

**THE BIO-ECOLOGY, ECONOMICAL IMPORTANCE AND CONTROL OF THREE
SATURNIIDS INJURIOUS TO FOREST TREES**

by

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RÉSUMÉ

The bio-ecology, economical importance and control of three saturniids injurious to forest trees.

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The pine emperor *Nudaurelia cytherea clarki* Geertsema, the poplar emperor, *Pseudobunaea irius* (F.) and the pine-bark emperor, *Holocerina smilax* (Westw.), are three important defoliators of especially *Pinus patula* Schlechtd. & Cham. trees.

These studies were undertaken to gain more knowledge of the biology and ecology of these insects, so that effective and economical methods of controlling them can be devised. A further aim was to make a comparison between the potential wood loss, as a result of defoliation, and the cost of insecticidal spraying.

Bio-ecology

a) *N. cytherea clarki* (the pine emperor)

The pine emperor appears mainly in eastern Transvaal, Natal and Swaziland.

In the field, under normal fluctuating temperatures and other weather factors, the egg stage lasts an average of 26 days at 20,2°C and 84 days at 13,7°C. Eggs are laid singly or in masses, with a mode of 10 on *P. patula* needles and 15 on the leaves of broad-leaved trees and shrubs.

Larvae appear from the beginning of March until the beginning of October. First and second instar larvae generally move to the tips of the pendulous *P. patula* needles, where feeding takes place. Third to fifth instar larvae are capable of bending pine needles and can, in this way, reach the tips of needles while still clinging to branches with their abdominal legs. Despite these efforts by larvae to reach the tips of the needles it usually happens that a certain length of the tip is severed and wasted. In this way an average of 2 573 needle tips are

severed and wasted by one larva during the whole of its larval life.

During the first three instars the larvae are noticeably gregarious.

The widths of frass pellets can be used to determine with reasonable certainty what instar larva produced them.

The digestion coefficient of larvae feeding on *P. patula* and *Rhus dura* Schonl. was calculated at 22,8 and 12,7 per cent respectively.

In the field, at approximately 15°C, the larval stages last about 100 days on *P. patula*. A large number of indigenous host plants of the pine emperor have been found. The pupal stage lasts approximately eight months, mainly during summer. Pupae appear in the needle mat up to 50 mm below the soil surface.

Adults appear from the first week of February to the first week of May. Sexual attraction and mating begin mainly between midnight and 0300 hours. Mating lasts from less than an hour to 17 hours and, in exceptional cases, as long as 37 hours.

Egg laying takes place mainly between 1900 and 2200 hours during the first three nights after mating. An average of 182 eggs are laid per female of which 159 develop normally.

The maximum distance of dispersion by marked adults was 5,3 km for a male and 1,9 km for a female. Only 9 per cent of the marked females dispersed more than 280 m, whereas 62 per cent of the males exceeded this distance.

b) *P. irius* (the poplar emperor)

The poplar emperor is present in almost the whole of southern Africa.

In the field, at an average temperature of 14,9°C, the egg stage lasts 16-21 days. Eggs are laid singly or in masses with a mode of two and three on pine needles and broad leaves respectively.

First generation larvae appear from the end of October to the end of February. Second generation larvae are unable to complete their development at the low winter temperature conditions prevailing in the Transvaal Highveld. These larvae develop from the middle of March, and are present until the beginning or middle of May and then die off. The gregarious inclination is not as strongly developed as in the case of pine emperor larvae. Fourth and fifth instar larvae are capable of

bending pine needles to start feeding at the tips in this way. Nevertheless, each larva severs and wastes an average of 2 132 needle tips during its lifetime.

Frass pellet widths can be used with reasonable accuracy to determine the instar of the larva producing them.

The digestion coefficient of larvae on *P. patula* needles was calculated at 17,1 per cent.

In the field, at an average temperature of about 18°C, the larval stages last about 63 days on *P. patula*.

The later in the season that pupation of first generation larvae takes place, the higher the percentage of pupae entering diapause. The pupal stage lasts about two months, or, where diapause occurs, about seven months. Pupae are present from just below the needle mat to 62,5 mm below the soil surface.

Adults occur in three colour forms. Two generations of adults appear per season, namely from October to December and during March.

Sexual attraction and mating usually begin between 2300 and 0200 hours. Mating lasts from about an hour to approximately 18 hours.

Most of the eggs are laid during the first two nights after mating. One female is capable of laying an average of 184 eggs, of which 156 develop normally.

c) *H. smilax* (the pine-bark emperor)

The pine-bark emperor is distributed over almost the whole of south eastern Africa.

At an average field temperature of approximately 16,6°C, the egg stage lasts 10-13 days. Eggs are laid singly or in masses with a mode of one on both pine needles and branches.

Larvae are present from the end of October to the beginning of December (first generation), from the end of January to the end of April (second generation) and from the beginning of May to the beginning of September (third generation). Only larvae in the first instar are slightly gregarious. The larvae are apparently not capable of bending needles as indicated for the other two species. One larva severs and wastes an average of 1 727 needle tips during its lifetime.

Frass pellet widths can be used to determine the instar of the larva producing them.

The digestion coefficient of larvae (with five instars) feeding on *P. patula* needles was found to be 21 per cent.

In the field, the larval stages last approximately 43 days on *P. patula* at an average temperature of 18°C.

The later that larvae of the second generation pupate, the larger the percentage entering diapause. The pupal stage lasts about three weeks or, when diapause occurs, about six months. Pupae are formed in cracks in the bark of tree trunks.

Sexual attraction and mating take place shortly after dusk. Mating lasts approximately 1–23 hours. A female is capable of laying an average of 119 eggs of which 109 develop normally.

Population studies

Population densities of the three species were determined by means of sampling the pupal, adult and larval populations directly as well as the larval population indirectly by noting the production of frass pellets. In general the results obtained by the different methods agreed fairly well. It was however found that the number of first instar larvae that could be predicted from the number of pupae or adults previously present, was much higher than larval sampling indicated. The most vulnerable period in the life cycle is therefore from the time of the emergence of adults until first instar larvae start to feed.

Damage caused

Defoliation by the pine emperor larvae takes place during the dormant period of the trees and is less injurious than defoliation by the other two species, which takes place during the active growth period of the trees. Two or more consecutive complete defoliations during the active growth period of the same or two consecutive seasons, result in certain trees dying back, or dying completely.

Control by insecticides

If more than one total defoliation of 10 year old trees by the pine emperor

can be expected, or one or more partial to complete defoliations of four year old trees on fertile soil, up to five insecticidal applications can be economically justified.

Whenever complete defoliation by the poplar or pine-bark emperor is expected, spraying is economically justifiable and absolutely essential if no other method of control would be effective. Larvae of all three species can be sprayed by hand if they occur on young trees or by aircraft if tall trees are infested.

Other methods of control

Wild or domestic pigs can be strongly recommended for the control of the pupal stage of the pine and the poplar emperors. The collecting and marketing of pine emperor and poplar emperor larvae for human consumption apparently have great possibilities, since it is a relished dish of certain Bantu tribes.

Natural enemies and diseases

A considerable number of parasites and predators were found to attack all three species. As far as parasites are concerned, the highest percentage mortality was caused by egg parasites in the case of the pine emperor, while pupal parasites claimed the heaviest toll in the cases of the poplar and the pine-bark emperors.

Predators appear to be of more importance than parasites. The most effective predators were baboons against the pine emperor, hawks against the poplar emperor, and guinea-fowls against the pine-bark emperor.

A number of pathogens of pine and poplar emperor larvae was found. Under certain circumstances some of these pathogens are apparently of great importance for larval mortalities.

SAMEVATTING

Die bio-ekologie, ekonomiese belangrikheid en bestryding van drie saturniiede skadelik vir bosboubome.

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Die dennepouoog, *Nudaurelia cytherea clarki* Geertsema, die populier pouoog, *Pseudobunaea irius* (F.) en die dennebaspouoog, *Holocerina smilax* (Westw.), is drie

belangrike ontblaarders van veral *Pinus patula* Schlechtd. & Cham. -bome.

Hierdie studies is onderneem om soveel moontlik van die biologie en ekologie van hierdie insekte te wete te kom, sodat effektiewe en ekonomiese beheermaatreëls gevind kan word. Verder is daar beoog om 'n vergelyking te tref tussen die potensiele houtverlies, as gevolg van ontblarings, en die koste van bespuiting met insekmiddels.

Bio-ekologie

a) *N. cytherea clarki* (die dennepouoog)

Die dennepouoog kom hoofsaaklik in oostelike Transvaal, Natal en Swaziland voor.

In die veld by normaal skommelende temperature en ander weersfaktore, duur die eierstadium gemiddeld 26 dae by 20,2°C en 84 dae by 13,7°C. Eiers word enkeld of in massas gelê, met 'n modus van 10 op *P. patula* naalde en 15 op die blare van breëblaar bome en struik.

Larwes kom van die begin van Maart tot aan die begin van Oktober voor. Eerste en tweede stadium larwes beweeg meestal tot by die punte van die hangende *P. patula*-naalde, waar hulle vreet. Derde tot vyfde stadium larwes is instaat om dennenaalde te buig en kan sodoende die punte van naalde bykom terwyl daar met die abdominale pote aan takkies vasgeklou word. Tenspyte van die pogings van die larwes om die punte van die naalde te bereik, gebeur dit gewoonlik dat 'n sekere lengte van die naaldpunte afgebyt en vermors word. So word 'n gemiddeld van 2 573 naaldpunte deur een larf gedurende die hele larwale leeftyd afgesny en vermors.

Tydens die eerste drie stadia is die larwes tot 'n groot mate gregaries.

Die breedte van miskorrels kan gebruik word om die stadium van die larf wat dit geproduseer het met 'n redelike mate van betroubaarheid te bepaal.

Die verteringskoëffisient van larwes wat op *P. patula* en op *Rhus dura* Schonl. voed word op 22,8 en 12,7 persent onderskeidelik bereken.

In die veld by sowat 15°C duur die larwale stadium op *P. patula* ongeveer 100 dae. 'n Hele aantal inheemse voedselplante van die dennepouoog is gevind. Die papiestadium duur ongeveer agt maande, waartydens dit oorsomer. Papië kom in die naaldmat tot 50 mm onder die grondoppervlakte voor.

Volwassenes kom vanaf die eerste week van Februarie tot die eerste week

van Mei voor. Geslagsaanlokking en paring neem meestal 'n aanvang tussen middernag en 0300 uur. Paring duur van minder as 'n uur tot 17 uur, en in uitsonderlike gevalle solank as 37 uur.

Eierlegging vind veral tussen 1900 en 2200 uur gedurende die eerste drie nagte na paring plaas. Een wyfie is in staat om gemiddeld 182 eiers te lê, waarvan 159 normaal ontwikkel.

Die maksimum verspreidingsafstand behaal deur gemerkte motte was 5,3 km vir 'n mannetjie en 1,9 km vir 'n wyfie. Slegs 9 persent van die wyfies het verder as 280 m versprei, terwyl 62 persent van mannetjies hierdie afstand oortref het.

b) *P. irius* (die populierpouoog)

Die populierpouoog kom oor byna die hele suidelike Afrika voor.

In die veld by 'n gemiddelde temperatuur van 14,9°C duur die eierstadium 16–21 dae. Eiers word enkeld of in massas gelê, met 'n modus van twee en drie op dennenaalde en breëblare onderskeidelik

Eerste generasie larwes kom vanaf die einde van Oktober tot aan die einde van Februarie voor. Tweede generasie larwes is nie in staat om hul ontwikkeling by die lae wintertemperatuurtoestande van die Transvaalse Hoëveld te voltooi nie. Hierdie larwes ontwikkel vanaf middel Maart, en kom voor tot begin of middel Mei en sterf dan uit. Die gregariese neiging is swakker ontwikkel as in die geval van die dennepouooglarf. Vierde en vyfde stadium larwes is in staat om dennenaalde te buig om sodoende die punte by te kom. Nietemin, word 2 132 naaldpunte deur een larf gedurende sy leeftyd afgesny en vermors.

Miskorrel-breedte kan met 'n redelike mate van betroubaarheid gebruik word om die stadium van die larf wat dit produseer vas te stel.

Die verteringskoëffisiënt van larwes op *P. patula*-naalde is op 17,1 persent bereken.

In die veld by 'n gemiddelde temperatuur van sowat 18°C, duur die larwale stadium ongeveer 63 dae op *P. patula*.

Hoe later in die seisoen dat verpopping van die eerste generasie larwes plaasvind, hoe groter die persentasie papies wat in diapouse gaan. Die papiestadium duur sowat twee maande, of, waar diapouse intree, ongeveer sewe maande. Papies

kom vanaf net onder die naaldmat tot 62,5 mm onder die grondoppervlakte voor.

By die volwassenes kom drie kleurvorme voor. Twee generasies motte kom voor en wel vanaf Oktober tot Desember, en in Maart.

Geslagslokking en paring begin meestal tussen 2300 en 0200 uur. Paring duur van sowat 'n uur tot ongeveer 18 uur.

Meeste van die eiers word gedurende die eerste twee nagte na paring gelê. Een wyfie is instaat om gemiddeld 184 eiers te lê waarvan 156 normaal ontwikkel.

c) *H. smilax* (die dennebaspouoog)

Die dennebaspouoog is oor byna die hele suidoostelike Afrika versprei.

By 'n gemiddelde veldtemperatuur van ongeveer 16,6°C duur die eierstadium 10–13 dae. Eiers word enkeld of in massas gelê, met 'n modus van een op beide dennenaalde en -takke.

Larwes kom voor vanaf einde Oktober tot begin Desember (eerste generasie), vanaf einde Januarie tot einde April (tweede generasie) en vanaf begin Mei tot begin September (derde generasie). Slegs eerste stadium larwes is effens gregaries. Die larwes is skynbaar nie instaat om raaalde te buig soos wat vir die ander twee spesies aangedui is nie. Gedurende sy leeftyd sny een larf gemiddeld 1 727 naaldpunte af, wat dan vermors word. Miskorrel-breedte kan gebruik word om die stadium van die larf wat dit geproduseer het vas te stel.

Die verteringskoëffisiënt vir larwes (met vyf stadia) wat op *P. patula*-naalde voed, is op 21 persent bereken.

In die veld by 'n gemiddelde temperatuur van 18°C duur die larwale stadium ongeveer 43 dae op *P. patula*.

Hoe later larwes van die tweede generasie verpop, hoe groter die persentasie wat in diapouse gaan. Die papiestadium duur ongeveer drie weke, of waar diapouse intree, sowat ses maande. Papiës word in barste in die bas van boomstamme gevorm.

Geslagslokking en paring vind veral kort na skemer plaas. Paring duur ongeveer 1–23 uur.

'n Wyfie is instaat om 'n gemiddelde van 119 eiers te lê, waarvan 109 normaal ontwikkel.

Bevolkingstudies

Bevolkingsdigthede van die drie spesies is direk vasgestel deur monsterring van die bevolkings van papies, volwassenes en larwes, terwyl larwale bevolkings ook indirek vasgestel is deur middel van 'n metode gebaseer op die produksie van miskorrels. Hierdie vier metodes het meestal byna dieselfde resultate gegee. Daar is egter gevind dat die aantal eerste stadium larwes, wat voorspel kon word op grond van die aantal papies of motte vroeër teenwoordig, baie groter was as wat die larwale monsterring aangedui het. Die kwesbaarste tydperk in die lewensloop is dus vandat die volwassenes uit die papies verskyn totdat die eerste larfstadium begin vreet.

Skade aangerig

Ontblaring deur dennepouooglarwes geskied tydens die rusperiode van die bome en is minder nadelig as ontblaring deur die ander twee spesies wat in die aktiewe groeitydperk van die bome geskied. Twee of meer opeenvolgende algehele ontblarings gedurende die aktiewe groeitydperk van dieselfde of twee agtereenvolgende seisoene, het tot gevolg dat van die bome kan terugsterf of heeltemal doodgaan.

Beheer met insekmiddels

Wanneer meer as een algehele ontblaring van 10 jaar oue bome deur die dennepouooglarf verwag kan word, of een of meer gedeeltelike tot algehele ontblarings van vierjarige bome op vrugbare grond, is tot vyf toedienings van 'n insekmiddel ekonomies regverdigbaar. Elke keer dat algehele ontblarings deur die populierpouoog of die dennebaspouoog verwag word, is bespuiting ekonomies regverdigbaar en gebiedend noodsaaklik indien geen ander beheermaatreël effektief sal wees nie. Die larwes van al drie spesies kan in jong bome met die hand bespuit word of met behulp van viiegtuie indien groot bome besmet is.

Ander beheermaatreëls

Ter bestryding van dennepouoog- en populierpouoogpapies word die gebruik

van wilde of mak varke sterk aanbeveel.

Die versameling en bemarking van dennepouoog en populierpouoog larwes vir menslike gebruik hou skynbaar groot moontlikhede in, aangesien dit 'n gesogte dis van sekere Bantoestamme is.

Natuurlike vyande en siektes

'n Hele aantal parasiete en predatore val die verskillende spesies aan. Sover dit parasiete betref, word die hoogste persentasie mortalitiet deur eierparasiete in die geval van die dennepouoog veroorsaak, terwyl papieparasiete die hoogste tol eis in die gevalle van die populier- en die dennebaspouoog.

Predatore skyn van meer belang as parasiete te wees. Die doeltreffendste predatore was bobbejane teen die dennepouoog, valke teen die populierpouoog en tarentale teen die dennebaspouoog.

By dennepouoog- en populierpouooglarwes kom 'n aantal patogene voor, wat skynbaar in sekere omstandighede van groot belang vir larwale sterftes is.

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CHAPTER 1 : INTRODUCTION

Nudaurelia cytherea clarki Geertsema, *Pseudobunaea irius* (F.) and *Holocerina smilax* (Westw.) are three important defoliators of especially *Pinus patula* Schlechtd. & Cham. trees. *P. patula* is planted on a large scale for timber and the manufacturing of pulp. Although some damage is annually done to trees, the three pests only appear sporadically in large enough numbers to cause serious or complete defoliation.

During 1941, an insect was reported damaging *P. patula* trees at Coetzee-stroom, Kaapsche Hoop, Transvaal. The insect was identified as *N. cytherea clarki*. Although *N. cytherea cytherea* (F.) was well-known as a pest in the Cape Province (Tooke & Hubbard, 1941), damage to afforested areas by *N. cytherea clarki* in other parts of Southern Africa apparently remained undetected. Subsequent inspections of plantations suddenly revealed that the species occurred over a wider region than originally supposed. This insect was popularly named the pine emperor after the Cape subspecies.

N. cytherea clarki appears in plague proportions in the Eastern parts of the Transvaal, in Natal and Swaziland. One generation of moths appears per year. Trees are defoliated from June to September, that is, during the resting period of the trees. Trees seldom die as a result of defoliation, but definitely receive a setback.

In the Transvaal, sporadic infestations occurred at: Brooklands, Sabie District in 1947; Doornhoek and Renosterhoek, Sabie District, Mac Mac, Graskop District and Witklip, White River District, in 1952; as well as Endahwin and Oosterbeek, Barberton District, in 1959. Populations of pest proportions were recorded at Ameide and Welgelegen, Barberton District, from 1950 to 1965 and 1957 to 1970 respectively; as well as at Weltevreden (Schagen), Nelspruit District, from 1960 to 1965. Although only scattered infestations have occurred in Natal since 1958, severe outbreaks were reported from Canaan and Enon, Richmond District, from 1963 to 1965 and Edenvale, Pietermaritzburg District, during 1964 and 1965. In Swaziland, the pest was recorded regularly at Usutu, Mhlambanyati and frequently at Piggs Peak as from 1955 and 1954 respectively. Sporadic outbreaks were also recorded from Havelock mine as from 1959.

In the Rietvlei and Pan plantations in the district of Middelburg, Transvaal, three colour forms of another emperor moth can be found. These colour forms, appearing at the same time, have been seen to mate with each other and to produce fertile eggs. Although these colour forms have been described as different species now placed in the genus *Pseudobunaea*, i.e. *P. epithyrena* (M. & W.), *P. natalensis* (Aur.) and

and *P. sjostedti* Aur., it is surmised that they are merely colour forms of *P. irius* and are here treated as one species. Rougeot (1955) is of the same opinion.

During 1947 and 1948, *P. irius* was found feeding on *Populus deltoides* Marsh. trees at the Kromdraai plantation, Piet Retief District, and so earned the popular name of the poplar emperor. In 1959/60 it caused damage to *P. deltoides* at Sheepmoor, Ermelo District. From 1961 to 1966 *Pinus radiata* D. Don and subsequently also *P. patula* were attacked at the Pan plantation, Middelburg District. During the 1964/65 season, reports of damage were also received from the Ajax plantation, Piet Retief District. From 1968 to 1970 *P. patula* trees were partly defoliated in the Rietvlei plantation, Middelburg District.

P. irius has thus far only been reported as a pest in the Transvaal Highveld. Two generations of moths appear per year i.e. during October – November and March. All pupae of the first generation do not develop into adults the same summer to produce the second generation of moths – some lie over until the next summer. Under Transvaal highveld conditions, larvae of the second generation die during winter. Trees are defoliated during their growth period from December to February. The defoliated trees must therefore survive the dry autumn and winter. If defoliation occurs for two or more consecutive years, many trees may die, resulting in grave losses.

The third emperor moth, *Holocerina smilax*, had, until recently, been noticed in small numbers only, especially in *P. patula* plantations. During the 1964/65 season it was found in the Ajax plantation, Piet Retief District, at Usutu, Mhlambanyati in 1965 and at Schoemansdal in 1969. During 1967/68 and 1968/69, about 20 ha of *P. patula* trees were completely defoliated at the Keerom plantation, Middelburg District. The population, however, decreased naturally, so that only a few individuals could be found in 1971. From 1968 a few individuals of this species were found at the Rietvlei plantation, Middelburg District. The population density increased until it reached pest proportions during the beginning of 1971.

Three generations of moths appear per year, of which the first two are considerably larger than the third and of much greater importance. Some of the second generation pupae enter diapause and give rise to the first generation of the following season. Defoliation may take place twice during the same growing season, i.e. during December – January and March – April. The first defoliation results in the trees budding again, thus ensuring some food supply for the second generation. Trees may die partially or completely after the first or second season's defoliations.

This species is also referred to as the variable prince (Pinhey, 1956) but as *H. smilax* pupate in cracks in the bark and the general coloration of the moth resembles that of bark, the popular name pine-bark emperor is suggested.

Taxonomic position

The following is the taxonomic position of these insect species as given by Pinhey (1956).

ORDER LEPIDOPTERA

Family Saturniidae

Subfamily Ludiinae

Holocerina smilax (Ang.) Westw.

Holocerina smilax (Westw.) is the currently accepted name (Pinhey, *in litt.* 1971).

Subfamily Saturniinae

Lobobunaea epithyrena (M. & W.)

Nudaurelia cytherea (F.)

Pseudobunaea irius (F.) is regarded (Rougeot, 1955) as the correct name for *L. epithyrena*.

Nudaurelia cytherea clarki is the name proposed for the subspecies of *N. cytherea* occurring in the Transvaal, Natal and Swaziland (Geertsema, 1970).

Literature review

Nudaurelia cytherea clarki

The species *Bombyx cytherea* was described by Fabricius (1775). *Phalaena capensis*, which later turned out to be the same species as *B. cytherea*, was described by Stoll (1780). This species was divided into two subspecies, namely *N. cytherea capensis* (Stoll) and *N. cytherea cytherea* (F.) (Gaede, 1927 according to Geertsema, 1970).

According to Geertsema (1970), the Cape Province subspecies should be known as *N. cytherea cytherea*, while the subspecies in Transvaal, Natal and Swaziland is to be known as *N. cytherea clarki*.

Tooke & Hubbard (1941) mention the occurrence of *N. cytherea clarki* and state that no damage to cultivated trees had been reported.

Hepburn (1961) reviews the occurrence of outbreaks in the Transvaal up to and including 1961. He also mentions hand-picking and spraying with insecticides to control the larvae. He reached the conclusion that the results of an aerial spraying were by no means entirely satisfactory and speculated that two sprayings per season would perhaps be necessary, that more effective aircraft would have to be used and that a thorough system of marking the aircraft runs (swaths) would have to be resorted to.

Van den Berg (1964, 1965) discusses an aircraft spraying campaign, as well as the seasonal history of this insect and the possible use of *Bacillus thuringiensis* Berlinger against its larvae. He also mentions the control of pupae by means of fire.

Taylor (1967) refers to some aspects of the biology and mentions a number of host plants.

Prinsloo (1967) isolated the bacteria *Serratia marcescens* Bizio from diseased *N. cytherea clarki* larvae.

Van den Berg (1968) mainly discusses the egg parasites of emperor moths, and also mentions the flight activities of moths and experiments with ultra-violet light traps. A summary of part of the work done on the egg parasites was published (Van den Berg, 1970).

Van den Berg (1969) describes a new method of employing pigs for the control of pupae, namely that of herding the pigs instead of allowing them a free run in fenced-in camps.

Geertsema (1970) gives descriptions of the different stages. The geographical distribution, a number of host plants and the biology in comparison with that of *N. cytherea cytherea* also receive attention.

Anonymous (1970) mentions a number of host plants of *N. cytherea clarki* (under the name *N. cytherea capensis*) as well as the fact that *P. patula* is defoliated in the Transvaal, Natal and Swaziland.

Pseudobunaea irius

This moth was described by Fabricius (1793) under the name *Bombyx irius*. The species was also described as *Bunaea epithyrena* by Maassen & Weymer (1886), the correct name of which was, until recently, considered to be *Lobobunaea epithyrena* (M. & W.).

Rougeot (1955) brought the taxonomic name of this species up to date i.e. *Pseudobunaea irius*. He also states that many variations of the species appear and that it is distributed throughout all African savannas and gives a number of host plants.

Hepburn (1961) states that *Populus deltoides* trees were defoliated and mentions the inability of pigs to destroy pupae under these trees. An insecticidal spraying experiment, in which DDT, nendrin and chlorfenvinphos gave the best results, is also described.

Prinsloo (1962) isolated the bacteria *Vibrio leonardi* Metalnikov & Chorine from field collected poplar emperor larvae of the second generation.

Van den Berg (1965) discusses the seasonal history, the possible use of *B. thuringiensis* against the larvae, as well as the development of pupae at different controlled humidities.

Hepburn, Prinsloo & Loedolf (1966) state that defoliation during a drought may cause the trees to die. A description of the immature stages, the biology and seasonal history, as well as recommendations for the control of pupae by means of pigs are also given.

Prinsloo (1967) states that *Serratia marcescens* was isolated from diseased larvae.

Van den Berg (1968) made a study of the egg parasites of *P. irius*.

Anonymous (1970) gives a number of host plants and mentions single large outbreaks of the poplar emperor.

Holocerina smilax

The adult moth was described by Westwood (1849) under the name *Saturnia (Henucha ?) smilax*.

A thorough description of one of the mature larval forms, compared with

the hemileucid larvae from America, is given by Packard (1914).

Janse (1946) states that different colour forms of the larvae occur.

Anonymous (1970) provides a number of host plants of the pine-bark emperor.

Motivation and main objectives

From the above study of the literature it can be concluded that our knowledge of the biology of these moths is still very fragmentary and incomplete, while that of their ecologies is in an even less satisfactory state. Of one species, namely *H. smilax*, virtually nothing is known. One of the objectives of the present study was, therefore, to learn as much as possible of the biology and ecology of each species, with the view to devising efficient and economic ways of controlling them.

From the brief history of outbreaks presented above, it appears that the first damage to pine trees by one of these indigenous insects in the eastern Transvaal, was noticed in 1941. It has been established, however, that pine trees (*P. patula inter alia*) had been introduced into this region as early as 1908–1913 (Kotze, 1926). That no damage had been reported much earlier than 1941 may therefore be highly significant; it certainly is noteworthy. It seems rather unlikely that the degree of damage recorded during the past decade or two, could have escaped all attention for such a long time. Complete defoliation of extensive blocks of trees for two or more consecutive growing seasons, would surely have attracted the attention of foresters directly concerned with such catastrophies. Furthermore, forest entomologists were active in the area probably as early as the late 1920's.

It may therefore be argued that these indigenous insects are gradually adopting certain exotic trees as food plants. Due to monocultural practices, fairly large areas are now occupied by one plant species to the practical exclusion of all others, and consequently also of many animal species associated with or dependent on these plants.

An insect capable of adapting itself to such a new and plentiful food supply may benefit in two ways. Obviously, it can thereby be enabled to multiply to excessive proportions where it had previously been unable to do so, maybe for lack of food, or maybe because of the way the food was distributed making it relatively more difficult to locate. It may, however, also benefit in a much more subtle way,

namely due to the gradual disappearance of enemies or competitors incapable of adapting themselves to the changed ecological conditions.

It may therefore be argued that the rather sporadic nature of outbreaks in the past, and possibly also at present, could gradually develop at more frequent intervals and may attain greater levels of severity in the not too distant future. What may at the moment be regarded as a minor pest, justifying little or no control, could gradually be transformed into a major pest causing serious losses almost every year, thus rendering frequent control imperative. It is therefore clear that thorough biological and ecological studies are highly desirable.

The chemical methods of control generally practised today, are in the opinion of timber growers, rather expensive and uneconomical. Whether this truly reflects the actual state of affairs is however highly uncertain. One of the objectives was, therefore, to devise some methods whereby the reduction in the amount and value of timber, produced as a result of different levels of defoliation during one or more seasons, can be satisfactorily measured. This knowledge would enable one to decide what expenditure on control would be economically justified.

A further objective was to compare a few of the methods of control with the view of establishing which of them would be the most efficient and economical way of keeping these insects under control. In this connection, it should be remembered that the soil is occupied for a fair number of years (usually up to 30 years) before the crop is ready for harvesting. Loss of growth at frequent intervals may, therefore, seriously delay the harvest time.

CHAPTER 2: BIO-ECOLOGICAL STUDIES ON *NUDAURELIA CYTHEREA CLARKI*

A. Experimental site

Experiments in connection with *N. cytherea clarki* were mainly carried out in the Welgelegen plantation, Barberton District and Usutu plantation, Mhlambanyati, Swaziland.

Welgelegen is situated 1 067-1 676 m above sea-level in mountainous terrain about 19 km from Barberton on the road to Havelock. It is 2 342 ha in extent, of which 80 per cent is occupied by *P. patula*. On the northern side it adjoins the Oosterbeek plantation and on the southern side extends up to 5 km from Peak Timbers in Swaziland. Indigenous vegetation occurs chiefly in ravines, along roads, streams and margins of the plantation.

The Usutu plantation lies about 25 km south-west of Mbabane, surrounding the village of Mhlambanyati in Swaziland. The area occupied by the plantation is, on the whole, flatter in comparison with that of Welgelegen. The plantation is relatively isolated and is situated 950-1 528 m above sea-level. It extends over 43 700 ha, of which 81 per cent is occupied by *P. patula*. Although the entire area under cultivation consists of an almost mono-culture and is extensively cultivated, a great deal of indigenous vegetation is found along roads, firebreaks and ravines.

B. Distribution

Every insect tends to disperse over the widest possible area. From optimal habitats the species will normally spread to marginal areas beyond which it cannot survive (Grobler, 1957).

N. cytherea clarki is an indigenous insect and must have had ample opportunity to disperse over as wide an area as conditions would allow it to exist. It is therefore highly probable that it occurred and was reported or collected from optimal as well as marginal habitats in the past years. To determine its distribution, data on collection localities were obtained from the Transvaal, Natal, South African, British and Rhodesian museums as well as from the Forest and Timber Insects Section and the National Collection of Insects of the Plant Protection Research Institute. From these sources the following list of localities was obtained, mentioning the date of collection where this is known and giving in brackets the name

of the first person who made the collection at that locality. Distribution data obtained from literature are also provided.

Natal

Durban ? (A.J.T. Janse); Ixopo, 8.vii.1964 (H.E. Prinsloo); Pietermaritzburg, Sept, 1963 (T. Bosman); Port Edward, 24.iv.1938 (H.M. Millar); Richmond, Aug, 1962 (E.D. Thomas); Thornville, 17.iii.1963 (M.A. van den Berg); Weenen, 22.i.1903 (G.F. Leigh).

Swaziland

Havelock (Van den Berg, 1965); Mhlambanyati (Hepburn, 1961); Piggs Peak (Hepburn, 1961).

Transvaal

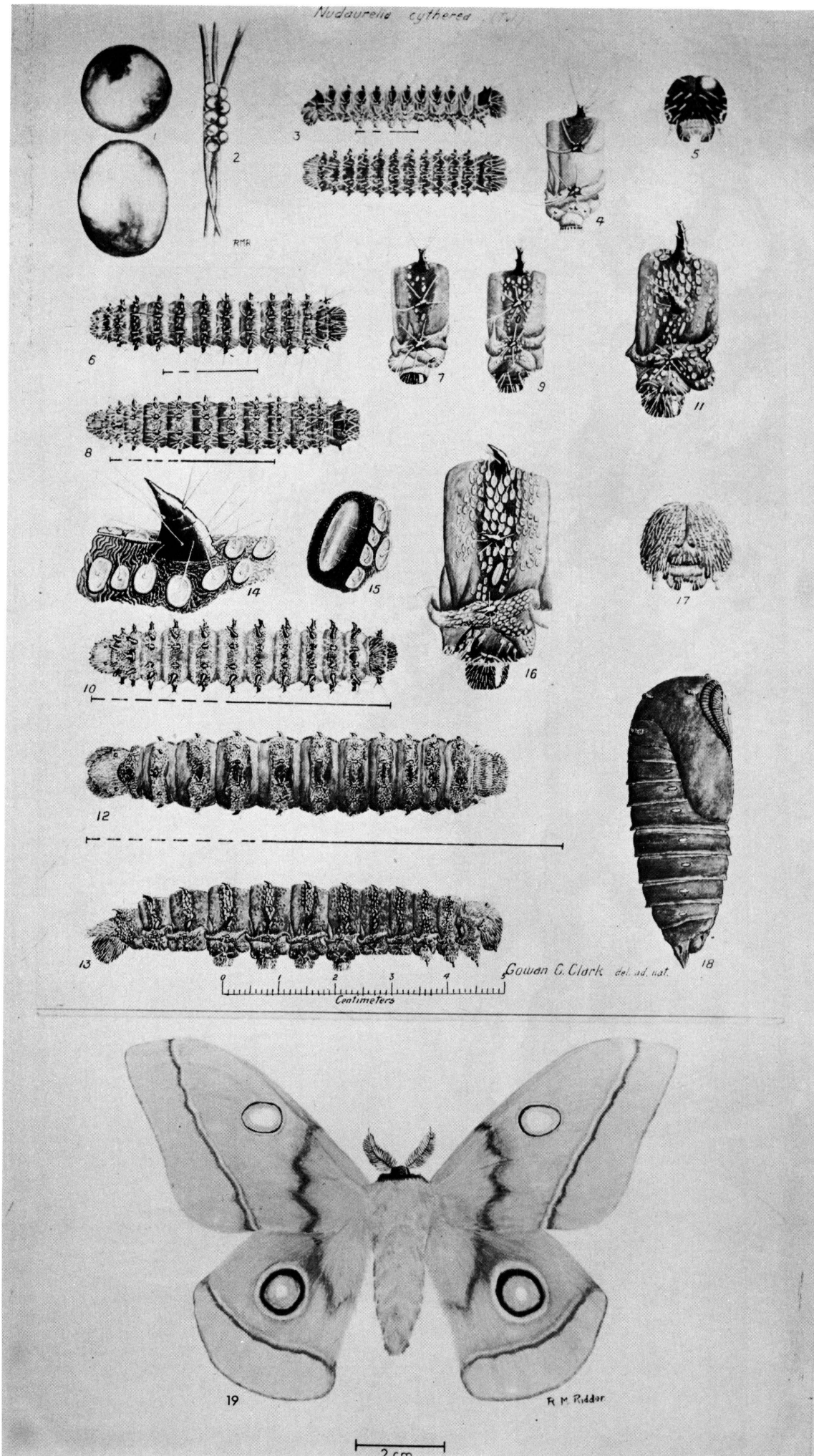
Barberton, 4.iii.1932 (? Rhod. Mus.); Bosbokrand ? (J.H. Grobler); Broederstroom (Haenertsburg) (Geertsema, 1970); Duiwelskloof, June, 1912 (J. Dicke); Graskop, 20.ii.1962 (Vari & Leleup); Haenertsburg, 24.xii.1921 (Swierstra); Jambila, 2.vi.1964 (H.E. Prinsloo); Johannesburg (Distant, 1911); Kaapche Hoop, July, 1941 (F.G.C. Tooke); Lochiel ? (J.H. Grobler); Lothair, Feb, 1959 (J.H. Grobler); Louis Trichardt, 7.iii.1966 (M.A. van den Berg); Louw's Creek, 21.ii.1968 (M.A. van den Berg); Lydenburg (Distant, 1911); Mariepskop, 20.iv.1955 (H. Cooksen); Nelshoogte, April, 1943 (? Nat. Coll.); Pilgrimsrest, 10.iii.1967 (Potgieter & Goode); Pietersburg, 1922 (? Rhod. Mus.); Premier Mine, 14.iii.1911 (A. Cochrane); Pretoria (Distant, 1911); Rustenburg, 29.iii.1924 (W. Impey); Sabie (Grobler, 1957); Schagen (Hepburn, 1961); White River, 24.viii.1951 (J.H. Grobler); Wolkberg, 27.ii.1965 (Killick).

Rhodesia

Changadze River, Jan, 1938 (G. van Son).

From 1903 to 1924 it was collected at Weenen (1903), Johannesburg (before 1911), Lydenburg (before 1911), Pretoria (before 1911), Premier Mine (1911), Duiwelskloof (1912), Haenertsburg (1921), Pietersburg (1922) and Rustenburg (1924), indicating that it was widely distributed over almost the whole of the Transvaal in those early days.

Subsequent collections were almost all done in the Eastern Transvaal, Natal



and Swaziland, which indicates that the insect probably occurs in much larger numbers in these regions. One collection was made in Rhodesia at Changadze River (1938). This is its most northerly distribution known.

C. The egg stage

1) General description

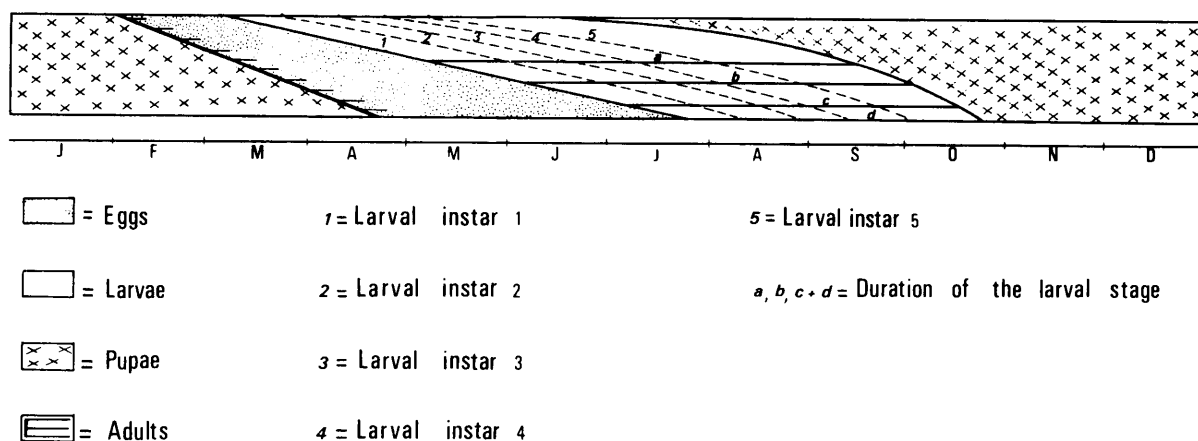
The egg is oval-shaped, the average length of 50 eggs being 2,72 mm, ranging from 2,56 – 2,88 mm and the width 2,38 mm, ranging from 2,25 – 2,50 mm. It is a cream- to pure-white colour, over which different irregular purple-brown to dark brown stripes of a sticky substance are smeared (Plate 1). This substance is initially soft and yellow-brown, but later becomes darker, hardens, and adheres the eggs to the leaves and to each other. This substance later fades and is also washed off by rain, so that older eggs frequently appear considerably lighter than eggs a few days old. No characteristic structures appear and the micropylar area is almost invisible to the naked eye. The eggs are conspicuous objects and very easy to locate, especially when they are laid in groups. For a more detailed description, refer to Geertsema (1970).

2) Oviposition and incubation period

The duration of the egg stage was determined by tying pine needles, with eggs deposited on them the previous night, onto small trees. These eggs were provided with labels. The date and the number of larvae which developed were noted.

Eggs are deposited from the first week in February to the beginning of May, and are found until July (Fig. 1). This extended oviposition period results from the temperature, to which the eggs are exposed, varying from an average of 23,3°C during February to 13,4°C during July. In the field, at a temperature of 20,2°C, incubation lasted an average of 26 days, whereas it lasted 84 days at an average temperature of 13,7°C (Fig. 2). This agrees with the findings of Taylor (1967) who states that the developmental period lasted from 29–76 days and to a certain extent with that of Geertsema (1970) who reports that the incubation period was from 24–44 days. Eggs of the same egg mass do not always hatch at the same time. For example, the eggs of one mass hatched in four groups on the 6th, 9th, 12th and 17th May, on which dates 5, 11, 14 and 3 individuals hatched respectively.

Fig.1: Time of occurrence of the different stages of the pine emperor in the Welgelegen (Barberton) plantation



3) Egg masses

Observations on egg laying pattern and the number of eggs per mass were made in the field on *P. patula* and other indigenous host plants.

Eggs are deposited in groups, or occasionally singly, on pine needles and broad leaves. From 2–44 eggs are deposited together on *P. patula* needles in one egg mass with a mode of 10 eggs for 613 masses (Fig. 3). On broad leaves such as *Rhus dura* Schonl., *Rapanea melanophloeos* (L.) Mez and *Psidium guajava* L., 2–83 eggs are deposited in masses with a mode of 15 eggs for 1 072 masses (Fig. 4). Geertsema (1970) found a mode of seven eggs per mass on *P. patula* and 15 on *Diospyros whyteana* (Hiern) F. White. Geertsema obtained his average for eggs on pine needles from material sent to him by post from Mhlambanyati

Fig 2 Duration of the egg stage of the pine emperor in the field

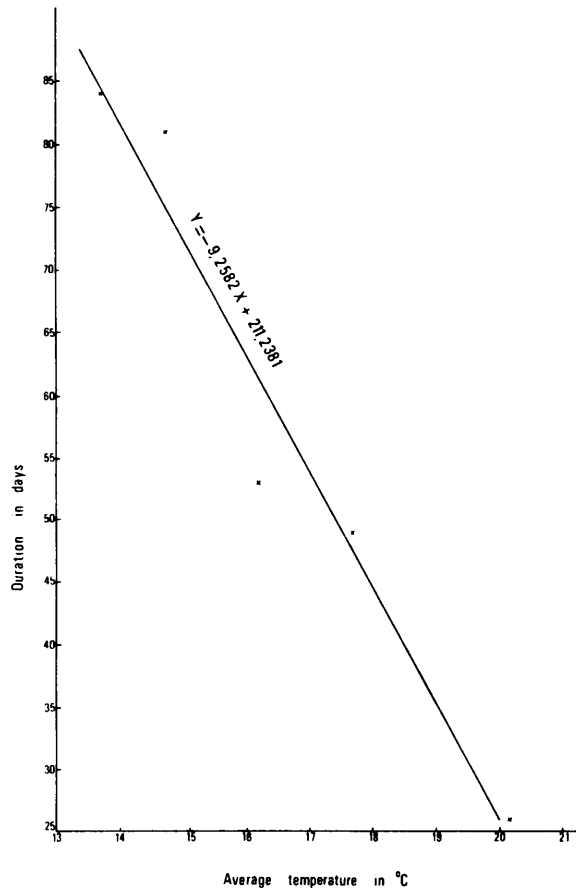


Fig. 3: Number of pine emperor eggs occurring singly or in masses on *P. patula* needles

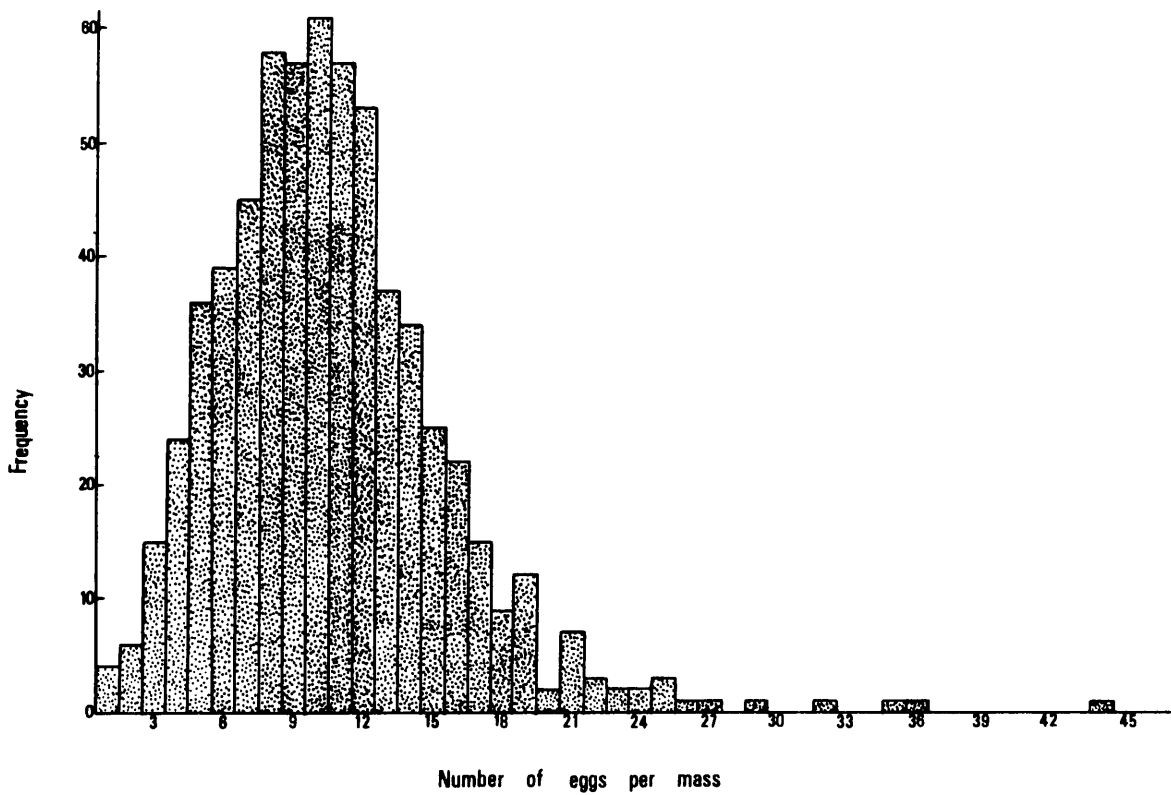
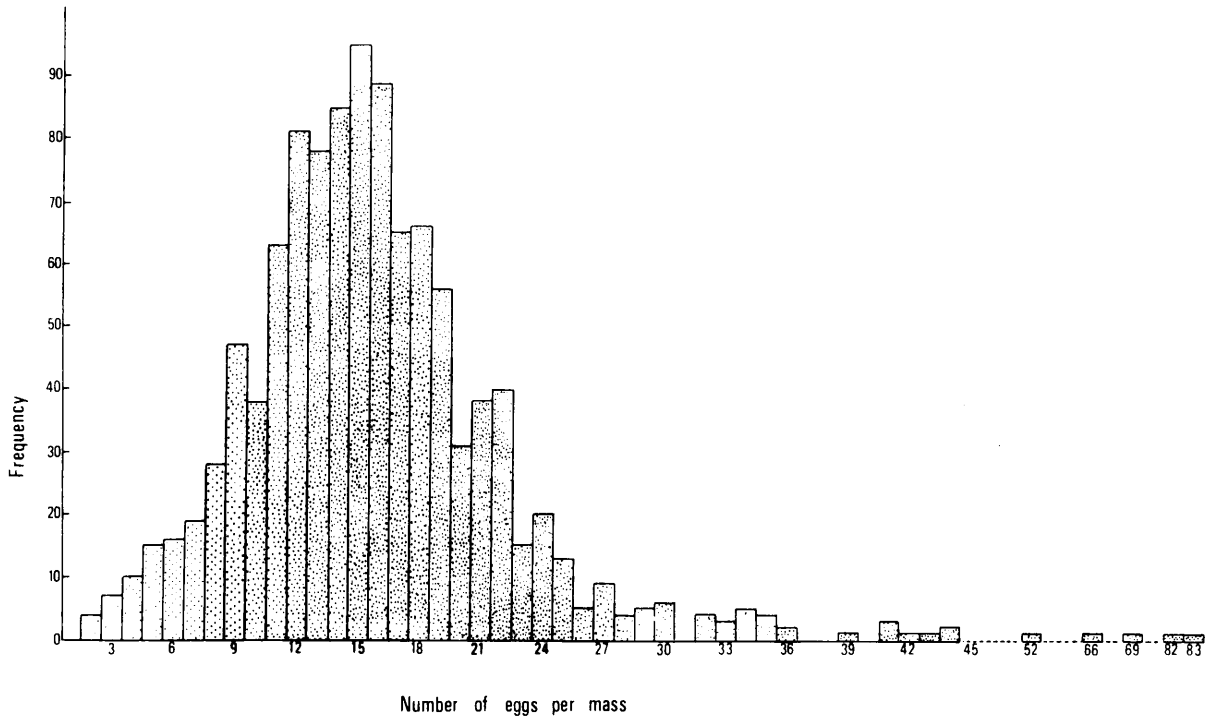


Fig 4: Number of pine emperor eggs occurring singly or in masses on broad leaves



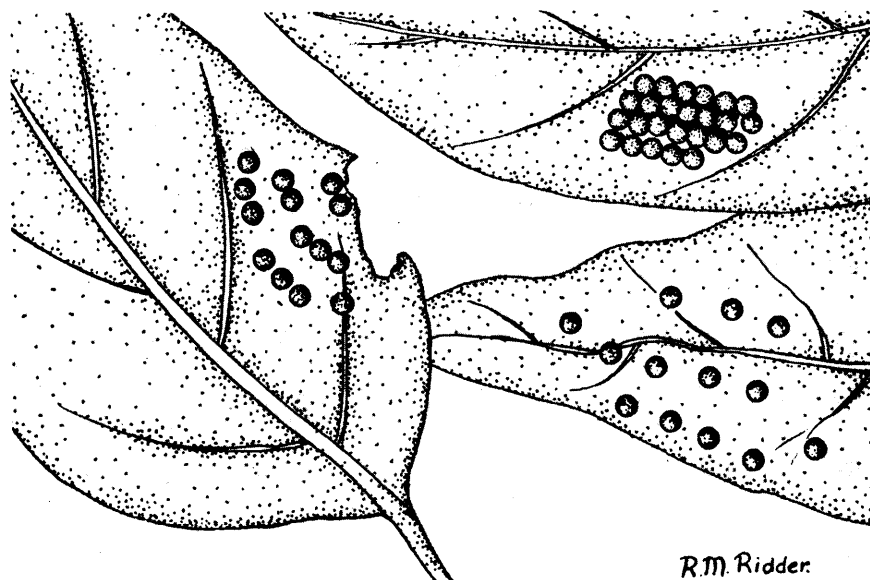
to Cape Town. During transit some of the eggs masses could have broken up into two or more smaller portions, each of which was then taken as one original egg mass. Geertsema's lower average figure for egg masses on *P. patula* needles may, therefore, have been due to such an eventuality.

Typical egg masses are depicted in Plates 1 (pine needles) and 2 (broad leaves). From these plates it can be seen that eggs in masses are usually laid in rows across

Plate 2: Pine emperor egg masses on broad leaves

Top right: normal arrangement

Left and bottom right: eggs spaced



R.M. Ridder

or down the length of pine needles, whereby up to 10 needles may become glued together by the sticky substance secreted by the ovipositing female. Eggs are usually laid alongside each other, but they may also be laid on top of each other. Eggs are deposited mainly on the lower surface of broad leaves. On broad leaves, a variation in the arrangement of the eggs occurs. The eggs are laid in rows against each other across the leaf, or in rows with more or less egg-size spaces between the rows or between all the eggs (Plate 2).

A small percentage of eggs are laid on growing branches, bark and brushwood. Eggs with other eggs on top of them do not usually hatch as the larvae are unable to gnaw through the double shell and therefore die inside the shells. If larvae hatching from the top eggs consume most of the chorion of these eggs before hatching of the bottom eggs begins, the bottom larvae can hatch normally.

Different sizes of eggs are sometimes deposited in the same mass. The width of these eggs can differ from 1,7 mm (small) to 2,5 mm (large). The small eggs do not develop: about half of them appear to be inviable while the others develop up to the stage where the larvae start to gnaw through the egg shells, but then die inside the shells. These egg masses containing small and large eggs are probably the last eggs laid by some of the older females.

Often many of the eggs laid in May (the last females) are inviable.

Eggs appear to be well protected against the usual fluctuations in weather conditions. If the eggs are, however, removed from the host plants, the emerging larvae mostly die of hunger. About seven per cent of the eggs laid on indigenous plants and small pine trees were washed or blown off during 1968.

During experiments with the pine emperor in the Barberton District, it snowed about 150–200 mm deep (3 June, 1968), resulting in tree tops being broken and branches torn off. Eggs lying in the snow were collected and placed in gauze cages (10 x 10 x 10 cm) together with snow, and left outside until the snow melted. Hereafter, the eggs were placed in a honey jar at room temperature in the laboratory. All eggs which did not develop were dissected. From the percentage hatch obtained, some idea could be formed of the cold-hardiness of the egg stage. No mortality was noticed amongst eggs dislodged by snow (152 eggs).

Newly emerged larvae can apparently crawl not more than 4 m in search of

food. Although these larvae can sometimes remain alive for up to 10 days without food, they are usually not in a condition to feed and/or to develop further after 4–7 days.

D. The larval stage

1) General description

The different larval instars are depicted in Plate 1.

First instar

General colour red-brown. A brown-black area is present on the dorsal aspect of every segment. Dorsally behind the head on the pro-thorax, a sclerotised saddle is present. This is black at the front becoming brown further back. Anteriorly on the saddle, there are two pairs of seta bearing scoli pointing forwards. On the same segment another pair of scoli is found laterally. With the exception of the last two segments, six seta bearing scoli are found on each segment in transverse as well as longitudinal rows across the larva's back and sides. On the penultimate segment, the two dorsal scoli are close to each other, while the last segment and also the clypeus each have four scoli. The setae on these scoli are more or less as long as the body is wide and are white to light grey. The head is dark brown to black, with a slightly shiny surface and a number of seta. The thoracic legs are brown to black. The abdominal legs are red-brown on the outside and pale orange-brown on the inside, which is also the colour of the ventral aspect of the body. The length varies from 5–11 mm.

Second instar

This instar differs from the first instar mainly in size. Other differences which appear are: The brown-black area on each segment extends further downwards, reaching the sides. A few yellow and white spots appear, especially on these darker areas. The scoli are slightly bigger and the setae slightly shorter. The length is between 11 and 17 mm.

Third instar

It differs from the second instar in that the general colour is lighter. The

brown-black areas are present on the back and sides. Some of the coloured spots are faintly blue. The scoli are more prominent and the setae slightly shorter. The length varies from 17–30 mm.

Fourth instar

Differs from the third instar as follows: The general colour is orange-brown. The brown-black areas are slightly larger and lighter and more coloured spots are present. Between the last two pairs of abdominal legs, yellow and white spots appear. The general length is between 29 and 63 mm.

Fifth instar

It differs from the fourth instar in that yellow and white spots appear between the pro- and meso-thoracic legs. The saddle is now brown. The scoli are thorny and point slightly backwards. The head is brown and possesses many setae. All the setae are relatively shorter than the width of the head capsule. The size varies from 61–114 mm.

For a more detailed description of the first and final instar refer to Geertsema (1970).

2) Key to the larval instars

- a) Yellow or white spots absent from back and sides of body of larva First instar
 Yellow and white spots present on back and sides b
- b) Bands around the body almost completely brown-black. White and yellow spots not very conspicuous Second instar
 Bands around the body a conspicuous white and yellow c
- c) No yellow and white spots visible between last two pairs of abdominal legs, or if present (shortly before moulting) much duller than those on sides and back Third instar

Yellow and white spots between last two pairs of abdominal legs as distinct as those on back and sides d

- d) No yellow or white spots present between pro- and meso-thoracic legs, or if present (shortly before moulting) not as distinct as those on sides and back Fourth instar
- Yellow and white spots between pro- and meso-thoracic legs as distinct as those on sides and back Fifth instar

3) Head capsule widths

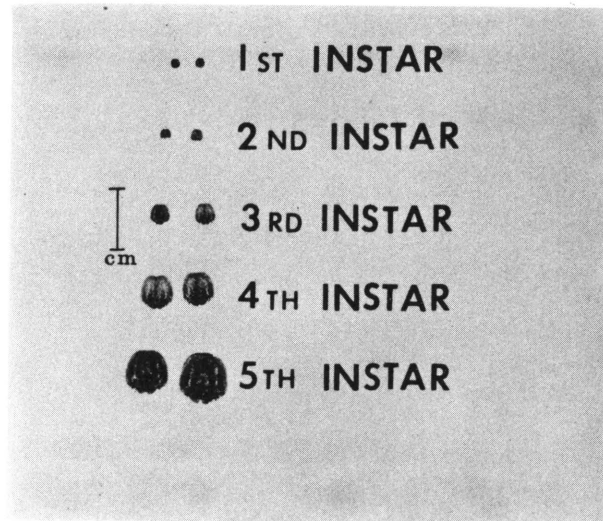
The widths of the head capsules of 40 larvae of each instar were determined with the aid of a standardised micrometer ocular. The results are supplied in Table 1.

Table 1: Head capsule widths of the different larval instars of the pine emperor (40 individuals of each measured).

Instar	Width in mm			Increase per instar (x)
	Min	Max	Aver	
1	1,50	1,63	1,58	—
2	2,19	2,44	2,30	1,46
3	3,12	3,63	3,40	1,48
4	4,77	5,41	5,06	1,49
5	6,84	8,27	7,57	1,50

According to this table, there are definite differences between the head widths of successive instars (Plate 3). An increase in size of between 1,46 and 1,50 times was found, which is in close agreement with the figure of 1,4 regarded as more or less characteristic for Lepidoptera (Dyar, 1890).

Plate 3: Head capsules of the different instars of the pine emperor



4) Time of occurrence

The time of occurrence of larvae was determined by direct observations on indigenous shrubs and young *P. patula* trees. Their presence could also be detected from needle drop and frass pellets under *P. patula* trees.

Larvae hatch from the beginning of March to the end of July. The first full-grown larvae enter the soil during the first week of June and the last towards the end of October. Larvae thus occur from the beginning of March to the end of October (Fig. .1)... This agrees with the findings of Hepburn (1961) who states that some of the larvae may already have turned into pupae while unhatched eggs of the same generation are still present. There is thus a considerable overlapping of the immature stages.

5) Larval behaviour

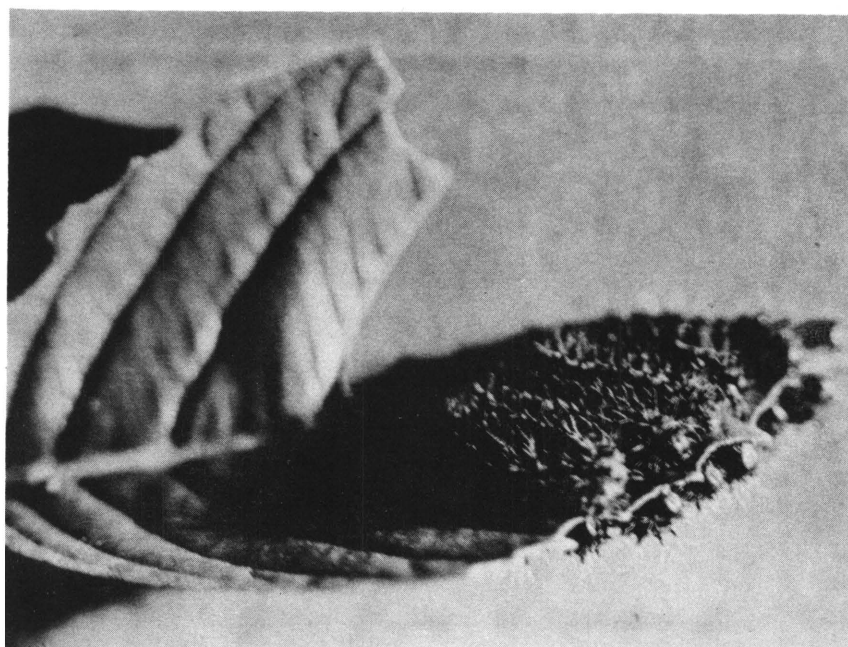
The unhatched larva gnaws an irregular hole through the dorsal side of the egg shell. The larva crawls through this opening which is just large enough for its head to pass through. Shortly after emergence the larva frequently feeds on the remaining egg shell. A large or small proportion of the egg shell may be consumed as explained below. During rainy weather, the larvae stay near the shells for up to 2–3 days. These larvae form circular groups around the shells and almost

completely consume all shell remains. On broad leaves, the outer shells of an egg mass may be consumed almost entirely, while those in the middle of a mass remain largely untouched. In warm sunny weather, the shells are often not devoured beyond the opening through which to emerge.

In the laboratory, newly hatched larvae are positively phototactic and congregate on the side of the petri-dish facing the light from a window, even crawling over food in this process. After a while the larvae begin to wander about in all directions, locating the food merely by chance. In the plantation, this phototactic response of newly hatched larvae will lead them to the tops of trees and tips of branches where developing young needles will be most abundant.

As no indigenous *Pinus* spp. occur in South Africa, the feeding habits of this insect must have originally been adapted to broad leaved trees. On broad leaves they move forward right to the edge of the leaf and then feed from the edge inwards, so that little of the leaf is wasted. The larvae tend to form compact groups on the lower surfaces of the leaves. They keep their heads pointing in the same direction towards the leaf margin, eating away the margin, and retracting gradually inwards as the leaf is consumed. Sometimes the group consists of larvae on both surfaces of the leaf, all eating away the same leaf margin (Plate 4).

Plate 4: Groups of pine emperor larvae feeding on both sides of a leaf



They evidently try to do the same on pine needles, but as these probably do not offer as firm a substrate to cling to, they do not move right to the tips of the needles; consequently a smaller or larger needle tip is bitten off and dropped.

The needles (leaves) of *P. patula* are borne in small clusters, usually three per cluster. The base of the cluster is enveloped in a common sheath – the scale leaf. Each cluster is borne on a very short stem, called the short branch. A varying number of clusters originate from a thicker common stem termed the long branch.

First instar larvae usually crawl forwards to feed near the tips of the pendulous *P. patula* needles; only short pieces are usually severed, not the complete needle. The feeding habits of second instar larvae are practically the same as those of the first instar, but longer pieces are severed. As the larvae grow larger and heavier (third and fourth instar) they do not move as far forward as smaller larvae but cling and feed closer to the base of the needles. Larvae of the third and later instars usually cling to branches with their abdominal legs, using their thoracic legs and mandibles to move along the needles, bending them in an attempt to reach the tip (Plate 5). Wherever the mandibles come into contact

Plate 5: A final instar pine emperor larva bending a needle to reach the tip



with the needle, a small piece is usually bitten out. The tip is then bitten off and by moving the thoracic legs backwards, the bent portion is gradually devoured and thus shortened. The rest of the needle is then consumed, without much waste. All the needles of a cluster may be bent and consumed at the same time. Sims (1903) states that the needle is "caught" by the final instar larva of *N. cytherea cytherea* leaning forwards. Tooke & Hubbard (1941) and Geertsema (1970) quoted this statement. Their further descriptions of the feeding habits of the final instar agree largely with what has been found in the present study. Third to fifth instar larvae occasionally leave the branches, moving forwards on groups of needles.

The first three instars frequently do not consume the needles entirely, but only partly along the length; such partly consumed needles are sometimes severed and can be recognized from the fact that they are not round and are usually short. Large portions can also be severed, probably when a larva moves backwards without feeding and then starts to feed again closer to the base of the needle. Larvae in the fourth and fifth instars may feed on only one of the three needles in a cluster; they may suddenly switch over to the other needles, of which portions are then severed at the point of switchover.

During the first three instars, the larvae are rather strongly gregarious. Larvae of the same size are frequently and larvae of different sizes and instars occasionally found together. On pine needles, from 2–5 larvae are often found feeding on a single needle or on the same cluster of three needles. These groups of larvae seem to prefer pendulous needles, such as those of *P. patula*, to which they cling with their heads pointing downwards, moving backwards as the needles are consumed.

Larvae dislodged from trees sometimes feed on pine needles dropped by feeding larvae; they may also move about in search of an object to ascend. They may crawl up against any object raised above the general level of the soil such as brushwood, logs, tree stumps, tree trunks and even stones. Recently cut branches of which the needles are still green and succulent are often ascended.

Some of these larvae may congregate at the highest point if the object ascended is relatively low. Larvae ascending objects other than trees may die of starvation, since they often show no tendency to descend.

When larvae are disturbed, for example by other larvae or the parasitic wasp

Apanteles maculitarsis Cam., they jerk the front part of their bodies from side to side. If the disturbance continues, the larvae may vomit drops of brown liquid. Most of this liquid is usually again imbibed after the disturbance is over.

6) Moulting

A larva preparing to moult first spins a type of silken moulting platform on a few needles, a branch or any other nearby object. This moulting platform is spun in such a manner that it is usually slightly longer than, and, on flat objects, about twice as broad as the larva itself, and is raised only very slightly above the surface. On broad leaves, a group of first to third instar larvae often spin a common moulting platform. The crochets of the abdominal legs are then hooked into the platform. Larvae on pine needles mostly hang with their heads downwards, with the three pairs of thoracic legs relaxed. The head is bent slightly downwards and the cervical membrane is stretched forward to make room for the developing head of the next instar inside the stretched out integument. Larvae may remain in this position for 4–6 days (depending on the prevailing temperature).

Shortly before the actual moult, the skin acquires a wrinkled appearance, whitish stripes appear at the level of the stigmata and the larva elongates slightly. The skin then splits along the mid-dorsal line of the thorax and the following instar emerges. The discarded head capsule often remains attached to the old skin. It may also cling to the mandibles, and is then rubbed off against any object to which the larva may be clinging. After moulting, the old skin usually remains on the moulting platform, with the larva nearby. Usually the larva returns and feeds on the old skin, causing the old cuticle of the head capsule to become dislodged. The larva is now of a lighter ground colour, the spots being very conspicuous and bright. Apart from bits of skin being eaten, usually no further feeding takes place on the day of moulting.

Larvae removed from their moulting platforms to moult elsewhere, often struggle to shed the old skin which adheres to the last segments, crumpled together in the form of a ring.

7) Needle drop and production of frass

Procedure

Daily needle drop and frass production during the different instars were stud-

ied, using 10 young pine trees 2-2,5 m high. These trees were pruned up to 1 m from the ground and the main stems cut off at 1,5 m, so that all branches could be reached from the ground. Around each tree a wooden frame (2 x 2 m and 1,5 m high) was erected with the stem in the centre. This frame served as a support for a detachable funnel constructed from cloth with its outlet slightly off-centre to miss the stem of the tree. One of the four sidepieces of cloth forming the funnel was therefore longer than the others. In this longer sidepiece a slit was cut through which the stem of the tree could pass. At the end of this slit a piece of cloth was provided, which could be formed into a sleeve pointing upwards to tie round the stem of the tree. The screw top of a fruit jar was attached to the outlet at the bottom of the funnel; into this a jar could be screwed.

From 10-20 newly hatched larvae were placed on each of these trees. Daily, at about the same time (1700 hours), two side pieces of each funnel were detached, the number of larvae on the trees counted and the funnel hooked onto the frame again. The tree was shaken slightly and the needles and frass were funnelled into the jars. The fruit jars were then unscrewed, numbered and clean ones screwed on. The needles and frass were counted and recorded for each tree. In order to limit these investigations to one instar at a time, all larvae developing conspicuously faster or slower than the majority were removed from the trees. The remaining larvae all moulted within the same day or two. Larvae preparing to moult could be distinguished by the fact that they spin moulting platforms after they have finished feeding during the specific instar. Apart from this reduction, a number of larvae also died or disappeared.

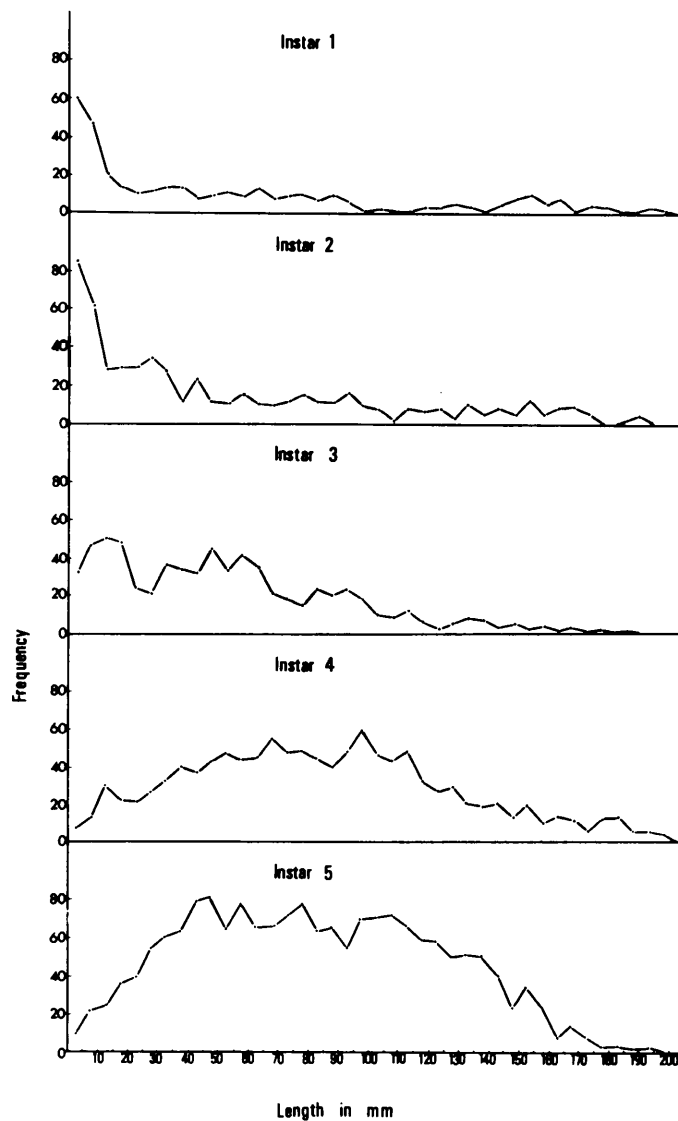
The apical portions of the needles severed can be distinguished, as the needles have sharp tips, which often appear to be somewhat dried out. The other end of a severed needle is blunt and clearly choppily bitten off. Middle portions of needles may also be severed and dropped to the ground, but usually not to the same extent as tips.

The lengths of all needles severed during the first two instars, were determined. Measurements were made of all needles cut off on the fifth to the eighth day for the third and fourth instars and all needles cut off on the seventh day for the fifth instar. The lengths of end and middle pieces were recorded separately.

Results

The frequency distributions of the lengths of apical needle sections severed during the different instars are shown in Fig. 5, which indicates that first and

Fig. 5: Number and length of needle tips severed by pine emperor larvae in the different instars



second instar larvae sever mostly up to about 30 mm of the distal end of the needle. Larvae in the third instar waste tips up to about 100 mm, while the figures for the fourth and fifth instars are from 30–120 mm and from 30–145 mm respectively.

The average lengths of apical and middle sections severed by each instar are summarized in Table 2. The average length of *P. patula* needles is 190,5 mm

(Loock, 1950). On the assumption that no needle is completely devoured (i.e. at least the apical section is dropped) the percentage total needle length wasted, could also be calculated.

Table 2: Average lengths and relative numbers of apical and middle sections severed by the different instars of the pine emperor and the percentage needle length wasted

Instar	Apical sections		Middle sections		Percentage total needle length wasted = $a + \frac{n_2}{n_1} b$ $\frac{n_1}{190,5} \times 100$
	no n_1	Average length in mm = a	no n_2	Average length in mm = b	
1	345	52,5	182	16,1	32,0
2	570	53,2	290	21,3	33,6
3	700	54,6	335	17,7	33,1
4	1 145	84,7	443	24,8	49,5
5	2 197	82,7	735	27,0	48,1
Percentage needle length wasted by all instars combined					47,7

From Table 2 it can be seen that the first three instars waste about a third of the needles, while the fourth and fifth instars waste nearly half of them. Included in these percentages wasted, is a basal part with an average length of 8,2 mm (2–30 mm for 300 clusters) of the needle which is not consumed and remains in and next to the sheath after the larvae have completed feeding on the needle. This part is, however, soon lost by the tree as it turns yellow and falls off. It can be concluded that an average of 47,7 per cent of the needles is wasted by the larvae, while 4,3 per cent of the damaged needles die and are shed by the trees.

Thirty frass pellets taken at random from those collected every second day of each instar were measured with the aid of a standardised micrometer ocular. The sizes of frass pellets can be seen from Fig. 6 and Plate 6.

According to Fig. 6, the lengths of frass pellets of consecutive instars overlap. However, only the maximum widths of the frass pellets produced during the last

Fig. 6: Lengths and widths in mm of 30 frass pellets produced every alternate day by the different larval

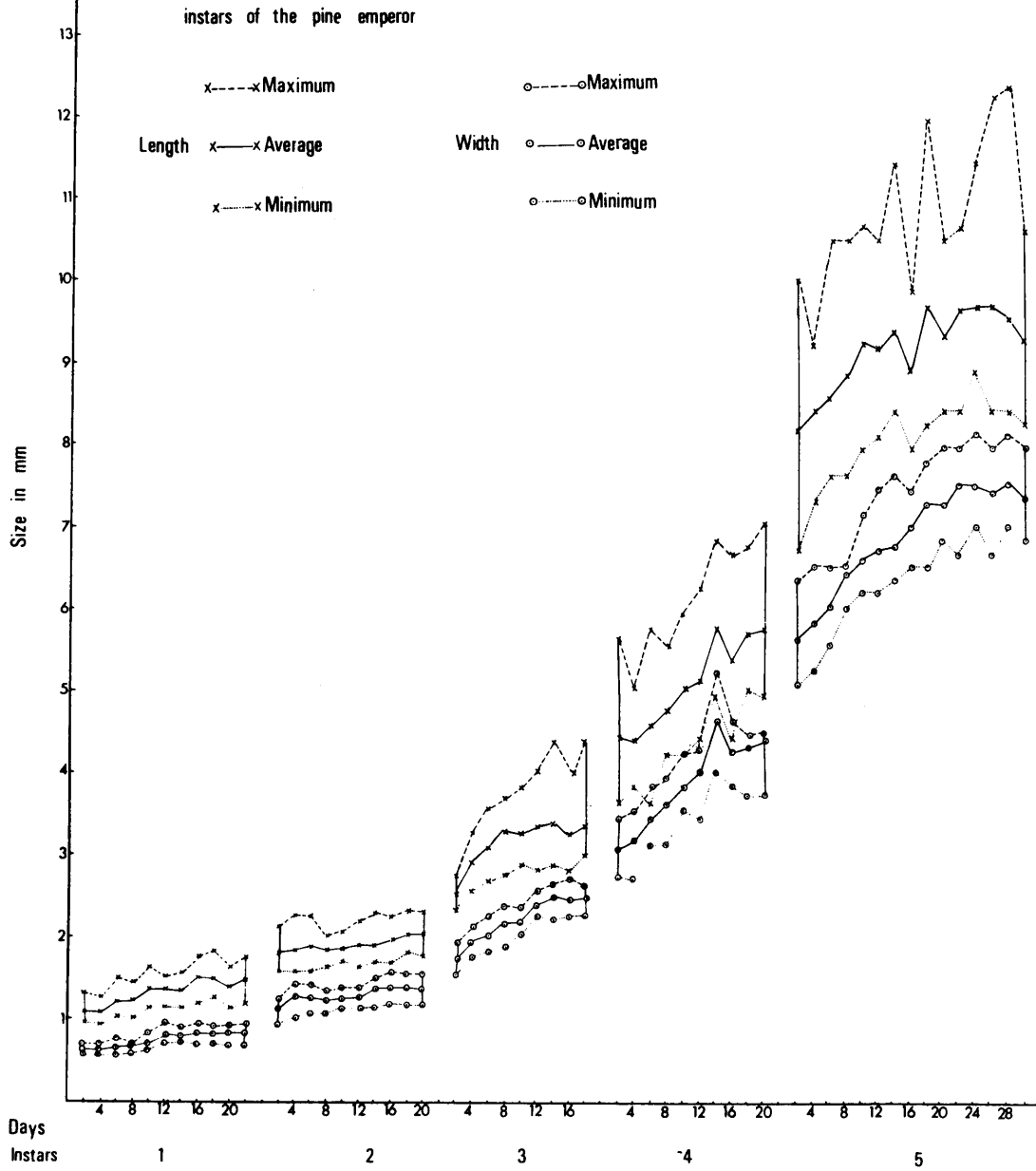
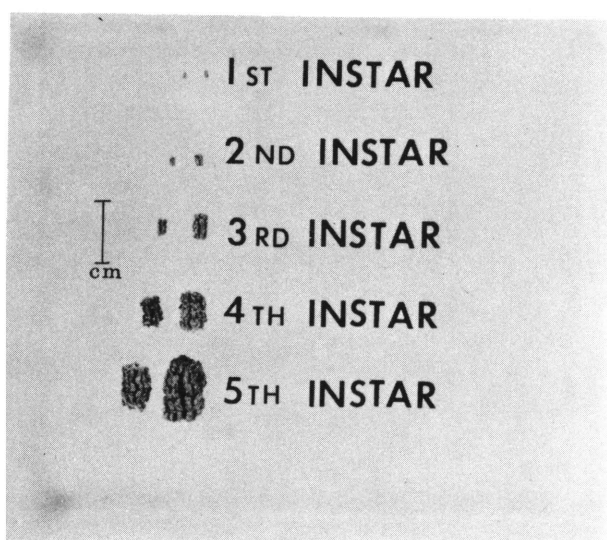


Plate 6: Frass pellets of the different instars of the pine emperor



few days of an instar overlap the minimum of those produced on the second day of the following instar. The widths of frass pellets can therefore be used to determine with reasonable certainty the instar of the larvae which produced them. It must however be stressed that the sizes mentioned here only apply to larvae on *P. patula*. On *R. dura* and other indigenous host plants the larvae attain a considerably larger size, resulting in proportionately larger frass pellets.

The numbers of needles and frass pellets obtained from larvae on funnelled trees, were also recorded for the full duration of each instar. The results can be found in Table 3.

Table 3: Needle sections severed and frass pellets produced by the different larval instars of the pine emperor

Instar	No. of larvae	Number of needle sections dropped			Number of frass pellets produced	Increase per instar (x)	
		Apical	Middle	Total		Needles	Frass
1	57	6,4	3,4	9,8	169,0	—	—
2	33	20,6	10,5	31,1	180,2	3,2	1,1
3	32	73,5	35,2	108,7	210,9	3,5	1,2
4	32	383,2	148,3	531,5	206,3	4,9	1,0
5	13	2 088,8	698,8	2 787,6	257,1	5,2	1,2
—		—	—	—			
Total		2 572,5 =2 573	896,2 =896	3 468,7 =3 469			

From this table it can be seen that the total number of apical needle tips severed during the larval stage is 2 573 per larva compared with 896 middle sections. As most of the remaining portions of needles are eaten and a small portion remains in and next to the sheath, later falling off, it can be assumed that one larva can destroy 2 573 needles. The severed sections increase roughly three fold per instar up to the third instar. Thereafter the increase is about five fold per instar. This means that they become progressively more wasteful feeders at an alarming rate. Apart from severing more needles, they drop larger pieces. Almost no increase in the number of frass pellets per instar was observed. The sizes do however increase greatly.

It is concluded that during the entire larval feeding period one larva eats or severs an average of 2 573 needles. Since an average of only 52,3 per cent of these needles is eaten, one larva will devour approximately 1 350 needles, provided that no wastage occurs.

8) The number of needles per *P. patula* tree

The number of needles per metre crown depth was determined as follows: After a tree had been chopped down, the branches were laid out, as far as possible, in their normal positions. Hereafter, long branches of each metre height from the top of the tree were cut off and the total lengths at which short branches appeared on them measured. From the branches of each metre section, 20 were taken at random, the number of clusters counted and the total cluster bearing length again measured. From this, the number of clusters and needles could be calculated for each metre crown depth. This was done on two 10 year old trees. The number of needles per *P. patula* tree obtained in this way is indicated in Table 4.

Table 4: Number of needles per *P. patula* tree

Distance from the top in metres	Number of clusters			Aver number of needles
	Min	Max	Aver	
1	1 360	3 789	2 575	7 725
2	5 103	15 621	10 362	31 086
3	6 057	23 276	14 667	44 001
4	7 171	35 699	21 435	64 305
5	8 247	33 281	20 764	62 292
6	12 557	32 864	22 761	68 283
7	7 776	24 865	16 321	48 963
Total			108 885	326 655

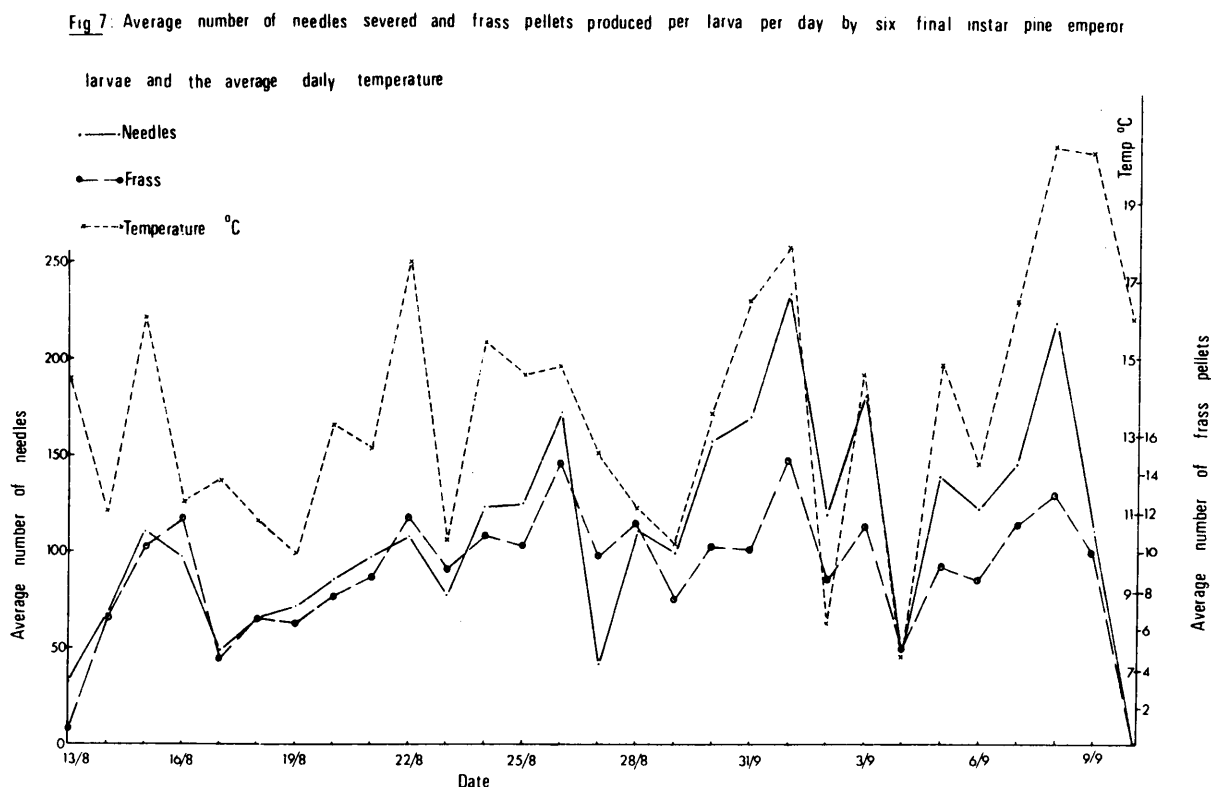
From Table 4 it can be seen that the top 2 m together, bear about as many needles as most of the other metre sections taken separately. If the top 2 m are considered as one section, thus dividing the 10 year old tree into six sections instead of seven, the general average is 54 443 needles per metre section.

The number of needles destroyed by one larva during the course of its life was estimated above at 2 573; therefore, 21 larvae could sever as many needle tips as normally occur in the top 2 m, or in each 1 m section lower down the tree. This damage is spread over 6–7 months in autumn and winter, during which period the tree can not repair the damage by adding new growth. About 126 larvae could completely defoliate one such tree. It is clear that even a small population per tree could significantly retard growth.

9) The influence of temperature on food intake

a) Average daily temperature

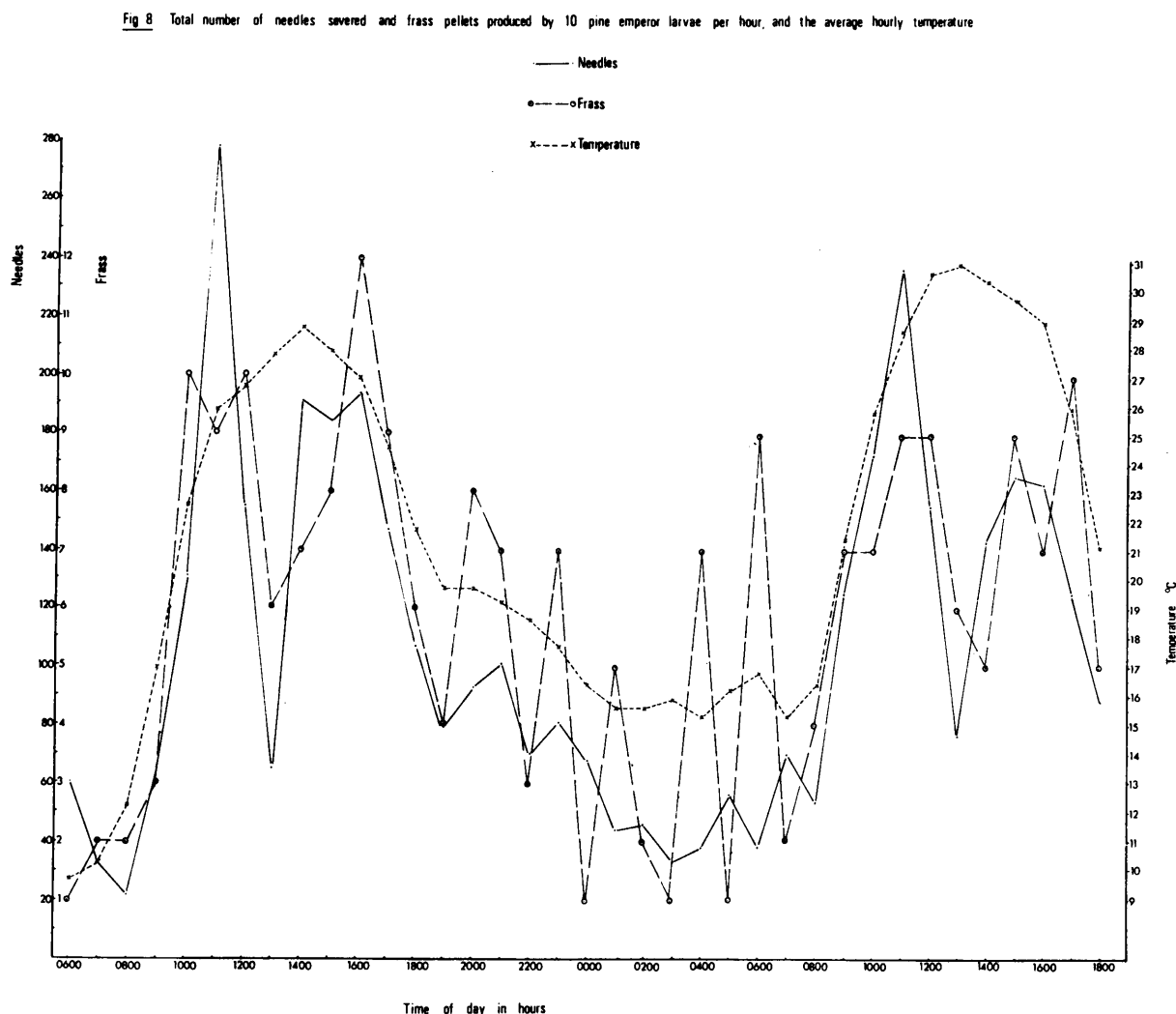
The total number of needles and frass obtained in the funnels per day from one group of final instar larvae, was compared with the average daily temperature (see Fig. 7).



From this fig. it can be seen that there is a positive correlation between temperature on the one hand, and needles severed and frass produced on the other, more needles being severed and more frass being produced at high than at low temperatures.

b) Average hourly temperature

The time of day at which active feeding takes place was studied only in the case of larvae that had been in the final instar for one week. This was done in the following manner: At 0500 hours a funnelled tree was lightly shaken, all the needles and frass pellets collected in the jar and a clean jar inserted. This was repeated at hourly intervals for 36 consecutive hours. At the same time hourly records were kept of the temperature. The results of this study are graphically represented in Fig. 8.



From this fig. it can be seen that the numbers of needles severed and frass pellets produced tend to rise and fall with temperature. However, needle drop and frass production fluctuate much more widely than temperature does. It may be concluded that larvae do not excrete frass at a steady rate, but at intervals in sudden spurts, particularly at night. This is also the case with needle drop, but much less conspicuously at night than by day. It also appears as if temperatures above 27°C or below 17°C tend to inhibit feeding to some extent.

This phenomenon of waves of feeding is all the more remarkable in view of the fact that 10 larvae were concerned in this study. One is tempted to suggest that feeding is somehow synchronized. Direct observations are necessary to throw more light on this question. It seems probable that the larvae feed together until hunger is stilled, then rest together until hunger again causes them to start feeding as a group. The intervals between feeding waves seem to be shorter during the night than during the day.

Temperatures above 27°C seem to stimulate the larvae to move about. On small trees they seem to move aimlessly in all directions. In large trees this movement may help them to reach shaded sites, where it would be cooler.

10) Food requirements

Procedure

In order to obtain some indication of the dry mass of food ingested the following experiment was conducted. Two groups, consisting of from 5–10 clusters with their scale leaves, were picked from the same long branch and placed in the two pans of a chemical balance. By adding bits of needles to the lighter side, the masses of the two groups could be equalized. The process could be repeated by emptying one of the pans and placing a third group of clusters and bits of needles in the other pan until balance was again achieved. For the purpose of this investigation, it is assumed that these different groups of needles would, for all practical purposes, also have the same dry mass, especially if the averages of a large number of determinations are compared.

A number of these groups of clusters were placed in petri-dishes (90 x 15 mm deep), one group per dish. One of these groups served as a control. The other groups were used as food for developing larvae. In order to keep the needles fresh,

the scale leaves of the clusters were pushed through a hole in the cork stopper of a small 3 ml glass vial filled with water. Small wood splinters were used as required to make the hole in the stopper watertight. The vial was then dried and laid flat in a petri-dish containing from 1–6 freshly emerged larvae. After the larvae had been feeding for 1–4 days they were removed and the dry mass of the frass and the uneaten remains of the needles determined after drying in an oven at 105°C until constant mass. The control needles were similarly dried and the dry mass determined. The difference between these two dry masses gives some indication of the dry mass of food actually consumed by the larvae.

This experiment was also done feeding the larvae on *Rhus dura* leaves. With *R. dura*, the stems bearing the leaves were cut to the same length. As the stems usually have a greater mass than the leaves, this method of obtaining the dry mass of food ingested, as described above, is probably less accurate than in the case of *P. patula*.

The moisture content of the needles and leaves was determined by finding the difference between the wet mass of the controls and their dry mass.

At the beginning of this experiment the larvae were transferred daily to freshly prepared needles or leaves, but since handling adversely affected them, they were later transferred at three- or four-day intervals. While the experiment was in progress, daily observations were made on larvae becoming immobile before moulting, in the act of moulting, or freshly moulted. Freshly moulted larvae were transferred to other petri-dishes prepared in the same way. From the third instar onwards larvae were placed singly in larger petri-dishes (130 x 25 mm deep) containing more needles (15–25 clusters); in these cases the scale leaves of the clusters were wrapped in moistened absorbent cottonwool before inserting them into glass vials; the cottonwool was remoistened at two day intervals.

The sexes are not distinguishable during the larval stage, and the larvae had to be bred until the pupal stage to determine their sex. Since the larvae were bred singly only from the third instar, the sex of each individual and thus the mass of food ingested by the different sexes could be determined from that instar onwards.

The last frass excreted by larvae directly before pupation is watery and darker

in colour than the normal frass. This frass sometimes contains jellylike inclusions. When such frass was noticed, the larvae were placed in clean petri-dishes for at least 6 hrs to ensure that no further excretion would take place and that all frass clinging to the larvae had been removed. Hereafter the larvae were placed in fruit jars, half full of damp earth, to pupate.

The mass of the larvae was determined directly after emergence and shortly after every moult. The sex and mass of each pupa were determined. In the male two swollen knobs are found latero-ventrally on the ninth abdominal segment, whereas in the female this segment is slightly elongated and provided with a longitudinal cleft on the mid ventral side.

Results

Breeding in the laboratory is a difficult and time consuming task. Of the 41 larvae bred on *R. dura*, only 20 developed to the pupal stage. Only 11 of the 132 bred on *P. patula* entered the soil, but none formed pupae. Taylor (1967) also stated that breeding is exceptionally difficult, whereas Geertsema (1970) did not succeed in breeding larvae in the laboratory. It was further observed that larvae occurring early in the season breed more successfully in the laboratory than those occurring later.

The average dry masses of *P. patula* needles ingested and frass excreted during the different instars are shown in Table 5.

From Table 5 it can be seen that during its larval stage an average individual ingests a total of 18 745 mg dry mass of *P. patula* needles, excretes 14 479 mg dry mass of frass and therefore utilizes 4 266 mg dry mass of plant material which is transformed partly into insect tissue and partly into energy. The increases in the dry masses of food ingested, frass excreted and plant material actually utilized, were more or less the same if the same two instars are compared. The increases were about 3–5 times per instar from the first to the fourth instars and about 6–7 times from the fourth to the fifth instars.

The digestion coefficient (Table 5) may be defined as the difference between the dry mass of food ingested and the dry mass excreted, expressed as a percentage of the dry mass of food ingested. On this basis the digestion coefficient of larvae bred on *P. patula* varied from 18,2–23,4 per cent for the different instars with an average of 22,8 per cent for all instars combined.

Table 5: Dry masses in mg of *P. patula* needles ingested and frass excreted by, and the digestion coefficient of the different instars of the pine emperor (both sexes)

Instar	n	Needles ingested			Increase of a per instar	Frass excreted			Increase of b per instar	Dry mass utilized (Difference between a and b)= c	Increase of c per instar	Digestion coeff = $\frac{c}{a} \times 100\%$
		Min	Max	Aver = a		Min	Max	Aver = b				
1	32	41,6	51,2	46,1	—	32,4	41,7	37,0	—	9,1	—	19,7
2	32	106,0	226,3	161,5	3,5	100,1	171,7	132,1	3,6	29,4	3,2	18,2
3	30	482,6	1 048,7	696,2	4,3	335,5	789,9	553,4	4,2	142,8	4,9	20,5
4	30	1 928,0	3 326,0	2 625,4	3,8	1 397,0	2 916,8	2 104,3	3,8	521,1	3,6	19,8
5	11	7 496,3	25 734,1	15 215,5	5,8	5 548,8	19 128,4	11 652,2	5,5	3 563,3	6,8	23,4
Total	—	—	—	18 744,7	—	—	—	14 479,0	—	4 265,7	—	22,8

The masses of larvae bred on *P. patula* shortly after hatching or moulting are given in Table 6.

Table 6: Live mass of pine emperor larvae of both sexes bred on *P. patula* shortly after hatching or moulting in mg

Instar	n	Min	Max	Aver	Live mass increase per instar
1	32	6,1	6,4	6,2	—
2	32	36,3	56,1	45,2	7,3
3	30	143,3	291,4	196,5	4,3
4	30	531,1	1 086,9	827,8	4,2
5	11	2 361,2	3 864,6	2 987,6	3,6
Pupa	0	—	—	—	—

According to this table, the mass of the larvae fed on *P. patula* increased from 6 mg shortly after emergence, to 2 988 mg at the beginning of the final instar. During the final instar the mass of the larvae increased a good deal more, but as no pupae were formed, pupal mass could not be determined. The increase in live mass was roughly 4–7 times per instar.

The average dry masses of *R. dura* leaves ingested and frass excreted during the different instars are provided in Table 7.

Females consume more, excrete more and utilize more than males. The increases in the dry masses of food ingested, frass excreted and plant material utilized, were more or less the same if the same two instars are compared, varying from 4–7 times per instar.

From a comparison of Tables 5 and 7 the following conclusions can be made. For each instar as well as for all instars combined, the dry mass of *R. dura* leaves ingested and frass excreted was about double that of *P. patula* needles. During the first instar, the dry mass *P. patula* utilized was about the same as that of *R. dura*, but during all other instars it was more or less a quarter lower on the former than on the latter. The digestion coefficient of each instar on *P. patula* was 1,5–2 times that on *R. dura*. This means that a larger mass of *R. dura* leaves will be required for complete larval development than would be the case with *P. patula*.

Table 7: Dry masses in mg of *R. dura* leaves ingested and frass excreted by, and the digestion coefficient of, the different instars of the pine emperor (M = male, F = Female).

Instar	Sex	n	Leaves ingested			Increase of a per instar	Frass excreted			Increase of b per instar	Dry mass utilized (Difference between a and b) = c	Increase of c per instar	Digestion coeff = $\frac{c}{a} \times 100\%$
			Min	Max	Aver = a		Min	Max	Aver = b				
1	M+F	36	46,7	90,4	85,0		36,3	82,4	76,0		9,0		10,6
2	M+F	30	239,1	425,7	308,9	3,6	199,1	378,6	269,5	3,5	39,4	4,4	12,8
3	M	13	1 047,4	1 405,7	1 195,7	4,2	951,4	1 237,0	1 070,7	4,2	178,5	4,5	13,6
	F	9	1 290,5	1 624,8	1 425,2		1 003,6	1 385,2	1 193,2				
4	M+F				1 310,4	4,1			4 747,1	4,2	635,8	3,6	11,8
	M	13	4 164,2	5 814,9	4 905,6		3 526,9	5 279,2	4 323,2				
	F	9	4 468,5	6 722,3	5 860,2		3 946,6	6 052,8	5 171,1				
5	M+F				5 382,9	6,6			31 022,2	6,5	4 545,8	7,1	12,8
	M	13	1 798,1	44 821,4	31 750,8		15 941,5	38 612,2	27 353,3				
	F	9	31 894,9	43 440,9	39 385,3		28 955,9	38 302,5	34 691,2				
Total	M+F				35 568,0				31 022,2				
	M				38 245,9				33 092,6				
	F				47 064,5				41 400,9				
	M+F				42 655,2				37 246,8		5 408,4		12,7

needles. In terms of plant material destroyed, this insect would therefore probably be a much more destructive pest on some of its indigenous than on its exotic host plants. The indigenous host plants usually occur isolated, trees and shrubs occurring sporadically, surrounded by unsuitable plants. Even with such a distribution, certain trees are sometimes totally defoliated. There is thus no absolute shortage of food, as only a small proportion of the available food supply is consumed. This was also found to be the case with *Thrips imaginis* Bagnall (Thysanoptera) (Davidson & Andrewartha, 1948 a & b). The host plants are so sparsely distributed that the chances of a moth locating food are minimal. If any of these indigenous trees were to be cultivated on a large scale, they would be especially vulnerable once they have been located.

The live masses of the different instar larvae bred on *R. dura* are summarized in Table 8.

Table 8: Live mass of pine emperor larvae bred on *R. dura* shortly after hatching or moulting (M = male; F = female)

Instar	Sex	n	Mass in mg			Live mass increase per instar
			Min	Max	Aver	
1	M + F	30	6,1	6,4	6,2	—
2	M + F	30	36,8	63,4	51,0	8,2
3	M	13	190,0	321,3	240,1	—
	F	9	217,5	361,5	267,2	—
4	M + F	22	—	—	253,7	5,0
	M	13	660,8	1 097,1	841,5	3,5
	F	9	747,8	1 237,3	1 005,3	3,8
5	M + F	22	—	—	923,4	3,6
	M	13	2 837,2	4 383,7	3 425,9	4,1
	F	9	3 322,2	5 023,8	4 186,0	4,2
pupa	M + F	22	—	—	3 806,0	4,1
	M	13	3 519,9	8 068,0	6 359,9	1,9
	F	9	6 643,6	9 896,3	8 482,5	2,0
	M + F	22	—	—	7 421,2	2,0

From this table it can be seen that they increase more than a thousand fold in mass before the pupal stage is reached. Females attained a larger mass than males, namely 8 483 as compared with 6 360 mg respectively. The live mass increase per instar was between about four and eight times per instar, while from the final instar to the pupal stage the mass was doubled.

Larvae bred on *P. patula* leaves in the laboratory were used to determine their moisture content. Directly after hatching or moulting, but before the larvae had an opportunity to feed, the live masses of 30 larvae of each instar as well as of 30 pupae were determined individually. The larvae or pupae were then killed in boiling water, placed in an oven at 105°C for 15–90 min until constant mass, left to cool and their dry masses determined. The results of these studies can be found in Table 9.

Table 9: Percentage moisture content of 30 larvae of each instar and 30 pupae of the pine emperor

Instar	Min	Max	Aver
1	72,3	73,9	72,8
2	81,7	88,8	87,0
3	82,9	91,4	86,5
4	86,2	90,5	88,0
5	83,6	88,9	87,3
pupa	62,7	76,6	69,8

From this table it is clear that the moisture content is lowest in newly hatched larvae and newly formed pupae. The moisture contents of the other larval instars are more or less the same. It is thus clear that larvae accumulate a fair amount of water in their tissues during the first instar, and lose about the same relative amount during pupation. This explains the high live mass increase during the first instar, and the low live mass increase from the final instar to the pupal stage. The loss of moisture before entering diapause has been reported for many insects (Andrewartha & Birch, 1954).

Larvae bred on *R. dura* obtained a larger mass per instar than larvae bred on *P. patula*. In addition, 22 larvae completed their development on *R. dura* in contrast to not a single one on *P. patula*. It is therefore clear that larvae in the laboratory thrive better on the former than on the latter; the same is possibly true of larvae in the field.

A summary of the relative increase in dry mass of food ingested, dry frass excreted, dry mass utilized and increase in live weights is given in Table 10.

Table 10: Summary of the relative increases in dry mass ingested, dry frass excreted, dry mass utilized and live weight of the pine emperor (both sexes)

Instars compared	Host plant	Relative increase in			
		dry mass ingested	dry frass excreted	dry mass utilized	live mass
1 + 2	<i>P. patula</i>	3,5	3,6	3,2	7,3
2 + 3	"	4,3	4,2	4,9	4,3
3 + 4	"	3,8	3,8	3,6	4,2
4 + 5	"	5,8	5,5	6,8	3,6
1 + 2	<i>R. dura</i>	3,6	3,5	4,4	8,2
2 + 3	"	4,2	4,2	4,5	5,0
3 + 4	"	4,1	4,2	3,6	3,6
4 + 5	"	6,6	6,5	7,1	4,1
5 + pupa	"	—	—	—	2,0

The increase in dry mass ingested, dry frass excreted as well as in dry mass utilized is in most cases higher with *R. dura* than with *P. patula*. These increases do not differ very widely for the two host plants if the same instar is compared. It is further noticeable that the increase is highest in the final, and usually lowest in the case of the first instar. Live mass, on the contrary, increases to a much greater extent during the first than during the fourth or fifth instars. The live mass increase per instar obtained with *P. patula* and *R. dura* does not differ greatly but is generally higher with the latter.

The overall efficiency of conversion of food into body tissue may be defined as the relationship between the gain in dry mass and the dry mass of food ingested. The percentage efficiency has been calculated for each instar as shown in Table 11.

Table 11: Percentage efficiency of conversion of *P. patula* and *R. dura* leaves into body tissue by pine emperor larvae

Instar	Host plant	At beginning of instar			During instar		
		% moisture content	Live mass (mg)	Calculated dry mass (mg)	Gain in dry mass (mg) = a	Dry mass food ingested (mg) = b	% efficiency = $\frac{a}{b} \times 100$
1	<i>P. patula</i>	72,8	6,2	1,7	4,2	46,1	9,1
2	"	87,0	45,2	5,9	20,6	161,5	12,8
3	"	86,5	196,5	26,5	72,8	696,2	10,5
4	"	88,0	827,8	99,3	280,1	2 625,4	10,7
5	"	87,3	2 987,6	379,4	—	—	—
Total	—	—	—	—	377,7	3 529,2	—
Average	—	—	—	—	—	—	10,7
1	<i>R. dura</i>	72,8	6,2	1,7	4,9	85,0	5,8
2	"	87,0	51,0	6,6	27,6	308,9	8,9
3	"	86,5	253,6	34,2	76,6	1 310,4	5,8
4	"	88,0	923,4	110,8	372,6	5 382,9	6,9
5	"	87,3	3 806,0	483,4	1 757,8	35 568,0	4,9
pupa	"	69,8	7 421,2	2 241,2	—	—	—
Total	—	—	—	—	2 239,5	42 655,2	—
Average	—	—	—	—	—	—	5,3

From this table it can be seen that the larvae could convert *P. patula* needles more efficiently into insect tissue than *R. dura* leaves, the percentage efficiency varying from 9–13, and 5–9 for the two host plants respectively.

The average percentage efficiency was 10,7 per cent when fed on *P. patula* and 5,3 per cent when fed on *R. dura*. According to Evans (1939) the percentage efficiency of *Agrias urticae* (L.) is 16,2 per cent and that of *Prodenia eridania* Cram. 33,5 per cent, both considerably higher than found during the present investigation on the pine emperor.

The average percentage moisture content of *P. patula* was higher than that of *R. dura* leaves, namely 61,1 and 55,0 per cent respectively. It is uncertain whether this difference in the moisture content of the leaves of the two host plants played an important role on the percentage of efficiency or not. However, it appears much more probable that *R. dura* leaves are either less nutritive to, or less digestible by pine emperor larvae than needles of *P. patula*.

From Table 11 it can also be deduced that to obtain a pupa with a dry mass of 2 241 mg, 42 655 mg dry mass *R. dura* leaves will be required. This represents approximately 94 790 mg of fresh leaves.

11) Duration of larval development

a) In the laboratory

Observations on the duration of larval development under fluctuating conditions in the laboratory are summarised in Table 12. The temperatures were registered by means of a thermograph.

As could be expected, temperature is an important factor in determining the duration of the different instars, the duration being longer at a low than at a high temperature. When fed on *P. patula*, instars one to five would probably last 18, 11, 12, 13 and 22 days at fluctuating laboratory temperatures with averages of about 20°C. From Table 12 it can also be concluded that on *R. dura* the two sexes develop at more or less the same rate during the final larval instar. There are indications that development is slightly faster on *R. dura* than on *P. patula*. Taylor (1967) and Geertsema (1970) also found that the host plant had an influence on the duration of the larval instars of *N. cytherea clarki* and *N. cytherea cytherea* respectively.

Table 12: Duration of the larval instars of the pine emperor fed on *P. patula* needles under fluctuating laboratory conditions (M = male; F = female)

Instar and host plant	Sex	n	Duration in days			Average temperature for period in °C
			Min	Max	Aver	
1. <i>P. patula</i>	M + F	20	12	16	12,7	21,3
	"	12	17	20	18,3	20,5
	"	6	17	19	18,0	20,2
<i>R. dura</i>	M + F	21	9	14	11,1	21,2
	"	12	18	19	18,4	20,2
2. <i>P. patula</i>	M + F	11	11	13	12,1	19,5
	"	6	12	14	13,3	19,3
	"	3	18	20	19,0	18,3
<i>R. dura</i>	M + F	12	11	13	12,2	19,5
	"	16	12	17	13,7	19,3
3. <i>P. patula</i>	M + F	12	9	15	12,3	20,0
	"	2	18	18	18,0	18,5
	"	8	14	21	16,0	17,2
<i>R. dura</i>	"	5	21	24	22,0	16,9
	M + F	11	8	10	8,4	20,3
	"	16	13	16	14,1	17,8
4. <i>P. patula</i>	"	3	19	22	20,0	16,5
	M + F	7	12	17	14,1	19,6
	"	9	15	20	17,1	18,1
<i>R. dura</i>	"	7	17	22	19,9	16,9
	M + F	9	13	14	13,6	19,6
	"	4	13	15	14,0	19,2
5. <i>P. patula</i>	"	12	20	24	21,3	16,8
	M + F	4	19	26	22,5	19,1
	"	2	26	28	27,0	17,8
<i>R. dura</i>	M	3	17	23	19,0	19,8
	F	1	20	20	20,0	
	M + F	4	—	—	19,5	
	M	5	18	20	19,4	19,2
	F	4	19	21	19,8	
	M + F	9	—	—	19,6	
	M	3	20	23	22,0	18,0
	F	2	20	23	21,5	
	M + F	5	—	—	21,8	
	M	2	23	25	24,0	16,8
	F	2	24	25	24,5	
	M + F	4	—	—	24,3	

b) **In the field**

The duration of the larval instars on naturally growing pine trees in a plantation appears in Table 13. The average temperatures as registered by a thermograph in the same plantation are also given.

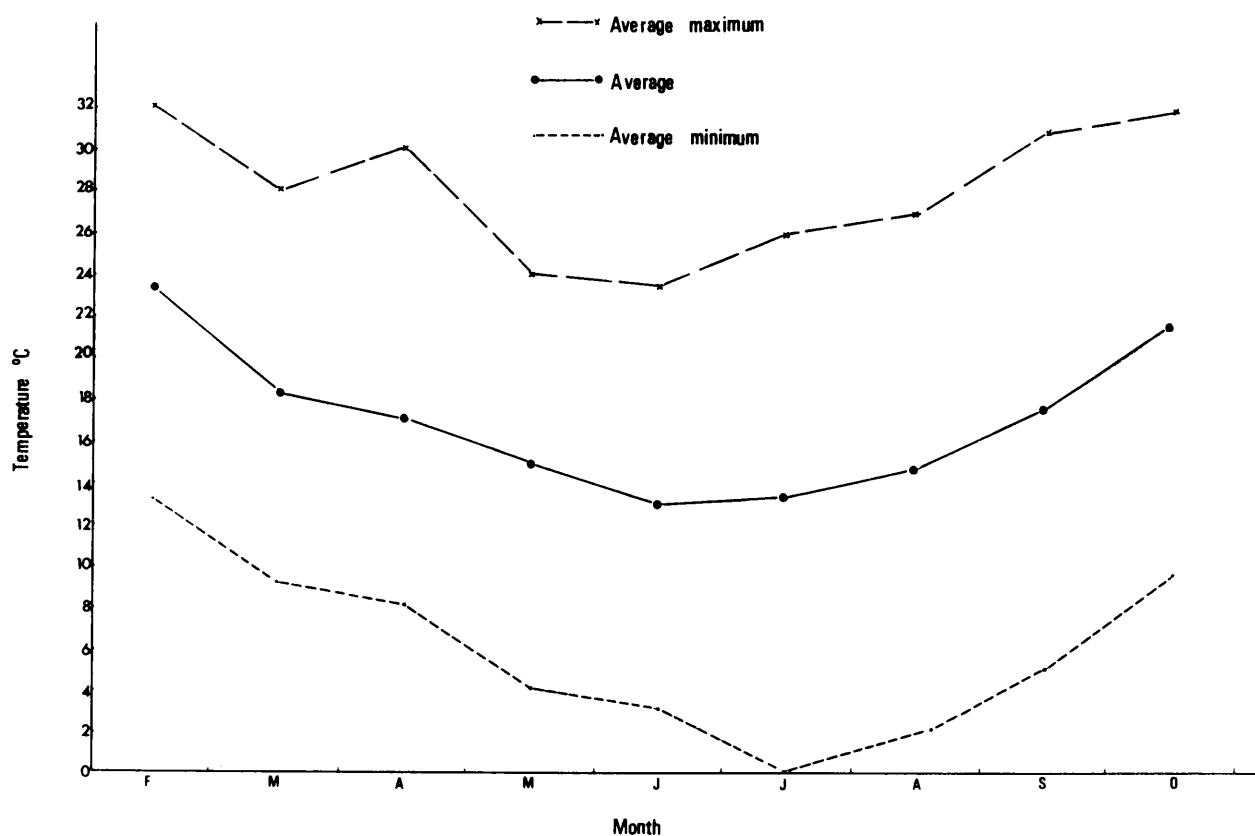
Table 13: Duration of the larval instars of the pine emperor feeding on growing *P. patula* trees under fluctuating field temperatures

Instar	n	Duration in days			Average temperature for period °C
		Min	Max	Aver	
1	20	13	16	14,8	18,0
	21	19	22	20,8	14,8
	23	21	24	22,9	14,8
2	19	16	21	17,3	14,3
	14	20	29	23,1	13,4
3	4	16	18	17,0	13,8
	31	21	27	24,0	12,6
4	9	17	21	19,1	15,9
	17	18	33	22,9	14,7
	2	21	21	21,0	13,4
	4	23	30	26,0	13,2
5	9	24	34	28,2	16,4
	3	26	33	30,7	13,5
	1	30	30	30,0	12,7

In the field, instars one to five would probably last about 21, 15, 15, 20 and 29 days respectively at fluctuating temperatures with an average of about 15°C. Both in the laboratory and in the field the fifth instar lasted the longest, and the first instar the second longest. The second instar lasted the shortest in both instances. Although the laboratory temperatures were much higher than those registered in the field, it seems that at the same average temperature, development would be slower in the laboratory than in the field. This is probably due to the larvae in the field feeding on growing foliage, while picked leaves were fed to larvae reared in the laboratory.

The average field temperature (Fig. 9) drops sharply from February, and reaches its lowest during June. A gradual increase in temperature then takes place until October. The temperature during the larval period is therefore highest during

Fig.9: Average monthly field temperature in the Welgelegen plantation for nine months during the years 1969 and 1970



March and September, and lowest during June and July. One result of fluctuating temperatures seems to be that larvae hatching late are somehow able to catch up on some of the earlier hatching larvae, instead of lagging further behind. For example, larvae hatching during the first week of May pupate during mid September (see a Fig. 1), those hatching during the first week in June pupate during the beginning of October (see b Fig. 1), while those hatching during the first and last weeks of July, pupate during the middle and end of October (see c & d Fig. 1) respectively. The average durations of these four batches of larvae are therefore 18, 16, 14 and 13 weeks respectively. The larvae hatching during July therefore

develop in a shorter period than those hatching during May and June.

Taylor (1967) states that the total duration of the larval stages during mid February to mid April averages 47,6 days (11 larvae) when fed on *Psidium guajava* and 50,3 days when fed on *Leucospermum cuneiforme* (Burm. f.) Rourke (15 larvae). Geertsema (1970) reports as follows on the duration of the different instars. The numbers of larvae indicated between brackets have been provided by Geertsema (*in litteris*) first instar: 15 days (10–21 days) (15 larvae); second instar: 11 days (9–12 days) (13 larvae); third instar: 11 days (9–12 days) (7 larvae); fourth instar: 16 days (no variation) (2 larvae) and fifth instar: 26 days (no variation) (2 larvae). Both above-mentioned authors do not however mention what the prevailing temperatures were when their observations were made.

During a snowfall on the 3rd June, 1968, a large number of larvae were dislodged from young trees. A number of these larvae were collected and placed in snow in gauze cages until the snow had melted. Larvae that outlived this treatment, were given *P. patula* needles and placed in gauze cages (30 x 30 x 45 cm) for further observation at room temperature.

During the snow, many branches gave way under the weight and about 70 per cent of the larvae on trees about 2 m high were dislodged. The bodies of larvae lying in the snow remained pliable and soft and apparently did not freeze. Of the 309 larvae collected and kept in snow, 59 died after the snow had melted and 10 during the following week. About 15,6 per cent of the total number of larvae on young trees were therefore killed. The greatest majority of the larvae therefore seem to be able to survive short periods of extremely cold weather.

12) Host plants

Host plants harbouring eggs or larvae were collected in the field. Neighbouring plants were also inspected for signs of defoliation or damage to minimise the chance of mistaking plants on which the larvae accidentally occur, for host plants. Where possible, plants were marked and later investigated to determine to which instar the larvae could develop on them. Samples of these plants were pressed, given a label showing the larval instar that was found on them, and later identified at the herbarium.

Larvae are frequently found on young indigenous trees and shrubs, which are

often defoliated early in the season so that the larvae have to locate other food. Movement from one type of host plant to another is therefore quite common in the case of indigenous vegetation. It was also observed that larvae do not necessarily complete their development on the same plant species as that utilized during the earlier instars.

The following authors were consulted to draw up the list of host plants that follows below:—

(a) Dickson (1945); (b) Hepburn (1961); (c) Taylor (1967); (d) Grobler according to Taylor (1967); (e) Geertsema (1970). In this list the author will be indicated by the corresponding letter (a) to (e) as used above. Only the author who first mentioned a host plant will be indicated. Original observations by the present author will be indicated by “(or. obs.)”. Anonymous (1970) mentions host plants already mentioned by other workers.

The most advanced instar mentioned by the author or recorded during this investigation on each host plant is indicated, where this is known, by the figure corresponding to the instar number.

a) List of indigenous host plants

- Aphloia theiformis* (Vahl) A. Benn. (or. obs.) (Is 1)
Burchellia bubalina (L. f.) Sims (or. obs.) (Is 5)
Canthium ventosum (L.) S. Moore (or. obs.) (Is 3)
Diospyros mespiliformis Hochst. ex A.DC. (d) (Is?)
Diospyros whyteana (Hiern) F. White (e) (Is 5)
Euclea divinorum Hiern (or. obs.) (Is 1)
Euclea natalensis A. DC. (or. obs.) (Is 1)
Euclea polyandra (L. f.) E. Mey. ex Hiern (a) (Is ?)
Faurea macnaughtonii Phill. (or. obs.) (Is 1)
Gerrardian foliosa Oliv. (or. obs.) (Is 3)
Halleria lucida L. (or. obs.) (Is 5)
*Leucospermum cuneiforme** (Burm f.) Rourke (c, in lab), (or. obs. in field) (Is 5)
Maesa lanceolata Forsk. (or. obs.) (Is 5)
Myrica conifera Burm f. (d) (Is ?)

* Not indigenous in areas where *N cytherea clarki* is found.

- Myrica pilulifera* Rendle (or. obs.) (Is 2)
Myrsine africana L. (or. obs.) (Is 4)
Ozoroa reticulata (Bak. f.) R. & A. Fernandes (or. obs.) (Is 2)
Protea caffra Meisn. (or. obs.) (Is 3)
Protea roupelliae Meisn. (or. obs.) (Is 5)
Protea rhodantha Hook. f. var. *rhodantha* (or. obs.) (Is 3)
Psychotria capensis (Eckl.) Vatke (or. obs.) (Is 1)
Pterocelastrus echinatus N. E. Br. (or. obs.) (Is 3)
Rapanea (Myrsine) melanophloeos (L.) Mez (d) (Is 5)
Rhamnus prinoides L' Hérit. (d) (Is ?)
Rhoicissus tridentata (L. f.) Wild & Drummond (or. obs.) (Is 3)
Rhus dura Schonl. (or. obs.) (Is 5)
Rhus lucida L. (d) (Is ?)
Rhus synstylica R. & A. Fernandes (or. obs.) (Is 5)
Rhus pyroides Burch. (or. obs.) (Is 1)
Rhus undulata Jacq. (or. obs.) (Is 1)
Syzygium cordatum Hochst. (or. obs.) (Is 5)
Vaccinium exul H. Bol. (or. obs.) (Is 2)

b) List of imported exotic host plants

- Eucalyptus grandis* (Hill) Maiden (e) (Is ?)
Persea gratissima Gaertn. f. (or. obs.) (Is 5)
Pinus caribaea Morelet (e) (Is 5)
Pinus patula Schlechtd. & Cham. (b) (Is 5)
Pinus radiata D. Don (or. obs.) (Is 5)
Pinus taeda L. (e) (Is 5)
Psidium guajava L. (c) (Is 5)
Pyrus malus L. var. *pumila* Henry (e) (Is 5)

It was noted that five third instar larvae moved from a defoliated *R. dura* tree to *Watsonia densiflora* Bak. (Liliaceae) where they remained for about a week before moving to another host plant. According to Skaife (1953), *N. cytherea cytherea* larvae are frequently found on *Watsonia* sp.. *W. densiflora* is, however, only very rarely eaten by *N. cytherea clarki* and is not considered a host plant. It was also observed that larvae feed on the skins of the guava fruit when leaves

become scarce.

From the long list of host plants it is clear that a wide variety of food plants exists for *N. cytherea clarki*. This subspecies has adapted itself so well to *P. patula* that its original host plants cannot be stated with certainty. Moreover, many of these host plants were found in the vicinity of *P. patula* plantations. Certain indigenous plants listed above are often defoliated near as well as more than 10 km away from plantations; they may therefore be regarded as some of the original host plants of *N. cytherea clarki*. These are: *Diospyros whyteana*, *Protea roupelliae*, *Rapanea melanophloeos* and *Rhus dura*. *R. melanophloeos* is also considered as one of the original host plants of *N. cytherea cytherea* (Tooke & Hubbard, 1941).

Most of the host plants regarded here as original, as well as some of the other host plants listed above occur in the two veldtypes designated as the North-Eastern Mountain Sourveld and Ngongoni Veld of Natal Mist Belt by Acocks (1953). When the distribution of these veld-types is compared with that of *N. cytherea clarki* (Fig. 10), it is seen that the insect has a very similar distribution to these veldtypes. Rainfall is probably one of the most important factors in determining the distribution of plants, thus indirectly determining the distribution of associated insects.

13) Pupation

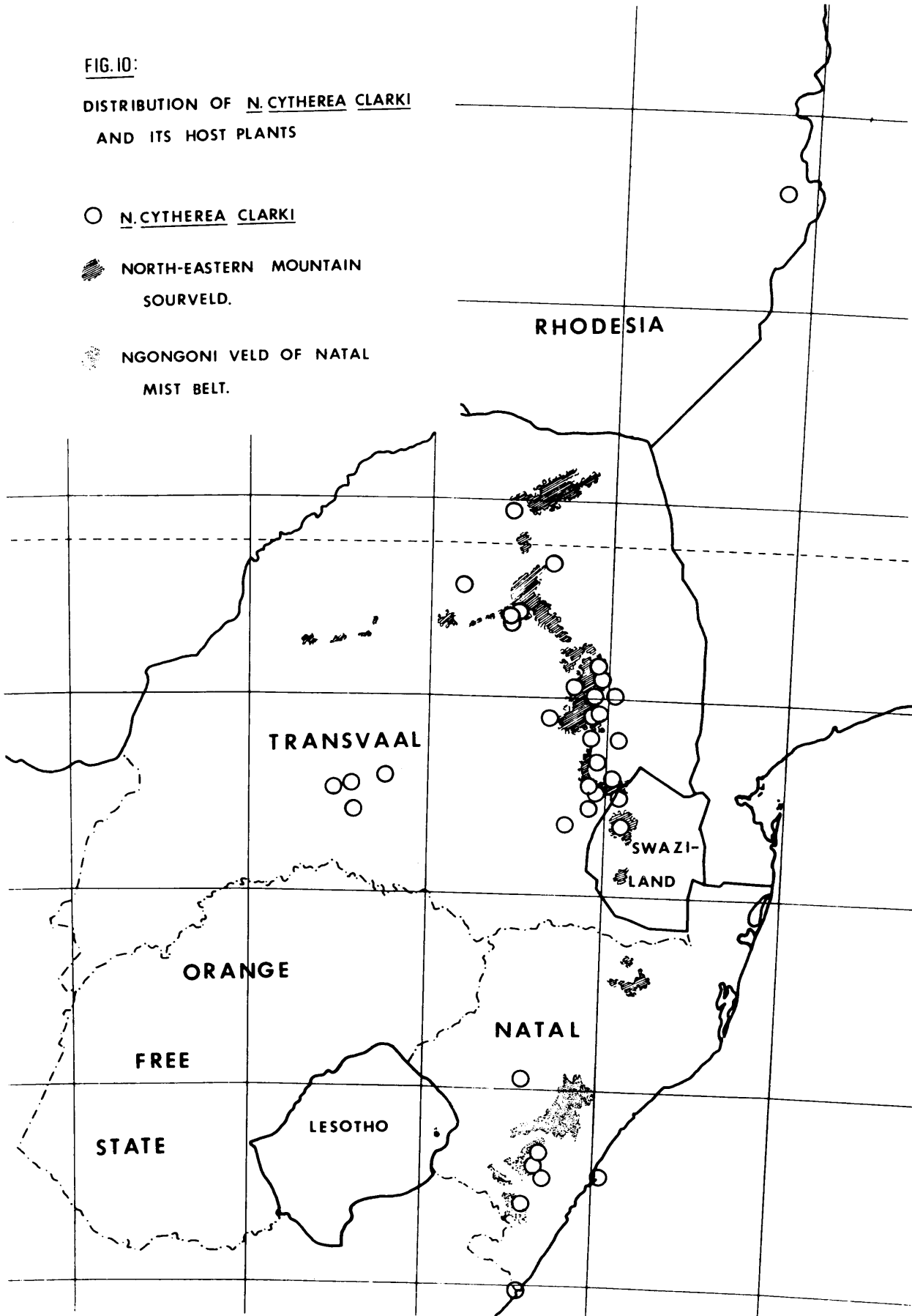
The full-grown larva stops feeding and becomes more or less immobile for about 30 min or more after which it starts to crawl about, apparently aimlessly. In the meantime it may excrete irregular frass pellets, of which at least the last one is watery. The larva then crawls down the tree or drops to the ground where it crawls about in search of a suitable site to pupate. From the time that the watery frass is excreted the larva gradually shrinks.

The movements of pine emperor larvae ready to pupate were studied during August, 1970 as follows: Shortly after larvae on funnelled trees had descended to pupate, five larvae were placed on more or less flat ground between young *P. patula* trees, where hoeing had been done a few months previously. The movements of these larvae were watched and their positions marked every 5 min.

Preliminary results indicated that the movements of the larvae could not be correlated with the position of the trees. Most larvae appeared to be crawling in

FIG. 10:
DISTRIBUTION OF N. CYTHEREA CLARKI
AND ITS HOST PLANTS

- N. CYTHEREA CLARKI
- ▨ NORTH-EASTERN MOUNTAIN SOURVELD.
- ◐ NGONGONI VELD OF NATAL MIST BELT.



a southerly direction, i.e. more or less away from the sun. If larvae attempting to burrow into the substrate are excluded, they progressed from 19–85 cm in 5 min. They crawled about for periods lasting from half an hour to more than two hours before finally burrowing into the soil. The total distance covered from the point of release was from 2,7–6,1 m. While crawling about, a larva may attempt to burrow into the substratum at more than one spot until a suitable site is found.

The searching larva eventually burrows into the needle mat and/or soil where it forms a type of hollow or cell. It usually comes to rest in this cell in a horizontal position, frequently just below the general level of the soil. The cell in the substrate is broadened by appropriate movements. A type of cocoon consisting of silk, saliva and earth particles is then constructed in the cavity. The larva then lies comparatively motionless for a few days, loses a great deal of its water content and shrinks from about 110 mm to about 40–50 mm in length. The skin then bursts on the mid-dorsal line and the pupa appears. The old larval skin usually remains attached to the hind part of the body. Under the prevailing conditions, the larval skin was shed from 10–19 days after entering the soil, the period being the shortest at higher

Table 14: Duration of the prepupal stage of both sexes of the pine emperor at fluctuating laboratory conditions

No of individuals	Duration in days			Average temperature for period in °C
	Min	Max	Aver	
13	17	19	18,5	16,8
5	15	18	16,4	17,6
7	10	14	11,9	19,8

temperatures (see Table 14). This is in close agreement with the findings of Geertsema (1970), who states that the prepupal stage lasts from 9–14 days during October.

E. The pupal stage

1) Description, size and sexual differences

The newly formed pupa is at first soft and a light yellow-brown, with the remains of the three pairs of scoli on the thorax, the two knobs above the antennae and the terminal abdominal segment dark brown. During the next two or three days,

the whole pupa changes in colour and becomes dark brown. After a few days the colour changes to a dull black and the integument hardens (Plate 1). Deep incisions separating the abdominal segments are characteristic. As previously described, the male has two swollen knobs, latero-ventrally on the ninth abdominal segment, whereas in the female this segment is slightly elongated and provided with a longitudinal cleft on the mid ventral line. The lengths and widths of 150 pupae of both sexes are indicated in Table 15.

Table 15: Measurements in mm of 150 male and 150 female pupae collected in the field

Sex	Lengths			Widths		
	Min	Max	Aver	Min	Max	Aver
Males	32	49	41,9	12	18	14,9
Females	35	51	45,2	13	20	16,2

From this table it can be seen that female pupae are slightly larger than males. For a more detailed description of the pupa see Geertsema (1970).

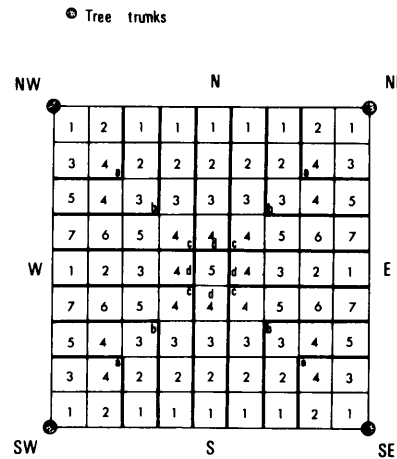
2) Seasonal occurrence

Pupae are formed from the beginning of June until the beginning of October. Emergence of adults ranges from the first week in February until the end of April (Fig. 1). The pupal stage lasts about 7–9 months (October to April and June to February), indicating that pupae formed during winter (June) develop at a slower rate than those formed during spring (October). Diapause during the pupal stage thus retards the earlier formed pupae by about two months, enabling later formed pupae to catch up on them. With the exception of May, pupae are present during all months of the year.

3) Spatial distribution

The depths and positions of pupae in relation to ground level and tree trunks were studied in 40 randomly chosen plots, half of them with and the other half without brushwood. Each plot covered a square area 2,7 x 2,7 m between four trees and was marked off by means of a rope fastened to the four trees. Each plot was subdivided into 81 subplots, 30 x 30 cm, as shown in Fig. 11. Pupae were carefully located by

Fig. 11: Lettering and numbering used to form groups of 30 x 30 cm subplots for statistical analysis of pupal distribution relative to tree trunks



systematically digging up the whole area occupied by each plot. The height of each pupa above or below the general ground level was measured to the nearest 5 mm. The perpendicular distances between each pupa and the two nearest ropes were also measured, so that the position of each pupa could be entered on a sketch-plan showing all the subplots.

Notes were kept of the point on the compass occupied by each of the four boundary trees, so that the number of pupae located in corresponding subplots in the 40 different plots (replications) were known and could be added together. In this way an overall picture could be formed of the distribution of pupae relative to tree trunks and brushwood in the plantation.

The depths at which pupae occurred in the needle mat and soil are summarized in Fig. 12. Free-hand curves were drawn from the points plotted. The statistical analysis of this data appears in Table 16.

From Fig. 12 it can be seen that more pupae were found in lanes without than in lanes with brushwood. According to the X^2 analysis in Table 16, pupae were found at highly significantly greater depths in lanes without than in lanes with brushwood. The pupae in brushwood lanes occur chiefly in the needle mat above the soil, while those in lanes without brushwood appear mainly on or in the soil.

Fig. 12: Depths at which pine emperor pupae occurred in needle mat and soil in lanes with and

without brushwood

●—● Lanes without brushwood

×---× Lanes with brushwood

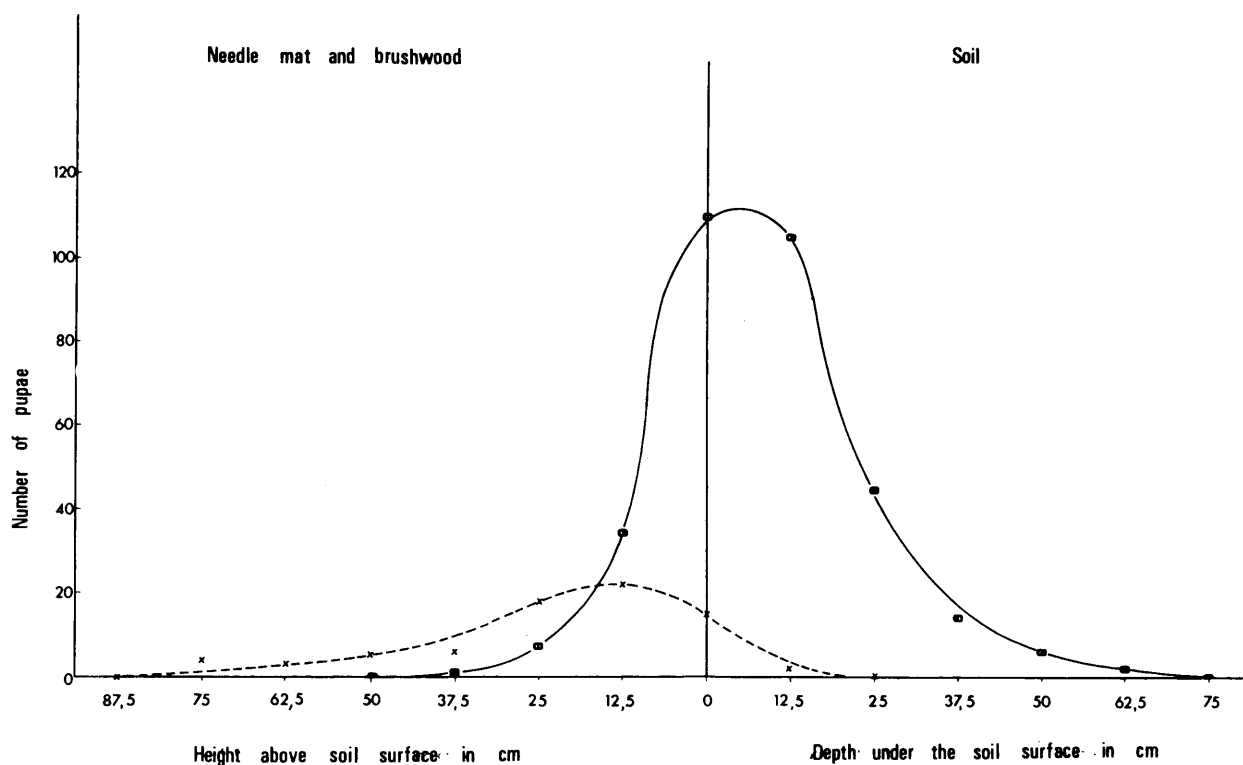


Table 16: Statistical analysis of data in Fig. 12.

	Lanes without brush- wood	Lanes with brushwood	
In needle mat	42	58	100
On or in the soil	281	17	298
	323	75	398

Continuity correction was applied

$$X^2 = 130,50^{**}; X^2_{1} (,01) = 6,63$$

For the purpose of statistical analysis the subplots were lettered and numbered, as indicated in Fig. 11, to form groups of subplots in the same relative positions in their respective plots. The brushwood was heaped together in every third lane running from east to west, so that a third of the soil surface was covered with brushwood while the rest was clear of it.

The actual number of pupae found in the different subplots can be found in Table 17 while the statistical analysis of the data in Table 17 can be found in Table 18.

Table 17: Numbers of pine emperor pupae found in the different subplots of 30 x 30 cm with lettering and numbering corresponding to that in Fig. 11

No	Lanes without brushwood				Lanes with brushwood			
	Subplot group a				Subplot group a			
	NW	NE	SW	SE	NW	NE	SW	SE
1	11	13	21	17	12	8	5	4
2	4	8	13	8	2	7	2	5
3	6	3	11	10	5	4	4	5
4	11	10	11	11	9	4	3	4
Aver for subplot group a	10,50				5,19			
	Subplot group b				Subplot group b			
	NW	NE	SW	SE	NW	NE	SW	SE
1	4	4	6	8	2	2	1	4
2	13	7	5	9	0	1	3	2
3	4	5	8	4	0	5	2	2
4	10	5	8	10	2	9	0	0
5	2	6	6	10	8	9	2	0
Aver for subplot group b	6,70				2,70			
	Subplot group c				Subplot group c			
	NW	NE	SW	SE	NW	NE	SW	SE
1	5	1	4	3	0	0	0	0
2	1	7	1	2	2	1	0	1
3	1	1	1	3	0	0	0	0
4	5	6	3	4	3	5	0	0
5	6	7	4	3	2	0	0	2
6	4	7	2	6	0	4	0	0
7	2	1	4	5	8	6	0	0
Aver for subplot group c	3,54				1,21			
	Subplot group d				Subplot group d			
	N	W	E	S	N	W	E	S
1	8	7	8	0	4	0	0	6
2	6	7	2	3	2	0	0	1
3	4	9	3	4	2	2	0	4
4	4	5	4	3	0	3	2	3
5	—	—	—	3	—	—	—	6
Aver for subplot group d	4,71				2,06			

Table 18: Analysis of variance of data in Table 17

a) Lanes without brushwood

Source of variation	SS	d.f.	MS	F
Between subplot groups	532,00	3	177,33	20,91**
Within subplot groups	652,69	77	8,48	
Total	1 184,69	80		

**Differs highly significantly at the 1% level ($F_{3,77} = 4,052$)

SSD(Fisher) at $t_{\alpha/2} = 1,973$ (5%) and 2,649 (1%)

Comparing a with b = 3,89; a with c = 7,63; a with d = 5,71; b with c = 3,71;
b with d = 2,07 and c with d = -1,31

a	b	d	c
10,50	<u>6,70</u>	<u>4,71</u>	<u>3,54</u>

Averages underlined by a continuous line do not differ significantly. Averages underlined by a dotted line do not differ highly significantly.

b) Lanes with brushwood

Source of variation	SS	d.f.	MS	F
Between subplot groups	165,81	3	55,27	9,37**
Within subplot groups	454,29	77	5,90	
Total	620,10	80		

**Differs highly significantly at the 1% level ($F_{3,77} = 4,052$)

SSD(Fisher) at $t_{\alpha/2} = 1,973$ (5%) and 2,649 (1%)

Comparing a with b = 3,05; a with c = 5,22; a with d = 3,70; b with c = 2,10;
b with g = 0,80 and c with d = -1,14

a	b	d	c
5,19	<u>2,70</u>	<u>2,06</u>	<u>1,21</u>

Averages underlined by a continuous line do not differ significantly. Averages underlined by a dotted line do not differ highly significantly.

From Table 18(a) and (b) it can be concluded that highly significantly more pupae could be found near the tree trunks (subplot groups a in lanes without as well as in lanes with brushwood) than anywhere else. Similarly, significantly more pupae could be found in subplot groups b than in groups c whether they contained brushwood or not. Although more pupae could be found in subplot groups b than in groups d, the differences were not significant. There is therefore convincing evidence that the chances of finding pupae would be best near tree trunks.

The actual number of pupae found in each of the subplots appearing in Table 17 were used to determine whether the number of pupae found in lanes with brushwood differed statistically from that in lanes without brushwood. The analysis appears in Table 19.

Table 19: Analysis of variance of the data in Table 17

Source of variation	SS	d.f.	MS	F
Between lanes with and without brushwood	466,83	1	466,83	41,39**
Within lanes	1 804,79	160	11,28	
Total	2 271,62	161		

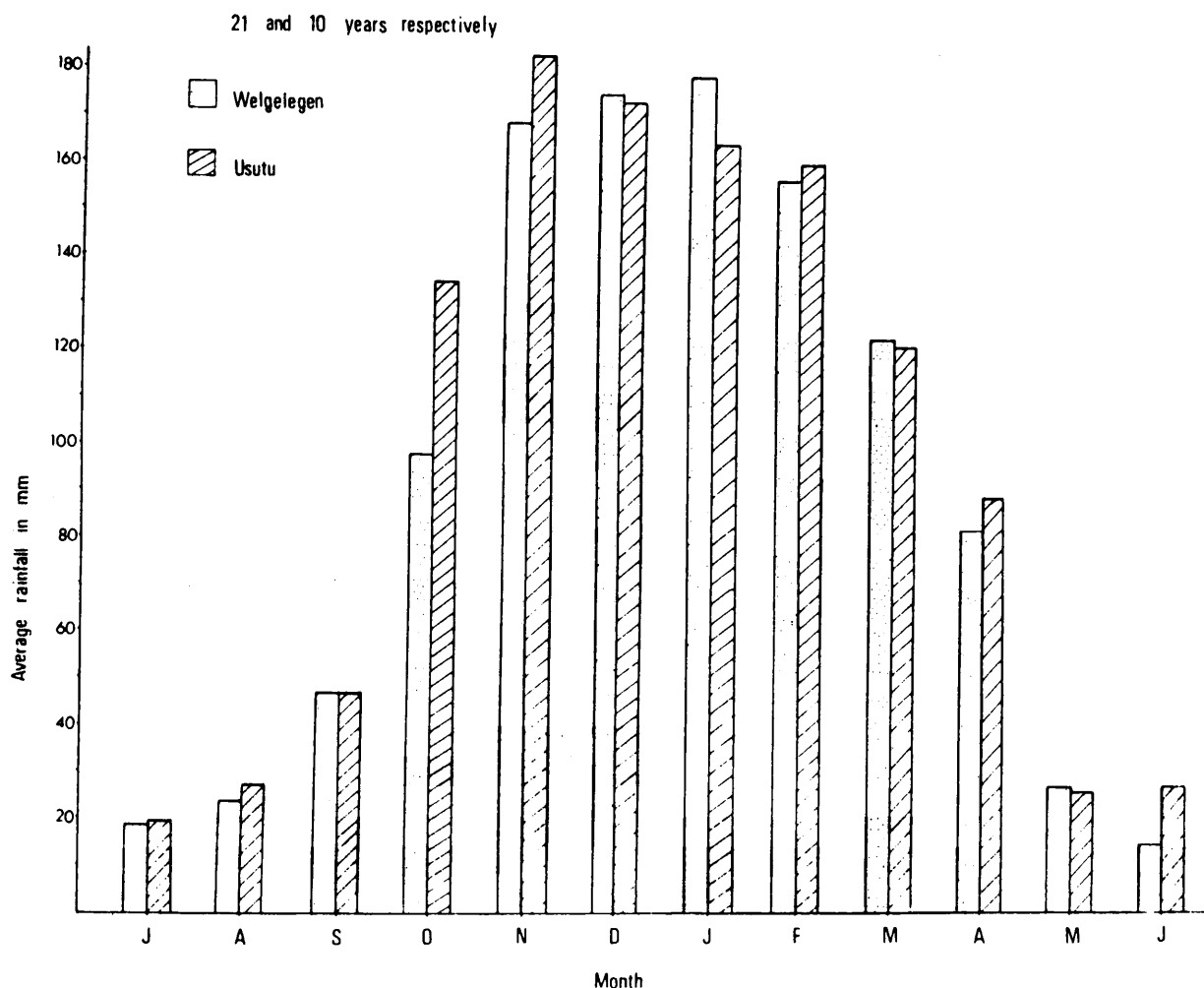
**Differs highly significantly $F_{(1,160)}(.01) = 3,91$

From the analysis in Table 19, it can be seen that highly significantly more pupae were found in lanes without than in lanes with brushwood. There appear to be two possible explanations for this. Firstly, larvae may be activated by the presence of twigs and branches on the substrate, and secondly, they may be repelled by decaying wood.

A certain amount of moisture is lost during and shortly after pupal formation. There is however a certain minimum moisture content below which normal development is not possible. Pupae exposed to dry conditions lose a certain amount of moisture, which can apparently not be reabsorbed. In extreme cases such pupae may die, or if the adult stage is reached, the wings are unable to expand normally and remain crumpled together. Such moths have been noticed in laboratory cultures. They may also appear in plantations in spite of heavy rains of as much as 75 mm a week prior to emergence.

In a pine plantation the pupae are usually well protected against temperature and moisture fluctuations under the pine needle mat and soil. According to the rainfall records (Fig. 13), it is dry during the early pupal stage (June to August).

Fig. 13: Average monthly rainfall for the Welgelegen and Usutu plantations over the last

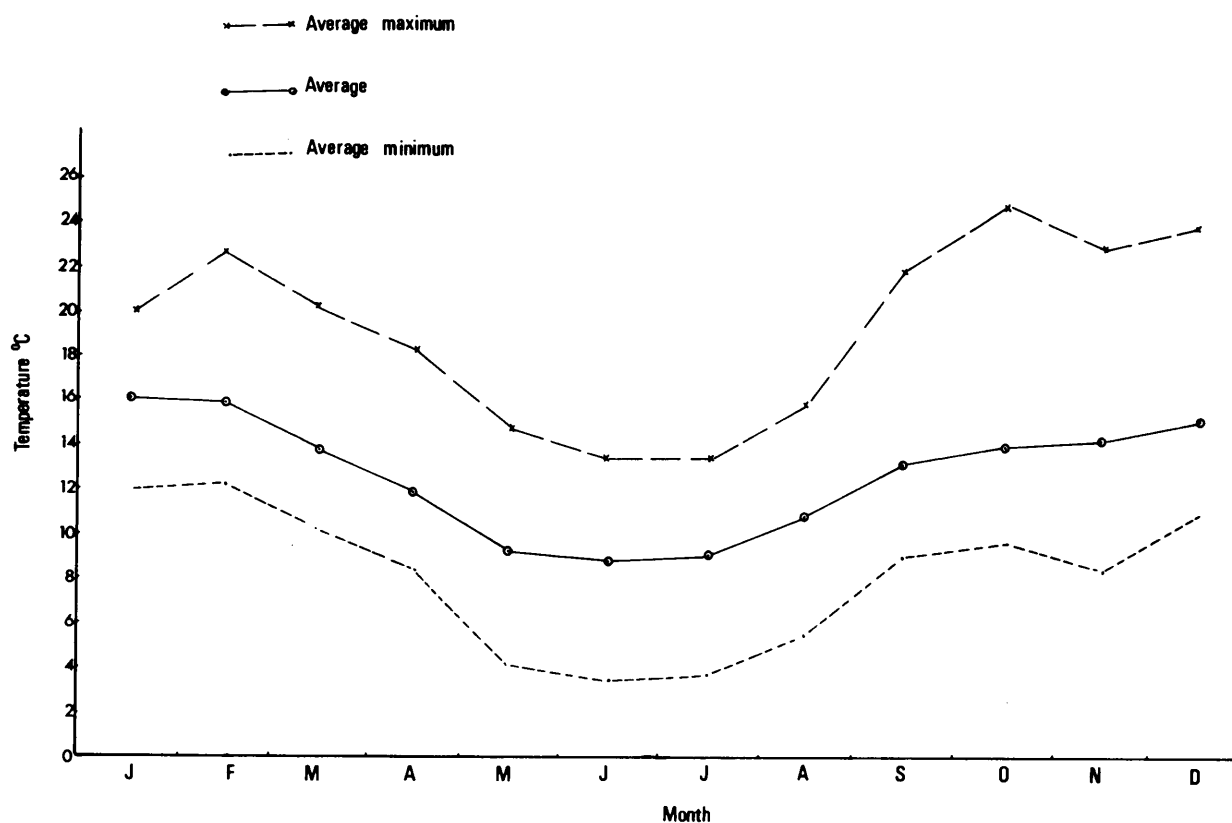


During the later pupal stage (October to March) it is moist, the average rainfall being about 150 mm per month for the six months. In dry soil the larvae are unable to burrow very deeply while the emergence of moths is facilitated by moist conditions. In low-lying areas, pupal mortality is often high, which is probably due to drowning.

The average monthly temperature recorded by a soil thermograph at a depth of 25 mm below the soil surface is represented in Fig. 14. From this figure it can be seen that pupae would normally be subjected to temperatures ranging from 8,5–16,0°C. During aestivation in the pupal stage, the minimum recorded tempera-

Fig.14: Average monthly temperature 25 mm below the soil surface in a *P. patula* plantation at Welgelegen

for the years 1969 and 1970



ture was 3,5°C which is nowhere near the freezing temperature. The maximum temperature of 25°C can be regarded as a very moderate temperature during summer. It thus seems hardly likely that temperatures within this range would be lethal.

F. The adult stage

1) General description

The adults of the pine emperor (Plate 1) are large heavy moths with wing spans of up to 172 mm. The wings are covered with short hairy scales on the outer edges, gradually changing to long hairy scales near their bases. The background colour is yellow to yellow-brown. The wings are divided more or less into thirds by two lines running parallel with their outer edges. The lines nearer the outer edges of the wings are thin and straight, displaying the colours grey-brown, pink and carmine from inside outwards. The line nearer the wing base is very irregular, with the same colour sequence indicated above, but arranged the other way round, i.e.

from the outside inwards. In the central part of each wing there is a round eye-spot of which the central area is completely transparent and surrounded by four concentric coloured rings displaying the colours yellow, black, pink and carmine from inside outwards. The transparent area of the forewing is considerably larger than that of the hindwing, but less conspicuous, the coloured rings being considerably narrower. The middle third of the hindwing is much darker than the rest of the wing, as a result of brown specks in the yellow. The body is hairy. The thorax and the abdomen are yellow dorsally and yellow-brown ventrally. The head and neck regions are carmine and the antennae orange-brown.

The basic colour constantly ranges from yellow to yellow-brown. The wing colour gradually fades with age and due to loss of scales. Old moths are therefore lighter in colour than newly emerged ones.

A colour variation of which the basic colour is bright yellow and the pink and carmine in the eye spots and dividing lines are replaced by white, was found in the Usutu, Swaziland plantation during 1971. This colour form is especially interesting as the pink and carmine colours around the eye spots are regarded as characteristic of *N. cythera clarki*, while the white colour is characteristic of *N. cythera cythera*. This colour form however, seems to occur in very small numbers as only two individuals could so far be found. This colour form is described as *N. cythera clarki* colour form *sulphuria* (Van den Berg – In Press).

For a taxonomic description, refer to Geertsema (1970).

2) Sexual dimorphism and size

For all practical purposes the two sexes occur in equal numbers (Van den Berg, 1968; Geertsema, 1970), The sexes can be distinguished by structural differences in the antennae and the shape of the forewings. The antennae of the male are broadly bipectinate whereas those of the female appear longer and almost filiform or at the most slightly serrated. Furthermore, the apex of the forewing of the male is slightly more acute than that of the female.

The wing spans of field collected moths vary from 124–172 mm for 50 females (average 154,7 mm) and from 108–172 mm (average 151,9 mm) for 170 males. Geertsema (1970) found average wing spans of 147,9 and 146,5 mm

for 34 females and 34 males respectively, i.e. values slightly below those found during the present investigation.

3) Seasonal occurrence

Since these moths are fairly large and conspicuous, the time of appearance of adults was determined by direct observation in the plantations. For this purpose 30 plots, each situated between two rows of trees 2,7 m apart and 91 m long, were laid out at three localities in a plantation. These blocks were chosen in such a manner that 10 were within an area with a very dense population, the second 10 within an area with a medium density and the rest within one with a sparse population. The total area was approximately 0,7 ha. From previous results it was possible to plan the counts at such a time of the day that the biggest possible proportion of freshly emerged moths would be recorded for every day. Pine emperor moths emerge mainly from 1800 hours to midnight. As the moths usually fly away at specific times, namely at dawn or dusk, countings could be made a few hours after all moths had emerged, i.e. about 0700 to 0900 hours. The freshly emerged moths can usually be found low down on stems and brushwood. Only freshly emerged adults were counted; this was done once per week, when the plots were thoroughly inspected. The number counted represented about a third of the moths that emerged during each night.

Besides these direct observations on seasonal appearance, moths were also caught in light traps and their numbers recorded. Two Rothamsted light traps (Williams, 1948) which were slightly modified, were used. The alteration was a gauze cage (60 x 60 x 30 cm) which was placed at the bottom of the funnel instead of a killing bottle. These light traps were in operation for three nights a week from 1900 hours to midnight throughout the year.

Adults occur in the field from the first week in February until the first week in May (Fig. 1). The egg and larval stages therefore occur during autumn and winter, and the pupal stage during spring and summer.

4) Emergence

Procedure

In order to determine at what time of day the adults actually crept out of the soil, 40 plots of 2,7 x 91 m were laid out in one continuous block (approximately

1 ha in total extent) and kept under more or less continuous observation for 48 hours. This was done at a time of peak emergence of moths. It took one observer just under one hour to complete the necessary observations over the 40 plots and to start afresh. With two observers relieving one another at set intervals these hourly observations of each plot could be extended over 48 hours. A torch was used to provide the necessary illumination during the night.

The observations were started at 1800 hours on the 10th March, 1971. The position of each freshly emerged moth was marked by means of a card (101 x 76 mm) fixed to some object nearby. On this card the date and time at which the moth was observed for the first time were recorded. Freshly emerged moths could be distinguished by their crumpled wings and their light coloured shiny eyes. On subsequent visits further observations on the same moth were recorded on the card, e.g. when the wings were fully expanded or hardened, when mating started or ended, when the moths flew away and so on.

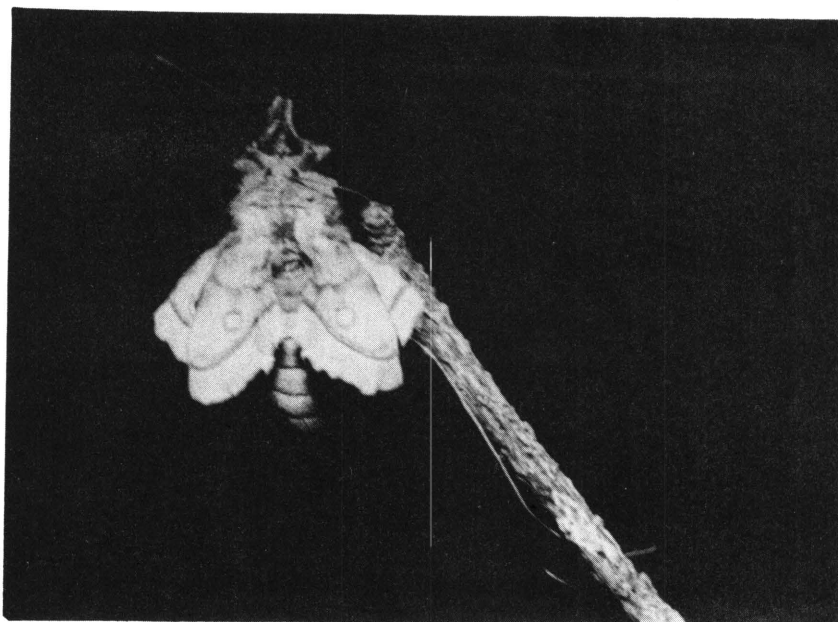
In a number of gauze cages of 50 x 30 x 30 cm and one of 1,8 x 1,5 x 1,5 m, emergence and mating could be studied more intensively on an open veranda. Field collected pupae were placed in these cages which were examined every quarter of an hour for 48 continuous hours. Moths which emerged in these cages could crawl up the sides of the cage and cling to the gauze at the top. The times at which the wings were fully expanded and hardened were noted for every moth. Each moth with fully expanded wings was marked distinctively by means of different combinations of various colours. For this purpose, fast drying pelican poster and gloss paints were used. Mating moths were also kept under direct observation.

Results

At the time of moth emergence, the pupal shell becomes softer at the wing tips and splits open along the posterior margin of the wings and the third thoracic segment. The moth then begins to crawl out of the pupal shell of which the ventral portion becomes detached and slides off. At this stage a whitish liquid is secreted through the anus and is usually left behind in the pupal shell. During the course of the present investigations no pupal shells or bits of shells could be found above the surface of the plantation floor such as Tooke & Hubbard (1941) found in the case of *N. cytherea cytherea*. These findings agree with those of Geertsema (1970),

who, however, states that a few moths appear above the ground with the cervical shield of the pupal shell still attached to them. After emergence the moths move along the plantation floor, crawl up branches or tree trunks and settle in a more or less vertical position (Plate 7) with their wings hanging downwards. Emergence

Plate 7: Pine emperor moth busy expanding wings



takes place from 1900 to 0300 hours, with peaks between 2100 hours and midnight for both sexes (Fig. 15). The wings expand and attain their full size within 1–2 hrs. At this stage the wings are still teneral, hanging downwards dorso-caudally, the forewings almost touching one another (Plate 8). The wings harden within 60–105 min for males and 90–150 min for females, after which they are folded against the body. Although the moths are then able to fly, they usually only commence doing so at dawn or dusk.

Under very dry conditions, emerging moths may be unable to crawl out of the pupal shell or the soil, or their wings may be so damaged that they do not unfold. This usually happens under young trees, in the absence of a pine needle mat. Females with withered wings are still able to copulate and usually lay part of their eggs on stems of trees or brushwood. These larvae may hatch, but usually starve to death.

Fig.15: Number of pine emperor moths emerging from their pupae at different times of the night

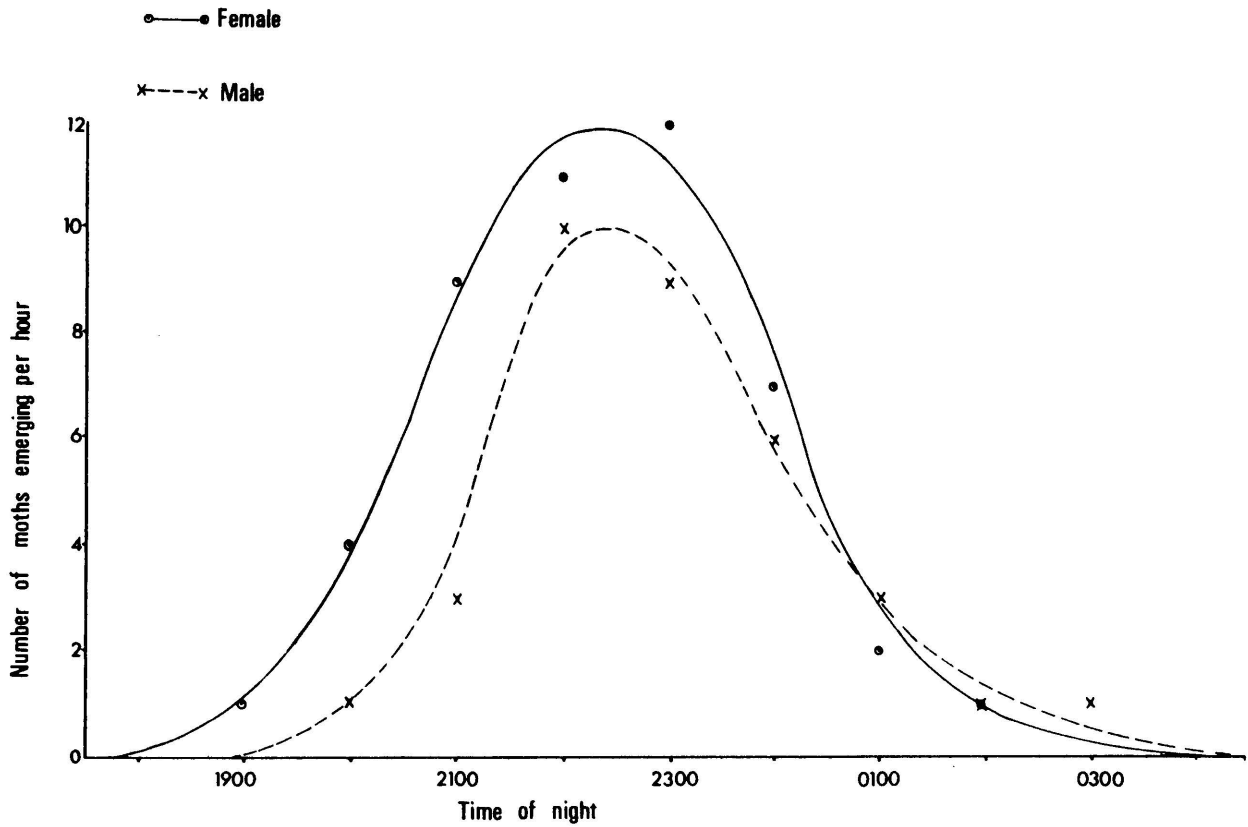


Plate 8: Pine emperor moth with wings fully expanded, but still teneral and hanging downwards



The abdomens of freshly emerged moths are more swollen and inflated than those of older moths. When moths are slightly disturbed, they generally open their wings, thus exposing their eye spots. When disturbed further, freshly emerged moths will squirt out a white to brownish liquid through the anus.

5) Sexual attraction and copulation

Sexual attraction and mating were studied, firstly, by making direct observations in the field on newly emerged females. Secondly, unmated females which had emerged from field collected pupae the previous night, were placed in pairs in ten gauze cages. These cages were placed at intervals of at least 20 m in the plantation. Males attracted to these females were counted and removed hourly.

Sexual attraction usually commences shortly after the wings of the female are folded against the body. It may, however, commence earlier i.e. before the wings are folded, or much later, i.e. during the following night. The last four to five abdominal segments are extended by telescopic movements and two small knobs which are probably scent glands are exposed and exerted. The two knobs are situated laterally between the second and third last segments. The abdomen can continuously be kept in this extended position for a few hours, but if the moth is disturbed, it is retracted immediately. Females extending their last abdominal segments the same night during which they emerged, only lure the males after 2300 hours and persist to do so, at intervals, until dawn. Females prevented from copulating for one or two nights, attract males at intervals from dusk to dawn. The intervals between luring periods lengthen progressively as the female ages. Although newly emerged females possess a greater attraction for males, older individuals also attract the males.

Male moths are attracted from a considerable distance, possibly up to more than 500 m. As soon as copulation commences, the female retracts her abdomen and other males in the vicinity lose interest. This behaviour also occurs in other Saturniidae (Skaife, 1953). When copulation commences the other males usually fly away, but if copulation commences at dawn, they may remain in the vicinity.

In the field, copulation usually commences between midnight and 0300 hours, but also as late as 0530 hours. Sometimes it lasts less than an hour (especially during rainy weather), but it could continue until dawn (about 5 hrs), go on for

nearly 17 hrs until the following evening, or in exceptional cases until the second evening (approximately 37 hrs).

Table 20: Duration of mating of the pine emperor in the field

Duration in hours	Less than 1	1-2	2-3	3-4	4-5	13-14	16-17	17-18	37-38
Number of matings	33	12	2	1	1	1	1	1	2

Females still copulating in the morning, frequently try to pull the males up the object or tree to which they are clinging. Usually they are unable to move much higher up, but in one case the female managed about 1 m.

Females have been observed to drop to the ground from rather high up in the trees. This frequently happens with females trying to free themselves from copulating males at dawn. These females often die near the point of impact with the ground. This is not surprising as they are very heavy. Other insects and millipedes have been observed to feed on dead females, usually leaving behind only the wings and eggs close together. The following were two of the most important insect scavengers: *Pteronemobius* sp. (Gryllidae) and a member of the family Anisotomidae (Coleoptera, probably *Anogdus* sp.)

After copulation, the females usually remain stationary during the same night, but if copulation is terminated during the mornings or evenings they usually move to other sites. A female may copulate more than once. Females usually copulate once the first or second night and then once more on the fourth to the sixth nights. Old females without eggs have also been observed to copulate. One or both individuals may die in copula, possibly due to old age. Males are probably able to copulate twice a night and five or more times during their lives, depending on their longevity and the number of unfertilised females that they encounter.

Newly emerged females, not busy mating, move higher up trees in the mornings, while older females generally appear high up in trees. Males, on the contrary, frequently remain near mating couples, while newly emerged males are usually found near the ground level. These circumstances lead to the fact that more males can usually be located than females. This may explain why it is sometimes wrongly concluded

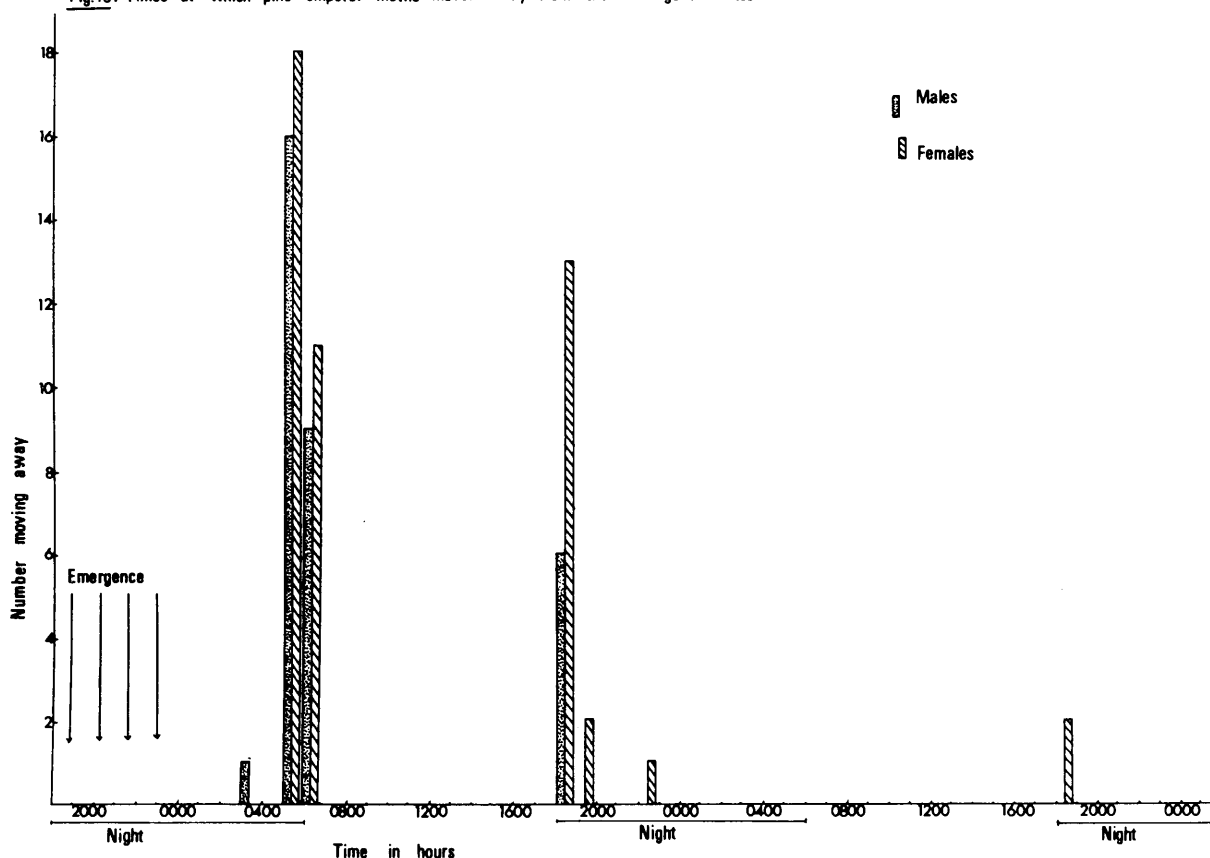
by laymen that more males than females occur.

6) Flight activity

Although the adults appear to be cumbersome and rather helpless during the day, they fly with great ease at night. They are very strong fliers and can rapidly disappear amongst the crowns of trees 20 m high. The moths mainly fly at night but, if they are disturbed, also during the day.

The times at which newly emerged moths leave the site of emergence are provided in Fig. 16. At dawn, 5–10 hrs after emergence, approximately

Fig.16: Times at which pine emperor moths moved away from their emergence sites



two thirds of the moths move away. At dusk, about 21 hrs after emergence, the remaining moths move away, with the exception of those still mating. The few females that remained near their emergence sites until dusk the second night (45 hrs after emergence) could not free themselves from the males and, but for this, would probably have moved away earlier. Moths that do not move away after emerging the previous night, will usually not fly even if they are flung up in the air. They will either fall down by keeping their wings closed or float to the

ground. Older moths treated in this manner will in most cases start to fly actively.

Males with freshly expanded and hardened wings, could fly from the object to which they had been clinging after emergence, or from the ground, during the night of emergence or at dawn the next day. As far as is known females do not fly before dusk the following evening. During this time, they climb up the stems of trees with wings flapping until they reach a branch, which is then followed up to its end point. The ends of branches probably offer suitable perches from which to fly away. Females usually commence flying from the ends of branches. Flying females sometimes lose height and may land on the ground again, in which case the whole process of finding a suitable perch is repeated.

According to Van den Berg (1968) females of the pine emperor mostly fly during the first half of the night and males during the latter half. The females probably fly about for one purpose only, namely to find suitable oviposition sites at each of which a few eggs are laid. Egg laying takes place mainly in the early evening (discussed under "Oviposition" p. 71). This could explain the flight activities of the females during the first part of the night.

Females emerging during the first half of the night usually commence copulating from midnight to 0300 hours early the next morning. In cages it was observed that males were active at dusk, during the latter half of the night and at dawn. This behaviour of males can either be environmentally or pheromonally controlled. Their activities during dawn and dusk may be environmentally controlled, while the activities during the latter half of the night may be pheromonally controlled. If this hypothesis about their activity during the latter half of the night is true, the explanation may be as follows: In an infested plantation there is most probably a rhythmic release of sexual pheromones during each day, so that the concentration of pheromones is always highest during the latter half of the night. It may be that the males are activated by this higher concentration of pheromones, causing them to fly around in search of females. This aspect of male behaviour needs more intensive study, and will receive further attention during the next season.

Considerably more males than females are attracted to light traps. These findings confirm those of Van den Berg (1968) and Geertsema (1970). From 77 females caught at light traps an average of 31 eggs (0–154 eggs) per female were

dissected. This is contrary to what was found by Geertsema (1970) for *N. cytherea cytherea*, in which case females appear to be attracted to light traps only after oviposition has been completed.

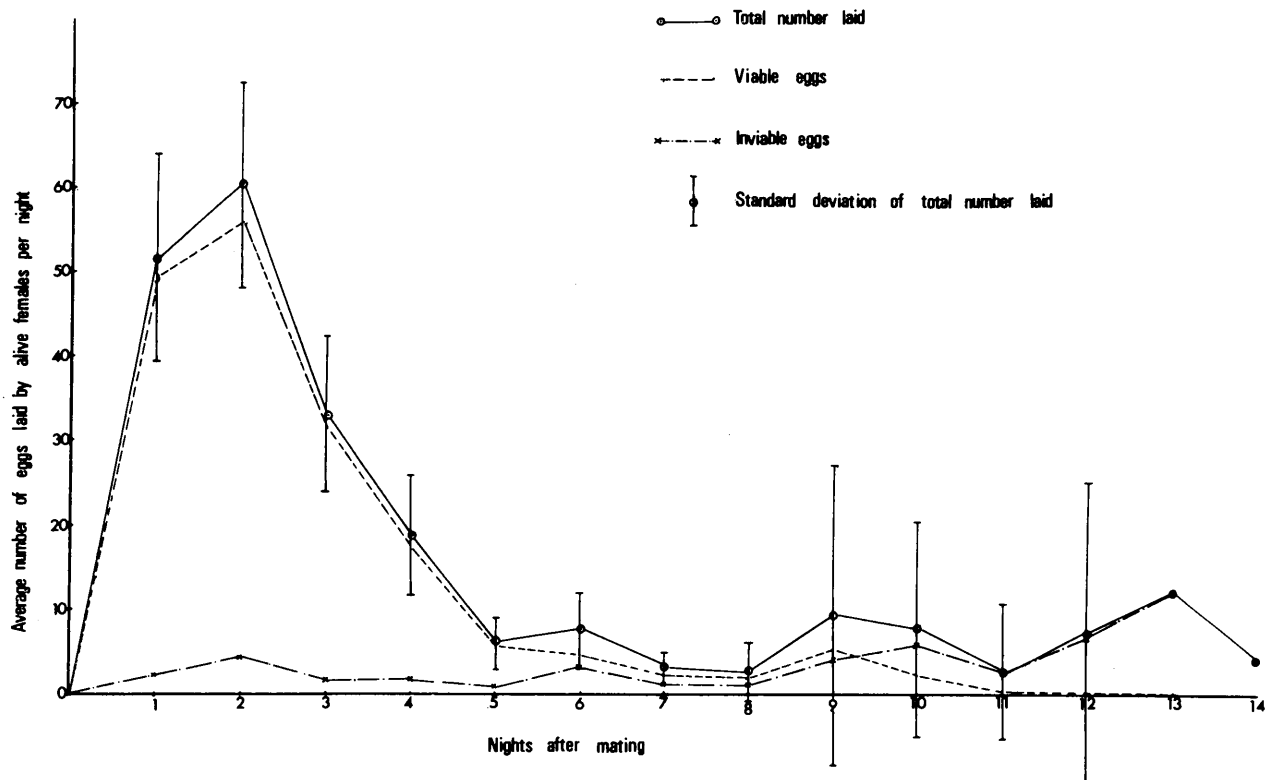
During the tests with light traps it was observed that drizzles did not prevent the moths from flying. Flight usually commences at 1830 hours and continues until 0600 hours (mid March, 1969). Moths only fly to the light traps when it is dark and usually settle within 7 m from the ultra-violet light where they usually vibrate their wings slightly. When a number of these moths are crowded together, as often happens near a light source, they severely damage their wings, and many die in the near vicinity. At sunrise, most of the unharmed moths fly away from the traps.

7) Oviposition

Since newly hatched larvae are able to crawl only short distances before they starve to death, they are almost entirely dependent on suitable food present at the oviposition sites, which are fastidiously selected by the female. Edible parts of the plant, such as leaves, are preferred by the female. Certain food plants such as *Rhus dura*, *Rapanea melanophloeos*, *Diospyros whyteana* and *P. patula* are preferred for oviposition. Frequently considerably smaller numbers of eggs are deposited on the leaves of the following plants often found in the same vicinity as those previously mentioned: *Euclea natalensis*, *Psychotria capensis*, *Vaccinium exul* and *Pinus taeda*. Eggs are seldom laid on plants totally unacceptable to larvae or parts of plants that are normally not eaten such as dead or dry branches, dry leaves, bark, tree trunks etc., as well as other totally unsuitable objects such as stones. In a few isolated cases eggs have for instance been found on *Smilax krausiana* Meison and *Viscum obscurum* Thunb., plants totally unacceptable to the larvae.

The number of eggs laid per night was determined as indicated below. Forty females which had emerged the previous night, and were busy mating, were collected in the field, and kept separately in 40 cages (30 x 30 x 30 cm). Eggs were collected from the cages every morning, recorded for the specific moth and night, and kept separately in honey jars to determine egg viability. The data are summarized in Fig. 17.

Fig.17: Average number of eggs laid by 40 pine emperor moths per night from the night after mating

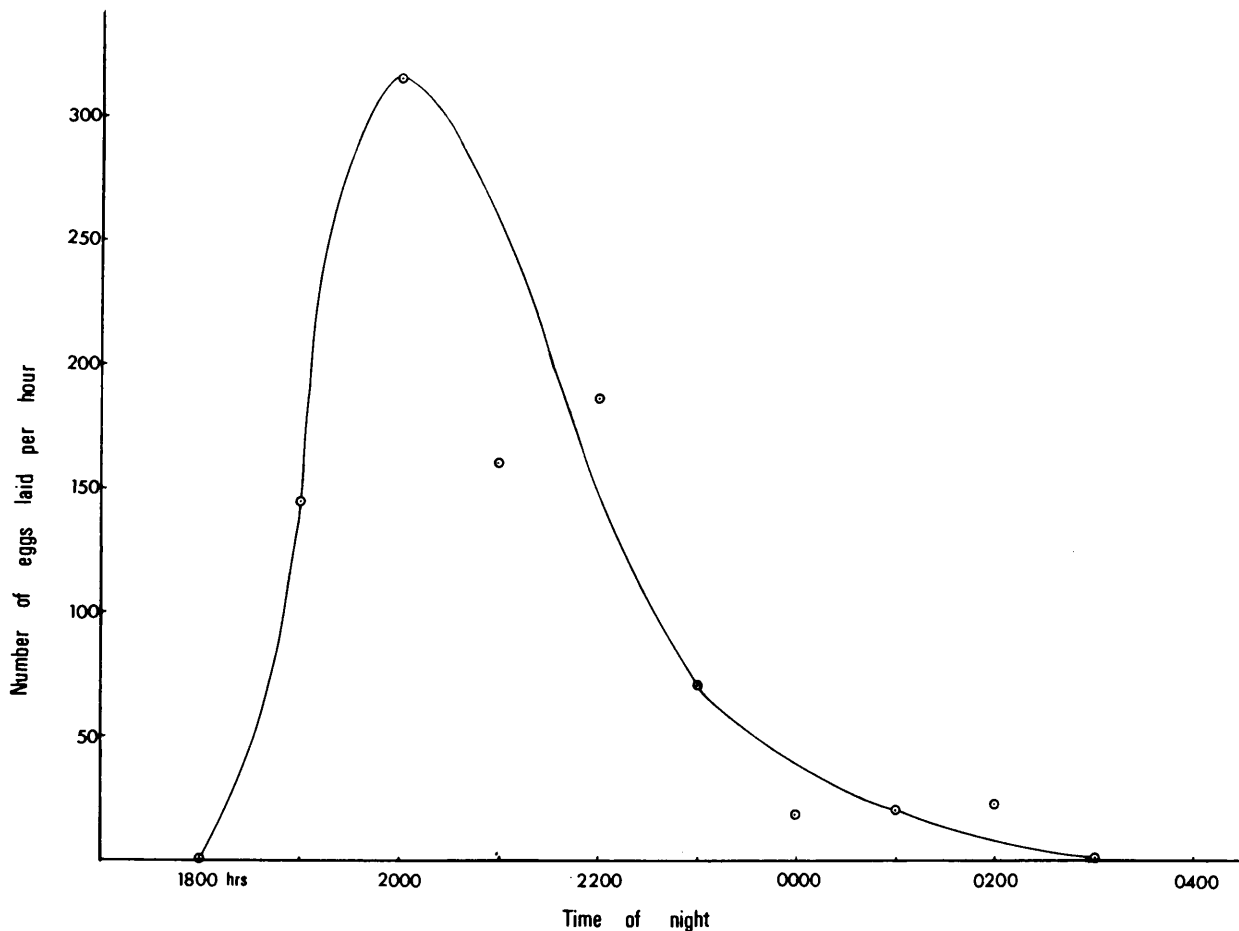


From this fig. it is clear that most eggs are laid during the first three nights after copulation. There is a regular increase in the ratio of inviable to viable eggs from the third to the fourteenth night. This increase could have resulted from a diminishing sperm supply. As females in plantations can, and probably do, mate more than once, the ratio of inviable to viable eggs may not be as high in nature as was found in this experiment with females that had mated only once. The average number of unlaidd eggs remaining in the bodies of dead caged females was 12,5, which is regarded as rather high in comparison with approximately 6,3 found in 52 field collected dead females. Twenty of the laboratory kept females had no unlaidd eggs while 14 of them had less than 20 unlaidd eggs in their bodies after death. The other dead females had 30, 37, 67, 68, 83 and 100 unlaidd eggs. Perhaps these six females were not properly fertilised and were trying to lure males for another mating, with the result that they died before all their eggs could be laid.

The time of egg laying during the night was determined on the 13th March and 3rd April, 1970 in the following manner. At 1700 hours, 20 field collected

females were placed singly in separate cages. The number of eggs laid during every hour of the night was counted and marked to distinguish them from eggs laid during the next hour. These eggs were removed from the cages the following morning, and recorded for each female every hour. The results are diagrammatically represented in Fig. 18. A free-hand curve was drawn from the points plotted.

Fig. 18: Total number of eggs laid per hour by 20 pine emperor moths at different times of the night



According to this fig. oviposition occurs between 1800 and 0300 hours, with a peak between 1900 and 2200 hours. During this time of night, females occurring naturally in the field will probably be actively flying about in search of suitable oviposition sites.

The heights at which eggs are laid in trees were determined by chopping down 20 *P. patula* trees and recording the distance of each egg mass from the top of the tree. For results see Table 21.

Table 21: Distance at which egg masses of the pine emperor moth were collected from the tops of 20 *P. patula* trees (14 years old)

Distance from the tops in m	0-1	1-2	2-3	3-4	4-5	5-6	6-7	Total
Number of masses	236	270	252	50	20	8	2	838

According to this table, the largest number of eggs are laid in the top 3 m and very few lower than 5 m from the top.

The females seem to prefer relatively open positions for oviposition, such as trees on the outskirts of plantations or blocks. These trees usually have more branches with needles as a result of more direct sunlight, and therefore offer a larger food supply. With a large population, there will therefore, generally speaking, be more larvae on trees on the outskirts of blocks than on those in the middle. Complete defoliation may start in the middle of blocks, but usually takes place almost simultaneously over the whole plantation, much as if the eggs were distributed in accordance with the food supply. Van den Berg (1968) states that eggs are usually laid high up in the trees and on trees on the outskirts, agreeing with the present findings.

8) Dispersion and longevity

Procedure

To study flight activity and survival of the pine emperor in the plantation, a method of marking and recapture was employed. A summary of the methods of marking moths for this purpose is supplied by Peterson (1955) and Grobler (1957). Although effective, most of these methods are too time-consuming to be applied where large numbers of moths are to be marked. As many different colours were needed, different colours of fast drying Pelican poster paint and gloss paint were used.

Freshly emerged moths were collected in the plantation and placed in gauze cages. These moths were liberated at four different localities after being marked. Different coloured dots on the right forewing were used to identify the different points of liberation. For subsequent liberations at the same locality, additional dots of the same colour served to identify the week of liberation. For each day of the

week a differently coloured dot was painted on the left wing. In this way, it could be determined where and when a moth was liberated as well as the duration of its survival. The marked moths were placed on platforms (1,5 x 1,5 m) raised 3,5 m above ground level, to keep them out of reach of baboons. The moths were recaptured at nine localities. At four of these, light traps were in operation every night from 1700 hours to midnight, while hand-collecting was undertaken daily at the other five localities over an area of about 1 ha for each. It should be mentioned that collections were not done in all possible directions from the points of release and that the adults most probably flew in all directions from these points.

Results

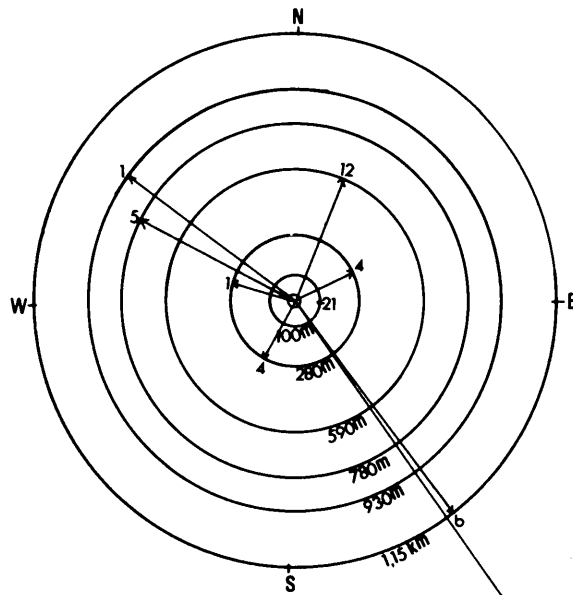
Of the more than 2 000 moths marked, 55 males and 33 females were recovered. The results of these experiments are summarised in Fig. 19 (a & b) and in Table 22.

From Fig. 19 a it is clear that males spread in nearly all directions from the points of release. The furthest point reached by a male was 5,3 km. The directions and distances flown by females are indicated in Fig. 19 b. From this it can be seen that only three females were recovered relatively far away from the point of release, i.e. 1,9; 1,6 and 1,2 km. Of the females recovered, 91 per cent flew less than 280 m, in comparison with 38 per cent of the males that flew less than this distance. This indicates that many more males than females fly long distances. It may also be concluded that females will usually lay most of their eggs within a relatively short distance from their emergence sites. The indications furthermore are that the females do not move great distances during the first three nights when the majority of their eggs are laid. It may be concluded that the dispersion of the species would be by relatively small steps with each generation. The female recovered at a distance of 1,9 km sat alongside two freshly laid eggs and, like the other two that flew long distances, did not possess any more eggs in her body. It is logical that females heavy with eggs will disperse less than those with few eggs. The few females which do cover relatively long distances, may enter areas not yet infested. The single females developing from these eggs will again lay most of their eggs in the same newly invaded area. The population of the next generation in these newly invaded areas is frequently large enough in number to cause complete defoliation during the same or a later season.

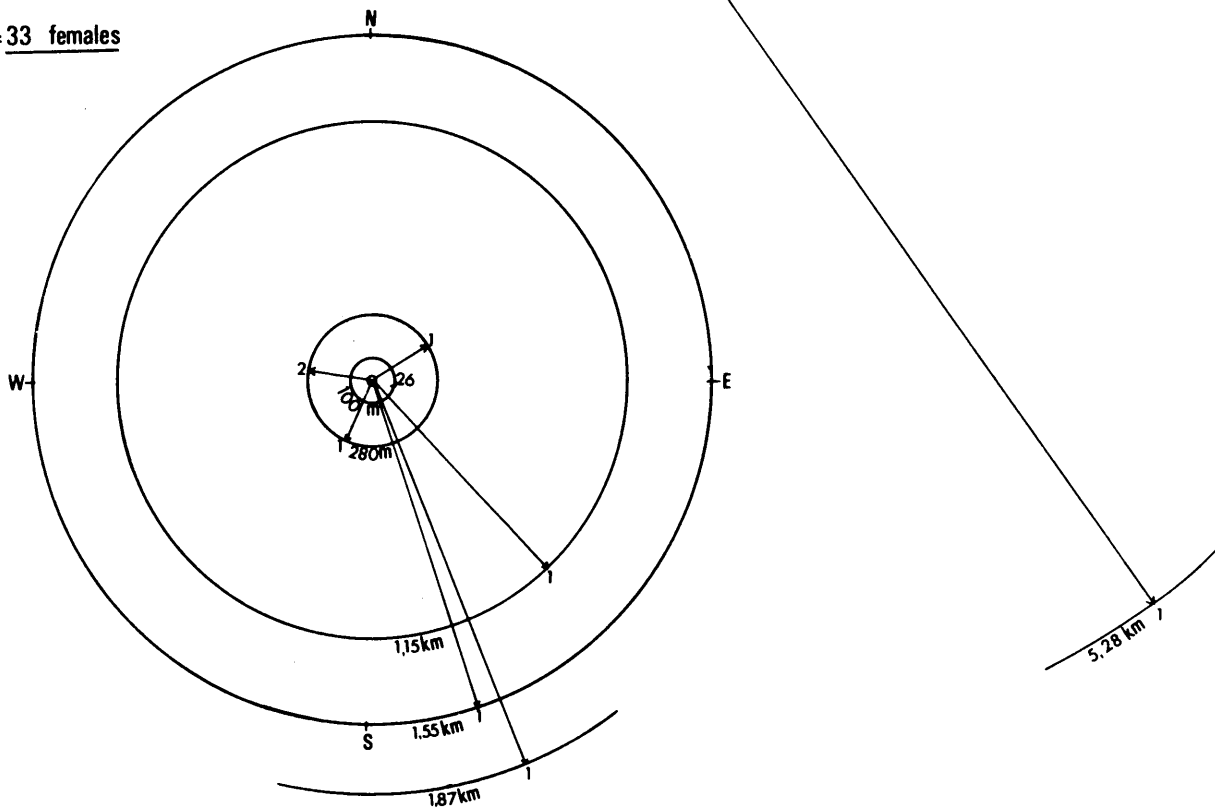
Occasionally, single trees of up to 3 m tall are almost completely defoliated, while

Fig.19: Distances and directions of recoveries from the point of release of pine emperor moths

a: 55 males



b: 33 females



no, or very few larvae, occur on surrounding trees. The larvae on such partly defoliated trees are often more or less the same size, and could therefore have originated from the same female. It may be assumed that single dispersing females are responsible for the infestation of isolated trees. Infestation of a plantation previously free of the pest most likely takes place in this manner, by moths dispersing from a neighbouring plantation or from nearby indigenous trees and shrubs. It is evident that a population sufficiently large to defoliate a large area must have been present in that area or in the immediate vicinity during the previous year or two.

From Table 22 it can be seen that one night after release, at least one male

Table 22: Distances at which pine emperor adults were recovered from the points of release during different nights after release

Nights after release	Males				No recovered	Females		
	No recovered	Distance in m				Distance in m		
		Min	Max	Aver		Min	Max	Aver
1	33	10	1 150	440	16	10	240	37
2	9	25	1 150	500	5	5	91	55
3	5	40	300	140	4	20	275	106
4	4	340	1 150	855	3	50	340	237
5	2	780	780	780	1	1 870	1 870	1 870
6	0	—	—	—	3	10	1 550	530
7	1	270	270	270	1	1 150	1 150	1 150
8	1	5 280	5 280	5 280	0	—	—	—

travelled 1 150 m and one female 240 m, indicating that males are about five times as active as females. The maximum distance reached by a male was 5,3 km which is about three times that reached by a female (1,9 km). If one ignores the one female recovered on the fifth night after release, a gradual increase is evident in the average distance reached by females with the lapse of time. It may be concluded that females will gradually drift further and further away from the localities where the adult stage was reached. To a certain extent this appears to be true for males as well. The fact that no clear increase in the distance is discernible for males, may be due to the fact that they tend to fly in whatever direction a female may be luring them. Since luring females can be found in

all directions, the movements of males would probably be random.

Four males marked and released at 0800 hours on 4 March, 1969, on a day when there was practically no wind, were found 1,2 km from the point of release at 2100 hours the same evening. If the moths commenced flying at 1830 hours as they usually do, the minimum speed at which these moths must have travelled was therefore 0,48 km per hour.

Of the marked moths one male was nine days old and one female eight days old when last seen alive. This is probably near the maximum age that would be attained under natural conditions. This agrees with Skaife (1953) who states that although saturniid moths appear to be very robust and strong, they only live a few days as adults, since they are unable to feed on account of their imperfect mouthparts.

9) Number of eggs and larvae per female

The number of eggs found in the ovaries of 80 females that emerged from pupae collected from the Welgelegen plantation during 1968 and 1969, varied from 119–288, with an average of 182,4 per female. Geertsema (1970) recorded an average of 128,6 eggs for 16 females, which is considerably lower than was found in the present study, indicating that the number of eggs per female may vary widely under fluctuating environmental conditions in nature.

In the field most females usually deposit all their eggs, but an average of 6,3 eggs (0–171 for 52 females) remain in the ovaries of dead females. Of the 52 females examined, the one with 171 eggs had probably not yet started to oviposit, and possibly died after falling from a tree before any eggs could be laid. Of the rest, nearly half (25) contained no eggs.

Of the 2 000 marked eggs on indigenous and young pine trees in the Welgelegen plantation during 1968, an average of 9,9 per cent were inviable (parasitism excluded). The calculated number of offspring was therefore about 159 larvae per female under the conditions prevailing at that time.

G. Climatic factors influencing population density

From studies on the pine emperor and the rainfall figures in a number of plantations where outbreaks occurred, the following conclusions were drawn in connection with probable mortality factors during the different stages.

Egg stage

During the egg stage (February to July), heavy thunderstorms or snow may dislodge many of the eggs. Larvae developing from such eggs usually die of starvation.

Larval stage

Snow can lower the larval population to some extent and may also cause their death by starvation.

Pupal stage

Pupae may drown in areas flooded during spring. Pupae exposed to extremely dry conditions may die due to dehydration.

Adult stage

Under very dry conditions some adults are unable to crawl out of the pupal shell, while the wings of others are so damaged that they are unable to fly or otherwise to locate suitable oviposition sites in time to lay all their eggs.

CHAPTER 3 : BIO-ECOLOGICAL STUDIES ON
PSEUDOBUNAEA IRIUS

A. Experimental site

Experiments in connection with *P. irius*, the poplar emperor moth, were carried out in the Rietvlei plantation, situated 24 km from Middelburg (Tvl) on the southern side of the Stoffberg road. The general topography is more or less that of flat plains at an altitude of 1 676 m above sea-level. It is 1 373 ha in extent of which 33 per cent is occupied by *P. patula* whilst no *P. radiata* or *Populus deltoides* are cultivated. On the southern side it adjoins the Pan plantation. Indigenous trees and shrubs are more or less absent.

B. Distribution

The poplar emperor is an indigenous insect and was thus probably reported or collected from optimal as well as marginal habitats. The following list of localities was compiled from the same sources mentioned earlier in this paper. The date of collection, where this is known, and the name of the first person who made the collection at that locality, are given between brackets.

Natal

Balgowan, Nov, 1934 (? Rhod. Mus.); Durban, 21.xii.1910 (C. Franks); Greytown, 1964 (Hepburn *et al*, 1966).

Transvaal

Barberton, 16.ix.1910 (? Tvl. Mus.); Letaba, 15.i.1966 (M.A. van den Berg); Middelburg, ?1965 (H.E. Prinsloo); Pretoria, 21.xii.1970 (H.D. Catling); Piet Retief, ? 1947 (G.A. Hepburn); Politsi, ? 1965 (M. Johannsmeier); Punda Milia, 18.i.1966 (M.A. van den Berg); Sabie, 21.iv.1968 (M.A. van den Berg); Shiluvane, May, 1902 (? Tvl. Mus.); Warburton, 9.xii.1970 (P.F. du Toit).

Mozambique

Dondo, Nov, 1967 (? Rhod. Mus); Savanie Forest, (Beira) Nov, 1967 (? Rhod. Mus.).

Rhodesia

Belingwe, Nov, 1916 (? Rhod. Mus.); Bulawayo, Jan, 1947 (? Rhod. Mus.); Gatooma, Dec, 1955 (? Rhod. Mus.); Khami, Jan, 1952 (? Rhod. Mus.); Nyamdandhlovu, Dec, 1958 (? Rhod. Mus.); Que Que, ? 1909 (? Tvl. Mus.); Salisbury, Dec, 1915 (? Rhod. Mus.); Vumba, Dec, 1958 (? Rhod. Mus.); Wankie, 1.ii.1926 (? Tvl. Mus.).

Malawi

Monkey Bay, Jan, 1944 (? Rhod. Mus.); Mlanje, Feb, 1945 (? Rhod. Mus.).

Zambia

Kabwe, ?1923 (? Rhod. Mus.); Lusaka, Dec, 1960 (? Rhod. Mus.); Mwinilunga, Sept, 1961 (? Rhod. Mus.).

Tanzania

Amani, Feb, 1955 (? Rhod. Mus.).

Kenya

Kilale, April, 1954 (? Rhod. Mus.).

Angola

Texeira da Sousa, Feb, 1965 (? Rhod. Mus.).

Zanzibar

? (Distant, 1911).

From 1902 to 1924 it was collected at Shiluvane (1902), Que Que (1909), Barberton (1910), Durban (1910), Zanzibar (before 1911), Salisbury (1915), Belingwe (1916) and Kabwe (1923). This indicates that it was widely distributed over the eastern half of Southern and Central Africa, i.e. from Zanzibar to Durban, in those early days. Subsequent collections were made in more or less the same regions, indicating that the species is probably more numerous there. The poplar emperor was also collected from Western Central Africa i.e. Angola during 1965.

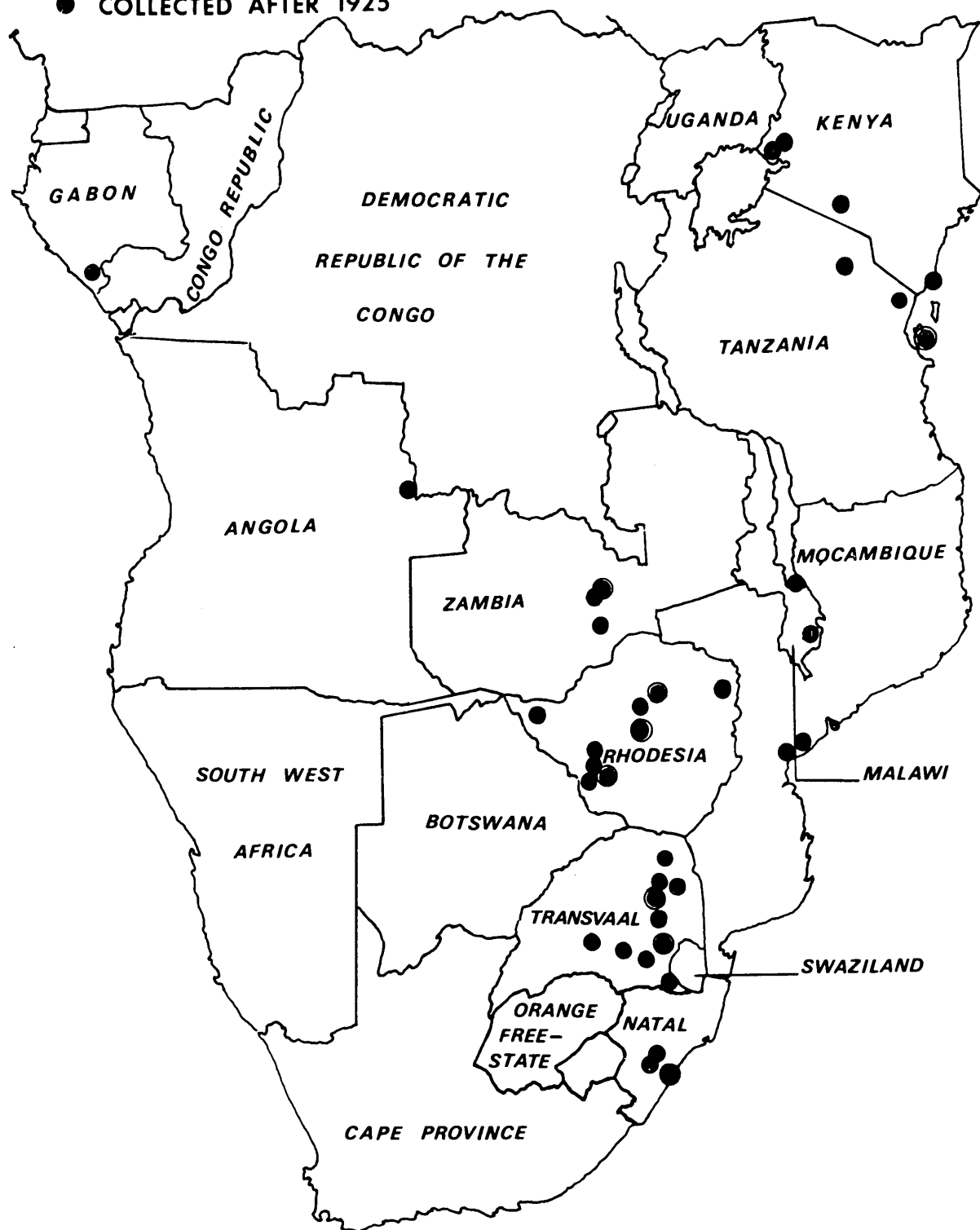
A distribution map is provided in Fig. 20. This indicates that *P. irius* is

FIG.20:

DISTRIBUTION OF P. IRIUS

● COLLECTED BEFORE 1925

● COLLECTED AFTER 1925



probably distributed over almost the whole of the southern half of Africa. According to Rougeot (1955), it occurs over almost the whole of the African savannas.

C. The egg stage

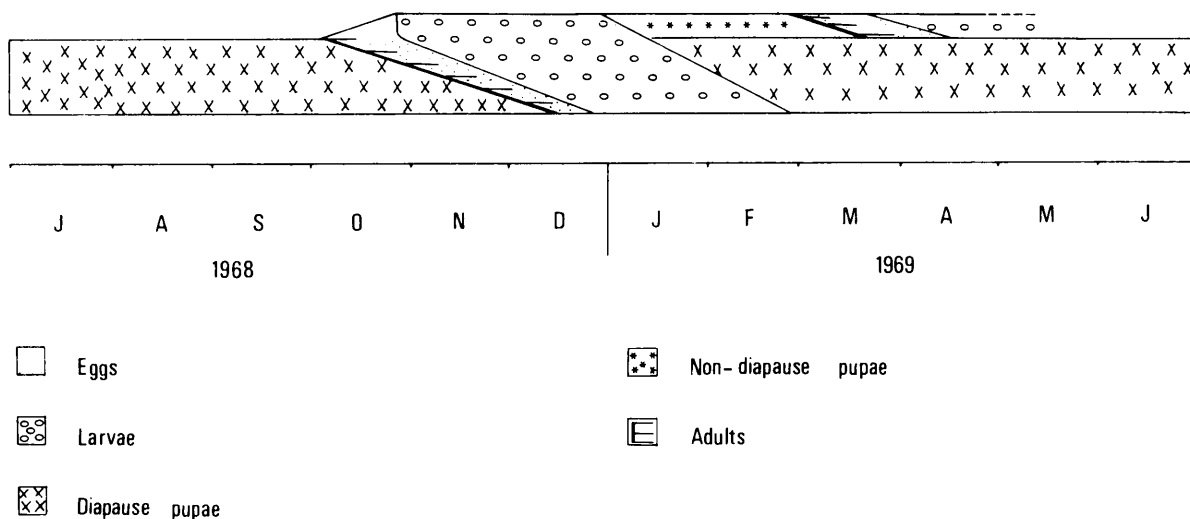
1) General description

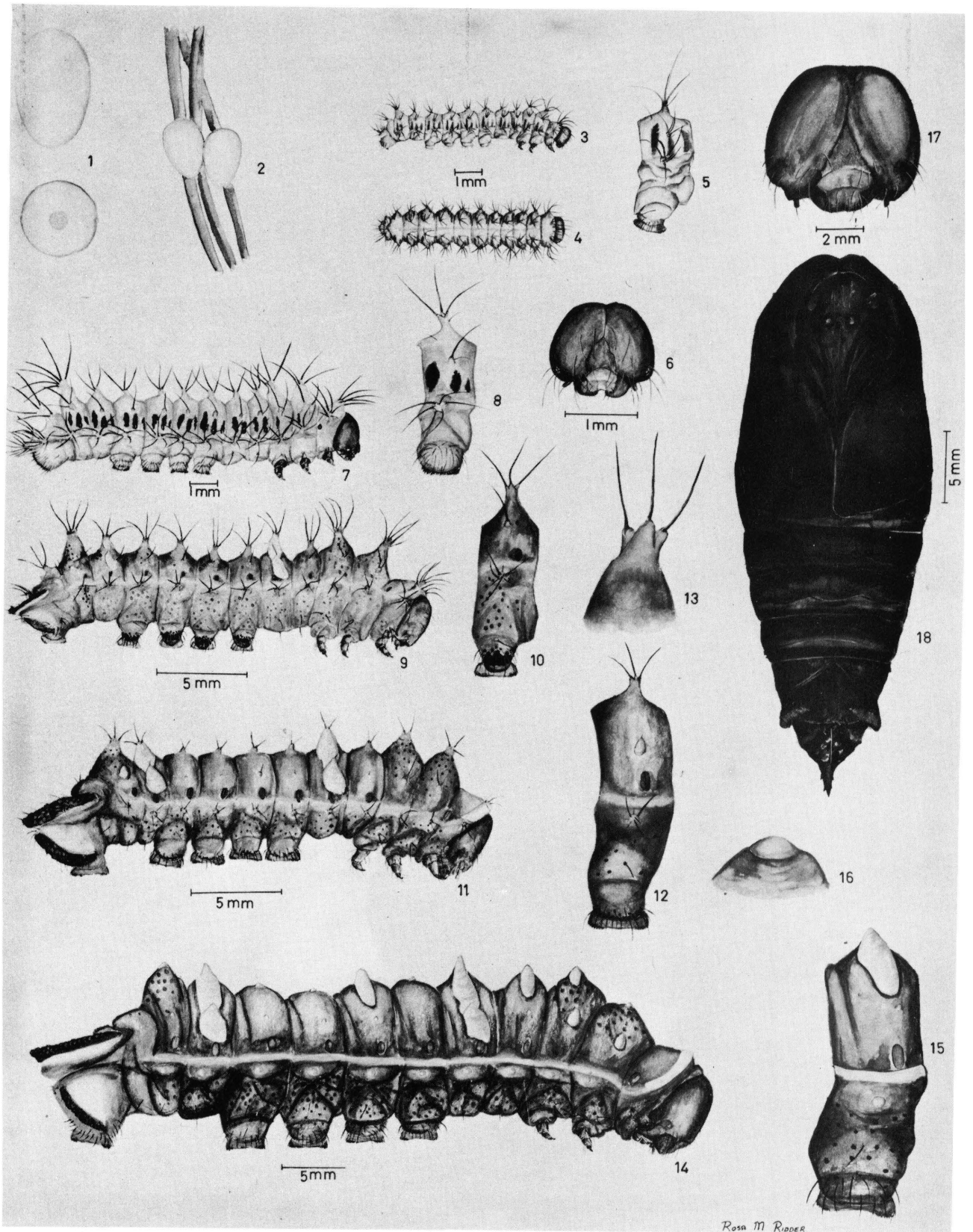
The egg is oval-shaped and frequently broader at the top (Plate 9). The average length of 50 eggs was 2,84 mm, ranging from 2,31–3,06 mm and the average width 1,91 mm, ranging from 1,75–2,06 mm. The eggs are usually cream-white to light cream-pink, whereas some appear slightly speckled with dark grey, apparently as a result of incomplete chorion formation. The eggs are glued to the substrate and to each other by a colourless secretion. The micropylar area is clearly situated on the broadest side and changes in colour from yellow to dark brown as development of the embryo proceeds. The average diameter of the micropylar area is 0,38 mm.

2) Oviposition and incubation period

Eggs of the first generation are deposited from the beginning of October to mid December, while the last eggs hatch during the end of December (Fig. 21).

Fig. 21: Time of occurrence of the different stages of the popular emperor in the Rietvlei (Middelburg) plantation





Oviposition by the second generation occurs from the end of February to the end of March. Eggs are found until mid April.

In the field, at an average temperature of 14,9°C, incubation lasted 16-21 days (average 18 days), and 10-15 days (average 13 days) at 19,3°C. Hepburn *et al* (1966) state that the incubation period lasts 12-16 days at a temperature of 25°C.

3) Egg masses

In order to obtain information on egg laying pattern, large numbers of eggs were inspected at random on pine trees and broad leaved plants, and the number of eggs recorded. From the information so collected, the frequency distributions appearing in Fig. 22 (on *P. patula*) and Fig. 23 (on broad leaves) have been drawn up. From this it can be seen that eggs are deposited singly or in groups, the egg masses on pine needles consisting of 2-16 eggs and those on broad leaves of 2-24 eggs, with modes of two and three respectively. Hepburn *et al* (1966) state that eggs are often laid singly, or in two's and three's, on pine needles. Typical egg masses are depicted in Plates 9 (pine needles) and 10 (broad leaves).

Eggs in a mass are laid next to each other, usually in rows across the length of pine needles and broad leaves. On broad leaves, eggs are frequently laid on the under surface, and as the basal ends are usually slightly broader than the rest of the egg, the masses are frequently slightly crescent shaped (Plate 10).

Plate 10: A typical egg mass of the poplar emperor on broad leaves

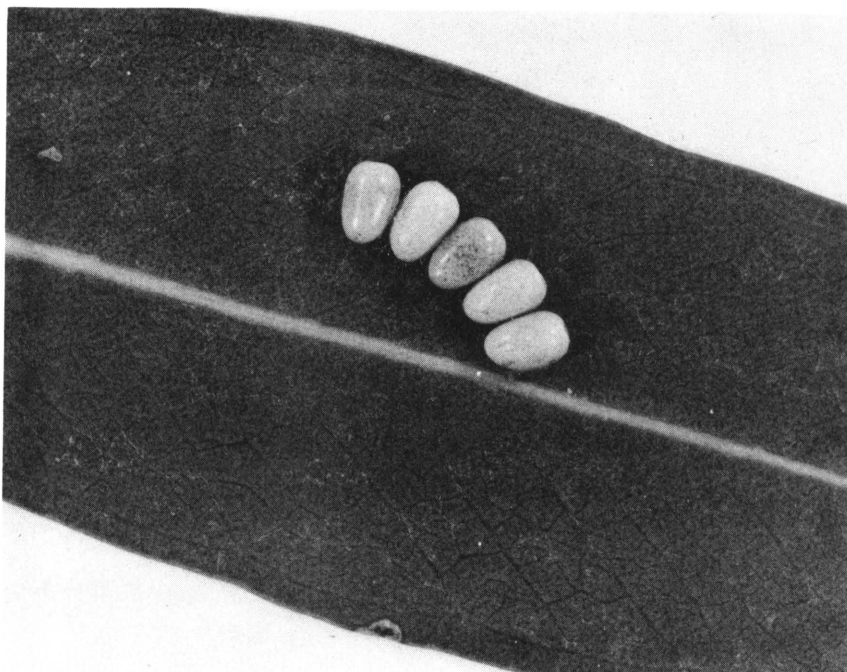


Fig. 22: Number of poplar emperor eggs occurring singly or in masses on P. patula needles

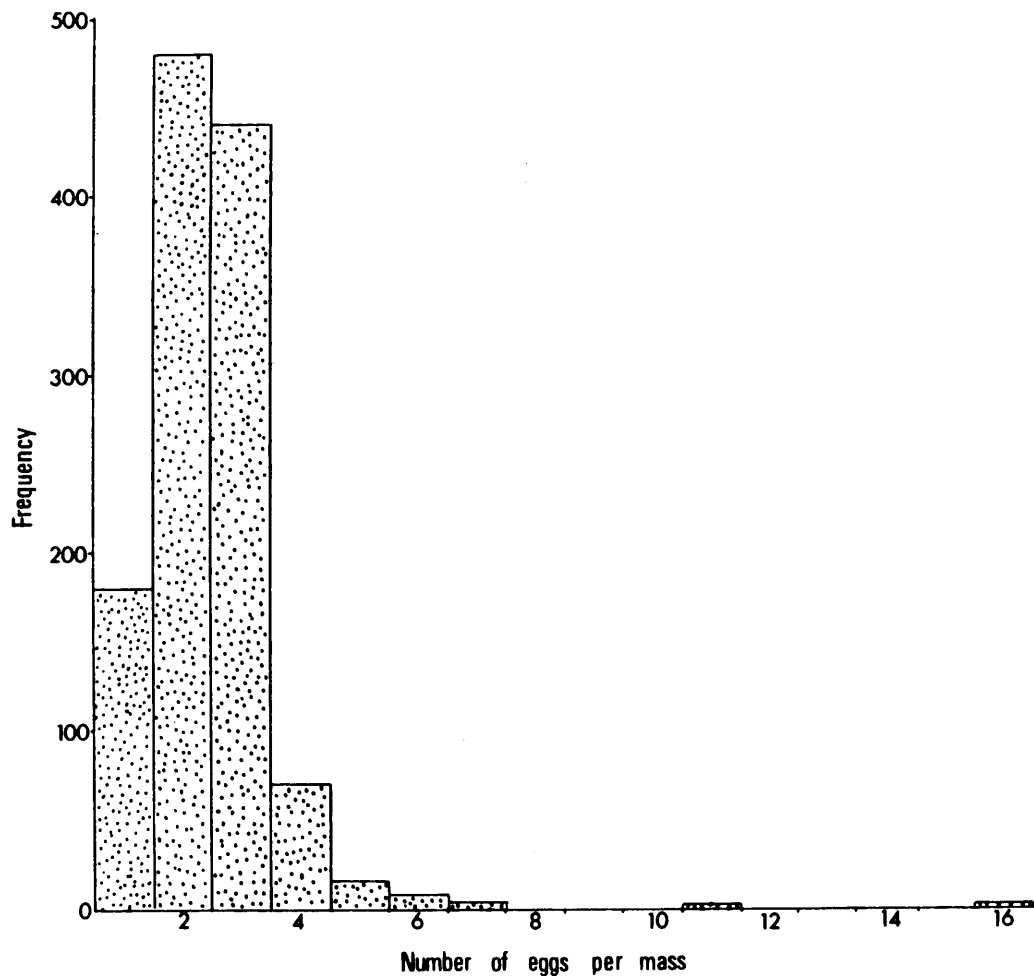
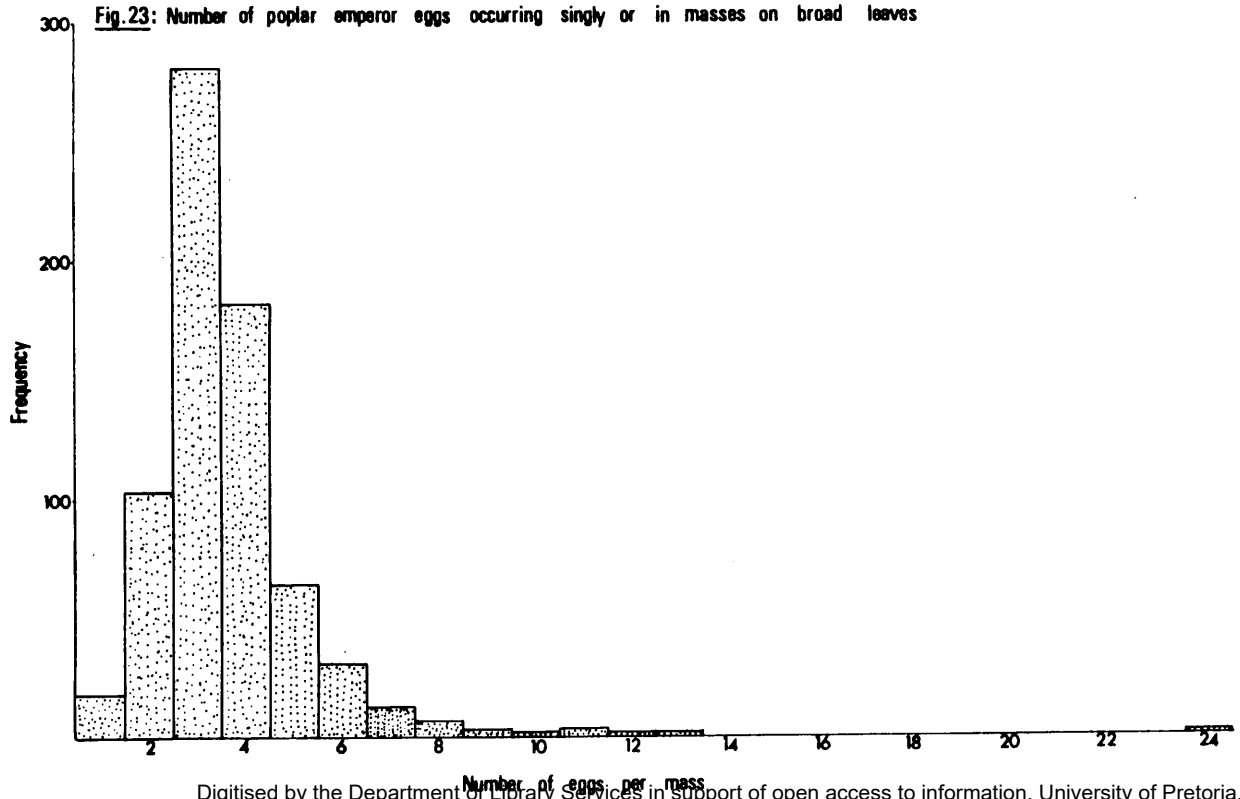


Fig. 23: Number of poplar emperor eggs occurring singly or in masses on broad leaves



As is the case with the pine emperor, different sizes of eggs are sometimes deposited in the same mass. The widths of eggs in such masses were found to vary from 1,63 mm (small) to 2,00 mm (large). The small eggs were all inviable. Sometimes eggs with transparent shells are deposited. Frequently these transparent eggs are small and inviable, but, if large, they sometimes develop normally.

According to field observations, it appears that eggs generally survive well. Thunderstorms are common in the Middelburg region, resulting in eggs occasionally being washed off needles and leaves. Larvae hatching from dislodged eggs usually die of starvation.

D. The larval stage

1) General description

The different larval instars are depicted in Plate 9.

First instar The general colour is yellow-brown. All body segments, with the exception of the first and last two, show three dark brown specks on each side next to the stigmata. There are six setae bearing scoli on each segment excluding the last two. One pair is situated dorsally and the other two pairs laterally. These setae are arranged in rows along the length of the back and sides of the body. On the penultimate segment, the two median scoli are fused, whereas only four appear on the last segment. The setae are brown and are approximately as long as the width of the head capsule. The ventral aspect of the larva is pale yellow-brown, whereas a red-brown line appears on the dorsal side. The head and thoracic legs are brown. Setae are also found on the head, legs and ventral parts of the segments. Body length varies from 5-9 mm.

Second instar Differs from the previous instar in that the colour is yellow-green. The specks close to the stigmata are black. Ventrally the larva is pale yellow-green and the setae are shorter than the width of the head. Body length varies from 8-15 mm.

Third instar The general colour is bright green. The head is a light greenish-brown. Four drop shaped silvery flecks appear on the sides of the fifth and tenth segments (one pair on each) and stretch from the dorso-ventral area to, and above, the dorsal setae. A yellow-green line extends from the neck region, below the

stigmata, to the last segment. The stigmata as well as the small areas next to them are an orange colour. The tips of the scoli are light blue. The length of the seta is approximately half the width of the head capsule. The tip of the clypeus and the dorsal portion of the last segment are sclerotized light brown. The thoracic legs are light brown. Body length varies from 14-24 mm.

Fourth instar The head is green. The setae are considerably shorter than half the width of the head capsule. The neck region is white. Drop shaped flecks occur on the fifth and tenth segments but may also be present on other segments. The sclerotized tip of the clypeus and the dorsal portion of the last segment are much more conspicuous than in the third instar, and are red-brown. Body length varies from 23-38 mm.

Fifth instar This instar differs from the fourth instar as follows: Generally, more than two pairs of silvery flecks are present on the larva's sides. No setae appear on the scoli. The areas directly surrounding the stigmata are green, while the stigmata themselves still appear orange. Body length varies from 36-66 mm.

Sixth instar The only sixth instar larva ever seen, appeared in all respects to be similar to the fifth.

The larval instars were also described by Hepburn *et al* (1966).

2) Key to the larval instars

- a) General colour orange-brown to brown First instar
 General colour yellow-green to green b
- b) No silvery drop-shaped marks on the sides Second instar
 Silvery drop-shaped marks present on the sides c
- c) Hind tip of last segment indistinctly
 sclerotized an orange-brown colour. No
 yellow colour present directly above this
 sclerotized tip Third instar
 Hind tip of last segment clearly sclerotized
 a red-brown colour. Sclerotized tip with
 yellow edge above d

- d) Setae present on the sides and frequently
 also on the back Fourth instar
 No setae present on the sides or the back Fifth instar

3) Head capsule widths

The widths of the head capsules of 30 field-bred larvae per instar were determined with the aid of a micrometer ocular. The results can be found in Table 23.

From this table it can be seen that there are noticeable differences between head capsule widths of successive instars. The width increases from 1,36 – 1,52 times per instar, agreeing fairly well with Dyar's law. The head capsules of the different instars are depicted in Plate 11.

Table 23: Head capsule widths of the different larval instars of the poplar emperor (30 individuals of each instar measured)

Instar	Width in mm			Increase per instar (x)
	Min	Max	Aver	
1	1,38	1,56	1,49	—
2	1,94	2,19	2,02	1,36
3	2,63	3,19	2,93	1,45
4	4,23	4,83	4,45	1,52
5	6,36	7,00	6,64	1,49

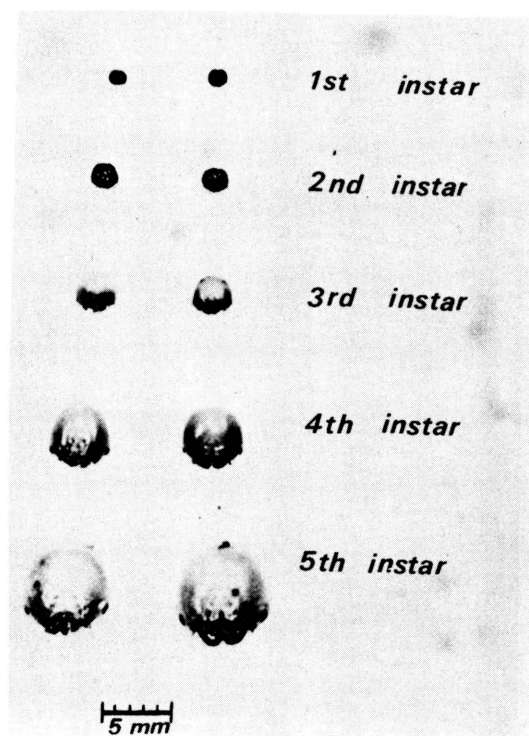
4) Time of occurrence

a) First generation

Larvae usually hatch from the end of October to the end of December, and enter the soil to pupate from the end of December to the end of February (Fig. 21). During the 1964/65 season the larvae at Pan plantation made their appearance slightly later, namely on 11.xi.1964, and could be found until 2.iii.1965 (Van den Berg, 1965).

During the 1968/69 season, larvae hatched from the last week in October to the beginning of December, and pupated from the end of December to the end of

Plate 11: Head capsules of the different larval instars of the poplar emperor



February. The following season (1969/70) larvae appeared approximately two weeks later. The larval stage thus lasts about two months in the field.

b) Second generation

Under Transvaal highveld conditions, larvae of the second generation do not develop to the pupal stage in the field. All larvae die during the first cold snap; the winter therefore seems to be too severe for them. Second generation larvae hatch from mid March to the end of April, and survive until the beginning or middle of May. No larvae have yet been seen in the Rietvlei, Pan (Middelburg District) or Ajax (Piet Retief District) plantations after mid May. The larvae seldom develop as far as the third instar. These results agree with earlier findings (Van den Berg, 1965), but Hepburn *et al* (1966), who speculated on spraying larvae of this generation, appear to have been unaware of their inability to survive the low temperatures during the Highveld winter. Second generation larvae develop normally under the warmer laboratory conditions.

5) Larval behaviour

An irregular hole is gnawed through the dorsal side of the egg shell by the hatching larva. The larva crawls through this opening which is just large enough for its head to pass through. The larva often feeds on what remains of the egg shell, sometimes consuming it almost entirely. Newly hatched larvae are positively phototactic and move to the tips of branches and leaves or needles.

Since eggs are laid in smaller masses than in the case of the pine emperor, fewer larvae normally occur per group. Larval gregariousness is less well developed than that observed with the pine emperor. From 2-5 first instar larvae usually feed together. During the second and third instars the groups are often smaller, while singly feeding larvae have also been observed. Fourth and fifth instar larvae do not appear to be gregarious at all.

The feeding habits of *P. irius* are most probably adapted to broad leaves which are devoured from the leaf edges inwards. On pine needles they evidently try to feed in the same way, but appear to be unable to reach the tips of the needles. Consequently a portion of the needle is bitten off and wasted.

When larvae in the first instar reach the tips of the needles, they move back a short distance before starting to feed. Usually only small pieces are severed. These larvae then retract gradually as the rest of the needle is consumed. The feeding habits of second instar larvae are nearly the same as those of the first instar, but bigger pieces are severed. Larvae in the third and fourth instars usually cling near to, or on to, the base of the needles and longer bits are wasted. Larvae in the fourth and fifth instars frequently cling to branches or the bases of needles with their abdominal legs, bending the needles in the same way as described for the pine emperor. Often only one or two needles of a cluster of three are bent and devoured from the tip inwards; when unbent needles are encountered in this process, they are bitten off, resulting in very long bits being wasted.

The tips of new needles remain alive and green during the growing season, and are frequently also eaten by final instar larvae. Some of the needles are thus devoured completely. Larvae may also bite off tips of needles, but instead of dropping them, turn them round with the mouthparts, devouring the tips from the severed end to their apices, i.e. the other way round to how fixed needles are consumed.

When the larva is disturbed, it often retracts the head, lifts the front part of the body slightly and then stays quite motionless for a while. In this position the larva is relatively well camouflaged against a green background such as leaves. If the larva is further disturbed, it frequently vomits drops of green to brown liquid, most of which may again be imbibed once the disturbance has ended.

6) Moulting

The preparations for moulting and the process of moulting are essentially the same as those described for the pine emperor. As the poplar emperor is exposed to higher temperatures, moulting takes place 2-4 days after the silken moulting platform has been spun, in contrast to the 4-6 days in the case of the pine emperor. The larva also returns and feeds on the old skin, which causes the old head capsule to become dislodged.

Larvae removed from their moulting platforms usually experience difficulty in getting rid of their old skins which stick to the last few segments.

7) Needle drop and production of frass

Daily needle drop and frass production during the different instars were studied on 10 young pine trees with a cloth funnel around each.

Measurements were made of all needles severed by one group of first and second instar larvae. In addition, measurements were made of needles severed by instars three and four from the fourth to the eighth days and by instar five on the seventh day. The results appear in Fig. 24.

From this fig. it can be seen that first and second instar larvae usually sever 40 mm or less of the distal end of the needle. Larvae in the third instar waste needles of nearly all possible lengths up to 140 mm long, while the lengths for the fourth and fifth instars are from 10-140 mm and from 5-150 mm respectively.

The relative number and average lengths of apical and middle sections severed by each instar and the percentage total needle length wasted appear in Table 24.

The calculation for the final instar is regarded as an overestimate as some of the needles may be completely devoured. From Table 24 it can be seen that first and second instar larvae wasted less than a fifth of the needles, while the

Fig. 24: Numbers and lengths of needle tips severed by poplar emperor larvae in the

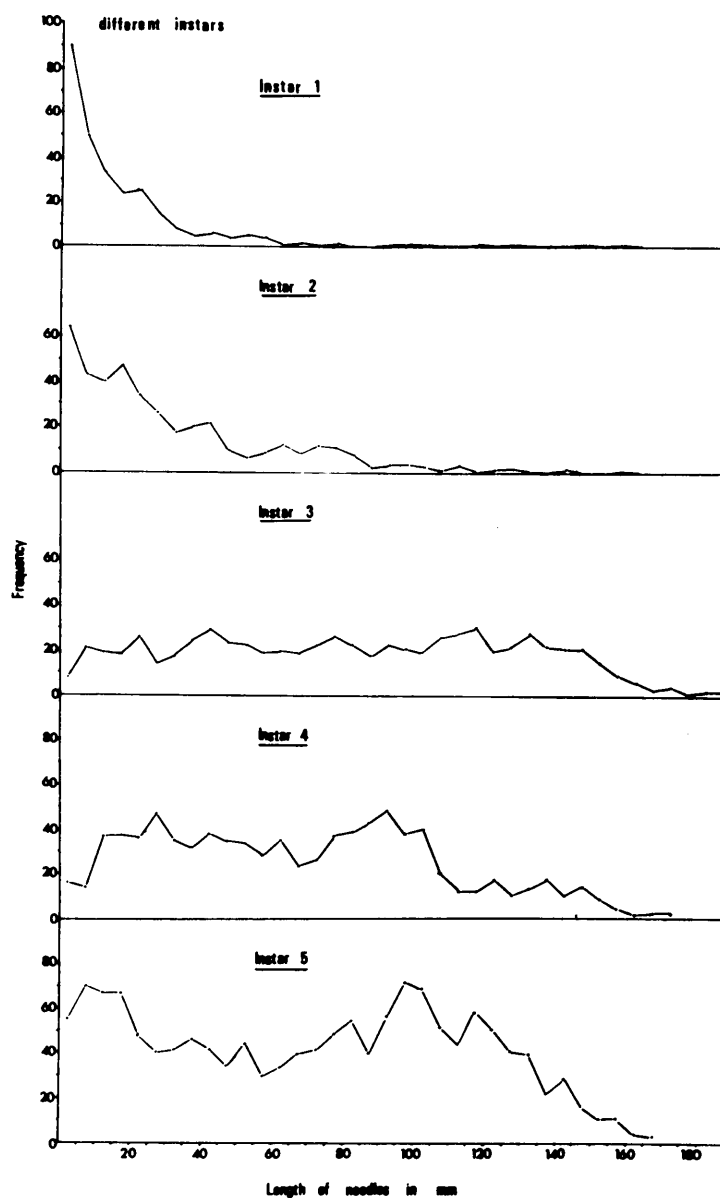


Table 24: Relative numbers and average lengths of apical and middle needle sections severed by the poplar emperor during the different instars and percentage total needle length wasted

Instar	Apical sections		Middle sections		Percentage total needle length wasted $= \frac{a + \frac{n_2 b}{n_1}}{190,5} \times 100$ = c
	No n_1	Average lengths in mm = a	No n_2	Average lengths in mm = b	
1	240	17,9	133	7,6	11,6
2	401	30,1	217	11,3	19,0
3	668	86,1	319	23,9	40,0
4	859	70,3	372	27,1	43,0
5	1402	74,6	590	27,1	45,1
Percentage needle length wasted by all instars					43,7

last three instars wasted nearly half. It must also be taken into account that some of the needles are not yet full-grown and thus the average needle length might possibly be less than the 190,5 mm accepted as the average. Thus the larvae probably waste more than the percentages indicated.

The average numbers of needles severed and frass pellets produced by one individual for the full duration of each instar, as determined on funnelled trees, are summarized in Table 25.

From this table it can be seen that the severed sections increase roughly five fold per instar from the first to the second instar. Thereafter the increase is from 3-4 fold per instar. This means that the larvae become progressively more wasteful feeders. Apart from severing more needles, they also waste larger pieces. Almost no increase in the number of frass pellets per instar was observed. The sizes do however increase greatly.

The total number of apical needle sections dropped during the larval stage is 2 132 per larva. The general average of needles for the top 2 m of a pine tree with a 7 m crown height, and for the other metre sections separately, was calculated at about 54 443 needles. During the spring and summer months when defoliation takes place, the tree may be able to repair some of the damage by adding new growth. About 25 larvae could sever as many needles as normally occur in the top 2 m of such a tree. The same applies for each metre height lower down in the tree. About 150 larvae could completely defoliate one such tree.

The average widths and lengths of 30 frass pellets produced every alternate day by the different instars, were measured with the aid of a standardized micrometer ocular. The information gained is graphically represented in Fig. 25. Frass pellets produced by the different instars are depicted in Plate 12.

From Fig. 25a it can be seen that the lengths of pellets produced by successive instars overlap to some extent. From pellets of certain lengths it would therefore be difficult to deduce which of two successive instars produced them. From Fig. 25b it is however clear that there is only a slight overlapping of the widths of the pellets produced by successive instars. Pellet width would therefore be a fairly reliable criterion from which to deduce what instar produced them. In the case of the fourth and fifth instars, the pellets produced towards the end of these instars gradually

Table 25: Average numbers of needle sections severed and frass pellets produced per poplar emperor larva for the full duration of each instar

Instar	No of larvae	Average number of needle sections dropped per larva			Average number of frass pellets produced per larva	Increase per instar (x)	
		Apical sections	Middle sections	Total		Needles	Frass
1	52	5,7	3,1	8,8	173,3	—	—
2	56	28,5	15,4	43,9	197,0	5,0	1,1
3	33	118,5	56,6	175,1	221,6	4,0	1,1
4	28	588,6	49,3	637,9	258,5	3,6	1,2
5	15	1 391,0	585,4	1 976,4	277,7	3,1	1,1
Total		2 132,3	709,8	2 842,1	1 128,1		

Fig.25: Lengths and widths of 30 frass pellets produced every alternate day by different larval instars of the poplar emperor

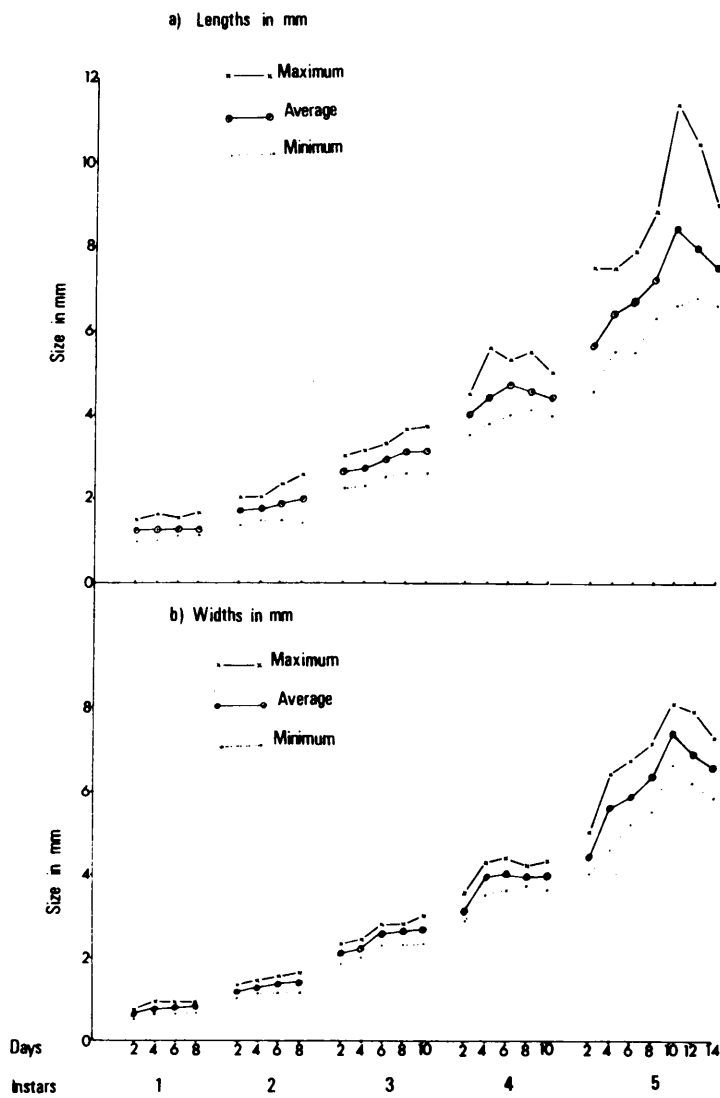
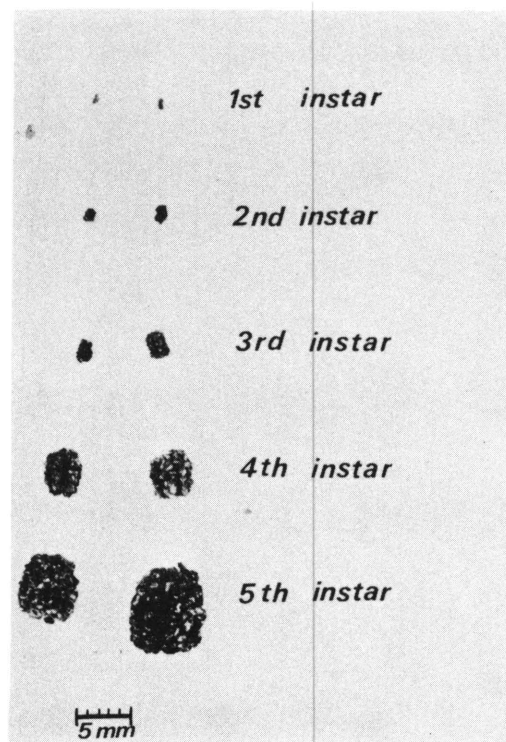


Plate 12: Frass pellets excreted by the different larval instars of the poplar emperor



become smaller. This could be explained by the fact that the more robust and larger larvae usually develop faster and moult or pupate earlier, while smaller larvae with smaller frass pellets take longer to complete their development. In addition, the last pellets produced by each instar are usually smaller than those produced the previous day, which may also cause the average to drop towards the end of an instar.

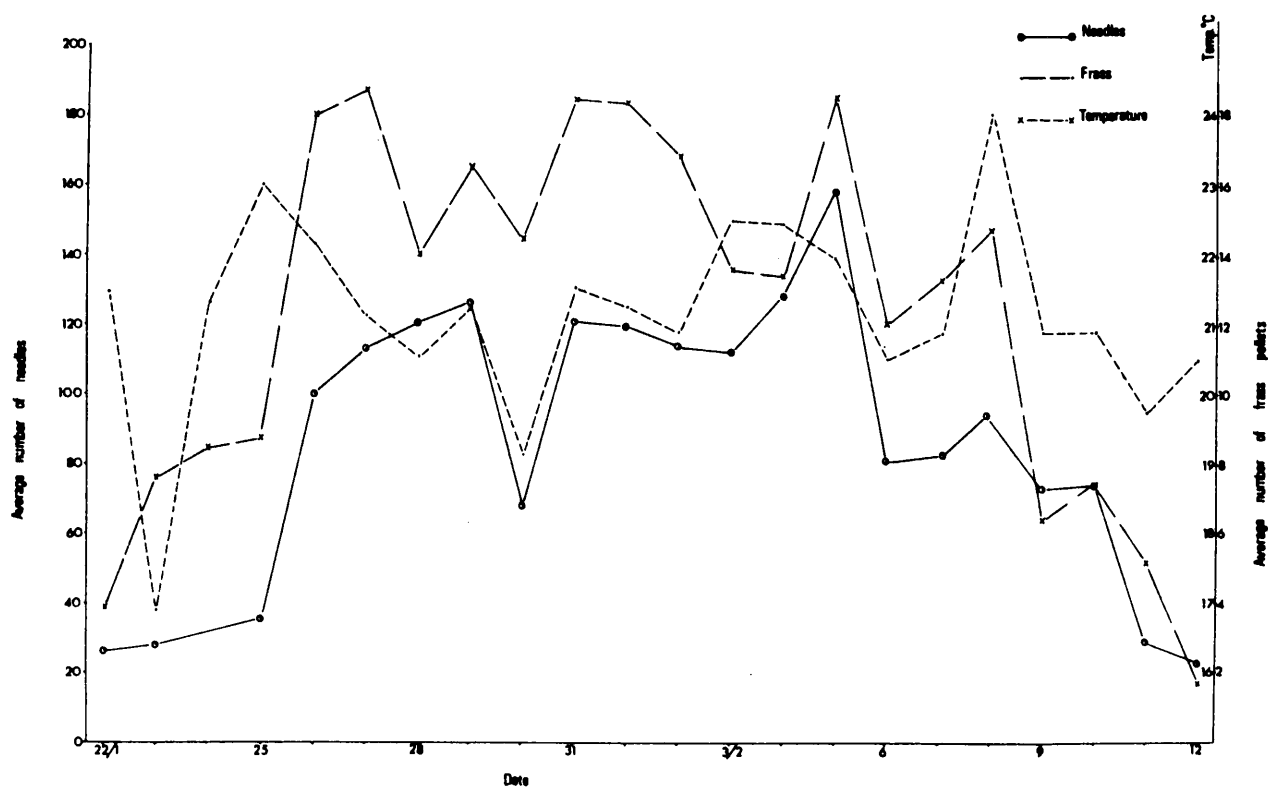
8) The influence of temperature on food intake

a) Average daily temperature

The influence of the average daily temperature on the number of needles cut off and frass pellets produced was studied on a funnelled tree. The results are graphically represented in Fig. 26.

From this it is seen that more needles are severed and more frass produced at higher than at lower temperatures, but that average temperatures above about

Fig.26: Average number of needles severed and frass produced per larva per day by 10 final instar poplar emperor larvae, and the average daily temperature



22°C seem to have a depressing effect. The amount of food after the 10th February may be ignored, because, at this time, larvae were nearing pupation.

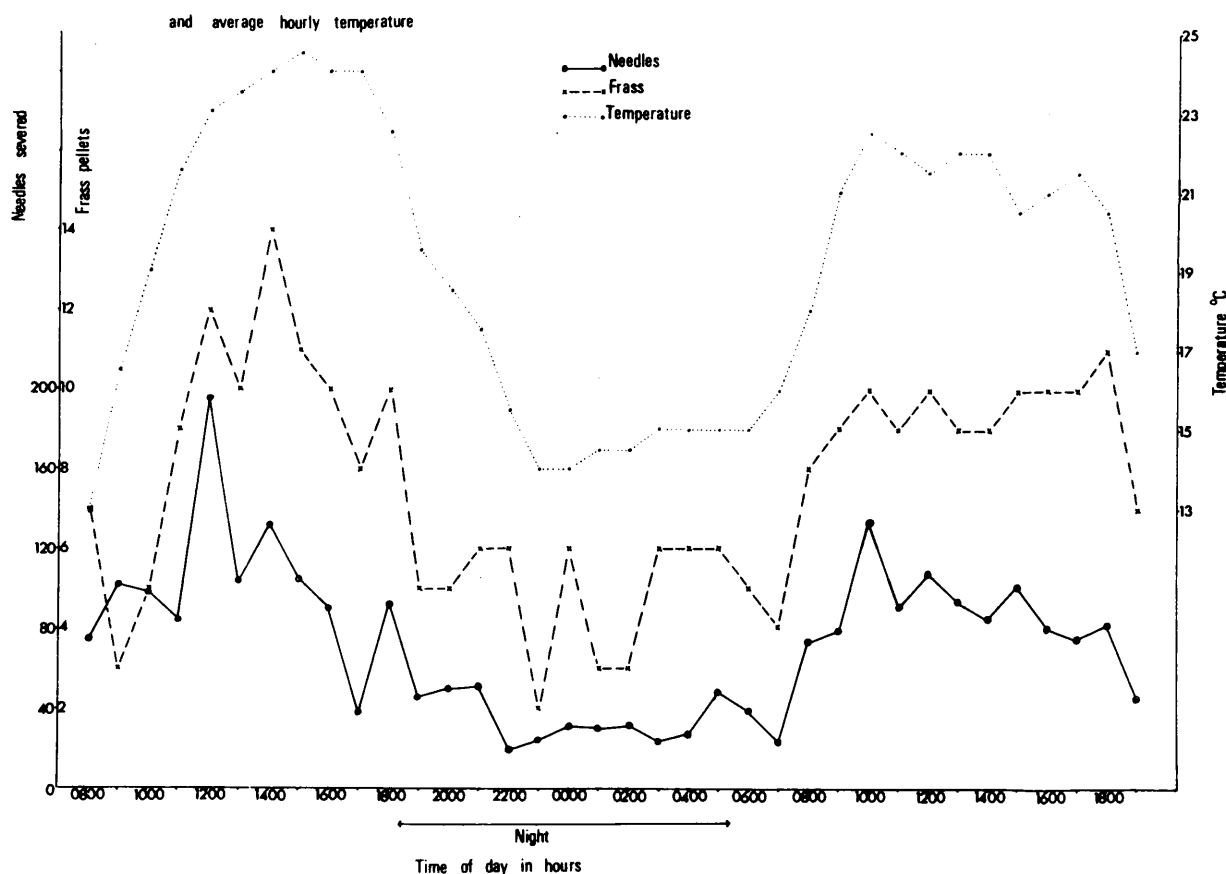
b) Average hourly temperature

The time of day at which active feeding takes place was studied with larvae that had been in the final instar for one week. At 0500 hours a funnelled tree was lightly shaken, all the needles and frass pellets collected in the jar, and a clean jar inserted. This was repeated at hourly intervals for 36 consecutive hours. Hourly records were also kept of prevailing temperatures.

The numbers of needles severed and frass pellets produced by 10 final instar larvae during each of 36 consecutive hours, and the average hourly temperatures are given in Fig. 27.

From this fig. it can be seen that the numbers of needles severed and frass pellets produced tend to rise and fall with temperature. The ups and downs of the curves appear to be of a random nature, indicating that the feeding and rest-

Fig. 27: Total number of needles severed and frass pellets produced by 10 poplar emperor larvae per hour,



ing periods of the different larvae are not well synchronized. It also appears that temperatures above 23°C or below 18°C tend to inhibit feeding to some extent.

In the case of larvae of the pine emperor there were indications that feeding does not take place at a steady rate but rather in sudden spurts at almost regularly spaced intervals. Furthermore, the feeding periods of the different larvae as well as their resting periods seemed to be somehow synchronized, especially during the night, resulting in more or less regular ups and downs in the curves for needle drop and frass production. This was not as evident in the case of *P. irius* where the fluctuations of the curves appear to be more of a random nature. One possible explanation for this difference in larval feeding behaviour may be the greater gregariousness of pine emperor larvae.

9) Food requirements

The masses of needles ingested and frass excreted by larvae were determined

by providing larvae with *P. patula* needles of the same mass as that kept as a control. After the larvae had eaten part of the food, the dry mass loss of the needles compared to that of the control was determined, as well as the dry mass of the frass. In this way, the total mass of needles ingested and frass excreted per instar could be obtained. Larval mass was determined shortly after emergence and after each moult. The mass of the pupae was also determined after being sexed.

Breeding in the laboratory, although still somewhat difficult, was more successful than with the pine emperor. Of 83 poplar emperor larvae bred on *P. patula*, 25 formed normal pupae.

The average dry masses of *P. patula* needles ingested and frass excreted during the different instars, and digestion coefficients are indicated in Table 26.

From the totals at the bottom of this table an idea can be formed of the total dry mass consumed and excreted during the larval feeding period by the average male, the average female or the average individual if the two sexes are combined.

The digestion coefficient was between 13,7 and 19,5 per cent, being higher for males than for females. It can however not be concluded that there is a better food utilisation by males than by females, or that males require less food to gain the same live mass as females.

Table 27 shows the minimum, maximum and average live masses of different instar larvae and of pupae, as well as the live mass increase per instar when bred on *P. patula* needles in the laboratory. From this table it can be seen that the increase in live mass from hatching until pupation is about 770 fold, which is achieved in about two months. The high increase from the first to the second instar (6,4 times) can most probably be attributed to moisture absorption, while the low increase of 1,7 times from the final instar to the pupal stage, may be due to loss of water before pupation.

The average moisture content of *P. patula* needles fed to the larvae in the laboratory was 65,7 per cent.

Table 26: Minimum, maximum and average dry masses in mg of *P. patula* needles ingested and frass excreted per poplar emperor larva in the different instars (M = Male, F = Female)

Instar	Sex	n	Dry mass of needles ingested per larva			Increase of a per instar	Dry mass of frass excreted per larva			Increase of b per instar	Dry mass utilized, difference between a and b = c	Increase of c per instar	Digestion coeff = $\frac{c}{a} \times 100\%$
			Min	Max	Aver = a		Min	Max	Aver = b				
1	M+F	70	34,3	44,1	38,9	—	26,4	35,0	31,3	—	7,6	—	19,5
2	M+F	43	100,2	190,5	139,7	3,6	80,5	151,0	113,0	3,6	26,7	3,5	19,1
3	M+F	32	420,3	635,6	521,0	3,7	319,7	496,1	424,3	3,8	96,7	3,6	18,6
4	M	13	1 803,8	2 302,1	1 965,9	—	1 455,2	1 892,1	1 644,3	—	321,6	—	16,4
	F	12	1 807,2	2 251,3	2 122,4	—	1 532,6	1 888,4	1 831,9	—	290,5	—	13,7
	M+F				2 044,2	3,9			1 738,1	4,1	306,1	3,2	15,0
5	M	13	7 985,3	12 049,0	10 441,8	5,3	6 801,0	9 919,4	8 590,4	5,2	1 851,4	5,8	17,7
	F	12	7 336,9	14 218,7	10 715,8	5,0	6 074,3	11 835,3	8 880,2	4,8	1 835,6	6,3	17,1
	M+F				10 578,8	5,2			8 735,3	5,0	1 843,5	6,0	17,4
Total	M				13 107,3				10 803,3		2 304,0		17,6
	F				13 537,7				11 280,6		2 257,1		16,7
	M+F				13 322,5				11 041,9		2 280,6		17,1

Table 27: Live mass of poplar emperor larvae bred on *P. patula* shortly after hatching or moulting (M = Male; F = Female)

Instar	Sex	n	Mass in mg			Live mass increase per instar
			Min	Max	Aver	
1	M+F	60	4,6	4,9	4,8	—
2	M+F	43	25,0	37,2	30,5	6,4
3	M+F	32	105,0	195,2	137,3	4,5
4	M	13	434,8	622,4	560,3	—
	F	12	557,2	755,0	663,8	—
	M+F				612,1	4,5
5	M	13	1 099,2	2 932,1	2 204,7	3,9
	F	12	1 697,2	2 667,2	2 207,9	3,3
	M+F				2 206,3	3,6
pupa	M	13	3 134,4	4 078,1	3 540,9	1,6
	F	12	3 160,0	4 589,6	3 860,9	1,7
	M+F				3 700,9	1,7

10) Duration of larval development

a) In the laboratory

The duration of the larval instars on *P. patula* under fluctuating weather conditions in the laboratory, is provided in Table 28.

Under laboratory conditions of average daily temperatures of about 20°C it would appear (Table 28) that the duration in instars one to five would probably last about 11, 10, 12, 12 and 17 days respectively. The duration of the final instar was 2-5 days longer for female than for male larvae.

In only one case out of the 30 larvae reared in the laboratory up to the pupal stage (of which 25 formed normal and 5 deformed pupae), did a larva pass through six instars; all other larvae passed through only five.

Hepburn *et al* (1966) state that the durations of the different instars bred on *Populus deltoides* are as follows: first instar 7-9 days; second instar 7-8 days;

Table 28: Duration of the poplar emperor larval instars on *P. patula* under fluctuating laboratory temperatures (M = Male; F = Female)

Instar	Sex	n	Duration in days			Average temperature °C
			Min	Max	Aver	
1	M+F	8	10	21	14,6	19,9
	"	12	9	14	11,5	20,1
	"	5	13	16	13,6	20,2
	"	13	9	13	10,0	20,3
	"	17	8	12	9,2	20,5
2	M+F	7	9	12	9,8	19,5
	"	10	8	14	9,6	19,7
	"	11	9	12	9,2	19,7
	"	8	9	12	9,7	19,8
	"	7	7	11	9,6	20,8
3	M+F	6	9	14	11,8	20,6
	"	10	8	11	9,0	20,9
	"	4	7	11	8,5	21,3
	"	4	7	10	8,8	22,8
	"	5	7	9	7,9	23,6
4	M+F	4	9	11	10,3	22,1
	"	13	9	11	10,3	23,3
	"	5	7	10	9,0	23,4
	"	9	8	16	10,9	23,6
	"	6	8	13	9,8	23,9
5	M	2	15	16	15,5	20,9
	F	1			18,0	
	M+F				16,8	
	M	4	17	19	18,3	22,4
	F	6	17	26	20,8	
	M+F				19,5	
	M	7	13	21	16,1	23,2
	F	5	16	23	21,6	
M+F				18,9		

third instar 8-10 days; fourth instar 8-10 days; fifth instar 9-11 days; sixth instar 10-12 days. The prevailing temperatures during the time that these observations were made, are unfortunately not mentioned. Their findings however are in fair agreement with those of the present study, except for the number of instars.

b) In the field

Observations on the duration of larval development on naturally growing pine trees in a plantation appear in Table 29. The average temperatures, as registered by a thermograph close to the experimental area are also given.

Table 29: Duration of the different larval instars of the poplar emperor feeding on growing *P. patula* under fluctuating field temperatures

Instar	n	Duration in days			Average temperature in °C
		Min	Max	Aver	
1	8	8	11	9,3	19,7
	25	7	13	10,5	19,3
	25	9	12	10,8	18,9
	27	7	10	8,0	17,7
2	10	8	10	9,1	17,9
	3	13	15	14,3	17,6
	18	10	12	10,4	17,4
	17	8	11	8,8	17,3
3	14	9	10	9,1	19,4
	8	9	10	9,6	18,7
	22	8	12	10,2	16,4
4	15	11	13	12,1	20,0
	7	12	15	13,1	19,8
	8	9	14	12,0	18,8
5	5	18	22	20,2	18,4
	10	17	27	18,7	18,3

In the field, instars one to five would probably last about 10, 9, 10, 13 and

20 days respectively at normal fluctuating temperatures with an average of about 18°C. Both in the laboratory and in the field the fifth instar lasted the longest, and the second instar the shortest.

The average monthly field temperatures are given in Fig. 28. From this

Fig.28: Monthly field temperature in the Rietvlei plantation

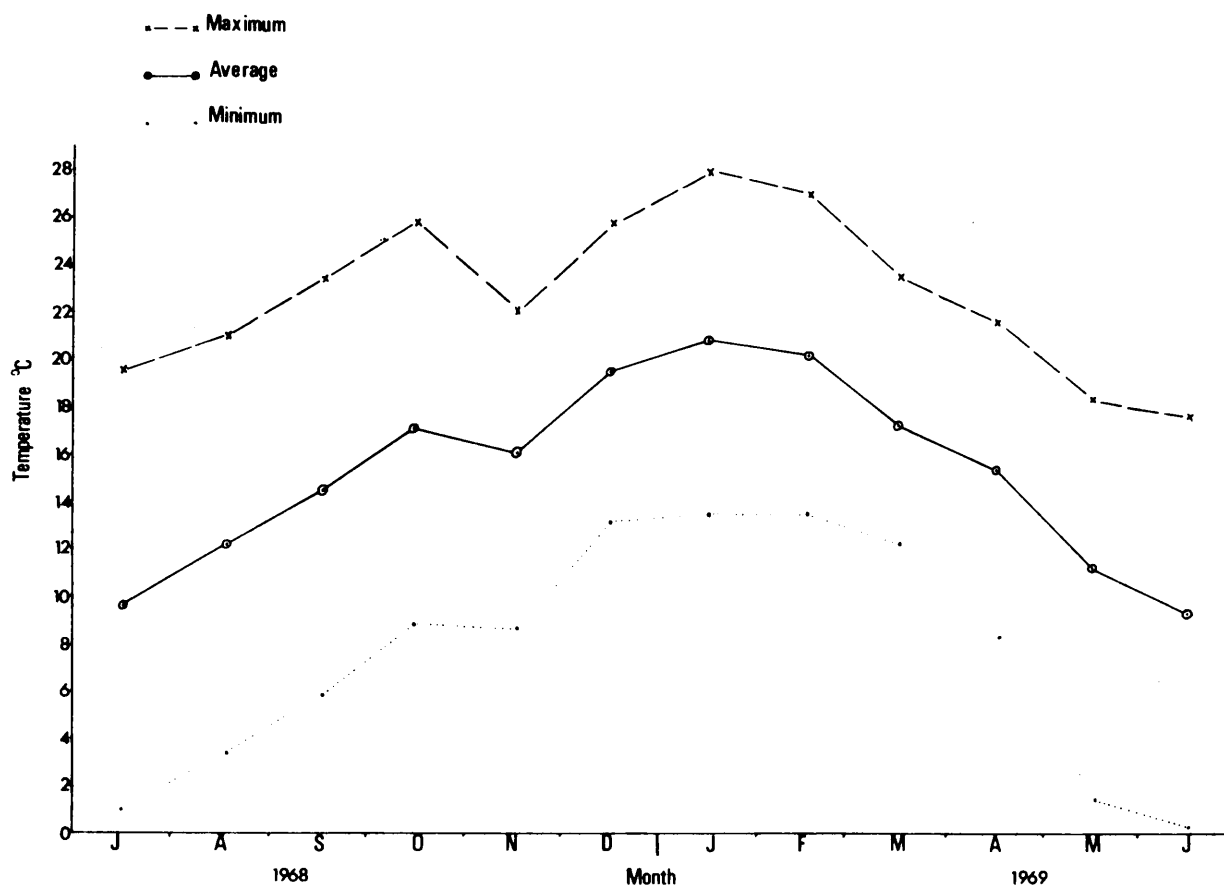


fig. it can be seen that, during the larval period of the first generation (October, 1968 to February, 1969), average monthly temperatures fluctuated between 16 and 20,8°C. Under these conditions, the total larval stage lasted from 7,5-9 weeks.

During the second generation, (March to May, 1969) the average temperature steadily dropped from 17,2 to below 11,2°C. The temperatures experienced from the end of April onwards are usually sufficiently low to kill all larvae. The minimum temperature recorded for May, 1969 was 1,4°C. It may therefore be stated that the larvae are not very cold-resistant. Since it was proved that larvae of the

second generation can develop at room temperatures such as experienced during the winter months in the Highveld, it may be concluded that in more tropical areas two generations will be completed per year.

11) Host plants

From field observations it became clear that early instar larvae of the poplar emperor may sometimes be found on plants on which they do not seem to be able to complete larval development. In the following list of host plants, the latest instar actually observed to be feeding on that plant will be indicated between brackets where this has been recorded.

The following authors were consulted to draw up a list of host plants.

(a) Platt (1921); (b) Rougeot (1955); (c) Hepburn (1961); (d) Van den Berg (1965); (e) Hepburn *et al* (1966). In this list the authors will be indicated by the corresponding letter (a) to (e) as used above. Only the first author to mention a specific host plant will be credited. Original observations will be indicated by "(or. obs.)". Authors who only mention host plants already indicated by other authors are Prinsloo (1962) and Anonymous (1970).

a) List of indigenous host plants

Berlinia paniculata Benth. (b) (Is ?)

Brachystegia randii Bak f. (a) (Is ?)

Piliostigma thonningii (Schumach.) Milne-Redh. (b) (Is ?)

Uapaca nitida Muell. Arg. (b) (Is ?)

b) List of imported exotic host plants

Acacia mearnsii De Wild. (e) (Is ?)

Cupressus glabra Sudw. (e) (Is ?)

Eucalyptus fastigata Dean and Maiden (or. obs.) (Is 5)

Eucalyptus macarthuri Dean and Maiden (or. obs.) (Is 5)

Eucalyptus nitens Maiden (or. obs.) (Is 4)

Pinus caribaea Morelet (e) (Is ?)

Pinus michoacana Martinez (e) (Is ?)

Pinus montezumae Lamb. (e) (Is 5)

Pinus patula Schlechtd. & Cham. (d) (Is 5)

Pinus pseudostrobus Lindl. (e) (Is ?)

Pinus radiata D. Don (d) (Is 5)

Populus deltoides Marsh. (c) (Is 5)

Quercus palustris L. (e) (Is ?)

From this list it is clear that larvae of the poplar emperor have been observed on exotic plants in six genera, in contrast to four indigenous genera. As this insect was recorded on *Brachystegia randii* before 1921, which is at least 25 years earlier than all records on exotic host plants, this plant species was most probably one of the original host plants, while *Piliostigma thonningii*, *Berlinia paniculata* and *Uapaca nitida* may also be among the original host plants.

Indigenous trees and shrubs are exceedingly scarce and very poorly represented in the savannah type of country in which Rietvlei and Pan are situated. The invasion of newly established plantations of exotic trees by the poplar emperor must therefore have been a very gradual and slow process, in spite of the fact that the adults are strong fliers. It may therefore be concluded that, if this pest were to be totally eradicated in all plantations in the general vicinity, re-invasion of the plantations would again be very slow.

12) Pupation

The full-grown larva stops feeding and starts to wander about, apparently aimlessly. A watery frass is excreted and the larva climbs down or falls to the ground. The larva crawls about on the pine needle mat and frequently tries to enter the mat. It sometimes partly succeeds but then crawls out again to try elsewhere. Sites where small holes already exist are preferred. These are mostly found in lanes containing brushwood. The larva then burrows into the mat and pupates in the same way as described for the pine emperor.

In the laboratory, the prepupal stage (i.e. from the time that the larva enters the soil until the pupa is formed) lasts from 6-9 days (25 prepupa at an average temperature of 22,1°C). According to Hepburn *et al* (1966), the prepupal stage lasts from 2-7 days; their minimum of two days appears to be rather short, but could have been due to much higher temperatures.

E. The pupal stage

1) Notes on diapause

Full-grown larvae wandering about in search of a site to pupate, were collected on three different dates in midsummer 1966, and placed in three different cages (2 x 1 x 1 m) with a 7 cm layer of soil at normal fluctuating temperatures in the laboratory. The larvae were allowed to burrow into the soil to pupate, which they all did within a day or two after being placed in the cages. Notes were kept on the number of adults emerging in each cage before as well as after the winter. From the data it could be calculated what percentage of pupae had entered diapause. The results obtained are summarized in Table 30.

Table 30: Number of diapause pupae obtained from full-grown poplar emperor larvae collected from the field on different dates

Collection date during 1966	Number collected	Diapause pupae	
		Number	Percentage
12th Jan	326	176	54,0
1st Feb	141	138	97,9
20th Feb	105	104	99,0

Admittedly the data are too fragmentary to warrant definite conclusions. There are however clear indications that the later the date of pupation, the greater the percentage of pupae entering diapause. The factor(s) inducing this diapause can not be stated with certainty at the present time.

Adults of the first generation do not emerge at a more or less fixed date each year, resulting in earlier or later oviposition and consequently a larger or smaller proportion of larvae pupating early. If the first generation makes its appearance early, a smaller percentage of pupae will thus enter diapause than would otherwise be the case.

If a method could be found by which the first generation of adults could be induced to emerge very early, the larvae would pupate early, resulting in non-diapause pupae. The second generation of larvae would then be killed by the cold and the poplar emperor eradicated in this way. Further research in this connection is planned.

2) Description, size and sexual differences

When newly formed, the pupa is yellow-brown and soft, but after a few days the integument hardens and the colour changes to shiny black (Plate 9). The incisions separating the abdominal segments are not very deep or conspicuous. The abdomen ends in a long sharp cremaster. Table 31 summarizes the dimensions of pupae of the two sexes.

Table 31: Average size of 40 male and 40 female poplar emperor pupae

Sex	Length			Width		
	Min	Max	Aver	Min	Max	Aver
Male	36	49	42,9	13	18	15,8
Female	42	53	46,6	15	19	16,8

From this table it is seen that female pupae are somewhat bigger than males. These dimensions are in close agreement with those of Hepburn *et al* (1966) who mention lengths of 43-51 mm and widths of 15-19 mm.

Latero-ventrally, on the ninth abdominal segment, the male has two swollen knobs. In the female the ninth segment is slightly elongated and a longitudinal cleft is visible on the mid ventral line.

3) Seasonal occurrence

Pupation begins from the end of December while the last larvae pupate at the end of February. A small proportion of adults emerge to form a second generation during the end of February to mid April (Fig. 21). The other pupae lie over from the beginning of the year to give rise to adults the following season, emerging from the beginning of October to mid December. Pupae are thus present during all months of the year. Individuals in diapause remain in the pupal stage for over seven months., i.e. from March until October. This extended pupal diapause may yet prove to be the weak link in the whole life cycle.

4) Spatial distribution

The brushwood in the Rietvlei plantation had been heaped together in alternate lanes running from east to west, so that approximately half of the soil sur-

face was covered with it. At the time that pupal distribution was studied, the brushwood had a height of only about 15 cm, being higher in the middle of the lanes than closer to the rows of trees. The brushwood was mostly dry, decaying very slowly.

Observations on the depths at which pupae occur in *Populus deltoides* plantations have not yet been made, but according to Hepburn *et al* (1966), they occur up to 125 mm below the soil surface.

The depths and positions of pupae relative to ground level, *P. patula* tree trunks and brushwood, were determined as described for the pine emperor. This was done in 30 plots each bordered by four trees, half of them in lanes with brushwood, and the other half in lanes without. In the case of lanes with brushwood, the northern and southern sides of each plot bordered on lanes without brushwood.

The depth at which pupae were found in lanes with and without brushwood was roughly the same, most of them being at the same level as the soil surface and the deepest at 62,5 mm below soil surface level.

For the purpose of statistical analysis, the same lettering and numbering system used for the pine emperor was employed to form groups of 30 x 30 cm subplots. The actual numbers of poplar emperor pupae found in the different subplots are indicated in Table 32. Statistical analysis of the data in Table 32 is given in Table 33a and b.

From Table 33a it can be concluded that in lanes without brushwood, highly significantly more pupae could be found near the tree trunks (subplots lettered a) than anywhere else. From Table 33b it follows that in lanes with brushwood this was not the case.

As the brushwood in the Rietvlei plantation was heaped on a strip about 150 cm wide midway between two rows of trees (with the highest brushwood in the centre), it was decided to compare the pupae in subplots within this strip with the pupae in the rest of the subplots (Fig. 29). The statistical analysis of the data in Fig. 29 is given in Table 34.

From this analysis it follows that, in lanes with brushwood, highly significantly more pupae were found in subplots within the central 150 cm wide strip than in

Table 32: Numbers of poplar emperor pupae found in the different subplots of 30 x 30 cm with lettering and numbering corresponding to that in Fig. 12

No	Lanes without brushwood				Lanes with brushwood			
	Subplot group a				Subplot group a			
	NW	NE	SW	SE	NW	NE	SW	SE
1	2	8	3	5	2	1	2	0
2	3	4	2	5	2	1	1	0
3	1	3	0	2	1	1	3	0
4	6	3	1	2	0	0	0	0
Aver for subplot group a	3,13				0,88			
	Subplot group b				Subplot group b			
	NW	NE	SW	SE	NW	NE	SW	SE
1	1	2	0	0	0	0	1	0
2	0	4	0	1	1	0	1	2
3	2	5	1	0	0*	2*	0*	2*
4	1	4	2	2	1*	1*	1*	4*
5	4	4	2	1	2*	1*	2*	2*
Aver for subplot group b	1,80				1,15			
	Subplot group c				Subplot group c			
	NW	NE	SW	SE	NW	NE	SW	SE
1	1	2	0	1	1	0	0	0
2	2	0	2	0	2	0	1	0
3	2	0	0	4	0*	3*	1*	4*
4	2	1	0	1	1*	2*	2*	1*
5	1	2	3	1	1*	2*	3*	2*
6	2	2	0	3	1*	0*	2*	2*
7	2	0	1	4	2*	3*	2*	1*
Aver for subplot group c	1,39				1,39			
	Subplot group d				Subplot group d			
	N	W	E	S	N	W	E	S
1	2	1	2	0	0	2*	0*	0
2	2	1	3	2	0	0*	1*	1
3	1	1	1	1	0*	0*	3*	0*
4	1	1	0	3	3*	6*	2*	2*
5	—	—	—	1	—	—	—	4*
Aver for subplot group d	1,29				1,35			

* Number of pupae in lanes with brushwood within the 150 cm strip midway between two rows of trees covered by brushwood

Table 33: Analysis of variance of data in Table 32a) **Lanes without brushwood**

Source of variation	SS	d.f.	MS	F
Between subplot groups	36,07	3	12,02	5,66**
Within subplot groups	163,51	77	2,12	
Total	199,58	80		

** Differs highly significantly $F_{(3,77)}(,01) = 4,05$

SSD(Fisher) at $t_{\alpha/2} = 1,973$ (5%) and 2,649 (1%)

Comparing a with b = 2,71; a with c = 3,19; a with d = 3,50; b with c = 0,96;

b with d = 0,93 and c with d = 0,09

a	b	c	d
3,13	<u>1,80</u>	<u>1,39</u>	<u>1,29</u>

Averages underlined by a continuous line do not differ significantly.

Averages underlined by a dotted line do not differ highly significantly.

b) **Lanes with brushwood**

Source of variation	SS	d.f.	MS	F
Between subplot groups	3,44	3	1,15	0,76 ⁻
Within subplot groups	117,10	77	1,52	
Total	120,54	80		

⁻ No significant differences occur ($F_{(3,77)}(,05) = 2,73$)

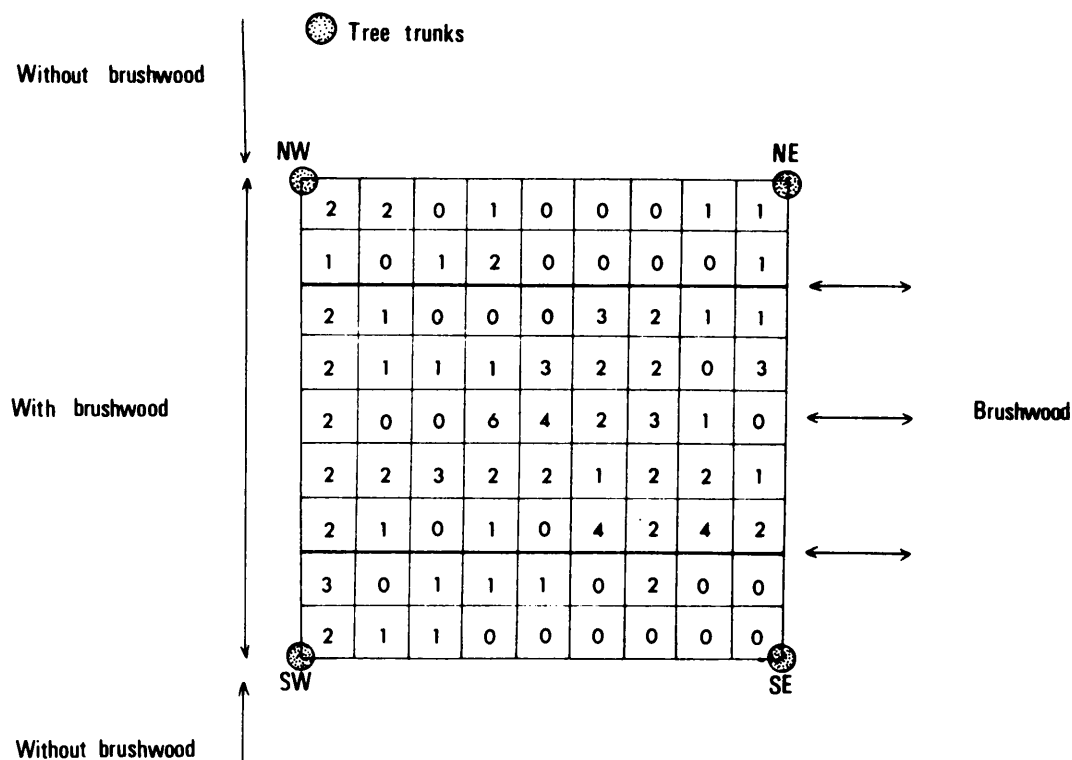
Table 34: Analysis of variance of data indicated by asteriks in Table 32

Source of variation	SS	d.f.	MS	F
Between subplot groups	20,90	1	20,90	16,59**
Within subplot groups	99,64	79	1,26	
Total	120,54	80		

** Differs highly significantly $F_{(1,79)}(,01) = 4,88$

Fig.29: Grouping of 30x30 cm subplots to compare the number of pupae in a 150 cm strip midway

between two rows of trees with that outside this strip



subplots on either side. This distribution is probably due to the fact that pupating larvae prefer sheltered sites, such as found within the central 150 cm wide strip covered with brushwood.

The actual number of pupae found in every subplot appearing in Table 32 was analysed to determine whether the numbers found in lanes with brushwood differed significantly from those in lanes without. The analysis can be found in Table 35.

Table 35: Analysis of variance of data in Table 32

Source of variation	SS	d.f.	MS	F
Between lanes with and without brushwood	14,23	1	14,23	7,12**
Within lanes	320,12	160	2,00	
Total	334,35	161		

** Differs highly significantly $F_{(1,79)}(,01) = 6,82$

From this analysis it follows that highly significantly more pupae were found in lanes without than in lanes with brushwood. In order to study the distribution further, the data in Table 32 indicated by asterisks (area under brushwood) have been compared with the rest (area without brushwood). This analysis is supplied in Table 36.

Table 36: Analysis of variance of data in Table 32

Source of variation	SS	d.f.	MS	F
Between subplots within the central 150 cm strip in brushwood lanes and all other subplots	1,56	1	1,56	0,75 ⁻
Within subplots	332,79	160	2,08	
Total	334,35	161		

No significant differences occur ($F_{(1,160)}(,05) = 3,91$)

From this analysis it follows that the pupae were more or less evenly distributed in the area covered with brushwood and in that without it.

From this study of pupal distribution it may be finally concluded that, if a concentration of pupae is desired for the purpose of collecting or destroying them, the brushwood should be heaped around the trunks of the trees.

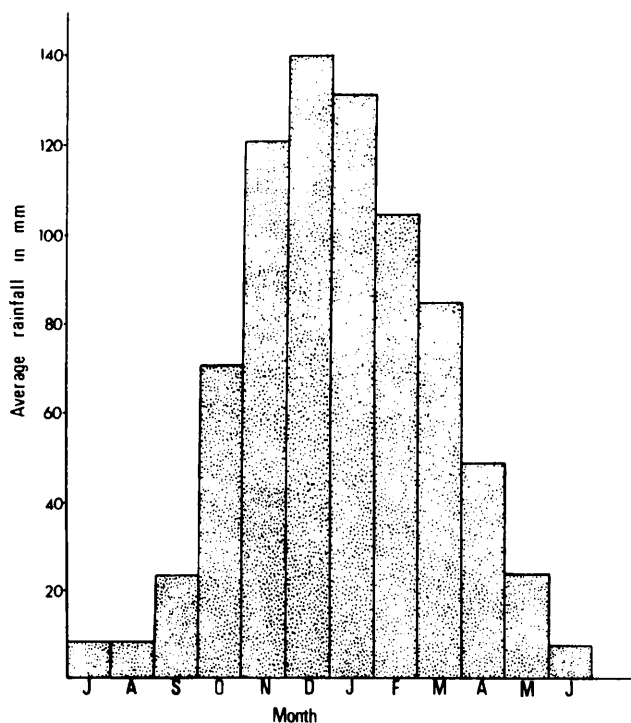
Hepburn *et al* (1966) also mention that pupae are often found near the stems, but under brushwood some are found far from the stems. This is in agreement with the findings of the present study.

The loss of a certain amount of moisture during and shortly after pupal formation is of great importance for cold-hardiness. There is however a certain minimum moisture content below which normal development is no longer possible. If pupae are therefore exposed to low moisture conditions for long periods they may lose an excessive amount of moisture which they are unable to reabsorb later. These pupae either die, or if they do develop into adults, their wings do not open normally. Van den Berg (1965; 1968) found that poplar emperor pupae kept at low humidities, such as between 20 and 50 per cent RH, gave rise to adults

possessing crumpled wings, while the wings expanded normally at 60-90 per cent RH. Adults with crumpled wings, have also been observed in plantations. The fact that most adults found in a plantation usually have normal wings, therefore indicates that humidities in the pupal cells must be fairly high (i.e. of the order of 60-90 per cent).

In a pine plantation the pupae are usually well protected against fluctuating moisture and temperature conditions. From the average monthly rainfalls in Fig. 30, it is evident that moist conditions prevail during the time of pupation (December to February), resulting in the larvae being able to burrow deeply into the soil. After about two months in the pupal stage, the soil dries out, but towards the end of the pupal stage moist conditions usually again prevail (September to November). The rain falling during September to November has a very

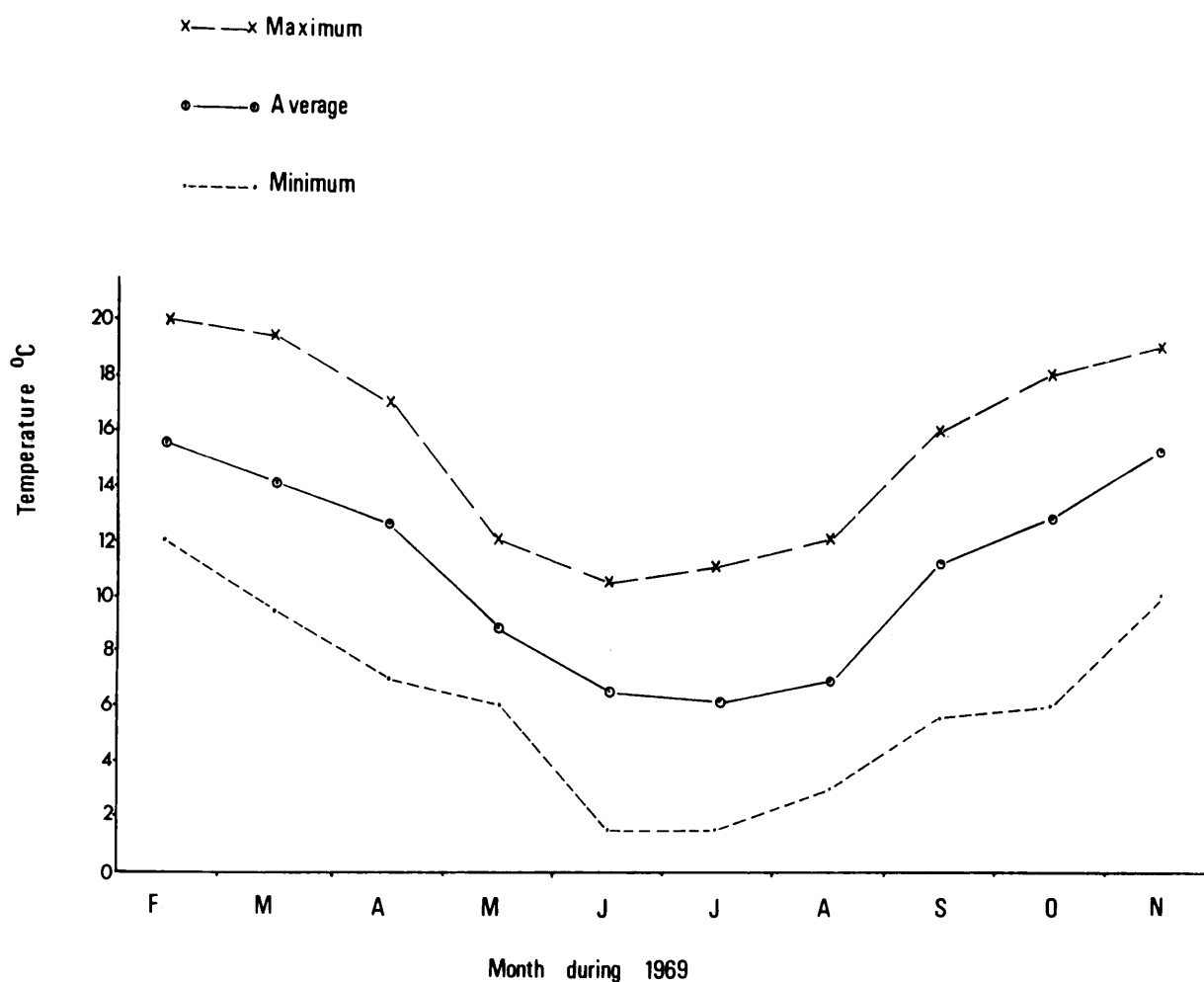
Fig.30: Average monthly rainfall for Pan plantation over 57 years (1914-1960)



important influence on adult emergence. If the soil had been soft and moist during pupation, enabling larvae to burrow deeply into the soil, but if it is hard and dry during the time of emergence, many adults fail to emerge.

The average monthly temperatures recorded by a soil thermograph at a depth of 25 mm below the soil surface, are represented in Fig. 31. From this it can be

Fig.31: Monthly soil temperature 25 mm below the soil surface in the Rietvlei plantation

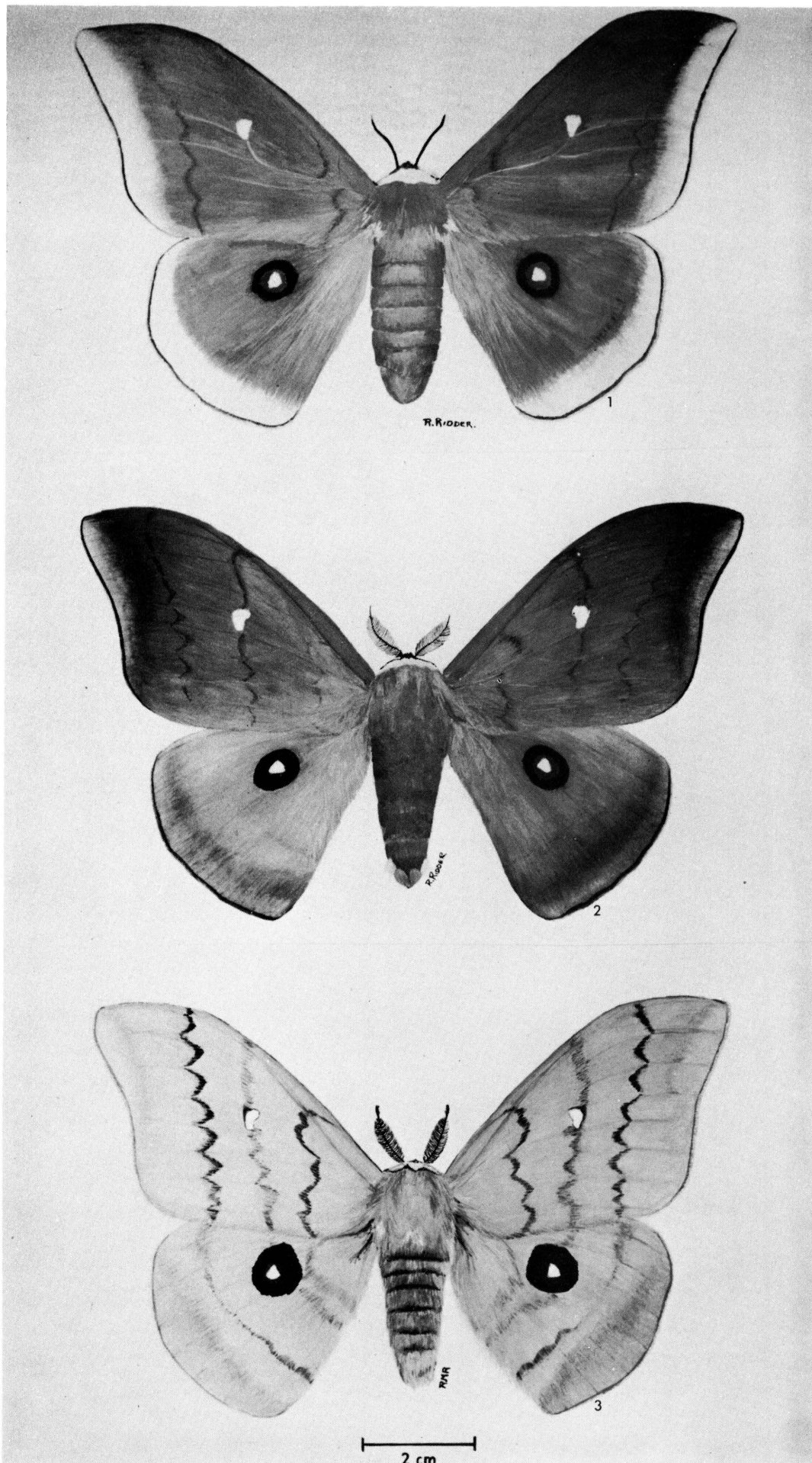


seen that pupae may be subjected to temperatures ranging from 1,4-20°C. During hibernation in the pupal stage, the minimum recorded temperature was 1,4°C, thus still above freezing point. It appears unlikely that even the lowest recorded soil temperatures during the dry winter months would prove lethal to diapausing pupae. The maximum temperature of 20°C can be regarded as moderate.

F. The adult stage

1) General description

Poplar emperor adults are large and heavy (Plate 13). The ground colour is variable, frequently grey-brown, red-brown or yellow. The forewing has more



or less the same colour throughout, except for a lighter portion of grey near the outer edge on grey-brown and yellow moths, and grey to red-brown on red-brown moths. The outer edge has a clear thin line of a slightly darker shade than the background colour. On the forewing there is a more or less triangular transparent spot, without encircling coloured rings. Frequently, three light to dark grey wavy stripes can be seen parallel with the outer edge of the wing. On the hindwing a clear eye spot is visible. It consists of a round to triangular transparent central area, with a dark grey inner and a black outer ring surrounding it. This eye spot is round to oval shaped, and lies in an orange to red-brown portion in grey-brown and red-brown moths. It is situated near the centre of the wing, slightly closer to the front edge. In yellow moths, this central area is of a brighter yellow shade than the background colour. The three light to dark grey stripes are often continued on the hindwing but do not appear in the orange to red-brown or brighter yellow portions of the wing. The body and thorax are hairy, matching the ground colour i.e. grey-brown, red-brown or yellow. The hairs continue over the proximal parts of the wings. On the ventral aspect the thorax and abdomen are white to a lighter shade of the ground colour. The head is brown-grey. Directly behind the head is a white collar. The antennae are brown-black.

2) Sexual dimorphism, size and colour variations

According to Hepburn *et al* (1966), the two sexes occur in more or less equal numbers, as was also found during the present study.

The antennae of the male are broadly bipectinate, while those of the female are almost filiform. The apex of the forewing of the male is also more acute than that of the female.

The wingspan of field collected moths varied from 103-145 mm for 95 females (average 126,7 mm) and 94-136 mm (average 120,0 mm) for 121 males.

The three previously mentioned colour forms were sent to Dr. E. Pinhey of the National Museum of Rhodesia for identification. The following colour forms occurred in the Rietvlei plantation: *f.epithyrena* (grey-brown), *f.natalensis* (red-brown) and *f.sjostedti* (yellow), in the proportions of about 9:3:1 respectively for both sexes during 1968 (204 females and 265 males).

3) Seasonal occurrence

The time of appearance of adults was determined by direct counts in 30 plots each 2,7 x 91 m, in the plantation. These plots were distributed in such a manner that 10 were situated in an area with a dense, 10 in a medium, and 10 in an area with a sparse population. Counts were made weekly at about 0700 to 0900 hours.

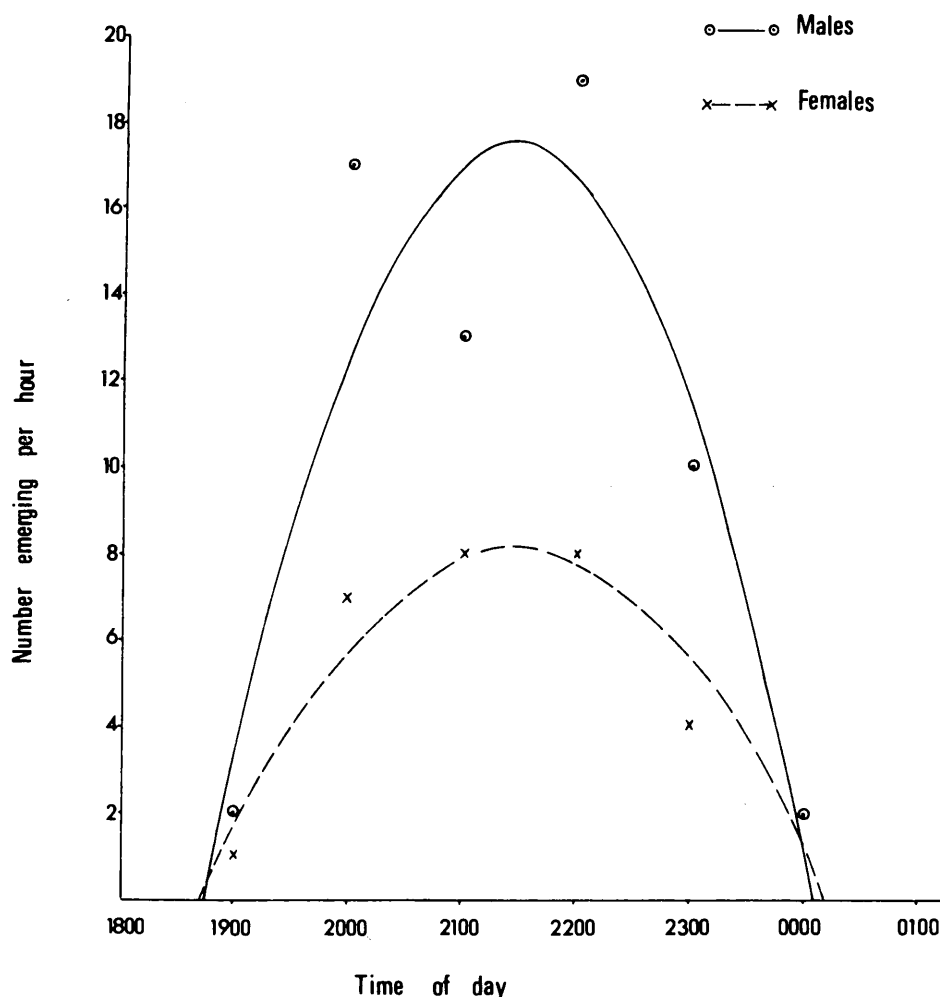
Two generations of adults occur per year. The first generation makes its appearance from the beginning of October to mid December and the second during the end of February to the end of March. Adults however do not annually emerge at the same time. For example, during the 1964/65 season, the first generation emerged between 10.x.1964 and 7.i.1965 (Van den Berg, 1965; Hepburn *et al*, 1966); during the 1968/69 season between 3.x.1968 and 21.xii.1968; and during the 1969/70 season between 18.x.1969 and 11.i.1970. This may be due to differences in weather conditions experienced by the diapausing pupae. The first generation of adults is much more numerous than the second, which agrees with previous findings (Van den Berg, 1965; Hepburn *et al*, 1966; Van den Berg, 1968). The percentage of the total population emerging as the second generation varies from season to season.

4) Emergence

Emergence was studied in 40 plots, each 2,7 x 91 m, in a continuous block. The observations started at 1700 hours on the 9th October, 1969, and lasted for a continuous period of 48 hrs. Each freshly emerged adult was marked by means of a card fixed to a nearby object. The date and time it was first seen, when the wings were fully expanded or hardened, when mating started or ended and when it flew away were recorded on this card.

Emergence of the poplar emperor agrees with that of the pine emperor as far as clinging to an object in a more or less vertical position and the unfolding and hardening of the wings are concerned. The numbers of adults that emerged at different times of the day during this 48 hour period have been diagrammatically represented in Fig. 32. From the points plotted, smooth curves have been drawn. From this it can be seen that both sexes emerge between 1900 hours and midnight. About two hours after emergence the wings are completely expanded and hardened, after which they are folded against the body.

Fig. 32: Time of emergence of poplar emperor moths in the plantation



5) Sexual attraction and copulation

Sexual attraction commences when the female telescopically extends her last few abdominal segments. Two small knobs situated latero-ventrally between the second and third last segments are then projected. These structures are evidently sexual attraction glands. Sexual attraction is more or less the same as described for the pine emperor, and usually commences shortly after the wings of the female are folded against the body. Mating usually commences between 2100 and 0300 hours, with a peak from 2300 to 0200 hours (14 copulations). In 12 cases mating continued for 1-2 hrs, in one case it lasted until dawn (about 6 hrs) while in another case it lasted until dusk the following night (about 18 hrs).

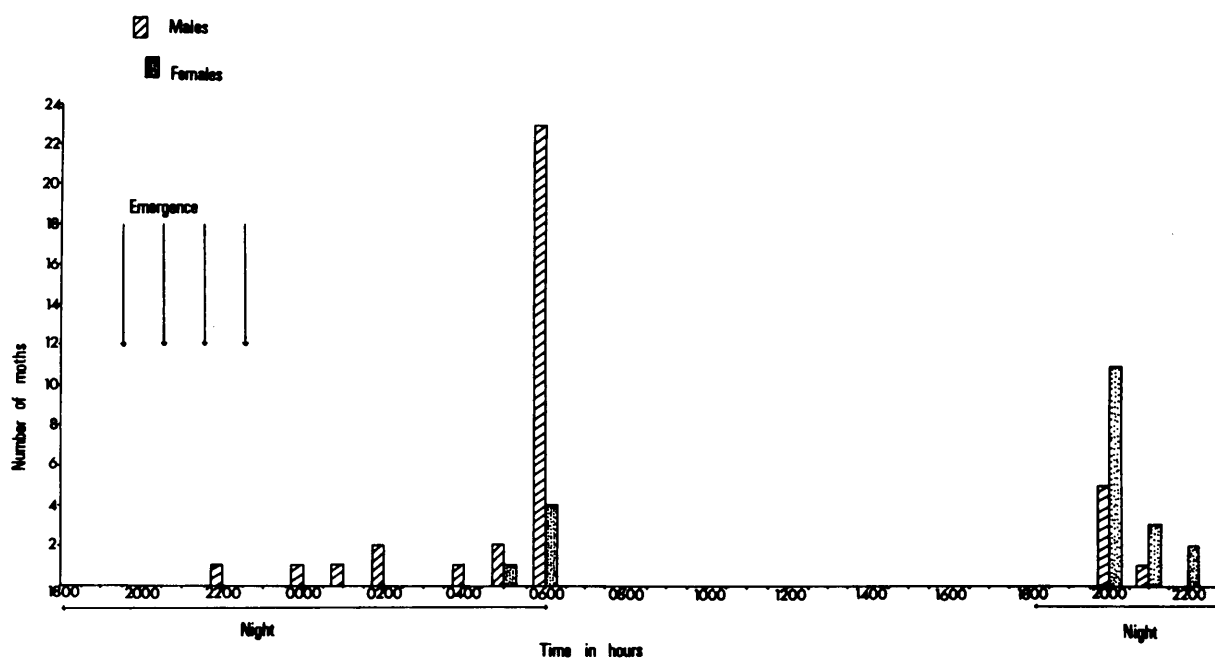
Females frequently mate more than once, while old females depleted of eggs may also copulate. One or both individuals sometimes die while in copula. Males can apparently mate twice during the same night and up to six or more times during their lifetime.

6) Flight activity

The adults fly very strongly and, in spite of their size, apparently without much effort.

Observations on the times at which newly emerged adults leave the sites of emergence are summarized in Fig. 33. From this it can be seen that some of the

Fig. 33: Times of first flights by poplar emperor moths relative to the time of emergence



males move away from their emergence sites during the night of emergence. The largest number wait until dawn (about 8 hrs after emerging) or dusk of the following day (about 23 hrs after emergence). Females usually crawl up tree trunks during the morning after the night of emergence, and then only fly away at dusk that night (about 22 hrs after emergence).

During the period of peak moth numbers, hourly records were kept of the sexes that arrived at ultra-violet light traps from dusk to dawn. The findings are summarized in Fig. 34. Free-hand curves were drawn from the points plotted. Statistical analysis of Fig. 34 is provided in Table 37.

According to this table, females are attracted to ultra-violet light traps highly significantly earlier than males. These different flying times for the two sexes may be explained along the same lines as for the pine emperor, namely that the females

Fig. 34: Total number of poplar emperor moths caught at a light trap per hour

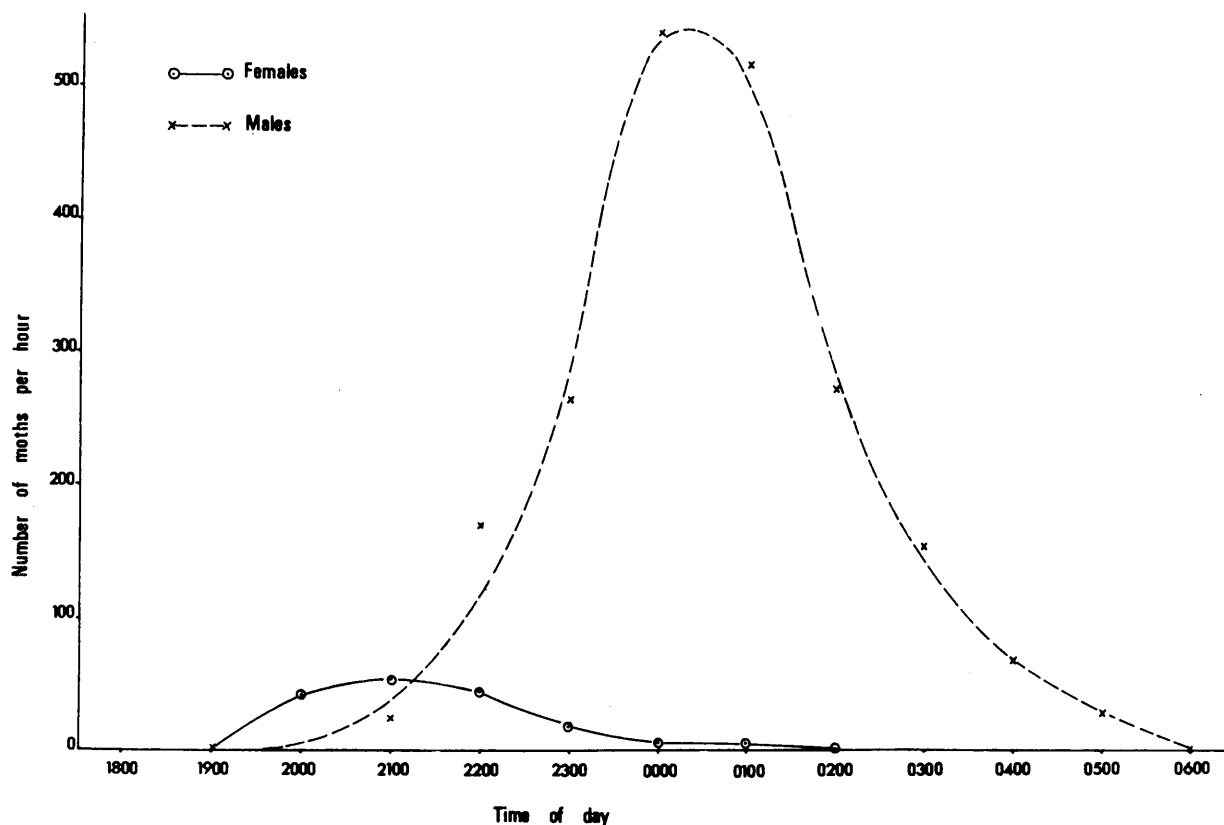


Table 37 : Statistical analysis of data in Fig. 34

	Males	Females	
Before 2300 hours	460	153	613
After 2300 hours	1 577	13	1 590
	2 037	166	2 203

Continuity correction was applied

$$X^2 = 366,6^{**}, X^2_1 (.01) = 6,63$$

fly from one egg laying site to another, while the males are most active during the period when virgin females usually begin to secrete the luring pheromone. The flight activity of poplar emperor males starts somewhat earlier than that of the pine emperor, which may be explained by the earlier commencement of pheromone secretion by females.

Hepburn *et al* (1966) caught 437 females and 281 males with the aid of an ultra-violet light, during the first 2,5 hrs after sunset, agreeing with the present findings on flight activity for the same time of night.

From Fig. 34 it is also clear that considerably smaller numbers of females than males are attracted to ultra-violet light traps. Gravid females occasionally come to light traps, whereas those containing few or no eggs are more generally attracted. This was also noted by Hepburn *et al* (1966).

Although the adults are good flyers, dispersion from an outbreak area to other nearby areas takes place very slowly. Hepburn *et al* (1966) state that the largest number of larvae were found at the same localities where the greatest damage had been done the previous year, indicating weak powers of dispersion.

7) Oviposition

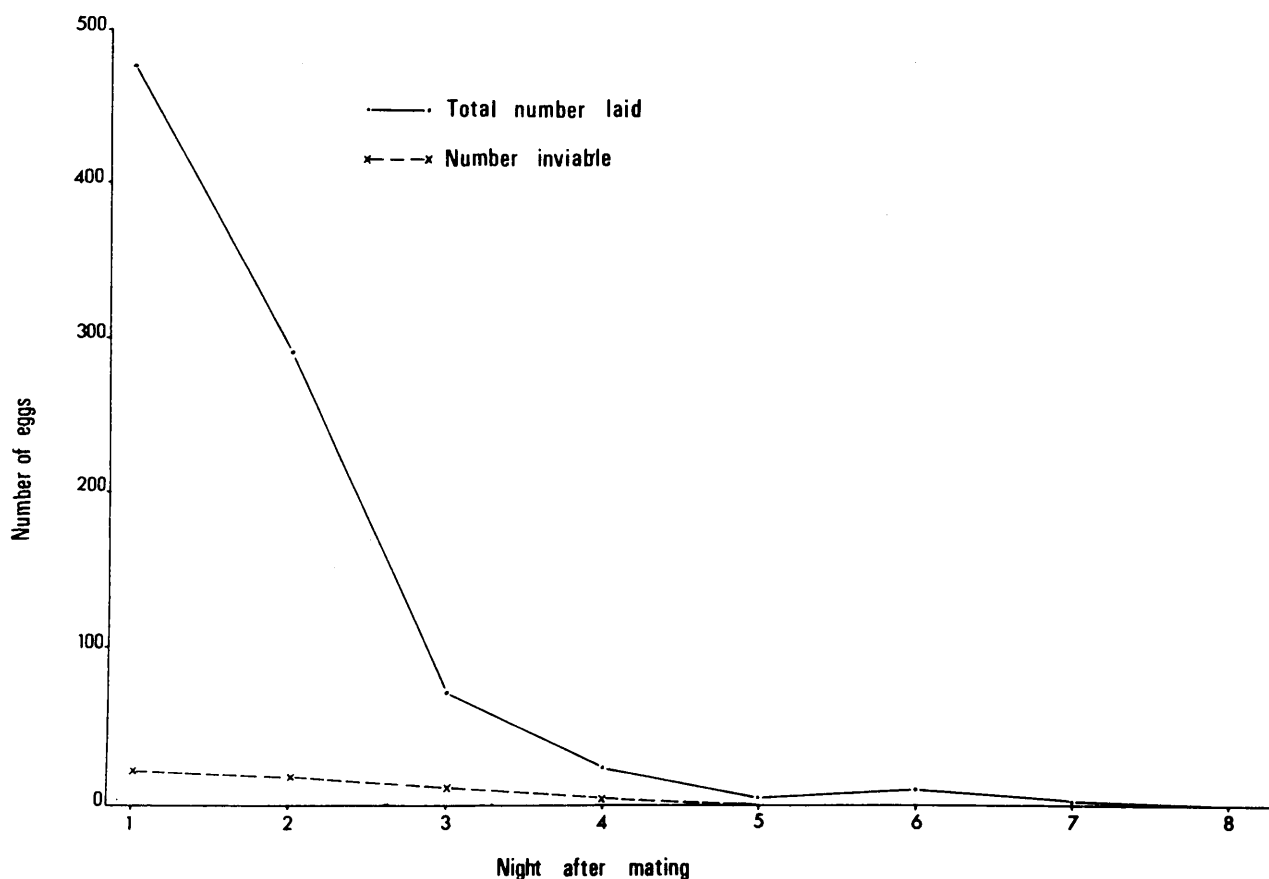
Oviposition behaviour of the female determines whether newly hatched larvae will be within reach of suitable food. Plant species preferred for egg laying are *P. patula*, *P. radiata*, *Eucalyptus nitens* and *Prunus persica* (peach). Egg laying takes place mainly on leaves, seldom on stems and dead branches. The larvae do not feed on peach leaves and eventually die of starvation; eggs laid on this plant are therefore wasted.

Females which had emerged the previous night, and were busy mating, were collected in the field and placed singly in 50 cages. Eggs laid during each night were collected from the cages the following mornings, and recorded for the specific moth and night, and kept separately in honey jars. The total numbers of eggs laid by these females on different nights after mating, are diagrammatically represented in Fig. 35.

From this fig. it can be seen that the greater bulk of eggs are laid during the first two nights after mating, the numbers rapidly declining afterwards. From

Fig.35: Total number of eggs laid by 50 field collected poplar emperor females

on different nights after the night of mating



the fifth night after mating hardly any further egg laying takes place. Of these 50 females, one died on the third night, slightly more than half of them (28) were still alive after five nights, while the last three died on the eighth night. The average number of eggs left in the ovaries after death was 2,3.

On *P. patula*, the female frequently lays an egg mass on a group of needles, and then moves about 5 cm down the pendulous needles to lay another mass.

The heights at which eggs are laid in trees were determined by chopping down 20 trees and recording the distance of each egg mass from the top of the tree. The results are given in Table 38.

From this table it can be seen that almost all the eggs are laid in the top 6 m of the trees. In this particular instance the average crown depth was approximately 6,5 m, the lower 2 m being devoid of branches and needles. It can also be seen from this table that slightly fewer masses are laid in the top 2 m

Table 38: Height at which poplar emperor eggs were found in 10 *P. patula* trees

Distance in m from the tops of the trees	Number of egg masses
0-1	24
1-2	91
2-3	158
3-4	241
4-5	191
5-6	141
6-7	37
7-8	21
8-9	5
9-10	0
stem	<u>2</u>
Total	911

sections together, than in the next four separate metre sections lower down. It was determined that the top 2 m sections possess almost as many needles as the other metre sections lower down separately. The number of egg masses laid at different heights is therefore more or less in proportion to the number of needles available at these heights. Only a small number of eggs was found on the lower branches and stems. Relatively exposed positions seem to be preferred for oviposition, such as trees on the outskirts of plantations or blocks, resulting in a denser larval population in these trees than on trees in the middle of blocks. Since trees on the outskirts possess more branches with needles, they offer a larger food supply and can support a larger number of larvae. As a result, defoliation, if it takes place, occurs almost simultaneously throughout the infested area.

8) Number of eggs and larvae per female

The average number of eggs found in the ovaries of 123 females developing

from field collected pupae was 184, ranging from 129-254 per female. Hepburn *et al* (1966) found an average of 179 eggs for 72 females, which is in very close agreement with the present findings.

Females occurring naturally in the field usually deposit most of their eggs, but an average of 2,1 eggs (0-14 for 50 females) remains in their ovaries.

Of the 2 104 eggs collected in the Rietvlei plantation during 1968/69 an average of 14,2 per cent were inviable (parasitism excluded). The average number of offspring produced is therefore about 156 larvae per female under the conditions prevailing at that time.

G. Climatic factors influencing population density

During this study the following factors were observed to have an influence on the abundance of the egg, pupal and adult stages.

Egg stage

Heavy thunderstorms may dislodge many of the eggs which are present from October to December. Larvae developing from these eggs generally die of starvation.

Pupal stage

Pupae exposed to extremely dry conditions may die due to dehydration.

Adult stage

Under very dry conditions some adults are unable to crawl out of the pupal shell, while the wings of others may be damaged so that they are unable to fly.

**CHAPTER 4: BIO-ECOLOGICAL STUDIES ON
*HOLOCERINA SMILAX***

A. Experimental site

Experiments in connection with *H. smilax*, the pine-bark emperor, were carried out in the Keerom and Kanonkop plantations, which are situated five and seven km from Middelburg (Tvl.) on the Loskop dam and Stoffberg roads respectively. Keerom is 346 ha and Kanonkop 132 ha in extent, of which 44 per cent is occupied by *P. patula* and 31 per cent by *P. radiata*. The plantations are situated 1 534 m above sea level and the general topography is a flat plain. The nearest cultivated pine trees are about 16 km from the Kanonkop plantation. Few indigenous trees and shrubs appear in the direct vicinity of these two plantations.

B. Distribution

Adults of this emperor moth are not strongly attracted to light traps. In addition, they are relatively small and less conspicuous in comparison with the other two species. It is possibly for these reasons that the distribution of this species is less well known than that of the other two.

The distribution of *H. smilax* was deduced from collection records from the same sources mentioned earlier. The date of the collections and the name of the first collector are given where known.

Cape

Port Elizabeth, 23.x.1961 (J.S. Taylor).

Transkei

Buntingville, 17.xii.1902 (? Nat. Collect.).

Natal

Balgowan, Nov, 1934 (? Rhod. Mus.); Durban (Port Natal) (Westwood, 1849); Howick, ?1907 (J.C. Cregon); Muden, Oct, 1954 (? Rhod. Mus.); Pietermaritzburg, ? 1882 (Peringuey); Umkomaas, Oct, 1933 (? Rhod. Mus.).

Swaziland

Mhlambanyati, 11.xii.1965 (M.A. van den Berg).

Transvaal

Barberton, Feb, 1909 (Miss de Beer); Bronkhorstspuit, 30.x.1958 (M.A. van den Berg); Hemlock, Jan, 1940 (W.H. Ghent); Middelburg, 17.xii.1968 (M.A. van den Berg); Piet Retief, ? 1964 (H.E. Prinsloo); Pilgrim's Rest, 22.xi.1962 (Vari & Leleup); Pretoria, Nov, 1923 (Wager); Schoemansdal, 21.iii.1969 (M.A. van den Berg); White River, Oct, 1911 (A.J.T. Janse).

Rhodesia

Balla Balla, Dec, 1955 (? Rhod. Mus.); Bulawayo, Nov, 1955 (? Rhod. Mus.); Khami, Feb, 1951 (? Rhod. Mus.); Rusape, Feb, 1961 (? Rhod. Mus.); Turk Mine, Jan, 1958 (? Rhod. Mus.); Umtali, March, 1932 (? Rhod. Mus.); Vict. Falls Road, Nov, 1939 (? Rhod. Mus.); Vumba, Dec, 1962 (? Rhod. Mus.).

Tanzania

Amani & Shinyanga (Pinhey, 1956).

Kenya

Kitale, ? 1945 (? Rhod. Mus.); Nairobi, Nyeri, Machakos & Teita Hills (Pinhey, 1956).

The distribution is also indicated in Fig. 36.

From this distribution list and Fig. 36 it is clear that the pine-bark emperor is very widely distributed, namely from Kitale in Kenya in the north, to Port Elizabeth in the south. Before 1925 the species already had a wide distribution, namely Durban (before 1849), Pietermaritzburg (1882), Buntingville (1902), Howick (1907), Barberton (1909), White River (1911) and Pretoria (1923). The insect could also be found in many places in the Republic after 1925. As this moth was known to be present in areas where *P.patula* had been cultivated a long time ago, it is noteworthy that the first damage was only reported in 1967 and 1968. It is therefore possible that the pine-bark emperor has only recently become adapted to this food plant. If this proves to be correct, heavier and more frequent outbreaks can be expected in the future.

C. The egg stage

1) General description

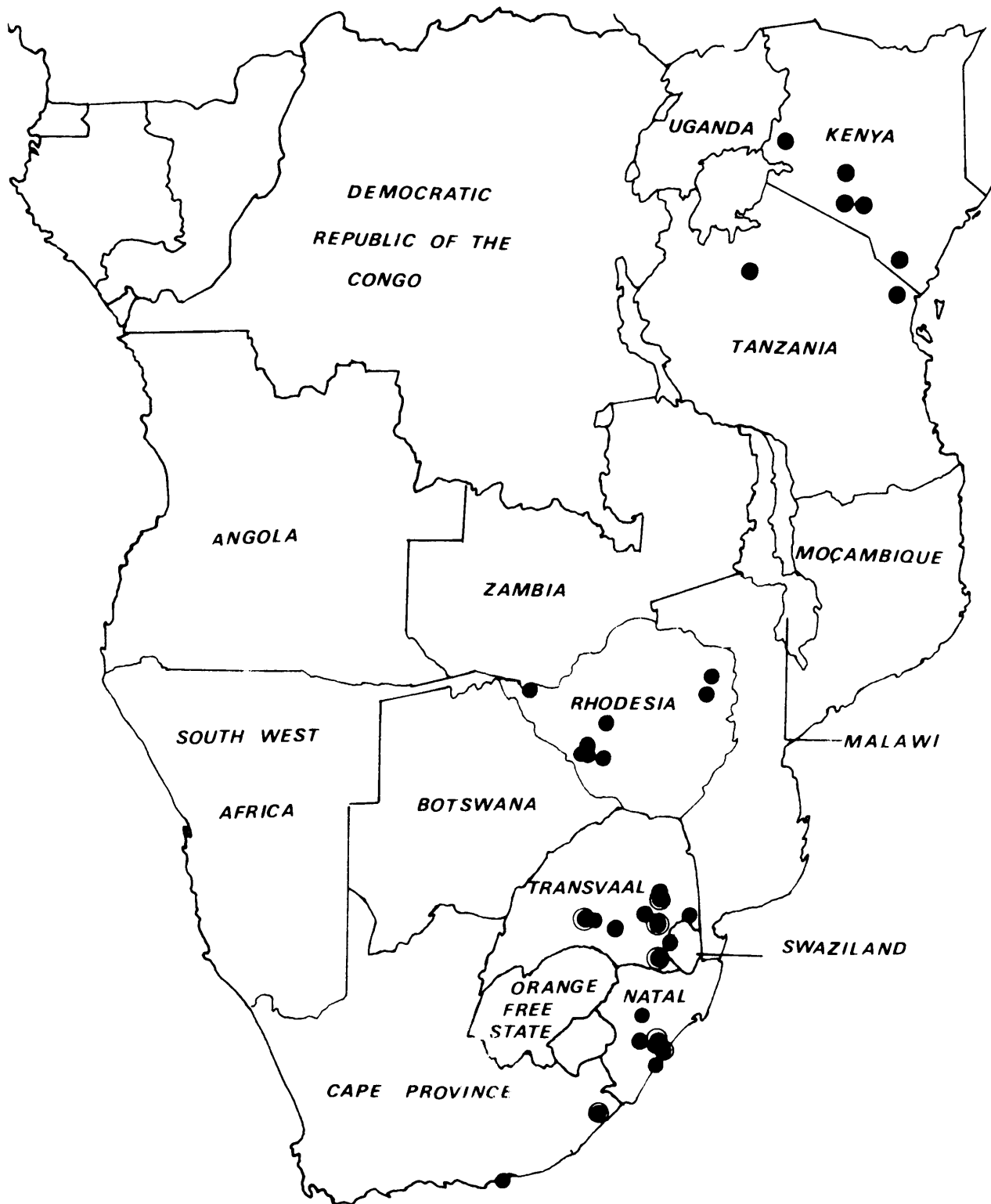
The egg is slightly oval-shaped and flattened (Plate 14). On the average it is 2,28 mm long, 2,01 mm wide and 1,75 mm high. (Table 39).

FIG.36:

DISTRIBUTION OF *H. SMILAX*

● COLLECTED BEFORE 1925

● COLLECTED AFTER 1925



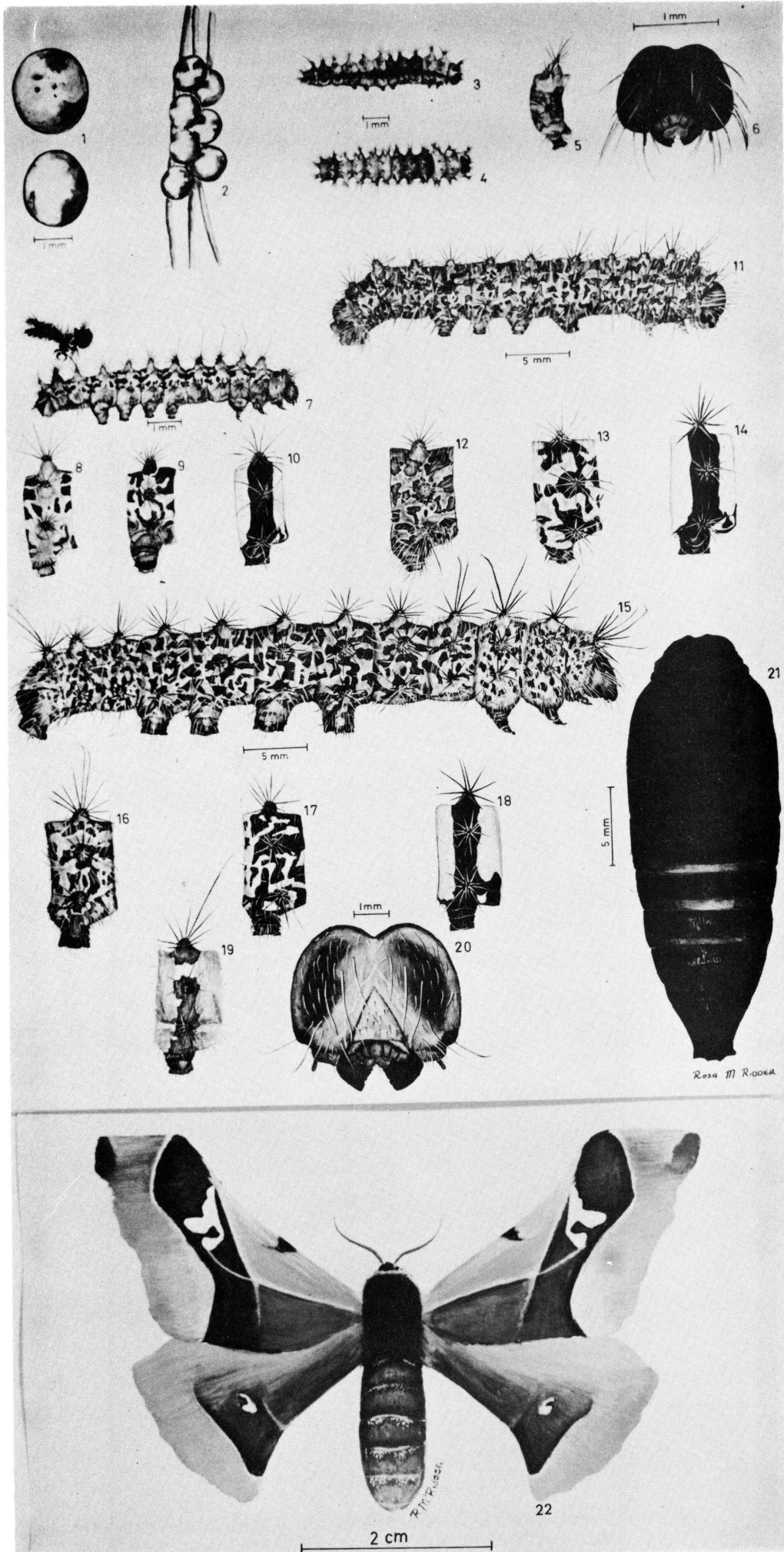


Table 39: Lengths, widths and heights of 34 pine-bark emperor eggs in mm

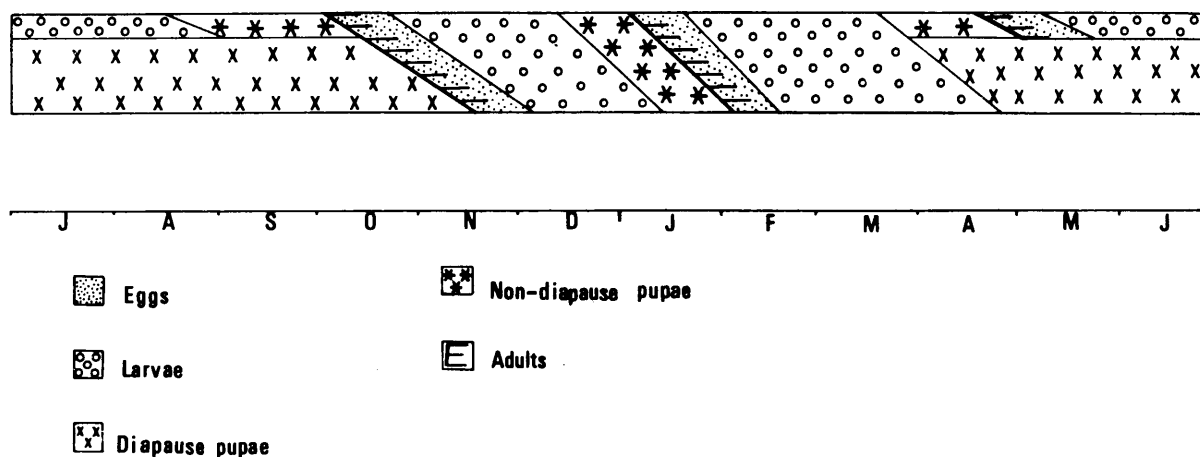
	Length	Width	Height
Min	2,13	1,88	1,63
Max	2,38	2,25	1,81
Aver	2,28	2,01	1,75

The eggs are creamy white, to which irregular strips of purple-brown adhesive substance adhere. This adhesive is originally light in colour, but darkens and hardens, glueing the eggs to the substrate and to each other. This adhesive later fades and washes off, so that older eggs sometimes appear almost cream-white. No characteristic structures appear on the egg and the micropylar area is invisible to the naked eye.

2) Oviposition and incubation period

The seasonal occurrence of the different stages and generations of the pine-bark emperor is diagrammatically represented in Fig. 37.

Fig.37: Seasonal occurrence of the different stages of the pine-bark emperor in the Keerom (Middelburg) plantation



First generation: In the field, egg laying takes place from the beginning of October to mid November. During this period eggs develop within 10-13 days.

The average temperature recorded in the plantation during 1969 was 15,5°C during October and 17,7°C during November.

Second generation: Eggs are deposited from the beginning of January to the beginning of February. The incubation period lasted from 9-12 days at an average of 19,8°C during January, and 17,8°C during February, 1970.

Third generation: Egg laying occurs from mid April to the beginning of May. These eggs were thus exposed to low temperatures, of 14,6°C during April and 10,3°C during May, 1970. They hatched after 14-20 days.

3) Egg masses

Eggs are deposited singly or in groups on pine needles, young growing branches and side branches. Eggs are usually laid next to each other, rarely on top of each other. On side branches, eggs are frequently laid on the undersurface. The number of eggs per mass found on *P. patula* needles varied from 2-8 (Plate 14, Fig. 38) and that on branches from 2-6 (Fig. 39), single eggs and pairs of eggs occurring much more frequently in both cases. Egg masses have not yet been located on broad leaved plants although larvae have been found on *Sclerocarya caffra* Sond.

Eggs apparently survive well in the field. As the eggs are often deposited on the undersurfaces of side branches, they will not be washed off easily during thunderstorms. Newly hatched larvae of *H. smilax* are very active and dislodged larvae might be able to find their way up the trees to reach the foliage.

D. The larval stage

1) General description

The larvae do not all pass through the same number of instars, the number being either four or five. Those passing through four instars cannot be readily distinguished from those passing through five. In addition, a great variation in colour forms exists, as can be seen in Plate 14. The existence of colour forms was also noted by Janse (1946).

First instar

Larvae in this instar are all very similar. The general colour on the back and

Fig.38: Number of pine-bark emperor
eggs per mass on *P. patula* needles

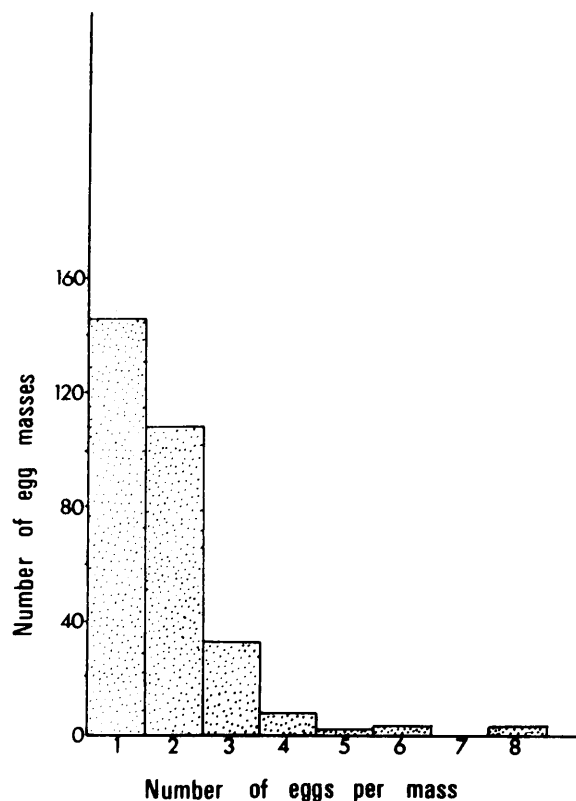
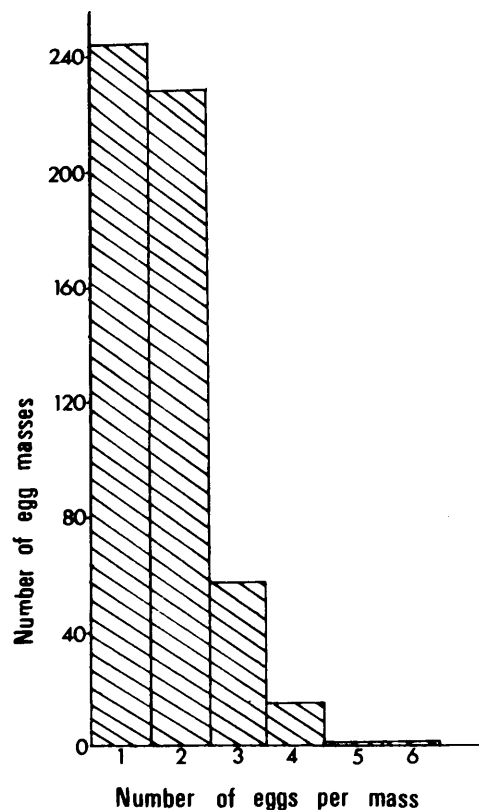


Fig. 39: Number of pine-bark
emperor eggs per mass on
P. patula branches



sides is dark to black. The third and fourth and the seventh to tenth segments are an orange-yellow dorsally. The ventral aspect is a grey-brown colour. The larvae are very hairy. With the exception of the last two segments, six seta bearing scoli are found on each segment, arranged in rows across the back and sides. On the second last segment there are five scoli and on the last segment four. The setae on the scoli and the thoracic legs are black. The length of the larva varies from 6-10 mm.

Second instar

The discarded skin of the previous instar frequently adheres to the hairs of the last few segments, and can not be pulled off without injuring the larva. Poisonous hairs, not yet well developed, appear on each scoli. The larva is from 9-19 mm long. Three distinguishable colour forms are found.

- a) **Variegated** These larvae are yellow to dark brown with black patterns

over them, often from the head down to the last segment. Frequently the larvae still have orange-yellow parts on the second and third, as well as on the seventh to tenth segments. It is mainly the scoli on these segments that are yellow with black patterns in between. The other scoli are black.

b) **Yellow-variegated** The ground colour is yellow and the scoli black. More or less square shaped black flecks are visible around the scoli. The spots on the same segment are joined with narrower black lines. Narrow black lines also occur between scoli of different segments, and between other black spots further away from the scoli.

c) **Yellow and black-zebra** The ground colour of these larvae is yellow, while the scoli and a thin connecting area between scoli of the same segment are black, forming black rings right around the body.

Third instar

The old larval skin does not adhere to the larva as in the second instar. The length of the larvae varies from 19-36 mm. From the variegated colour form of the second instar, two forms develop:-

a) **Purple-variegated** This is the most common colour form during this instar. The larvae are purple-brown, alternated with blue-green. The pattern is much the same from the first to the last segment.

b) **Orange and black-zebra** These larvae are orange with the scoli and a thin connecting area between the scoli of the same segment black (as depicted for the fourth instar in Plate 14).

Two other colour forms i.e. the yellow-variegated and yellow and black-zebra occur as described for the second instar. Thus four colour forms exist.

Fourth instar

The same four colour forms as described for the third are present in the fourth instar. Most larvae pupate at the end of this instar in the field. The length is from 33-72 mm.

Fifth instar

The same four colour forms found in the third and fourth instars were also

present in larvae which had five instars in the laboratory. The length of the single fifth instar larva seen in the field was more or less the same as that of fourth instar larvae.

The purple-variegated form found in the third to fifth instars was also described by Packard (1914).

Poisonous hairs

All larvae, except those of the first instar, have poisonous hairs of the so called spine type (Gilmer, 1925). These hairs are present on all the scoli and cannot be retracted. They cause a burning and itching irritation to the softer parts of the skin, persisting for up to two days. They do not usually break off, but merely prick the skin. When driven deeper into the skin they may however break off and remain in the skin, resulting in more acute irritation over a longer period. No additional ill effects of these hairs have so far been reported.

2) Key to the larval instars

- | | | |
|----|---|--------------------------|
| a) | The second, third and seventh to tenth segments an unpatterned yellow | First instar |
| | If yellowish, these segments are patterned | b |
| b) | Shed skin of the previous instar adhering to last few segments | Second instar |
| | Shed skin of the previous instar not adhering to larva | c |
| c) | Yellow hairs absent from the first, second and the last segments | Third instar |
| | Yellow hairs present on the first, second and the last segments | Fourth and fifth instars |

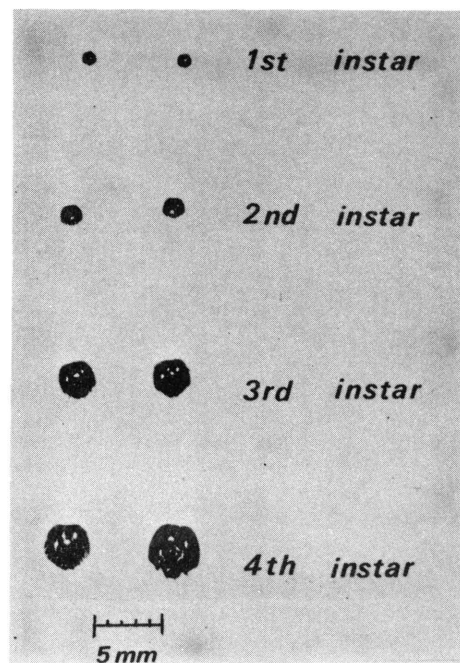
3) Head capsule widths

Head capsule widths of 30 field bred larvae of the first to fourth instars were determined with the aid of a micrometer ocular. The results are given in Table 40, while head capsules of the various instars are depicted. in Plate 15.

Table 40: Head capsule widths of the different larval instars of the pine-bark emperor (30 individuals of each instar measured)

Instar	Width in mm			Increase per instar (\bar{x})
	Min	Max	Aver	
1	1,13	1,25	1,19	—
2	1,69	1,88	1,77	1,49
3	2,69	3,06	2,87	1,62
4	3,75	4,63	4,30	1,50

Plate 15: Head capsules of the first to the fourth instar of pine-bark emperor larvae



From this table it is clear that there are definite differences between head capsule widths of successive instars, increasing from 1,49–1,62 times per instar, slightly more than the 1,4 times laid down in Dyar's law. In the field, usually only four instars are found, whereas five instars are frequently completed in the labora-

tory. The head capsules of laboratory reared larvae are noticeably smaller than those occurring naturally in the field.

4) Time of occurrence

The seasonal occurrence of the different larval generations can be found from Fig. 37.

First generation Hatching takes place from the end of October to the beginning of December and pupation from the end of December to the end of January.

Second generation Larvae hatch from the end of January to the end of February. The first larvae start to pupate from the middle of March to the end of April. A small number take much longer to complete their development, namely till the beginning of June.

Third generation Larvae of this generation are exposed to very low temperatures, and consequently take exceptionally long to complete their development. Eggs hatch during May and development can be prolonged until mid August and the beginning of September.

5) Larval behaviour

The unhatched larva gnaws an irregular hole through the egg shell, and crawls through this opening which is just large enough for its head to pass through. The larva often feeds on the remaining egg shell, consuming either a part of, or almost the whole egg shell. The larvae are very active and positively phototactic; they consequently move to the periphery of the tree where young developing needles will be found. During the first instar the larvae are slightly gregarious, but later instars are seldom found together.

As indicated for the other two species of emperor larvae, the feeding habits of the pine-bark emperor must originally have been adapted to broad-leaved trees. On broad leaves the larvae move forward to reach the edge of the leaf. On pine needles they probably try to do the same, but as the needles do not offer as firm a substrate, they do not move to the tips of the needles.

First instar larvae crawl forward and feed heads down, near the tips of the pendulous *P. patula* needles. Small pieces are severed, the larvae moving backwards

as the needles are consumed. The feeding habits of all other instars are practically the same, but as these larvae are larger and heavier they feed closer to the base of the needles and sever larger needle tips. Larvae in instars three and four occasionally move forwards on groups of needles, and can then feed near the tips. Pine-bark emperor larvae can apparently not bend the pine needles as described for the other two species.

The larvae crawl about considerably, frequently feeding at various different sites during the same instar. In dense populations it has often been noticed that larvae in the third and fourth instars climb down 20 m high trees that have been partly or completely defoliated. They then crawl about on the ground until a tree is again encountered, which they then ascend.

Disturbed larvae have the habit of curling themselves up in spirals, thus protecting themselves with their poisonous hairs.

6) Moulting

The preparations for moulting and the actual moulting process agree with those described for the pine emperor. The old larval skin is apparently not eaten by the newly moulted larva. The preparation for, and the moulting process itself take from 1,5–3 days during summer, and up to six days during winter.

7) Needle drop and production of frass

Needle drop and frass production during the different instars were studied on 10 young pine trees with cloth funnels around them.

The frequencies of different lengths of apical needle tips severed during the different instars are shown in Fig. 40. First and second instar larvae mainly sever 20 mm of the distal ends of needles. Larvae in the third instar waste tips of about 50 mm, while those in the fourth instar sever bits 40-100 mm long. This means that more advanced larvae waste larger pieces.

The average lengths of apical and middle sections severed by each instar are given in Table 41.

Assuming that the average needle is 190,5 mm long and that no needle is completely devoured, the percentage of the total needle length wasted can be calculated as shown in this table. From this table it can be seen that fourth

Fig. 40: Number and length of needle tips severed by pine-bark emperor larvae in the different instars

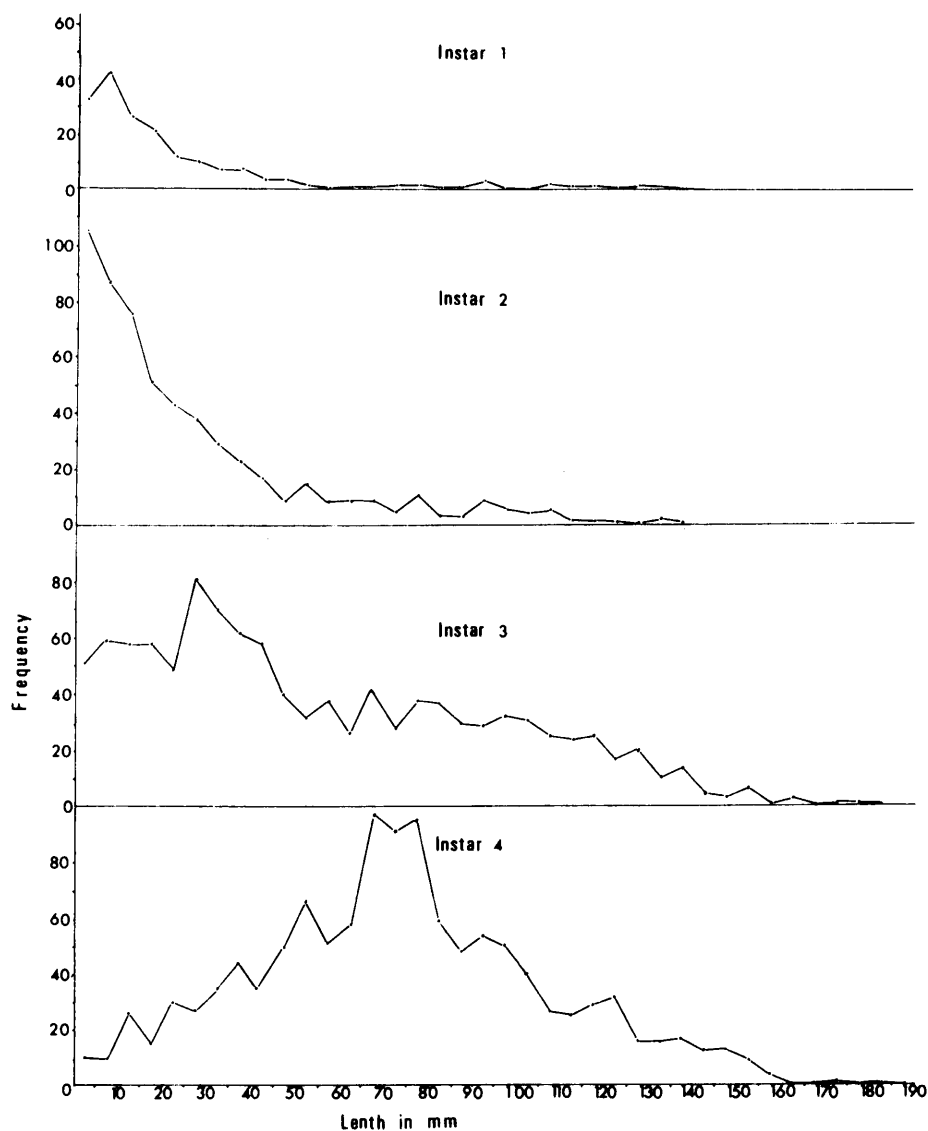


Table 41: Average lengths and relative numbers of apical and middle sections severed by different larval instars of the pine-bark emperor and percentage of total needle length wasted

Instar	Apical sections		Middle sections		% of the totale needle length wasted $= \frac{a + \frac{n_2}{n_1} b}{190,5} \times 100$
	no n_1	Average length in mm = a	no n_2	Average length in mm = b	
1	181	22,1	49	11,6	13,2
2	582	28,0	302	14,4	18,6
3	1 110	56,5	526	14,0	33,1
4	1 197	73,9	808	21,0	46,2
Percentage needle length wasted by all instars combined					44,8

instar larvae are by far the most destructive feeders, wasting almost half of the total food supply.

The number of needles severed and frass pellets produced for each instar are summarized in Table 42.

From this table it can be seen that the severed sections increased from 6,6--12,0 times per instar. This means that they become progressively more wasteful feeders. The number of frass pellets increased between 1,3 and 1,9 times per instar.

During its whole larval period, one pine-bark emperor larva severs 1 727 needle tips, and wastes 44,8 per cent of the needles. The pine emperor larva severs 2 573 tips and wastes 47,7 per cent of the needles, while the figures for the poplar emperor are 2 132 tips and 43,7 per cent respectively. It is therefore clear that, of the three species, the pine emperor causes the most and pine-bark emperor the least damage per individual.

The lengths and widths of 30 frass pellets produced every alternate day during each instar, are given in Fig. 41a and b, while the frass pellets of the different instars are depicted in Plate 16.

From Fig. 41a it can be seen that the lengths of the frass pellets of one instar overlap those of the previous or the next instar. There was no such overlapping of the frass pellet widths of the different instars, (Fig. 41b). It is thus clear that frass pellet widths can be used to determine the instars present at a particular time.

8) The influence of the average daily temperature on food intake

The average daily temperature has a positive influence on the number of needles severed and frass excreted. Fig. 42 shows that more needles are severed and more frass produced at a higher than at a lower temperature.

9) Food requirements

Larvae of the pine-bark emperor can be bred much more easily in the laboratory than the other two species. Of 59 larvae bred on *P. patula*, 31 pupated normally. The moths developing from these pupae mated and produced normal offspring.

Table 42: Needle sections severed and frass pellets produced per pine-bark emperor larva in the different instars

Instar	n	Number of needle sections dropped			No of frass pellets produced	Increase per instar	
		Apical sections	Middle sections	Total		Needles	Frass
1	140	2,9	0,8	3,7	171,1	—	—
2	112	20,6	10,6	31,2	225,6	8,4	1,3
3	67	138,7	65,7	204,4	282,9	6,6	1,3
4	36	1 564,5	888,2	2 452,7	540,6	12,0	1,9
Total		1 726,7	965,3	2 692,0	1 220,2		

Fig. 41: Lengths and widths of 30 frass pellets produced every alternate day during each instar by pine-bark emperor larvae

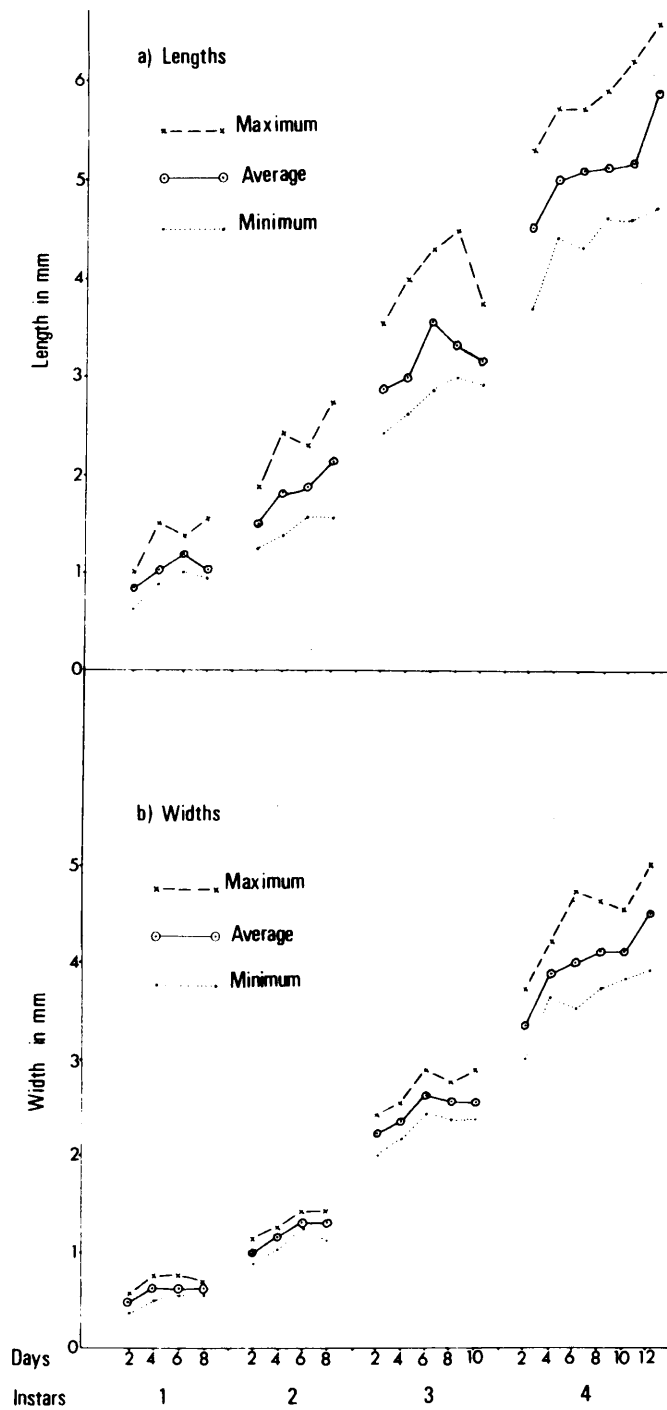


Plate 16: Frass pellets of the first to the fourth instar larvae of the pine-bark emperor

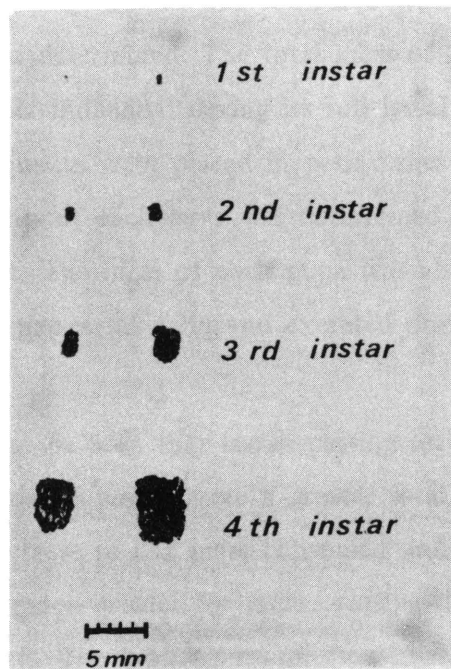
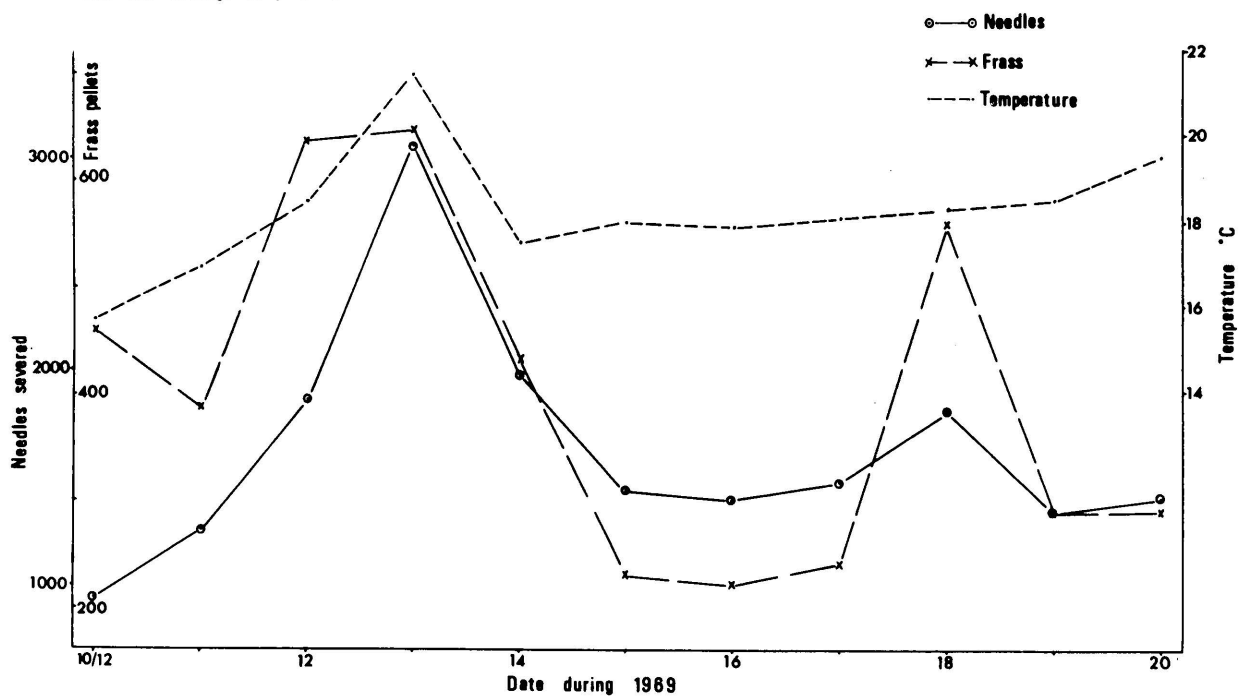


Fig. 42: Total number of needles severed and frass pellets produced per day by 14 pine-bark emperor larvae (final instar), and the average daily temperature



The masses of needles ingested and frass excreted were determined as follows: Two groups of *P. patula* needles with the same mass were placed in separate petri-dishes. One of these groups served as a control, while the other was fed to larvae in the different instars. After the larvae had consumed part of the food provided, the dry mass of the remaining needles was compared with that of the control. The mass of the frass was also determined. The total mass of needles ingested and frass excreted per instar and per individual during its full larval life could thus be obtained. Larvae ready to pupate were placed in petri-dishes containing paper torn into small shreds. The mass of each larva was determined shortly after emergence and also after each moult. The mass of each pupa was also determined after being sexed. The average dry masses taken in and excreted during the different instars are shown in Table 43.

From Table 43 it can be seen that larvae passing through five instars consume a greater total mass of needles and excrete a greater total mass of frass than those with four instars. The increase in dry mass consumed and excreted from the third to the fourth instar was much greater for larvae passing through four than for those passing through five instars. The largest consumption increases per instar appeared from the penultimate to the last instar (third to fourth instar for larvae with four, and fourth to fifth for larvae with five instars). The dry mass consumed during the third instar was more than twice as much for larvae with four than for larvae with five instars. From the dry mass consumed during the third instar one would be able to predict whether a larva will pass through four or five instars.

Larvae in the field generally have only four instars. As the larvae that were bred in the field and in the laboratory were all obtained from the same group of field collected eggs, the difference in the number of instars probably results from changed conditions prevailing in the laboratory. Larvae on growing pine needles generally obtain food in a fresher state than those in the laboratory fed on picked needles, even though kept as fresh as possible by inserting their scale leaves in water. It may therefore be concluded that it is during the third or even earlier instars that the number of moults is determined.

It is further noticeable that a greater proportion of females than males had five instars i.e. about 66 per cent in contrast to 50 per cent. It was found with *Pachypasa capensis* L. (Lasiocampidae) that females also had more instars than males (Van Dyk, 1969).

Table 43: Dry masses of *P patula* needles ingested and frass excreted by the different larval instars of the pine-bark emperor in mg (M = Male, F = Female)

Instar	Sex	No of instars in life cycle	n	Needles ingested			Increase of a per instar	Frass excreted			Increase of b per instar	Dry mass utilized (Difference between a and b) = c	Increase of c per instar	Digestion coeff = $\frac{c}{a} \times 100\%$
				Min	Max	Aver = a		Min	Max	Aver = b				
1	M+F	4+5	34	28,9	42,9	32,8		25,3	35,3	26,2		6,6		20,0
2	M+F	4+5	31	82,1	203,1	142,6	4,4	65,9	154,6	113,8	4,3	28,8	4,4	20,2
3	M	4	6	656,6	823,2	734,8		496,2	600,8	574,5		160,2		20,9
	F	4	6	850,5	1082,4	967,5		639,4	885,1	772,4		195,2		
	M+F	4				851,2	6,0			673,5	6,9	177,7	6,2	
	M	5	6	176,6	418,8	292,4		149,5	369,4	244,9		47,5		
	F	5	13	167,4	756,8	347,7		135,0	387,6	284,5		63,2		
	M+F	5				320,1	2,2			264,7	2,3	55,4	1,9	
4	M	4	6	3766,9	7082,7	5234,1		3015,9	5129,8	4064,3		1169,9		22,2
	F	4	6	6163,5	9818,1	7174,1		4811,0	7500,9	5590,7		1583,4		
	M+F	4				6204,1	7,3			4827,5	7,2	1376,6	7,7	
	M	5	6	583,3	1576,1	986,3		500,2	1321,0	823,0		163,2		
	F	5	13	965,9	1730,6	1222,9		689,4	1296,5	964,9		258,0		
	M+F	5				1104,6	3,5			894,0	3,4	210,6	3,8	
5	M	5	6	3669,8	7038,1	5418,5		2824,9	4775,8	4371,3		1047,2		21,5
	F	5	13	7066,8	9873,8	8285,8		5608,5	7257,0	6384,4		1901,5		
	M+F	5				6852,2	6,2			5377,8	6,0	1474,3	7,0	
T	M	4	6			6144,3				4778,8		1365,5		22,0
	F	4	6			8317,0				6503,1		1813,9		
	M+F	4				7230,7				5641,0		1589,7		
T	M	5	6			6872,6				5579,2		1293,4		21,0
	F	5	13			10031,8				7773,8		2258,1		
	M+F	5				8452,2				6676,5		1775,7		

The average percentage of moisture in *P. patula* needles was 65,1 per cent during this experiment.

To complete larval development, the following masses of *P. patula* needles are ingested by the pine emperor, poplar emperor and pine-bark emperor (with five instars): 18 745; 13 323, and 8 452 mg, their digestion coefficients being 22,8 , 17,1 and 21,0 per cent respectively. This indicates that the pine emperor ingests about one and a half times as much as the poplar emperor, and twice as much as the pine-bark emperor. The percentage utilisation of *P. patula* needles was highest for the pine emperor and lowest for the poplar emperor.

The following digestion coefficients have been recorded: *Bombyx mori* L.: 24 per cent (Peligot, 1867 according to Trager in Roeder, 1953); *Prodenia eridania* Cram: 48,5 per cent (Crowell, 1941); *Agrias urticae* (L.) 25,7 per cent; *Malacosoma neustria* (L.): 34,0 per cent; *Phalera bucephala* (L.): 35,0 per cent and *Pieris brassicae* (L.): 36,3 per cent (Evans, 1939). The digestion coefficients of all three emperor larvae studied here are considerably lower than those of these other lepidopterous larvae, yet comparable with those of at least some of these other species.

The live mass of larvae is provided in Table 44.

Female pupae with four instars attained a smaller mass than those with five instars, while the mass of males with four or five instars was practically the same. The live mass increase per larval instar was in all cases much higher for larvae with four than for those with five instars. The increase from the first to the second instar was highest, while it was the lowest from the final instar (fourth or fifth instar) to the pupal stage. This is probably attributable to absorption of moisture during the first instar and loss of moisture during pupal formation.

10) Duration of larval development

a) In the laboratory

Under fluctuating conditions in the laboratory, larvae completed their develop-

Table 44: Live mass of pine-bark emperor larvae bred on *P. patula* shortly after hatching or moulting (M = Male; F = Female)

Instar	Sex	n	No of instars	Mass in mg			Live mass increase per instar
				Min	Max	Aver	
1	M+F	31	4 & 5	2,9	3,5	3,3	—
2	M+F	31	4 & 5	19,0	31,2	26,3	7,9
3	M	6	4	93,2	107,3	100,6	—
	F	6	4	117,0	131,7	123,4	—
	M+F		4			112,0	4,3
	M	6	5	46,0	76,4	64,5	—
	F	13	5	63,9	113,1	78,6	—
	M+F		5			71,5	2,7
4	M	6	4	570,6	715,4	638,6	—
	F	6	4	615,4	829,6	707,0	—
	M+F		4			672,8	6,0
	M	6	5	201,8	302,2	244,6	—
	F	13	5	191,5	446,2	326,8	—
	M+F		5			285,7	4,0
5	M	6	5	483,0	870,9	687,6	—
	F	13	5	963,2	1562,4	1185,8	—
	M+F		5			936,7	3,3
pupa	M	6	4	961,0	1400,0	1156,5	—
	F	6	4	1668,7	2322,9	1868,8	—
	M+F		4			1512,6	2,2
	M	6	5	980,6	1428,8	1151,2	—
	F	13	5	1912,8	2545,2	2202,6	—
	M+F		5			1676,9	1,8

ment in either four or five instars. The duration of the larval instars, together with average temperatures recorded by a thermograph in the laboratory, can be found in Table 45.

Table 45: Duration of the larval instars of the pine-bark emperor fed on *P. patula* needles and average temperatures recorded in the laboratory (M = male; F = female)

Instar	Sex	n	No of instars	Duration in days			Aver temp in °C
				Min	Max	Aver	
1	M+F	11	4 & 5	9	17	13,0	18,7
	"	6	4 & 5	10	15	11,7	19,9
	"	16	4 & 5	8	13	9,4	22,0
2	M+F	5	4 & 5	9	13	11,0	20,9
	"	7	4 & 5	7	12	8,9	21,1
	"	10	4 & 5	7	16	9,4	23,4
	"	5	4 & 5	6	9	7,8	23,6
3	F	1	4	10	10	10,0	21,1
	M	2	4	8	9	8,5	21,7
	F	1	4	8	8	8,0	
	M+F		4			8,3	
	M	4	4	6	10	8,8	23,3
	F	4	4	9	14	10,3	
	M+F		4			9,5	
	F	3	5	7	8	7,3	21,1
	M	3	5	6	7	6,3	21,7
	F	8	5	5	9	6,1	
	M+F		5			6,2	
	M	3	5	5	8	6,7	23,3
	F	2	5	6	7	6,5	
	M+F		5			6,6	
	4	M	3	4	10	11	10,3
F		3	4	11	12	11,7	
M+F			4			11,0	
M		3	4	10	11	10,3	21,7
F		3	4	10	13	11,7	
M+F			4			11,0	
M		3	5	5	13	8,7	21,1
F		7	5	6	9	7,5	
M+F			5			8,1	
M		3	5	6	7	6,3	21,7
F		6	5	6	12	8,5	
M+F			5			7,4	
5	M	3	5	9	20	13,3	20,9
	F	6	5	10	16	12,7	
	M+F		5			13,0	
	M	3	5	9	16	12,7	21,3
	F	7	5	9	17	11,0	
	M+F		5			11,8	
	M	1	5	13	13	13,0	23,3

Temperature is an important factor in determining the duration of the larval stage, higher temperatures speeding up development. Under fluctuating laboratory conditions at an average of about 20°C, the larval instars will probably last about 12, 12, 9 and 12 days respectively (total 45 days) for larvae with four instars and 12, 12, 7, 9 and 14 days respectively (total 54 days) for larvae with five instars. Therefore larvae with four instars are full-grown about a week sooner than those with five. The developmental period of the two sexes did not differ noticeably.

b) In the field

Observations on the duration of the larval instars were made in a plantation on growing pine trees during October, 1969 to January, 1970. Under these conditions 36 larvae completed their development in four instars, while only one completed it in five. The duration of the larval instars together with the average prevailing temperatures are summarized in Table 46.

Table 46: Duration of the larval instars of the pine-bark emperor feeding on growing *P. patula* trees under fluctuating field temperatures

Instar	n	Duration in days			Average temperature in °C
		Min	Max	Aver	
1	47	7	12	8,4	16,4
	11	9	14	10,0	16,7
	32	6	10	8,4	17,2
	40	6	9	8,0	19,7
2	43	8	15	9,9	17,5
	55	7	11	8,9	17,7
	14	7	9	8,6	19,1
3	8	10	13	12,3	17,7
	36	8	11	9,1	17,8
	16	7	10	8,3	17,8
	7	8	10	8,9	18,5
4	12	11	27	16,5	16,5
	8	14	19	15,6	18,1
	16	13	28	19,7	18,4
5	1	16	16	16,0	19,4

In the field, instars one to four would probably last about 8, 9, 8 and 18 days respectively at an average temperature of about 18°C. During the first generation, the average monthly field temperatures (1969/70) from October to January, were 15,5; 17,7; 18,3 and 19,8°C respectively. Under these conditions the larval stages lasted from 50-70 days. During the second generation the average monthly temperatures for January to April were 19,8; 17,8; 17,2 and 15,3°C respectively. The larval stages then took from 48-85 days. The third generation is present during winter. The average monthly temperatures for May to September were 10,3; 8,9; 9,9; 10,4 and 14,0°C respectively. Under the prevailing conditions the larval stages lasted from 90-120 days.

Larvae of the third generation completed their cycles during 1969 and 1970. These years were not particularly cold, the minimum recorded temperatures being -1,5°C (1969) and -1,9°C (1970). Further research is necessary to determine the fate of the third generation during exceptionally cold winters.

11) Host plants

Little research has yet been done on the development of the pine-bark emperor on indigenous trees or shrubs. In the list that follows the following authors were consulted:— (a) Packard (1914); (b) Platt (1921); (c) Taylor (1946); (d) Anonymous (1970). Original observations will be indicated by “(or. obs.)”. Only the first author mentioning a food plant will be credited. Mention will also be made of the most advanced instar found on a particular plant where this is known.

a) List of indigenous host plants

Ekebergia capensis Sparrm. (b) (Is ?)

Protorhus longifolia (Bernh.) Engl. (b) (Is ?)

Rhus laevigata L. (b) (Is ?)

Rhus macowanii Schonl. (b) (Is ?)

Sclerocarya caffra Sond. (or. obs.) (Is 4)

b) List of imported exotic host plants

Jasminum pubigerum D. Don (a) (Is 4)

Pinus caribaea Morelet (d) (Is?)

Pinus patula Schlechtd. & Cham. (d) (Is 4)

Pinus radiata D. Don (or. obs.) (Is 4)

Psidium guajava L. (d) (Is?)

Psidium sp. (c) (Is ?)

Quercus sp. (Oak) (a) (Is 4)

Quercus robur L. (d) (Is ?)

Schinus molle L. (c) (Is 4)

Since this aspect of the biology has not yet been seriously studied, it is highly probable that more host plants will be discovered with further research. The larvae on *S. caffra*, were found in Pretoria, far away from any cultivated pine trees. *E. capensis*, *P. longifolia*, *R. laevigata*, *R. macowanii* and *S. caffra* may be regarded amongst the possible original host plants of the pine-bark emperor.

12) Pupation

Larvae about to pupate excrete a watery frass, then crawl down the trunks in search of suitable openings or cracks in the bark. If these can not be found on some trees, other trees may be ascended. Once suitable sites have been located, cocoons consisting of silk and pieces of bark are formed. In vertical cracks, as is usually the case on pine trees, the pupae are always orientated with heads facing upwards.

E. The pupal stage

1) Notes on diapause

Observations on second generation laboratory reared larvae that gave rise to diapause and non-diapause pupae, together with pupation dates, are supplied in Table 47.

Table 47: Number of diapause and non-diapause pupae obtained from laboratory reared pine-bark emperor larvae during autumn 1970 (M' = Male, F = Female and T = Total)

Pupation date	No. of pupae						Percentage in diapause		
	Non-diapause			Diapause			M	F	T
	M	F	T	M	F	T			
15-21/3	4	2	6	0	1	1	0	33	14
22-28/3	2	1	3	0	1	1	0	50	25
29/3-4/4	0	3	3	1	4	5	100	57	63
5-11/4	0	0	0	1	2	3	100	100	100
12-18/4	0	0	0	1	3	4	100	100	100
19-25/4	0	0	0	3	1	4	100	100	100

From this table and from general observations on pupae formed on funnelled trees, it appears that most of the pupae formed before or during the week of 22-28/3/70 did not enter diapause, while all pupae formed during or after the week of 5-11/4/70 entered diapause. From this it may be concluded that the later the date of pupation, the more pupae will enter diapause. During this time of the year the photoperiod gradually decreases while the temperature steadily drops. One or both of these factors may induce diapause (Lees, 1955). Further research is also necessary to determine what stage or instar in the development is most sensitive to the stimuli inducing diapause.

2) Description, size and sexual differences

The newly formed pupa is yellow-brown with the distal end of the wings green-brown. When the integument hardens, the colour of the pupa changes to a dull brown to black (Plate 14). The inter-segmental membranes have a smooth appearance, are soft and of a lighter brown colour. Characteristically, the colour of the ventral third of abdominal segments four to six and a small portion of abdominal segment seven is the same as that of the inter-segmental membranes. These portions are also smooth but fairly hard. Pupal dimensions are summarized in Table 48.

Table 48: Average size of 100 male and 100 female pine-bark emperor pupae in mm

Sex	Length			Width		
	Min	Max	Aver	Min	Max	Aver
Male	21	31	26,79	7	10	8,34
Female	27	37	31,44	8	12	10,19

From this table it can be seen that female pupae are somewhat bigger than males.

Sexual differences are the same as indicated for the pine emperor. The two sexes occur in more or less equal numbers (534 males : 595 females).

3) Seasonal occurrence

The times of the year during which pupae may be present can be found in

Fig. 37. The first summer generation pupates from the end of December to mid January, and the resulting adults emerge from the beginning of January to the beginning of February. Larvae of the second generation pupate between the end of March and the end of April. A portion of these pupae give rise to a third generation of adults during the end of April to the beginning of May. The rest enter diapause. The third generation of larvae pupate during mid August to the beginning of September, giving rise to adults at the same time as diapausing pupae, namely from the beginning of October to the middle of November. Pupae are thus present during all months of the year with only one exception, namely March.

4) Pupal sites

Pupation takes place on the stems and branches of trees, as was found on *P. patula* and *P. radiata*, thus simplifying observations on their distribution.

Pupae may be found at any height on the trees. As there are more cracks on the lower (thicker) parts of pine tree stems, more suitable pupation sites, and thus pupae, can be found here. Pupae are however also formed in the forks between branches.

Pupae formed on *P. radiata* appear to be covered with less bark and are thus not as well protected as those formed on *P. patula*. This is probably due to differences in stickyness of the bark of the two species of pine trees.

Resistance to dehydration is well developed in the pupal stage. In the laboratory, adults emerge normally from pupae kept in open containers, exposed to relatively low humidities.

F. The adult stage

1) General description

In comparison with the other two species of emperor moths, the adults are relatively small with wing spans of up to 86 mm (Plate -14). The ground colour is orange-red to purple maroon-brown. The wings possess small scaly hairs, but long hairy scales appear near the base and lower edges. The wings are roughly divided into thirds by two bands of a lighter red or purple-brown shade running more or less parallel with the outer edge. The middle third of each wing is considerably darker than the outer parts and possesses a clear transparent eye spot. The eye spot

on the forewing has three lobes. The spot on the hindwing of the females has two lobes; usually single lobed spots are found on the hindwings of males. The transparent spots are each surrounded by two rings, displaying a darker and a lighter shaded line of the ground colour. The basal third of the forewing is divided lengthwise into two differently coloured areas. The top half is greyish to a lighter shade of the ground colour, while the bottom part is darker and more or less the same colour as the middle third. On both wings and the body, small irregularly scattered white spots occur. The head, dorsal side of the thorax and abdomen are the same colour as the ground colour i.e. orange-red to purple maroon-brown, while the ventral aspects of the thorax and abdomen are frequently of a slightly lighter shade. Directly behind the head there is a light grey portion changing gradually to a dirty white. In the male, the antennae are proximally grey and distally light brown, while they are light brown in the female. For a taxonomic description, see Westwood (1849).

2) Sexual dimorphism and size

The sexes can be distinguished by structural differences in the antennae and the shape of the forewings. The antennae of the male are broadly bipectinate at the base while the distal halves are almost filiform, whereas those of the female appear longer and are almost filiform or slightly serrated. The apex of the forewing of the male is extended to a noticeable round tip, whilst that of the female is not extended and is sharper.

The wing spans of field collected moths vary from 67-86 mm for 30 females (average 78,3 mm) and from 52-59 mm (average 56,1 mm) for 30 males.

3) Seasonal occurrence

The time of appearance of adults was determined by direct counts in a plot of 0,856 ha in the plantation. Counts were made weekly at about 1700 hours.

Three generations of adults are found per year. The first and second generations occur in much larger numbers than the third. The months of the year during which adults may occur can be seen in Fig. 37. The first generation of adults emerges from the beginning of October to the middle of November, the second from the beginning of January to the beginning of February and the third from mid April to mid May. Adults live for up to 13 days in the laboratory, and

probably about as long in the field; adults may therefore be present in the field for about one to two weeks after the last ones have emerged. Adults can therefore be found during six months of the year, i.e. October, November, January, February, April and May.

4) Emergence

Emergence was studied in 30 plots, measuring 2,7 x 91 m each, in a continuous block. The observations started at 0600 hours on the 20th October, 1969, and lasted for a continuous period of 48 hrs. Freshly emerged adults were marked by means of a card fixed to the tree trunk. On this card records were made of the date and time it was first seen, when the wings were fully expanded or hardened and when it flew away. Emergence was also studied more intensively in the laboratory. Field collected pupae were placed in open petri-dishes, and were examined every quarter of an hour from 0600 to 1800 hours each day for two weeks. The adults that emerged, were allowed to crawl up a rough wall.

When emergence begins, the pupal shell splits open along the posterior margin of the wings and the third thoracic segment, while a transparent liquid is secreted through the mouth. The adult then crawls out of the pupal shell, and secretes a whitish liquid through the anus. The transparent liquid moistens the cocoon, and might help to dissolve adhesives on the silk. The adult crawls out of the cocoon and a short distance up the tree trunk. It settles in a vertical position with the wings and body hanging vertically downwards. Data on the time of day that adults emerge from their cocoons have been summarized in Fig. 43, and the statistical analysis in Table 49. Free-hand curves were drawn from the points plotted.

From this fig. it can be seen that emergence takes place from 0800 to 1700 hours, with peaks between 1100 and 1400 hours for both females and males. It seems that males emerge slightly earlier than females, but no significant difference could be found (Table 49).

Data on the time taken for adults to expand their wings can be found in Table 50 and the statistical analysis in Table 51.

From Table 50 it can be seen that the wings usually enlarge and attain their full size within about 26 – 40 min. From Table 51 it can be concluded that females take highly significantly longer to expand their wings than males. At this

Fig.43: Time of emergence of pine-bark emperor adults in the field

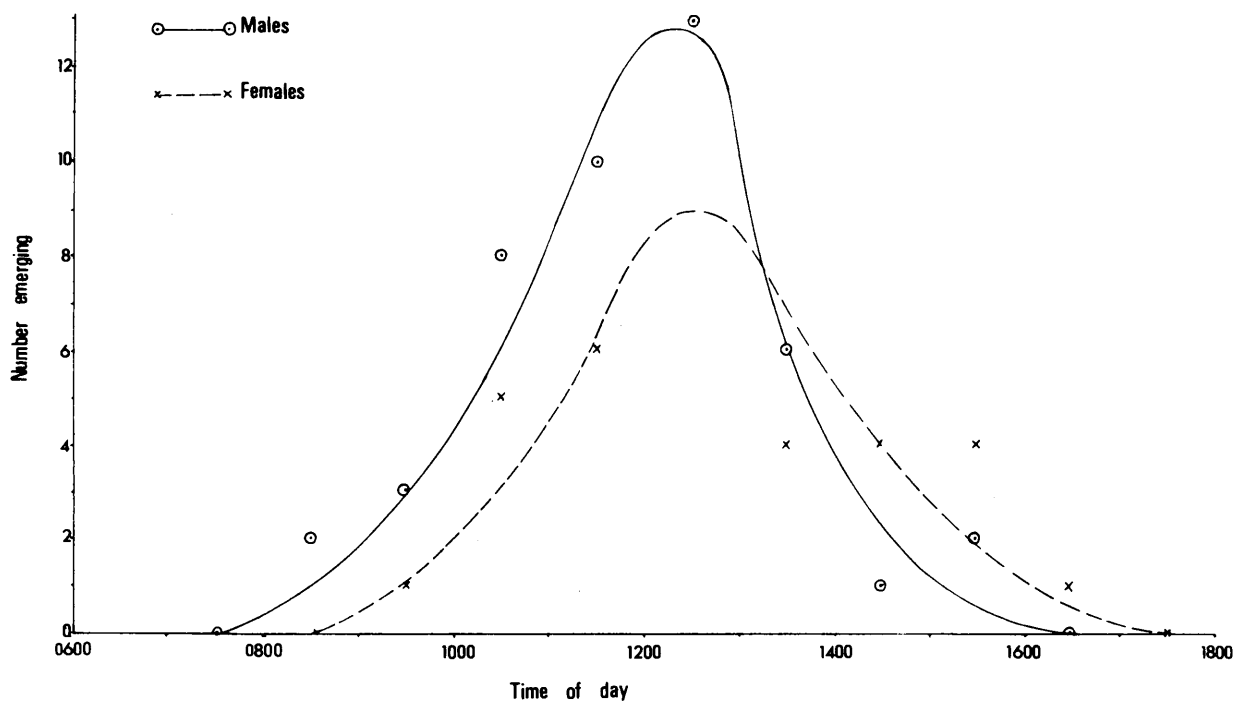


Table 49: Statistical analysis of data in Fig. 43

	Males	Females	
Before 1300 hours	36	21	57
After 1300 hours	9	13	22
	45	34	79

Continuity correction was applied

$$X^2 = 2,36^-; X^2_1 (,05) = 3,84$$

stage the wings are not yet fully hardened, being kept suspended against each other. Subsequently the wings harden and dry within average periods of 59 and 53 min for males and females respectively. The wings are then folded against the body.

Table 50: Time elapsing from emergence until the wings are fully expanded

Time in minutes	Number of adults		Total
	Males	Females	
16 - 20	1	0	1
21 - 25	6	1	7
26 - 30	7	3	10
31 - 35	9	11	20
36 - 40	5	11	16
41 - 45	0	8	8
46 - 50	0	7	7
51 - 55	1	2	3
56 - 60	0	0	0
61 - 65	0	4	4
66 - 70	0	0	0
71 - 75	0	1	1

Table 51: Statistical analysis of data in Table 50

	Males	Females	
Less than 35 min	23	15	38
More than 35 min	6	33	39
	29	48	77

Continuity correction was applied

$$X^2 = 14,8^{**}; X_1^2 (,01) = 6,63$$

5) Sexual attraction and copulation

Sexual attraction and mating were studied by placing unmated females, which developed in the laboratory from field collected pupae, in pairs in 10 gauze cages

in the plantation. This was done for five successive nights at 1700 hours on the same day that emergence took place. Males which were attracted to five of these cages, were counted and removed hourly. Males attracted to the other five cages were let in to mate.

After the wings have hardened, the females stay at the same site until dusk. They then fly to reach perches higher in the trees, from where sexual attraction takes place. Sexual attraction commences shortly after dusk, usually from 1700 to 2000 hours. The abdominal segments are then extended in the same manner as described for the pine emperor, and the two scent glands are exposed. As soon as mating commences, the extended abdominal segments are retracted and the scent glands withdrawn.

In cages placed in the field, mating commences between 1700 and 1845 hours (11 matings). The duration of mating is variable; in seven matings it was observed to last 80 min to 4 hrs, in one mating 10 hrs; and in three others 23 hrs. Mating is usually terminated at dawn or dusk. It was further noticed that about one third of the females did not expose their scent glands to attract males the first night after emergence, but only on the second night.

6) Flight activity

Shortly after dark, females fly away from the site of emergence (before 1900 hours on 20/10/69) and males about half an hour later (1920 hours). All seem to be heading for the crowns of the trees.

An experiment with ultra-violet light was carried out to determine the time of flight activity. The results of this experiment are supplied in Fig. 44 and the statistical analysis in Table 52.

From Fig. 44 it can be seen that the adults fly early in the evenings, with a peak between 1900 and 2100 hours. No significant difference was found between the times of activity of males and females.

7) Oviposition

As first instar larvae of *H. smilax* are very active, the actual site where the

Fig. 44: Total number of pine-bark emperor adults caught at an ultra-violet light trap during one week when the population was high

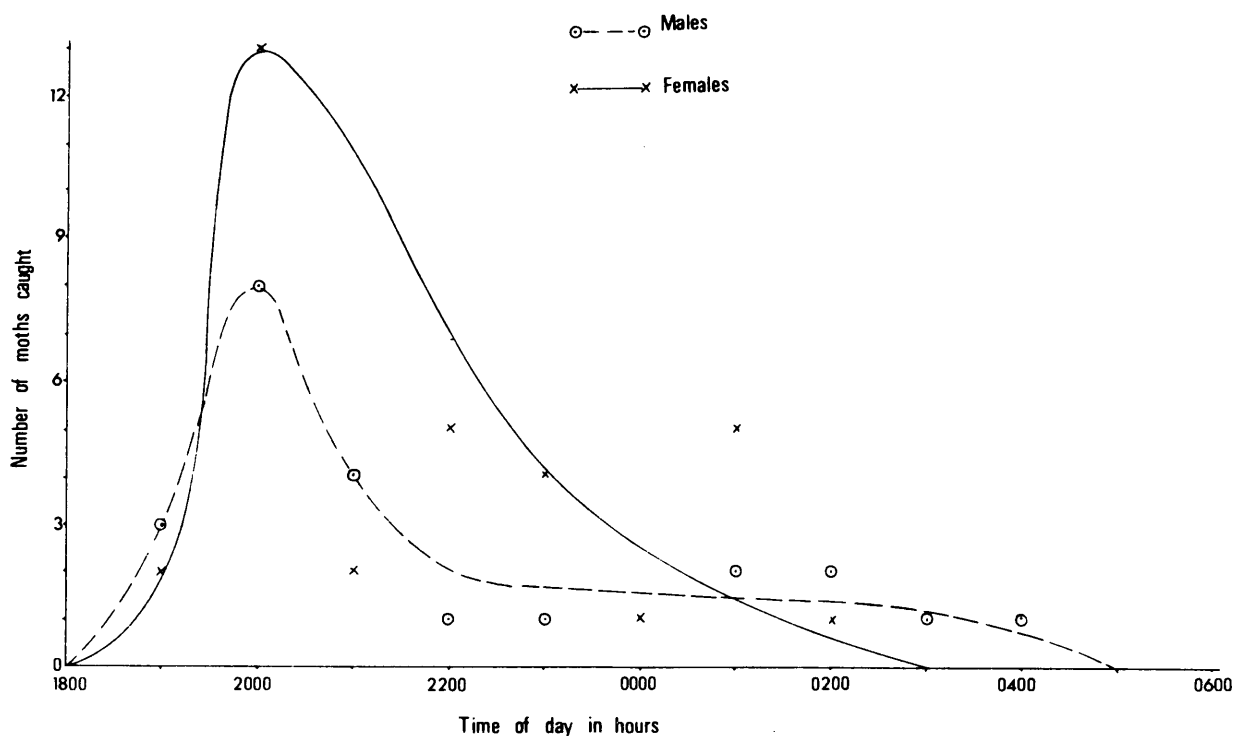


Table 52: Statistical analysis of data in Fig. 44

	Males	Females	
Before 2100 hours	11	15	26
After 2100 hours	12	18	30
	23	33	56

Continuity correction was applied

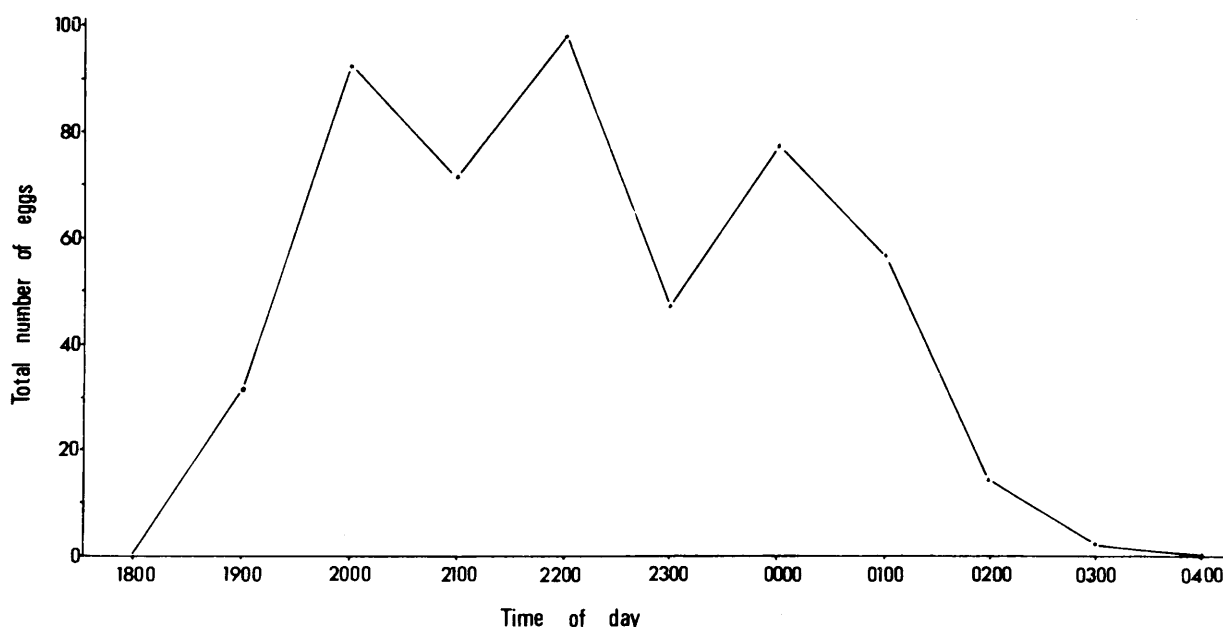
$$X^2 = 0,02; X^2_1(,05) = 3,84$$

eggs are laid is not very critical. Eggs are frequently laid on the lower surfaces of side branches up to about 4 m from edible foliage, or on pine needles. They may also be deposited on stems, dead branches or grass, but this is exceptional.

Plants such as *P. patula*, *P. radiata* and *Schlerocarya caffra* are the most usual host plants.

The time of egg laying during the night was determined by placing 15 females found mating in the plantation in separate cages. The eggs laid were marked every hour, and the number recorded for each female. Observations were also made in cages where copulation was studied. The data have been summarized in Fig. 45.

Fig.45: Number of eggs laid per hour by 15 pine-bark emperor females



From this fig. it can be seen that, in cages, oviposition begins shortly after dark (1900 hours), and continues until approximately 0300 hours, the peak period being from 2000 hours to about midnight. Oviposition usually commences during the same night that mating has taken place.

The heights at which eggs are laid in trees were determined by chopping down 10 trees and recording the distance of each egg mass from the tops of the trees. The results can be found in Table 53.

From this table it can be seen that very few egg masses could be found in the top 2 m of the crown, the number in these 2 m sections together being approximately half that found in the separate metre sections lower down the tree. With the exception of the tops of the trees and the stems, the eggs appear to be deposited more or less randomly at all heights. This distribution is probably due to

Table 53: Heights at which pine-bark emperor eggs were found in 10 *P. patula* trees

Distance from the top in m	Number of egg masses
0-1	4
1-2	45
2-3	102
3-4	105
4-5	90
5-6	86
6-7	75
7-8	77
8-9	97
9-10	82
stem	1
Total	764

the fact that more eggs are usually laid on branches than on needles.

Although more eggs can often be found on trees on the outskirts of plantations, this is not invariably the case. It has frequently been observed that certain trees may be totally defoliated while other trees next to them still possess more than 50 per cent of their leaves. This is especially noticeable during periods when the population is at a low level, indicating a weak dispersal power of the female.

8) Number of eggs and larvae per female

The average number of eggs laid by 71 females emerging from pupae collected from the field was 119 (ranging from 75-172). Of 478 eggs collected from *P. patula* shortly after oviposition (October and November, 1969), 91,8 per cent developed, the rest being inviable (no egg parasites could be found). The average number of larvae per female can therefore be calculated at about 109.

G. Climatic factors influencing population density

This species appears to be well adapted to the conditions in pine planta-

tions. Eggs which frequently occur on the underside of side branches are not easily washed off by rain. As the larvae are very active, many of those developing from the few eggs washed off by rain may ascend the trees and reach the foliage. Pupae are relatively resistant to dehydration. As they occur on tree trunks, the moisture content and hardness of the soil do not influence emergence.

CHAPTER 5 : STUDIES ON POPULATION DENSITIES AND DAMAGE CAUSED

A. Population density of *N. cytherea clarki*

The chief aim of this investigation was to devise a method of predicting future damage, as well as to determine the damage caused by a given population density.

Detailed studies were undertaken in three blocks, each covering 0,856 ha and containing three degrees of infestations, estimated to fall in the three categories: severe (Block A), moderate (Block B) and low (Block C). The blocks were at least 5 km apart and each population was regarded as a separate entity. The ages of the trees in Blocks A, B and C were respectively 17, 15 and 5 years during 1969.

1) Pupal counts

Procedure

At the commencement of this experiment, as well as a year and two years later, pupal counts were carried out after all larvae had pupated, but before adults had emerged.

In each Block, the number of pupae in 100 plots, each 2,5 m² (2,74 x 0,91 m) in extent, was determined by digging up each plot and replacing the pupae in their respective plots. The plots were distributed in such a way that 34 were situated against tree trunks, 33 in lanes without brushwood and 33 in lanes with brushwood.

Results

The number of pupae located every January from 1968 to 1970 in 100 plots of 2,5 m² each, is given separately for every year in Table 54. The number of pupae per surface area of 100 m² was calculated and is also provided.

According to this table, the pupal populations in Blocks A and B declined by about 50 per cent during each year. The population in Block C on the other hand, gradually increased. This increase was however noticeably lower than

Table 54: Number of pine emperor pupae per 2,5 m² plot in each of three blocks during January of each year (100 plots per block)

Block	Year	Min	Max	Average and confidence interval	Calculated number in 100 m ²
A (17 yr)	1969	0	6	2,47 ± 0,24	99*
	1970	0	4	1,40 ± 0,21	56
	1971	0	3	0,60 ± 0,15	24
B (15 yr)	1969	0	4	1,89 ± 0,19	76*
	1970	0	5	0,90 ± 0,17	36
	1971	0	3	0,51 ± 0,12	20
C (5 yr)	1969	0	3	0,86 ± 0,14	34*
	1970	0	4	0,97 ± 0,15	39
	1971	0	4	1,18 ± 0,16	47

*Pupal counts at beginning of investigations

can be expected if the biotic potential of the insect is taken into consideration.

The number of viable eggs is about 159 per female and the sex relationship is almost even. During other studies it was determined that the moth population was reduced by 65,6 and 48,1 per cent by baboons during the 1969 and 1970 seasons respectively. The effect of other predators such as monkeys and birds was calculated at about 5 per cent. Eggs may be dislodged from pine needles by wind and rain (average about 7 per cent) and parasitised by egg parasites (average 8,3 per cent). The combined effect is set at 15,3 per cent for both 1969 and 1970. The calculations of the expected number of first instar larvae are indicated in Table 55.

From this table it is clear that the number of larvae calculated per 100 m² would, under optimal conditions, have been enough to defoliate at least certain of the trees to a great extent.

2) Adult counts

Procedure

In every block, 10 plots of 91 x 2,7 m each, were laid out at regular intervals.

Table 55: Calculated number of first instar larvae originating from known populations of pine emperor pupae

Block	Year	Number of pupae/100 m ²	Percentage predatism of adults*	Remaining adults = a	Viable eggs /female = $\frac{159}{2} \times a$	Number of first instar larvae/100 m ² after 15,3% reduction of eggs**
A	1969	99	70,6	29	2 305	1 952
	1970	56	53,1	26	2 067	1 751
B	1969	76	70,6	22	1 794	1 520
	1970	36	53,1	17	1 352	1 145
C	1969	34	70,6	10	795	673
	1970	39	53,1	18	1 431	1 212

*Predatism by baboons, monkeys and birds

**Decrease as a result of parasitism and dislodging by rain and wind

The lanes in five of the plots were heaped up with brushwood while those in the other five were clean of it. Some of the adults emerging during the night can be found on the lower 2 m of tree trunks or on brushwood the next morning. All such newly emerged moths in these plots were counted once a week from the beginning of February until the beginning of May. These counts were carried out early in the mornings (0700 – 0900 hours), before predation by baboons started. It had been shown previously (Ch. 2, p., 67) that approximately two thirds of all newly emerged moths move away at dawn following the night of emergence. For this reason the counts made were estimated to reflect about one third of the total number of adults emerging in the plots during the previous 24 hours. An estimate of the total number of adults emerging in 100 m² during each season could thus be formed.

Results

The number of newly emerged adults recorded at weekly intervals in 10 plots (91 x 2,7 m) is provided in Table 56. The calculated total number of adults and the expected first instar populations are also given.

From this table it can be seen that the population in Block A was slightly denser than that in Block B, and considerably denser than that of Block C in 1969. During 1970 a decrease in the population occurred in Blocks A and B and a slight increase in Block C.

Table 56: Total number of newly emerged pine emperor adults counted once per week in 10 plots (91 x 2,7 m each) and calculated total adult and expected populations per 100 m² (W = Week)

Block	Year	February				March				April				Total for one day per week = a	Calculated total number of adults/ 100 m ² / season = $\frac{ax 100 \times 7 \times 3}{2457} = b$	Expected no of larvae /100m ² after a 15,3% reduction of eggs = $\frac{b \times 159 \times 0,847}{2}$	
		W1	W2	W3	W4	W1	W2	W3	W4	W1	W2	W3	W4				
A	1969	0	7	17	28	11	5	5	1	3	0	0	0	2	79	68	4 579
	1970	0	0	4	8	14	6	8	0	1	0	0	0	0	41	35	2 357
B	1969	1	9	18	11	21	9	4	2	0	1	0	0	0	76	65	4 377
	1970	0	1	3	5	6	10	3	1	0	0	0	0	0	29	25	1 683
C	1969	0	2	3	11	13	5	2	2	0	0	0	0	0	38	32	2 155
	1970	0	1	6	7	15	9	11	3	1	2	0	0	0	55	47	3 165

From the calculated number of adults per 100 m² (Table 56), it is clear that these numbers are approximately 20 per cent lower than the calculated number of pupae in Table 54. In one case, the number of adults was higher than the number of pupae. During other experiments it was found that pupal parasitism and predatism together amounted to about 0,5 per cent. Natural enemies were therefore probably not responsible for the lower number of adults found. It therefore appears as if the proportion of moths actually recorded was closer to a quarter than the original estimate of one third of the total daily population.

Due to the activities of various scavengers, it was unpractical to record the number of dead adults at the end of each season as was done by Tooke & Hubbard (1941) for *N. cytherea cytherea*.

3) Larval counts

Two methods were used to determine larval population densities: Counts were made, firstly, of frass pellets and needle drop, and secondly of adult larvae.

a) Counts of frass pellets

Procedure

In each of the blocks, 48 containers (48,1 x 37,7 cm and 25 cm deep) were placed out as follows: 20 containers were placed against tree trunks – five in the direction of each of the four main points on the compass; 16 were placed on the diagonal lines of four different squares each formed by four trees (four in each of the four main directions) at a distance of 1 m from the tree trunks (i.e. a quarter of the length of the diagonals); and 12 were placed on the diagonals, (three in every main direction) at distances of 1,9 m from tree trunks (i.e. just inside the point where the two diagonals cross). Thus, for every five containers against tree trunks there were four situated 1 m and three situated 1,9 m away from tree trunks. This distribution of containers relative to tree trunks was recommended by a statistician.

From direct observations made in the plantation, it was established that frass pellets dropping in the containers used (25 cm deep) did not bounce out again. Initially, cardboard boxes were used but were found to be not sufficiently durable. Containers made of milboard and painted with gloss paint proved to be ideal as they could be used for two or three seasons.

The needles and frass pellets in all containers were counted once a week. The

frass pellets in 10 randomly taken containers per block were individually compared with those produced by known larval instars. In this way the instars of larvae present in the trees could be determined, as well as in approximately what relative proportions they occurred.

An anemometer was erected in order to determine whether wind had any influence on the results.

Results

A summary of the total number of frass pellets produced by each of the larval instars during the full duration of each instar, the daily average number of frass pellets produced and the average duration of each instar as determined earlier, are provided in Table 57.

Table 57: Total number of frass pellets produced by the different larval instars of the pine emperor

Instar	Total number of frass pellets produced	Duration in days	Average number of frass pellets per day
1	169,0	19,6	8,6
2	180,2	19,8	9,1
3	210,9	19,7	10,7
4	206,3	22,1	9,3
5	257,1	29,6	8,7

The total number of frass pellets collected at weekly intervals from 48 containers per block, as well as the relative numbers of larval instars present (according to the size of the frass pellets) are provided in Tables 58 (1969) and 59 (1970).

From these tables it can be seen that more frass is produced from April till June, when many of the larvae are in the smaller instars, than later in the season.

Some of the severed needles and frass pellets landing on branches or between needles are held back on the trees. These are usually dislodged during strong winds. As a result, needles and frass from different weeks may be present in the same weekly sample or only some fraction of the weekly drop may be sampled. Over the whole larval period the effect of this screening is probably minimal.

Table 58: Total number frass pellets produced by pine emperor larvae collected weekly in 48 containers each with a surface area of 1 811 cm² in the different blocks during 1969 and calculated number of larvae in the different instars as deduced from frass pellets (Bl = Block; Is = Instar)

Week ending on	Total number of frass pellets in 48 containers = a			Relative numbers of frass pellets of the different instars in 30 containers					Calculated number of larvae per 48 x 1 811 cm ² surface area = $\frac{a}{y^*} \frac{x}{Sx}$														
									Block A					Block B					Block C				
	Bl A	Bl B	Bl C	Is 1 =x ₁	2 =x ₂	3 =x ₃	4 =x ₄	5 =x ₅	Is 1	2	3	4	5	Is 1	2	3	4	5	Is 1	2	3	4	5
29/3	216	107	27	274	0	0	0	0	25	0	0	0	0	12	0	0	0	0	3	0	0	0	0
5/4	703	432	148	349	62	0	0	0	69	12	0	0	0	43	7	0	0	0	15	2	0	0	0
12	1923	851	310	303	124	5	0	0	157	61	2	0	0	69	27	1	0	0	25	10	0	0	0
19	2333	1794	575	131	93	1	2	0	157	105	1	2	0	120	81	1	2	0	39	26	0	1	0
26	2434	2516	481	196	156	52	9	0	134	101	29	6	0	139	104	30	6	0	27	20	6	1	0
3/5	2450	3167	601	181	192	76	13	0	112	112	38	7	0	144	145	49	10	0	27	27	9	2	0
10	1817	2158	387	47	53	46	8	4	63	67	49	10	5	75	80	59	12	6	13	14	11	2	1
17	1715	1850	253	29	68	49	17	6	34	76	46	19	7	37	82	50	20	8	5	11	7	3	1
24	801	900	289	16	59	50	18	4	10	35	25	11	3	11	40	29	12	3	4	13	9	4	1
31	803	611	344	30	113	138	41	5	9	30	32	11	1	7	23	24	8	1	4	13	14	5	1
7/6	1243	1535	528	17	74	124	66	31	8	32	46	28	14	10	40	57	35	18	3	14	19	12	6
14	1028	1370	411	3	18	28	27	9	4	24	32	35	13	6	32	42	47	17	2	10	13	14	5
21	745	949	409	5	49	75	62	14	2	20	25	24	6	3	25	32	31	7	1	11	14	13	3
28	734	1122	382	10	44	68	60	23	4	17	23	23	9	6	26	35	35	14	2	9	12	12	5
5/7	679	1114	354	3	31	104	99	47	1	8	23	25	13	1	13	38	42	21	0	4	12	13	7
12	504	658	182	0	19	33	46	35	0	8	12	19	15	0	10	15	24	20	0	3	4	7	6
19	657	853	231	3	14	49	31	17	2	9	26	19	11	3	12	34	25	15	1	3	9	7	4
26	219	381	143	4	7	40	46	12	1	2	8	10	3	2	3	13	17	5	1	1	5	6	2
2/8	302	379	176	0	5	15	66	83	0	1	3	13	17	0	1	3	16	21	0	1	1	7	10
9	336	462	119	0	0	3	29	58	0	0	1	12	25	0	0	1	16	34	0	0	0	4	9
16	289	241	138	0	0	5	22	146	0	0	1	4	28	0	0	1	3	23	0	0	0	2	13
23	225	264	82	0	0	0	5	71	0	0	0	2	24	0	0	0	2	28	0	0	0	1	9
30	227	179	45	0	2	7	21	16	0	1	3	11	9	0	1	3	9	7	0	0	1	2	2
6/9	142	81	21	0	0	3	30	52	0	0	0	5	10	0	0	0	3	6	0	0	0	1	1
13	124	54	15	0	0	1	3	7	0	0	1	4	9	0	0	0	2	4	0	0	0	0	1
20	57	23	6	0	0	0	0	5	0	0	0	0	7	0	0	0	0	3	0	0	0	0	1
Total									792	721	426	300	229	688	752	517	377	261	172	192	146	119	88

* = average number of frass pellets produced per day by the different instars (see Table 57).

Table 59: Total number frass pellets produced by pine emperor larvae collected weekly in 48 containers each with a surface area of 1 811 cm² in the different blocks during 1970 and calculated number of larvae in the different instars as deduced from frass pellets (Bl = Block; Is = Instar)

Week ending on	Total number of frass pellets in 48 containers = a			Relative numbers of frass pellets of the different instars in 30 containers					Calculated number of larvae per 48 x 1 811 cm ² surface area = $\frac{a \times x}{y^* S_x}$														
	Bl A	Bl B	Bl C	Is 1 = x ₁	2 = x ₂	3 = x ₃	4 = x ₄	5 = x ₅	Block A					Block B					Block C				
									Is 1	2	3	4	5	Is 1	2	3	4	5	Is 1	2	3	4	5
28/3	128	75	142	84	0	0	0	0	15	0	0	0	0	9	0	0	0	0	17	0	0	0	0
4/4	375	208	419	317	0	0	0	0	44	0	0	0	0	24	0	0	0	0	49	0	0	0	0
11	514	363	641	297	105	0	0	0	44	15	0	0	0	31	10	0	0	0	55	18	0	0	0
18	965	572	806	209	182	17	3	0	57	47	4	1	0	34	28	2	0	0	48	39	3	1	0
25	1007	899	1002	342	319	65	12	0	54	48	8	2	0	48	43	7	2	0	54	48	8	2	0
2/5	1442	953	1514	389	365	94	23	0	75	66	15	4	0	49	44	10	3	0	79	70	15	4	0
9	2212	1188	1546	240	216	175	11	2	96	82	56	4	1	51	44	30	2	0	67	57	39	3	1
16	1801	620	817	231	270	251	120	13	55	60	48	26	3	19	21	16	9	1	25	27	22	12	1
23	2365	1329	1836	210	281	339	198	38	54	69	70	47	10	32	38	39	27	5	42	53	55	37	8
30	2100	945	1406	146	229	266	183	47	41	61	60	47	13	18	27	27	21	6	27	41	40	32	9
6/6	1669	627	934	109	190	234	158	51	29	47	49	38	13	11	18	18	14	5	16	26	28	21	7
13	2351	822	1011	125	217	301	342	95	32	52	61	80	24	11	18	21	28	8	14	22	26	34	10
20	990	373	530	21	89	252	327	80	3	13	30	45	12	1	5	11	17	4	2	7	16	24	6
27	647	207	320	37	82	125	192	73	5	11	15	26	11	2	4	5	8	3	3	6	7	13	5
4/7	616	179	269	11	75	102	181	109	2	11	12	25	16	0	3	4	7	5	1	5	5	11	7
11	945	215	329	5	44	116	172	127	1	10	22	38	30	0	2	5	9	7	0	3	8	13	10
18	534	140	282	0	33	97	214	116	0	4	11	27	15	0	1	3	7	4	0	2	6	14	8
25	345	178	234	0	38	86	105	51	0	5	10	14	7	0	3	5	7	4	0	3	7	9	5
1/8	220	191	231	0	7	20	72	115	0	1	2	8	14	0	1	2	7	12	0	1	2	8	14
8	154	140	219	0	1	7	39	58	0	0	1	6	10	0	0	1	6	9	0	0	1	9	14
15	95	139	249	0	0	3	29	72	0	0	0	3	8	0	0	0	4	11	0	0	1	7	20
22	47	126	130	0	0	0	6	50	0	0	0	1	5	0	0	0	1	13	0	0	0	1	13
29	33	99	104	0	0	0	5	47	0	0	0	0	3	0	0	0	1	10	0	0	0	1	11
5/9	17	45	53	0	0	0	0	34	0	0	0	0	2	0	0	0	0	5	0	0	0	0	6
12	3	35	58	0	0	0	2	11	0	0	0	0	0	0	0	0	1	3	0	0	0	1	6
19	0	25	40	0	0	0	0	13	0	0	0	0	0	0	0	0	0	3	0	0	0	0	5
Total									607	602	474	442	197	340	310	206	181	118	499	428	289	257	166

y* = average number of frass pellets produced per day by the different instars (see Table 57)

Taking into consideration the average duration of the different instars, and that the sampling surface was $48 \times 1\,811 \text{ cm}^2$, the number of larvae in the different instars can be calculated for 100 m^2 as indicated in Table 60.

Table 60: Calculated number of pine emperor larvae per 100 m^2 in the different blocks during 1969 and 1970

Block	Instar	Calculated total number of larvae per day/ $48 \times 1\,811 \text{ cm}^2 = a$		Duration of instar in days $= b$	Calculated number of larvae per 100 m^2 / season $= \frac{a}{b} \times \frac{100}{48 \times 0,1811}$	
		1969	1970		1969	1970
A	1	792	607	19,6	465	356
	2	721	602	19,8	419	350
	3	426	474	19,7	249	277
	4	300	442	22,1	156	230
	5	229	197	29,6	89	77
B	1	688	340	19,6	404	200
	2	752	310	19,8	437	180
	3	517	206	19,7	302	120
	4	377	181	22,1	196	94
	5	261	118	29,6	101	46
C	1	172	499	19,6	101	293
	2	192	428	19,8	112	249
	3	146	289	19,7	85	169
	4	119	257	22,1	62	134
	5	88	166	29,6	34	65

From this table it is clear that a decrease occurred in the larval populations of Blocks A and B during the two years, while the number of larvae in Block C increased. During 1969 the population was highest in Block B and lowest in Block C. During 1970 however, it was highest in A and lowest in B.

From a comparison of the number of first instar larvae calculated in Tables 60 and 55, it is clear that the number in the first mentioned table is considerably

lower than that in the latter. Although some mortality is to be expected during the first instar, it is clear that the two methods used yield widely different results. The following are some of the possible explanations for the smaller number of larvae as calculated from frass drop. A certain proportion of the females could have laid their eggs in other areas or other predators of adults, eggs and/or first instar larvae, not detected during this experiment, could have lowered the population.

The numbers of larvae in all instars are reduced to a great extent by natural enemies and diseases. From Table 60 it can be seen that the decrease was greatest during the third to the fifth instars. In two cases more second than first instar larvae were recorded, indicating shortcomings in the method employed. If the calculated number of final instar larvae in Table 60 is compared with the number of pupae present during the 1970 and 1971 seasons (Table 54), it is clear that the figures based on frass drop are higher than those based on pupal counts. The difference is, however, to be expected, as final instar larvae are known to be subject to reduction by natural enemies and diseases.

b) Adult larval counts

Procedure

Adult larvae of the pine emperor descend trees to find a suitable locality to pupate. As the larvae are large they can easily be seen. These larvae can be distinguished from those accidentally dropping from trees since the latter search for an object to ascend, and do not wander about or attempt to enter the soil. Full-grown larvae usually crawl about for an average of almost two hours before entering the soil to pupate.

When adult larvae appeared, counts were made at weekly intervals in ten plots (each being 2,7 x 91 m) at approximately 1400 hours. These plots were taken at random and were all in lanes without brushwood.

Results

The number of pupating larvae is summarized in Table 61. As it takes almost 2 hours to locate the pupation site and as this process takes place mainly during the day, about a sixth of the daily total number were counted once a week.

Table 61: Total number of pupating pine emperor larvae observed once a week in 10 lanes of 2,7 x 91 m

Block	Year	Total number of larvae observed once a week in 10 lanes = a	Calculated numbers of pupating larvae in 100 m ² during the season = $\frac{6 \times 7 \times 100}{91 \times 2,7 \times 10} \times a$
A	1969	67	115
	1970	42	72
B	1969	58	99
	1970	29	50
C	1969	16	27
	1970	33	56

A comparison of the figures in Tables 54 and 61 shows that the number of pupating larvae in Blocks A and B was almost 2–3 times as high as the number of pupae found in these blocks after these larvae pupated. The number of pupating larvae in Block C was closer to the pupal counts. As the trees in Block C were only five years old, a considerable amount of grass and undergrowth was still present. This fact probably aided pupating larvae in finding suitable pupation sites in a shorter time. Larvae were also much less conspicuous in this Block. The numbers of final instar larvae calculated according to frass pellet counts (Table 60), agree to a large extent with the number of pupating larvae calculated here (Table 61). This method offers a comparatively effective estimate of the number of adult larvae per unit area. It is also clear that a considerable number of larvae seemingly disappeared before they were able to form pupae. This reduction is most probably mainly due to predation by baboons.

From these studies it is clear that the results obtained by the four different methods of estimating the population differed somewhat, but every method has its merits. As the pupae remain immobile in the soil for a long time (about four months), pupal counts appear to be the most practical and accurate method. Counting freshly emerged adults would however require much less labour. It should however be kept in mind that forecasts of future developments based on these two methods are not absolutely reliable. Firstly,

mortality factors may vary drastically from season to season. Secondly, the adults are strong fliers and may migrate fair distances, thus considerably altering the local distribution of the next generation.

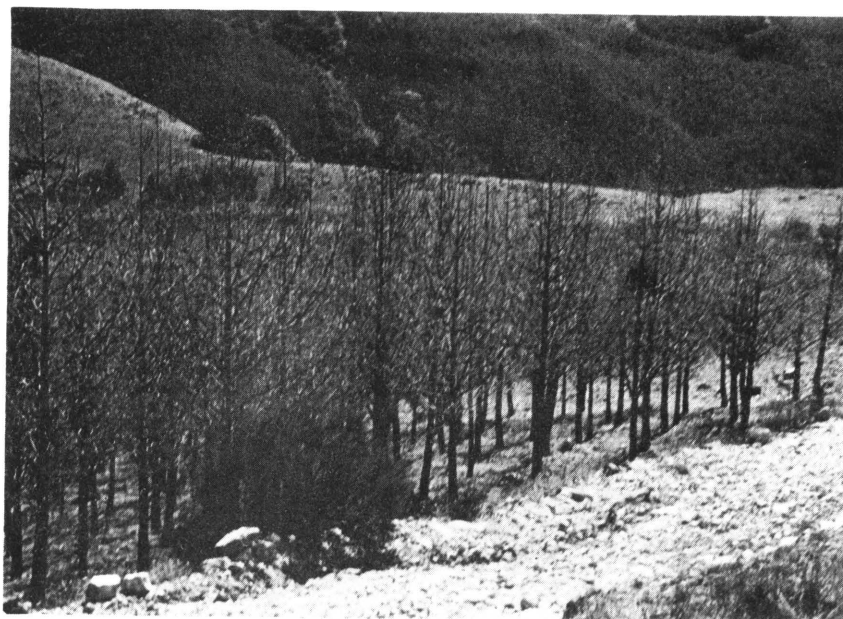
B. Estimation of damage by *N. cytherea clarki*

This investigation was aimed at determining the amount of wood increment lost as a result of defoliation. An attempt will also be made to compare potential loss with estimated aircraft spraying costs.

Defoliation by this species is confined to the dormant period of the trees. In the summer rainfall regions this period is followed by rains commencing during spring, stimulating new growth. Consequently it seldom happens that trees die back or are killed completely as a result of even complete defoliation.

During years when total defoliation of *P. patula* is brought about by this moth (as depicted in Plate 17), it is usually achieved by about August or September.

Plate 17: Total defoliation of *P. patula* trees in the Ameide plantation during 1959 (photo Mr. D. v.V. Webb)



In severely infested areas, defoliation may be completed somewhat earlier, i.e. at the end of June or during July. Trees in the 3-17 year age groups are most

susceptible to defoliation, as was also found by Geertsema (1970). Although many eggs are frequently deposited on younger or older trees, these trees do not seem to be damaged to the same extent as those 3 – 17 years old. On the other hand, older trees weakened years previously by a hail storm for example, are more susceptible to defoliation. Further investigations are necessary to explain these phenomena. Perhaps the nutrients required by developing larvae are not as fully provided by trees in certain age groups or in certain physiological states than in others.

In order to demonstrate the effects of different soil conditions at different localities in the same plantation, use was made of the site index (S.I.) as outlined by Bruce & Schumacher (1950). In the R.S.A., S.I. is based on the heights of pines after 20 years instead of 50 years as stipulated by Bruce & Schumacher.

The S.I. of a specific area therefore is the height of the average tree in feet (304,8 mm) at the age of 20 years, giving some indication of the effect of different climatic and soil factors.

The average yearly rainfall for the Welgelegen plantation is 1 108 mm. For the season 1968/69 to 1970/71 the figures were 1 166; 942 and 1 300 mm respectively, which could be regarded as more or less normal.

1) **Partial defoliation in population study plots**

Procedure

Four groups of nine trees each, situated in the four main directions about 30 m away from each of the three blocks (0,856 ha each) where population studies were in progress, were selected as control trees. As far as possible, each control tree was surrounded by eight other trees (four at a distance of 2,7 m and four at 3,8 m). The bark of each control tree was smoothed at breast height (135 cm from ground level). The circumference at breast height (c.b.h.) was determined, a white band painted around the stem where measured, and the tree numbered. Inside each block, another 36 trees were marked; the c.b.h. of each of these trees corresponded with that of one of the control trees and received the same number. Where a control tree was used with one or more of the eight surrounding trees missing, the same applied to the corresponding tree inside the block.

The trees inside the three blocks were subjected to normal defoliation by pine

emperor larvae. The control trees as well as surrounding trees up to 3,8 m away from each group of nine trees, were dusted with a five per cent mercaptothion dust whenever needle drop was observed in cardboard boxes underneath the control trees. The dust was applied by means of a power duster (Holder 1,5 metric hp) with a long detachable and flexible polythene delivery tube.

The heights of the 72 trees in and around each block were determined with the aid of a clinometer.

In each block the 48 containers were placed out to determine frass pellet and needle drop.

The extent of defoliation during each year was established in each block after all larvae had pupated. The total number of severed needles per tree was calculated from the total numbers collected in the 48 containers. From the average crown depth of the 36 trees per block, the average number of needles normally present per metre crown depth and the needle drop under these trees, it was possible to estimate the percentage defoliation. The c.b.h. and height of all the trees were determined twice at yearly intervals. Where a difference occurred between the control and defoliated trees, the effect on growth was also determined by means of stem analysis. At the end of the growing season following the second defoliation, the trees were felled and sections (about 30 mm thick) were cut out at 2,5 m intervals along the lengths of the stems of all 72 trees. After the sections had been allowed to dry, one surface of each was sanded and two straight lines drawn at right angles through the centre. Four measurements were made of the width of each year ring for the past two years as well as four measurements of the radii of the section, two along each of the two lines drawn across the section. These measurements were done by means of a micrometer caliper.

Results

The assumption is made here that each needle tip collected in the container represents the loss of one whole needle by the tree concerned. The number of needles lost could therefore be calculated for the soil surface occupied by a tree (2,7 x 2,7 m). As indicated previously in this report, the average number of needles on trees of different heights could be calculated, and therefore also the percentage defoliation. These results are supplied in Table 62.

Table 62: Percentage defoliation calculated from average crown depth, average number of needles per metre crown depth (= c), and number of needle tips severed per 48 containers (c = 54 453)

Block	Year	Total number severed needle tips in 48 x 1 811 cm ² = a	Average crown depth = b	Percentage defoliation $\frac{a \times 48 \times 0,1811}{2,7 \times 2,7} \times 100$ = $\frac{a}{c(b-1)} \times 100$
A	1969	20 142	6,72	7,71
	1970	11 225	7,44	3,82
B	1969	25 741	5,93	11,43
	1970	4 884	6,59	1,91
C	1969	6 369	1,99	14,09
	1970	7 433	3,11	7,71

From this table it can be seen that the percentage defoliation was highest in Block C during both years.

In Blocks A and B the needle drop during 1970 was much lower than during 1969. In Block C the drop was slightly higher during 1970. This is in agreement with changes in the population density in the specific blocks. The decrease in Block B was however much more drastic than that in Block A which was perhaps due to a higher larval mortality as a result of a virus epidemic. Although the number of needles severed in Block C was higher in 1970, the percentage defoliation was only about half that of the previous year. This was due to the crown depth of the trees increasing by more than a third.

The average c.b.h. and heights of the 72 trees in and around each block, are provided in Table 63 and the statistical analysis in Table 64.

From these tables it is evident that the difference in growth was minimal and that there were no significant differences between the volumes of the control and defoliated trees in the three blocks. Consequently, no stem analysis was attempted. It is clear that defoliations of 8, 11 and 14 per cent followed by lower defoliations one year later, have no visible effect on the growth of trees in the 17, 15 and 5 year age groups respectively.

Table 63: Average wood increment of 36 partly defoliated *P. patula* trees and 36 control trees per block (D = Defoliated trees; C = Control)

Block	Commen- cing age in years	No of trees /ha	Tree group	April 1969			% defo- liation	April 1970			Vol wood in- crem ent	% defolia- tion	July 1971			Vol wood in- crement	Total vol wood incre- ment
				c.b.h. in mm	height in m	Vol in m ³		c.b.h. in mm	height in m	Vol in m ³			c.b.h. in mm	height in m	Vol in m ³		
A	17	391	D	679	15,86	0,221840	7,71	714	16,89	0,259440	0,037600	3,82	740	17,85	0,295300	0,035860	0,073460
			C	679	15,92	0,220240	0	715	16,96	0,261090	0,040850	0	746	18,10	0,300740	0,039650	0,080500
			C-D			-0,001600					0,001650	0,003250				0,005440	0,003790
B	15	650	D	595	13,26	0,144870	11,43	620	13,91	0,164230	0,019360	1,91	642	14,65	0,182580	0,018350	0,037710
			C	595	13,19	0,143720	0	618	14,03	0,164940	0,021220	0	637	14,68	0,185090	0,020150	0,041370
			C-D			-0,001150					0,000710	0,001860				0,002510	0,001800
C	5	1327	D	168	3,88	0,003326	14,09	277	5,00	0,011754	0,008428	7,71	286	6,06	0,020730	0,008976	0,017404
			C	168	3,90	0,003293	0	278	5,00	0,011760	0,008467	0	340	6,08	0,021324	0,009564	0,018031
			C-D			-0,000033					0,000006	0,000039				0,000594	0,000588

Table 64: T values of data in Table 63 comparing defoliated and control trees (t = t values during specific years)

Block	t April 1969	t April 1970	t July 1971
A	0,111	0,103	0,314
B	0,086	0,048	0,161
C	0,140	0,006	0,409

$$t_{70} (,05) = 1,994$$

2) Complete defoliation by artificial populations

Procedure

Trees in the 15, 10, 10 and 4 year age groups at the commencement of these studies, were used to compare the growth of trees defoliated two or three times in succession with that of uninfested trees. The stand S.I. of all four groups was 70.

In three of the four groups, 10 pairs of trees with the same c.b.h. were chosen, whereas 20 pairs were used for the other group. These pairs of trees were distributed in the same plot and were all the same age. The control trees were situated more than 8,1 m away from the treatment trees of the same group in an area smaller than 1 ha. Lots were then drawn to decide which of each pair would serve as a control, and which as an experimental tree. A white band was painted around the stem where the c.b.h. was measured, and the trees numbered. The height of trees less than 3 m was directly measured, while the heights of taller trees were determined with the aid of a clinometer. The observations were further extended to trees four years old established in stands with S.I. 50 and 90. In the case of trees four years old established in a stand of S.I. 70, an additional treatment of about 50 per cent defoliation was included to compare with totally defoliated and control trees.

Small trees, (up to about 4 m high), may be completely defoliated in spite of having been free of infestation the previous year. In the case of taller trees, infestations extending over one or more years are necessary before complete de-

foliation is preceded by at least one partial defoliation. For this reason it was so arranged that complete defoliation of taller trees was preceded by a 50 per cent defoliation during the previous season.

Trees less than about 4 m high may be totally defoliated for three successive years, and taller trees for two consecutive years. In very exceptional cases, defoliation may be extended over longer periods.

The eight (or fewer) surrounding trees within 3,6 m from the trees used in the experiment, received the same treatment as the experimental trees. The extent of defoliation was obtained by placing pine emperor larvae on the trees and/or removing the needles from the trees by hand. Defoliation by hand was carried out during the peak of larval activity, and was spread over approximately three months for each tree, to simulate defoliation by pine emperor larvae.

Partial or complete defoliation of all age groups was carried out during three successive seasons, with the exception of one of the 10 year old tree groups which was defoliated for two seasons only.

The c.b.h. of the four year old trees in stands of S.I. 70 was determined monthly to study the effect of the actual time of defoliation in relation to the active growing period of the trees. This method of indicating the time of defoliation in relation to the growing period of trees was also used by Rose (1958) during experiments in connection with defoliation of *Populus tremuloides* Michx. trees by the forest tent caterpillar (*Malacosoma disstria* Hbn.).

The c.b.h. and height of all trees were determined annually. After the completion of the experiment, stem analysis was done at 2,5 m intervals along the lengths of the stems.

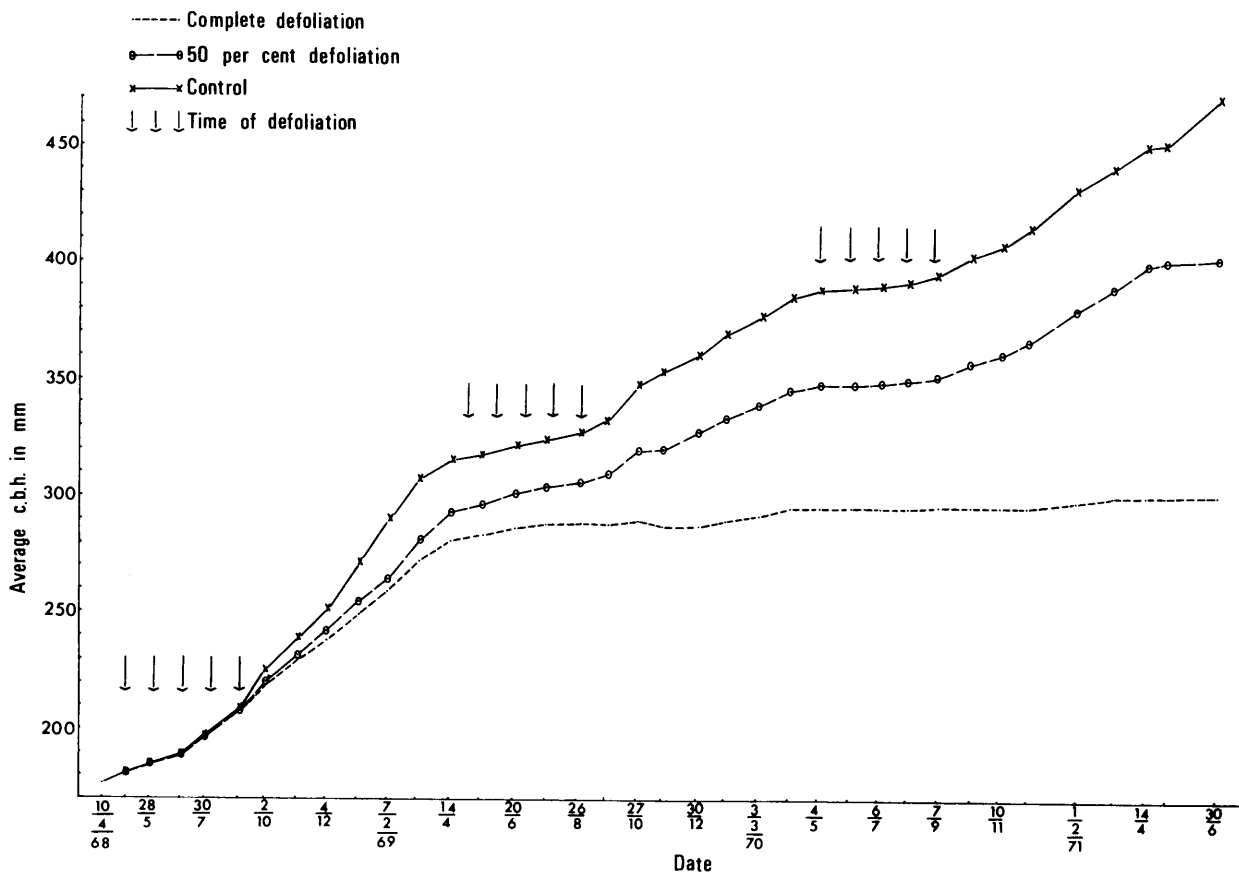
The values of wood mentioned here are considered by the Department of Forestry to be the average current prices for the different thicknesses of wood.

Results

Monthly c.b.h. measurements of the four year old trees in stands of S.I. 70 are provided in Fig. 46.

From this fig. it is clear that growth is cyclical, being mainly confined to the months October to April. It can further be seen that defoliation occurs from

Fig. 46: Average monthly c.b.h. measurements of four year old *P. patula* trees on stand S.I. 70, of which two groups of 10 trees each were defoliated by pine emperor larvae



May to August, i.e. while the trees are in a relatively dormant state. During the dormant season after attaining the age of four years, the effect of one total defoliation did not appear to be very serious. Total defoliation of the same trees for a second and third season however, results in the trees adding almost no growth at all. The effect of 50 per cent defoliation during successive seasons is less serious, but still very noticeable.

The average wood increment of different *P. patula* age groups and the level of defoliation by pine emperor larval activity is provided in Table 65. The volumes of the trees were calculated as shown in Table 65 and a summary of the statistical analysis of these volumes is given in Table 66.

From Tables 65 and 66 it is clear that, at the commencement of these observations, the volume of the experimental trees did not differ significantly from that of their control trees (see commencing *t* values). The following conclusions can further be made:—

Table 65: Average wood increment of different ages of *P. patula* trees and level of defoliation during the time of pine emperor larval activity (D = Complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Stand S.I.	No. of trees/ha	n	Tree group	April 1968			% defoliation	April 1969				% defoliation	April 1970				% defoliation	July 1971				Total vol/ wood increment in m ³ = d - a			
					c.b.h. in mm	height in m	Vol. in m ³ = a		c.b.h. in mm	height in m	Vol. in m ³ = b	Vol wood increment in m ³ = b - a		c.b.h. in mm	height in m	Vol. in m ³ = c	Vol. wood increment in m ³ = c - b		c.b.h. in mm	height in m	Vol. in m ³ = d	Vol. increment in m ³ = d - c				
15	70	454	10	D	771,4	16,96	0,303540	50	806,1	18,40	0,360090	0,056550	100	829,8	19,11	0,398170	0,038080	100	834,1	19,93	0,417050	0,018880	0,113510			
				C	771,4	16,92	0,302030	0	800,3	17,91	0,344960	0,042930	0	825,7	18,81	0,386440	0,041480	0	850,0	19,87	0,433050	0,046610	0,131020			
				C-D								-0,013620*											0,027730	0,017510		
10	70	687	10	D	509,0	13,20	0,102170	50	534,2	15,02	0,128140	0,025970	100	546,9	15,89	0,142140	0,014000	100	552,5	16,80	0,153380	0,011240	0,051210			
				C	509,0	13,20	0,102470	0	537,4	14,92	0,129750	0,027280	0	557,7	15,96	0,149250	0,019500	0	584,8	16,97	0,174260	0,025010	0,071790			
				C-D								0,001310											0,013770	0,020580		
10	70	1108	20	D	-	-	-	-	505,9	26,50	0,099391	-	50	518,7	27,82	0,111280	0,011889	100	520,9	28,79	0,115820	0,004540	0,016429			
				C	-	-	-	-	505,9	26,25	0,098394	-	0	529,8	27,95	0,116810	0,018216	0	555,6	29,62	0,135740	0,018930	0,037146			
				C-D																			0,006327	0,014390	0,020717	
4	90	1192	10	D	361,6	7,06	0,027822	50	460,4	8,67	0,058234	0,030412	100	484,0	10,03	0,070709	0,012475	100	487,5	11,06	0,079454	0,008745	0,051632			
				C	361,6	7,06	0,027936	0	465,8	9,06	0,062727	0,034791	0	536,1	11,09	0,095652	0,032925	0	591,4	12,26	0,128490	0,032838	0,100554			
				C-D								0,004379											0,020450	0,024093	0,048922	
4	70	1160	10	D	176,5	4,61	0,004368	100	280,2	5,78	0,014551	0,010183	100	294,3	6,19	0,016311	0,001760	100	303,9	6,45	0,018063	0,001752	0,013695			
				H	176,5	4,65	0,004397	50	292,1	6,35	0,017512	0,013115	50	345,0	7,71	0,028138	0,010626	50	411,6	8,69	0,044149	0,016011	0,039752			
				C	176,5	4,65	0,004459	0	314,8	6,62	0,021199	0,016740	0	385,1	8,04	0,037365	0,016166	0	471,8	9,01	0,061447	0,024082	0,056988			
				C-D								0,006557												0,014406	0,022330	0,043293
				C-H								0,003625													0,005540	0,008071
4	50	1094	10	D	51,3	2,17	0,000173	100	94,9	2,78	0,000936	0,000763	100	116,7	3,25	0,001422	0,000486	100	138,4	3,55	0,002116	0,000694	0,001943			
				C	51,3	2,17	0,000176	0	121,8	3,59	0,001957	0,001781	0	195,1	4,71	0,004582	0,002625	0	273,5	5,80	0,013134	0,008552	0,012958			
				C-D								0,001018												0,002139	0,007858	0,011015

* The wood increment after 50 per cent defoliation was larger than that of the control

Table 66: T values of data in Table 65 (t = t values during specific years; D = Complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Stand S.I.	Treatments compared	t 1968	t 1969	t 1970	t 1971
15	70	C & D	0,052	0,435	0,294	0,364
10	70	C & D	0,031	0,125	0,479	1,270
10	70	C & D	—	0,308	1,738	4,887**
4	90	C & D	0,036	0,734	3,178**	4,791**
4	70	C & D	0,141	2,905**	5,570**	7,276**
		C & H	0,100	1,652	2,206*	2,582*
		H & D	0,048	1,694	4,461**	6,881**
4	50	C & D	0,095	4,766**	6,508**	9,105**

*Indicates significant differences

**Indicates highly significant differences

a) 15 year old trees (Stand S.I. 70 and 454 stems per ha)

According to the increase in the volume of wood during the period April, 1968 to April, 1969, it would appear that 50 per cent defoliation had no effect on the wood increment. In fact, the experimental trees added more growth than the control trees. After the trees had been completely defoliated during the following season, the situation was reversed, the difference in volume, however, being not significant. After the second complete defoliation, its effect was more pronounced. Although no significant differences could be found, the average volume of the control trees was greater than that of the experimental trees.

b) 10 year old trees (Stand S.I. 70 and 687 stems per ha)

During the period April, 1968 to April, 1969, the experimental trees added less growth after 50 per cent defoliation than the controls. After two consecutive complete defoliations, the difference between the volumes of the two groups of trees became more noticeable. No significant differences could however be found.

c) 10 year old trees (Stand S.I. 70 and 1 108 stems per ha)

In this group, 20 paired trees were used. After 50 per cent defoliation in

1969, the experimental trees showed a smaller average wood increment up to April, 1970 than the control trees. The difference in volume was, however, not significant. After the trees had been completely defoliated during the following season, the volume of wood of the control trees was highly significantly bigger than that of the experimental trees (July, 1971) ($t = 4,887$; $t_{38} (,01) = 2,713$).

d) **4 year old trees** (Stand S.I. 90 and 1 192 stems per ha)

It was found that 50 per cent defoliation had an insignificant influence on the growth of the experimental trees during the period April, 1968 to April, 1969. The volume of wood of the control trees was, however, highly significantly bigger than that of the experimental trees (April, 1970; July, 1971) after both the first complete and the second consecutive complete defoliation (first complete defoliation $t = 3,178$; second consecutive complete defoliation $t = 4,791$; $t_{18} (,01) = 2,878$).

e) **4 year old trees** (Stand S.I. 70 and 1 160 stems per ha)

In this instance a comparison will be made between complete and 50 per cent defoliation, and the control. It was found that 50 per cent defoliation resulted in less than half as much wood loss than complete defoliation. After the first year (April, 1968 to April, 1969) the volume of the control trees was highly significantly bigger than that of the completely defoliated trees ($t = 2,905$; $t_{18} (,01) = 2,878$). After the second year (April, 1969 to April, 1970) the volumes of both the control trees and the 50 per cent defoliated trees were highly significantly bigger than those of completely defoliated trees ($t = 5,570$ and $t = 4,461$ respectively; $t_{18} (,01) = 2,878$). The volume of the control trees was significantly bigger than that of the 50 per cent defoliated trees ($t = 2,206$; $t_{18} (,05) = 2,101$). After the third consecutive defoliation, the volumes of both the control and the 50 per cent defoliated trees were highly significantly bigger than those of the completely defoliated trees, July, 1971, ($t = 7,276$ and $t = 6,881$ respectively; $t_{18} (,01) = 2,878$), while the volume of the control trees was significantly bigger than that of the 50 per cent defoliated trees ($t = 2,582$; $t_{18} (,05) = 2,101$).

f) 4 year old trees (Stand S.I. 50 and 1 094 stems per ha)

After all three consecutive complete defoliations, the volume of the control trees was highly significantly bigger than that of the completely defoliated trees (first defoliation $t = 4,766$; second defoliation $t = 6,508$; third defoliation $t = 9,105$; $t_{18} (,01) = 2,878$).

The percentage wood loss as a result of different degrees of defoliation was calculated and is given in Table 67.

Table 67: Percentage wood loss per year as a result of defoliation, as calculated from Table 65

Commencing age	Stand S.I.	First year		Second year		Third year		Total % loss
		% defoliation	% wood loss	% defoliation	% wood loss	% defoliation	% wood loss	
15	70	50	-31,73*	100	8,20	100	59,49	13,36
10	70	50	4,80	100	28,21	100	55,06	28,67
10	70	50	34,73	100	76,02	—	—	55,77
4	90	50	12,59	100	62,11	100	73,37	48,65
	70	100	39,17	100	89,11	100	92,72	75,97
	50	50	21,65	50	34,27	50	33,51	30,24
	50	100	57,16	100	81,49	100	91,88	85,01

* The wood increment after 50 per cent defoliation was larger than that of the control

From this table it is clear that for stand S.I. 70, the younger the tree, the greater the percentage wood loss. It is also clear that the percentage wood loss per year increases after every additional defoliation. In many cases this increase in wood loss is almost doubled after a second or third complete defoliation. The effect of 50 per cent defoliation is not too severe. After the first two 50 per cent defoliations the effect was almost half that of total defoliations, whereas after the third defoliation the effect remained almost the same as the previous year.

If a comparison is made between defoliation on 90, 70 and 50 S.I. stands, it can be seen that the largest percentage wood loss is experienced on a stand S.I. 50, and the second largest on a stand S.I. 70. This means that the poorer the soil, the greater the ill effects of defoliation. This was also found by Sherry &

Ossowski (1967) with defoliation of wattle (*Acacia mearnsii*) by *Kotochalia junodi* (Heyl.).

Grobler (1957) found that 10 year old *P. patula* trees defoliated by *Euproctis terminalis* during the winter to early spring months, added approximately 59 per cent less growth than what could have been expected from these trees. In this case, complete defoliation was preceded by two partial defoliations. The percentage loss reported by Grobler is more or less of the same order as that found in the present investigation with trees of approximately the same age.

The average volumes of usable wood increment calculated from stem analysis of the different groups of trees are indicated in Table 68.

From this table it can be seen that the results agree to a great extent with the volumes calculated in Table 63. As the volumes in Table 68 only represent usable volume at the time of felling, the method based on volumes calculated according to height and c.b.h. (Table 64) is the more accurate for determining the amount of damage done.

Thinning of *P. patula* is more or less generally practised as described below. Normally 1 334 nursery trees are planted per ha. This number is more or less maintained by replanting. After 10 years they are thinned to 642 per ha; after 15 years to 371 per ha; after 20 years to 247 per ha; and at the age of 25 years to 148 trees per ha. Clear felling takes place when the trees are 30 years old. In the calculations that follow, this recommended practice of thinning was kept in mind.

If thinning is practised normally and if the wood increment is normal during the growing season following the last defoliation (about 15 months after defoliation), the loss due to different degrees of defoliation at different ages can be calculated as indicated in Table 69.

The wood added during the year is in the form of a hollow cone on the outside of the tree. The top part of the tree with a diameter of less than 50 mm is considered unusable. Only part of the wood lost during the year that the tree is felled would therefore have been of economic importance. However, if the tree is felled more than two years after defoliation, it may be assumed that all the wood lost two years earlier would then be of economic consequence.

Table 68: Average wood increment of different ages of *P. patula* trees as calculated according to stem analysis (D = Defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Stand S.I.	Tree group	July 1968–July 1969		July 1969–July 1970		July 1970–July 1971		Total difference in vol wood increment in m ³
			% defoliation	Vol wood increment in m ³	% defoliation	Vol wood increment in m ³	% defoliation	Vol wood increment in m ³	
15	70	D	50	0,039519	100	0,032796	100	0,028773	-0,006812
		C	0	0,025138	0	0,037370	0	0,031768	
		C-D		-0,014381		0,004574		0,002995	
10	70	D	50	0,023968	100	0,020624	100	0,011938	0,022088
		C	0	0,025196	0	0,024200	0	0,029222	
		C-D		0,001228		0,003576		0,017284	
10	70	D		—	50	0,022937	100	0,016379	0,003630
		C		—	0	0,021382	0	0,021564	
		C-D		—		-0,001555		0,005185	
4	90	D	50	0,023207	100	0,010816	100	0,005273	0,045380
		C	0	0,029031	0	0,026133	0	0,029512	
		C-D		0,005824		0,015317		0,024239	
4	70	D	100	0,010183	100	0,002350	100	0,002412	0,025994
		H	50	0,010469	50	0,009302	50	0,011921	
		C	0	0,012033	0	0,012342	0	0,016564	
		C-D		0,001850		0,009992		0,014152	
		C-H		0,001564		0,003040		0,004643	
		H-D		0,000286		0,006952		0,009509	
4	50	D	100	Not usable	100	0,000595	100	0,000563	0,006190
		C	0		0	0,003385	0	0,003963	
		C-D				0,002790		0,003400	

Table 69: Calculation of financial loss per ha due to defoliation by pine emperor larvae

Age during 1968	Percentage and times of defoliation	Average loss of wood/tree in m ³	Stems/ha during 1968-71	Trees felled at 10 yr			Trees felled at 15 yr			Trees felled at 20 yr			Trees felled at 25 yr			Trees felled at 30 yr			Total discounted financial loss in R/ha
				Number felled/ha	Financial loss at 69c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 93c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 127c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 166c/m ³ in R	Discounted return in R/ha*	Clear felling	Financial loss at 194c/m ³ in R	Discounted return in R/ha*	
15	50x1	-	371	-	-	-	-	-	-	124	-	-	99	-	-	148	-	-	-
	100x1,5	-																	
	100x2,5	0,017510									2,76	2,06		2,88	1,61		5,03	2,10	5,77
10	50x1	0,001310	642	-	-		271	0,33	0,25	124	0,21	0,12	99	0,22	0,09	148	0,38	0,13	0,59
	100x1,5	0,006810									1,72	1,28		1,12	0,47		1,96	0,66	3,01
	100x2,5	0,020580									5,19	3,88		3,38	1,41		5,91	2,00	9,10
10	50x1	0,006327	642	-	-		271	1,59	1,19	124	1,00	0,56	99	1,04	0,43	148	1,82	0,62	2,80
	100x1,5	0,020717									5,22	3,90		3,40	1,42		5,95	2,01	9,15
4 (S.I. 90)	50x1	0,004379	1334	692	2,09	1,47	271	1,10	0,59	124	0,68	0,27	99	0,72	0,21	148	1,26	0,28	2,82
	100x1,5	0,024829			11,86	8,36		6,26	3,30		3,91	1,54		4,08	1,20		7,13	1,57	15,97
	100x2,5	0,048922			23,36	16,47		12,33	6,50		7,70	3,03		8,04	2,37		14,05	3,09	31,46
4 (S.I. 70)	100x1	0,006557	1334	692	3,13	2,21	271	1,65	0,87	124	1,03	0,41	99	1,08	0,32	148	1,88	0,41	4,22
	100x2	0,016595			9,92	5,58		4,18	2,20		2,61	1,03		2,73	0,80		4,76	1,05	10,66
	100x3	0,043293			20,67	14,57		10,91	5,75		6,82	2,69		7,11	2,09		12,43	2,73	27,83
4 (S.I. 50)	50x1	0,003625			1,73	1,22		0,91	0,48		0,57	0,22		0,60	0,18		1,04	0,23	2,33
	50x2	0,009165			4,38	3,09		2,31	1,22		1,44	0,57		1,51	0,44		2,63	0,58	5,90
	50x3	0,017236			8,23	5,80		4,34	2,29		2,71	1,07		2,83	0,83		4,95	1,09	11,08
	100x1	0,001018	1334	692	0,48	0,34	271	0,25	0,13	124	0,16	0,06	99	0,17	0,05	148	0,29	0,06	0,64
4 (S.I. 50)	100x2	0,003157			1,51	1,06		0,80	0,42		0,50	0,20		0,52	0,15		0,91	0,20	2,03
	100x3	0,011015			5,26	3,71		2,78	1,46		1,73	0,68		1,81	0,53		3,16	0,69	7,07

* Present value of return discounted at 6 per cent rate of interest

From Table 69, it is clear that the financial loss, as a result of wood loss, varies considerably for the different age groups. Spraying costs (including that of the insecticide) amount to approximately R4,50 per ha, which should therefore be regarded as an additional investment. This amount will have to be recovered from the trees per ha i.e., during thinnings and clear felling.

The prevention of losses may be regarded as the return to expenses incurred to control the insect, and thus as a future revenue resulting from the control. However, financial returns accruing after different intervals of time are not directly comparable. Revenue which may be obtained in say ten years time, is not of the same value at the beginning of the 10 year period. The present value can be obtained by determining which present amount of money, if invested at a compound rate of interest, would grow to the future value to be obtained. This procedure is known as the discounting of future revenues (Bishop & Toussaint, 1958).

In Table 69, the present value of the future income discounted at a 6 per cent rate of interest was thus calculated. These calculations were done using the following formula: $V = R / (1 + i)^n$, where V is the present value of the future return R , and i is the rate of interest received over a period of n years.

In order to decide whether it would be economically sound to spray, the probabilities of different degrees of defoliation must be taken into consideration. Unfortunately these probabilities are not sufficiently well known. To gain this knowledge would demand observations and accurate records in as many different localities as possible over extended periods of the order of two decades. However, there is some evidence that certain localities are especially prone to outbreaks of this pest. It may therefore be worthwhile to instigate intensive studies in such localities with the view of identifying the processes involved within a much shorter period than would be needed elsewhere.

For the purpose of this discussion the writer is of the opinion that the following probabilities could in the meantime be accepted as a general guide:-

Trees 15 years old: S.I. 70: The chances of one partial and two complete defoliations are relatively small. Although one application of the insecticide would be economically sound, the gain to be made would be small and uncertain. Therefore, spraying can be recommended only for localities known to be specially prone to outbreaks.

Trees 10 years old: S.I. 70: The probability of one partial and two complete defoliations before the age of 17 years is attained, is relatively high. Two applications of the insecticide can be definitely recommended, but a third application would not be economically justifiable.

Trees 4 years old: S.I. 90: The probabilities are that these trees would be completely defoliated about three to four times before the age of 17 years is attained. On such good soil this should not be allowed to happen. Four or even five applications of the insecticide would still be economical. In areas especially prone to outbreaks, it is recommended that these trees be inspected regularly at the beginning of the larval period to determine what degree of defoliation could be expected, so that action could be taken in time to avoid serious damage.

Trees 4 years old S.I. 70: The probabilities of complete defoliation are as indicated above, i.e. three or four times. The recommendations are the same as for S.I. 90, although the approach should be somewhat more critical. After two applications, the matter would have to be seriously considered before spraying again.

Trees 4 years old: S.I. 50: Although the probabilities of defoliation are as indicated above for 4 year old trees, the approach should be extremely critical. Spraying can be recommended only for localities especially prone to outbreaks, i.e. where it is almost certain that at least three complete defoliations would occur.

Summarising this, it can be said that more than one complete defoliation must occur in the case of 10 to 15 year old trees, before the cost of wood lost is more than the cost of spraying. More than one complete or partial defoliation must occur on four year old trees on S.I. 70 and 90 stands, before the loss in wood is higher than spraying costs. For four year old trees on a S.I. 50 stand, more than two complete defoliations must occur before spraying would be economically sound.

It must however be indicated that at a higher rate of interest, say 9 per cent, the total discounted financial loss will be considerably lower, and certain sprayings will not be rewarding.

C. Population density of *P. irius*

Intensive studies were undertaken in three blocks, each 0,856 ha in extent. The blocks were situated in areas where infestations of the poplar emperor were estimated

to fall in the following categories: severe (Block A); moderate (Block B) and low (Block C). These blocks were about 5 km apart and the three populations could be regarded as distinctly separate and different.

1) Pupal counts

Pupal counts were done during August, 1968 and February, 1969, in 100 plots, each 2,5 m² (2,74 x 0,91 m), of which 34 were situated against stems, 33 in lanes with brushwood and 33 in lanes without brushwood. The results of these pupal counts are supplied in Table 70.

Table 70: Number of poplar emperor pupae per 2,5 m² plot and calculated number per 100 m² in each of three blocks during August 1968 and February 1969 (100 plots per block)

Block	Sampling date	Min	Max	Average and confidence interval	Calculated number per 100 m ²
A (10 yr)	Aug, 1968	2	11	5,01 ± 0,39	200
	Feb, 1969	0	10	4,60 ± 0,45	184
B (7 yr)	Aug, 1968	0	3	0,64 ± 0,15	26
	Feb, 1969	0	3	0,83 ± 0,17	33
C (7 yr)	Aug, 1968	0	2	0,06 ± 0,06	2
	Feb, 1969	0	3	0,47 ± 0,15	19

The average number of viable eggs per female is 156 and the sex ratio is about even. According to other observations, natural enemies of pupae and adults could be expected to reduce the population by about 2 per cent. Egg parasitism and rain could cause a total mortality of about 5 per cent. The calculations shown in Table 71 have been based on these assumptions, and on the data in Table 70.

Table 71: Calculated number of first instar poplar emperor larvae expected to originate per 100 m² from known pupal populations

Block	Number of pupae	Number of adults after a 2% reduction = a	Viable eggs = $\frac{156}{2} \times a$	Number of first instar larvae after a 5% reduction of eggs
A	200	196	15 288	14 524
B	26	26	2 028	1 927
C	2	2	156	148

From this table it is clear that the expected population in Block A would be dense enough to completely defoliate the trees.(see p. 92).

2) Adult counts

Counting of adult insects was done once a week between 0700 and 0900 hours in 10 plots (91 x 2,7 m each) per block (five lanes with and five without brushwood). The number actually recorded was estimated to reflect about half of the total number of adults that had emerged in the plots the previous 24 hrs. (see p. 119).

The total number of newly emerged adults counted per block, and the calculated number per 100 m², are provided in Table 72.

Table 72: Total number of newly emerged poplar emperor adults counted once per week in 10 plots (91 x 2,7 m each) and calculated number of eggs/100 m² (W = Week)

Block	October				November				Total for one day per week = a	Calculated total number in 100 m ² / season $= \frac{a \times 7 \times 10 \times 2}{91 \times 2,7} = b$	Expected no of larvae/100 m ² after 5% reduction of eggs $= \frac{b \times 156}{2} \times 0,95$
	W 1	W 2	W 3	W 4	W 1	W 2	W 3	W 4			
A	8	35	43	129	190	5	2	0	412	235	17 414
B	1	4	5	24	19	4	2	1	60	34	2 519
C	1	2	3	16	12	3	1	0	38	22	1 630

If Tables 70 and 72 are compared, it is evident that there is a fair agreement between the number of pupae known to have been present and the calculated number of emerging adults.

3) Larval counts

The same two methods used to determine larval populations of the pine emperor, were used for the poplar emperor.

a) Counts of frass pellets

In each of the three blocks, 48 containers (48,1 x 37,7 cm and 25 cm deep) were placed out as described earlier. The frass pellets and severed needles were counted once a week. The frass pellets of 10 containers per block were compared individually with those of larvae of known instars.

A summary of the average number of frass pellets produced by each of the larval instars during the full duration of each larval instar, as well as the average duration of each instar are supplied in Table 73.

Table 73: Total number of frass pellets produced by the different larval instars of the poplar emperor

Instar	Total number of frass pellets produced	Duration in days	Average number of frass pellets per day = y
1	173,3	9,7	17,9
2	197,0	10,7	18,4
3	221,6	9,6	23,1
4	258,5	12,4	20,8
5	277,7	19,5	14,2

The total number of frass collected weekly in 48 containers per block, is supplied in Table 74. In this table the relative proportions of the different larval instars are given, as determined from the size of frass pellets in 10 containers per block.

From this table it can be seen that frass drop was high, especially during December, when many of the larvae were still in earlier instars.

The average duration of the different instars, and the fact that the sampling surface was $48 \times 1\,811 \text{ cm}^2$, have been taken into consideration to calculate the numbers of different instar larvae per 100 m^2 as indicated in Table 75.

If the calculated numbers of first instar larvae per 100 m^2 in Tables 71 and 72 on the one hand are compared with the calculated number of first instar larvae in Table 75 on the other, it may be concluded that there is a very high mortality from the time that the adults emerge until their progeny starts to feed in the first instar. This was especially the case in Block A where the population was high.

These decreases could have been brought about by predators or other factors not yet known.

All larval instars are subjected to natural enemies and diseases. From Table 75 it is however clear that fifth instar larvae were drastically reduced especially

Table 74: Total number frass pellets produced by poplar emperor larvae collected weekly in 48 containers each with a surface area of 1 811 cm² in the different blocks during 1968/69 and calculated number of larvae in the different instars as deduced from frass pellets (Bl = Block; Is = Instar)

Week ending on	Total number of frass pellets in 48 containers = a			Relative numbers of frass pellets of the different instars in 30 containers					Calculated number of larvae per 48 x 1 811 cm ² surface area $\frac{a \cdot x}{y^* \cdot Sx}$														
	Bl A	Bl B	Bl C	Is 1 =x ₁	2 =x ₂	3 =x ₃	4 =x ₄	5 =x ₅	Block A					Block B					Block C				
									Is 1	2	3	4	5	Is 1	2	3	4	5	Is 1	2	3	4	5
17/11	375	146	20	37	0	0	0	0	21	0	0	0	0	8	0	0	0	0	1	0	0	0	0
22/	607	331	87	52	7	0	0	0	30	4	0	0	0	16	2	0	0	0	4	1	0	0	0
29/	1214	565	125	71	15	0	0	0	56	12	0	0	0	26	5	0	0	0	6	1	0	0	0
6/12	1236	707	157	51	44	11	5	0	32	27	5	3	0	18	15	3	2	0	4	3	1	0	0
13/	1760	997	184	113	62	36	18	0	49	26	12	7	0	27	15	7	4	0	5	3	1	1	0
20/	6455	2302	750	143	203	133	80	0	92	127	66	44	0	33	45	24	16	0	11	15	8	5	0
27/	8362	1173	278	80	192	204	118	13	62	144	122	78	13	9	20	17	11	2	2	5	4	3	0
3/1	2514	441	159	2	17	349	521	126	0	2	37	62	22	0	0	7	11	4	0	0	2	4	1
10/	2446	416	139	0	0	287	752	355	0	0	22	63	44	0	0	4	11	7	0	0	1	4	2
17/	2426	554	129	0	0	68	539	510	0	0	6	56	78	0	0	1	13	18	0	0	0	3	4
24/	2777	662	148	0	0	0	211	743	0	0	0	30	152	0	0	0	7	36	0	0	0	2	8
31/	335	133	133	0	0	0	56	391	0	0	0	2	21	0	0	0	1	8	0	0	0	1	8
7/2	169	38	73	0	0	0	0	62	0	0	0	0	12	0	0	0	0	3	0	0	0	0	5
14/	10	5	10	0	0	0	0	7	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
Total									342	342	270	345	343	137	102	63	76	78	33	28	17	23	29

y* = average number of frass produced per day by the different instars (see Table 73)

Table 75: Calculated number of poplar emperor larvae per 100 m² in the different blocks

Block	Instar	Calculated total number of larvae per day/48 x 1 811 cm ² = a	Duration of instar in days = b	Calculated number of larvae per 100 m ² during 1968/69 = $\frac{a}{b} \times \frac{100}{48 \times 0,1811}$
A	1	342	9,7	406
	2	342	10,7	368
	3	270	9,6	323
	4	345	12,4	320
	5	343	19,5	202
B	1	137	9,7	162
	2	102	10,7	110
	3	63	9,6	75
	4	76	12,4	71
	5	78	19,5	46
C	1	33	9,7	39
	2	28	10,7	30
	3	17	9,6	20
	4	23	12,4	21
	5	29	19,5	17

in Blocks A and B. This decrease may be attributed to predation by hawks. The number of final instar larvae calculated in Table 75 is very nearly the same as the number of pupae later found during February, 1969 (Table 70). The slight decrease in Block A is probably also due to predation by hawks.

b) Adult larval counts

When adult larvae appeared, counts were carried out once per week in 10 plots (each 91 x 2,7 m) at approximately 1400 hours.

The total number of pupating larvae recorded once per week in 10 lanes per block is summarized in Table 76. The time spent by the larva to locate a suitable pupation site is probably of the order of 1,5 hours. As this process

usually takes place during the day, it is estimated that about one eighth of the daily total had been recorded once a week.

Table 76: Total number of pupating poplar emperor larvae observed once a week in 10 lanes of 2,7 x 91 m during the 1968/69 season

Block	Total number of larvae observed once a week in 10 lanes = a	Calculated numbers of pupating larvae in 100 m ² during the season = $\frac{a \times 8 \times 7 \times 100}{91 \times 2,7 \times 10}$
A	142	324
B	31	71
C	0	0

From Table 76, it is clear that the populations in Blocks B and C must have been exceptionally low. The number of pupating larvae estimated for Blocks A and B is considerably higher than the pupae recorded after pupation (Table 70, February, 1969). This decrease can be attributed to predation by hawks.

D. Estimation of damage by *P. irius*

Defoliation by the poplar emperor takes place during the growing season of the trees. In addition, the rainfall on the Highveld is relatively low for pine cultivation and droughts also occur frequently.

Total defoliation of *P. patula* and *P. radiata* trees generally takes place from the end of December to the end of January. As the larvae are full-grown in a relatively short time (approximately eight weeks), defoliation takes place at a rapid rate. It appears as if pine trees of all ages, with the exception of trees younger than three years, can be defoliated, but trees older than seven years seem to be preferred.

The average rainfall for the Rietvlei plantation is 774 mm per annum. For the 1968/69 to 1970/71 seasons it was 761, 820 and 762 mm per year. Rainfall was therefore more or less normal when the experiment was carried out.

1) Partial defoliation in population study plots

For this experiment, 36 treatment trees (situated in each block) and 36 con-

trol trees (situated around each block) were laid out as previously described.

The trees in each block were subjected to normal defoliation for only one year. As defoliation during one season may have an influence on the wood increment of the following year, all trees were kept free of the pest the following season by dusting with 5 per cent mercaptothion.

The percentage defoliation calculated from average crown depth and the total number of needles collected in 48 containers, are indicated in Table 77.

The c.b.h. and height of all trees were determined at the commencement of this experiment and at the end of the following season (July, 1970), as indicated in Table 78 and statistically analysed as shown in Table 79.

Table 77: Percentage defoliation by the poplar emperor during the 1968/69 season determined from the average crown depth of the trees, the average number of needles per metre crown depth (= c), and the number of severed needle tips in 48 containers (c = 54 453)

Block	Total number of severed needle tips in 48 x 1 811 cm ² = a	Average crown depth = b	Percentage defoliation $= \frac{a \times 48 \times 0,1811}{c(b-1)} \times 100$
A	65 813	7,38	22,6
B	15 379	6,30	6,4
C	7 209	5,93	3,2

From Table 79, it is clear that the volumes of the 36 trees in the blocks before defoliation and the control trees did not differ statistically significantly from each other (November, 1968). At the end of the experiment, there were still no statistical significant differences between the volumes of the control and defoliated trees.

It can however be stated that 22,6 per cent defoliation of 10 year old trees in Block A, lowered the percentage wood increment by about 17,9 per cent, which represents 4,1 m³ per ha. The degree of defoliation in the other blocks (6,4 per cent Block B and 3,2 per cent Block C) had a minimal influence on the wood increment.

Table 78: The average wood increment of 36 partly defoliated *P. patula* trees and 36 control trees per block (D = Defoliated trees; C = Control)

Block	Commencing age in years	No of trees /ha	Tree group	November 1968			% defoliation	July 1970			Vol wood increment
				c.b.h. in mm	height in m	Vol in m ³		c.b.h. in mm	height in m	Vol in m ³	
A	10	1263	D	442	11,2	0,068449	22,6	477	13,3	0,086510	0,018061
			C	442	11,1	0,067320	0	483	13,3	0,088611	0,021291
			C-D								0,003230
B	7	1290	D	437	9,3	0,053344	6,4	506	12,0	0,091890	0,038546
			C	437	9,5	0,054420	0	505	12,1	0,091755	0,037335
			C-D								-0,001211
C	7	1311	D	401	8,9	0,042659	3,2	452	12,0	0,072631	0,029972
			C	401	9,4	0,044621	0	455	12,3	0,075429	0,030808
			C-D								0,000836

Table 79: T values of data in Table 78 comparing defoliated and control trees (t = t values during specific years)

Block	t November 1968	t July 1970
A	0,180	0,268
B	0,365	0,034
C	0,014	0,014

$$t_{70} (,05) = 1,994$$

2) Complete defoliation by natural populations

In the Pan plantation, where complete defoliation occurred one or more times, these trees were investigated for a number of years with periods of 3-6 months between visits. The condition of the trees was recorded during each visit. In this locality a gradual increase in the population had also occurred, so that the trees had been partly defoliated for at least one season before complete defoliation.

The average rainfall for Pan plantation is 774 mm per annum. During 1964/65 it was 677 mm and during 1965/66 only 455 mm. The low rainfall during the 1965/66 season most probably had an effect on the results.

The influence of total defoliation on crown mortality and death of trees, is given in Table 80.

Table 80: Effect of complete defoliation by the poplar emperor on *P.radiata* trees subjected to conditions of drought during the 1965/66 season

Tree age during 1966	Stems per ha	Period of complete defoliation	Number of dead trees	Crown mortality	Normal trees	Percentage dead or abnormal trees
24	457	1964,65+66	178	132	207	59,96
21	741	1966	67	27	446	17,41
19	593	—	0	2	471	0,42

From this table it can be seen that three complete defoliations of the 24 year old trees caused much damage, whereas one defoliation was proportionately less

severe. Besides this obvious effect, there was possibly also a great loss in the wood increment. It is therefore clear that the effect of total defoliation by this pest should not only be measured in wood increment lost, but also in trees killed.

3) Complete defoliation by artificial populations

Procedure

The *P. patula* trees used to determine the effect of two consecutive defoliations were 10, 7 and 3 years old. All three were in stands with S.I. 70 and 10 paired observations on c.b.h. were made. The heights were also determined. In the case of seven year old trees, two other treatments were also included, namely, one group was completely defoliated the first year only and the other about 50 per cent during two successive seasons.

Trees less than about 6 m high can be completely defoliated without having been infested previously. On taller trees, a gradual increase in the population must first take place and complete defoliation is preceded by at least one partial defoliation. For this reason, the 10 year old trees were first 50 per cent defoliated and then completely the following year.

All trees within 3,6 m from the marked trees received the same treatment as the treatment trees. The required degree of defoliation was obtained by placing larvae on trees and/or by removing the leaves by hand. Defoliation by hand was done during larval activity over a period of about six weeks for each tree, to simulate defoliation by poplar emperor larvae.

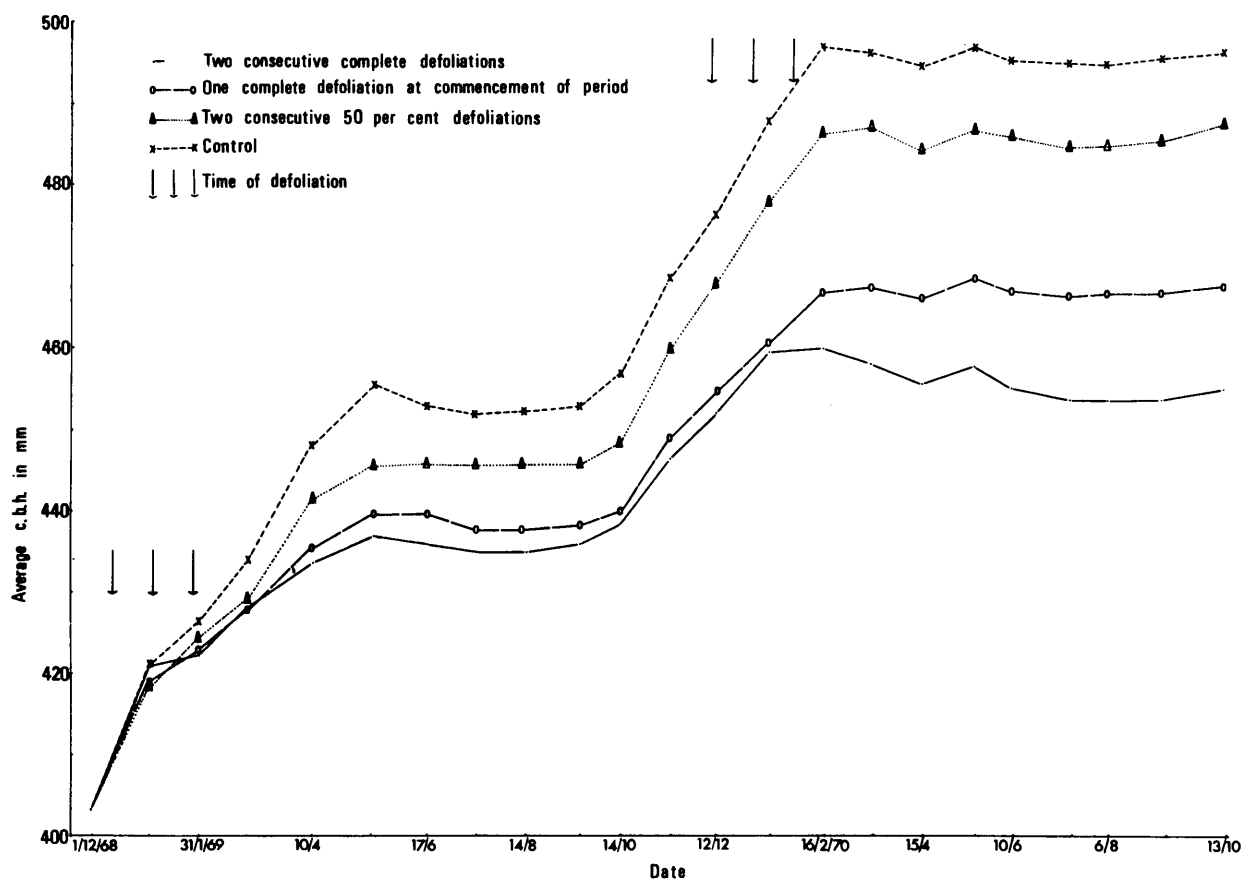
The c.b.h. of the seven year old trees was measured once a month. The c.b.h. of all other trees as well as the heights of all the trees were measured after one year and again after 2,5 years. Notes were also taken of dying trees.

The completely defoliated trees are not felled for the reason that they might recover. As dead trees can not be used unless they are felled shortly after death, they can be regarded as a dead loss.

Results

The average monthly c.b.h. measurements of each group of trees in the seven year old age group are indicated in Fig. 47.

Fig. 47: Average monthly c.b.h. measurements of seven year old *P. patula* trees of which three groups of 10 trees each were defoliated by poplar emperor larvae



From this fig. it is clear that growth was the same as found for trees at Welgelegen (i.e. cyclical, and mainly confined to the months October to April). It can further be seen that defoliation takes place when approximately two thirds of the yearly wood increment has already been added. During the growing season, after attaining the age of seven years, the effect of total defoliation is of such a nature that very little growth takes place after defoliation. Partial defoliation inhibits growth to a smaller degree. Two total defoliations of the same trees suppress growth almost completely. Trees defoliated during one year only, grow almost normally during the next. The effect of one complete defoliation was greater than that of two partial defoliations.

The average wood increment of the three different age groups, as well as the degree of defoliation at the time that poplar emperor larvae are active, are indicated in Table 81. Data in connection with the statistical analysis of the volumes are given in Table 82.

Table 81: Average wood increment of different ages of *P. patula* trees on stand S.I. 70, and degree of defoliation at the time of poplar emperor larval activity (D = Complete defoliation; H = Half defoliation; F = First year defoliation; C = Control)

Com-mencing age in years	No of trees/ha	n	Tree group	October 1968			%defo- liation	October 1969				% defo- liation	Num- ber of trees dead during 1970	July 1971				Total vol wood incre- ment = c - a
				c.b.h. in mm	height in m	Vol in m ³ = a		c.b.h. in mm	height in m	Vol in m ³ = b	Vol wood increment in m ³ = b-a			c.b.h. in mm	height in m	Vol in m ³ = c	Vol wood in- crement in m ³ = c-b	
10	1287	10	D	528	14,2	0,117330	50	565	14,5	0,137990	0,020660	100	2	579	15,1	0,149900	0,011910	0,032570
			C	528	13,9	0,114850	0	573	14,8	0,143570	0,028720	0	0	625	15,6	0,180183	0,036613	0,065333
			C-D			-0,002480			0,005580	0,008060						0,030283	0,024703	0,032763
7	1305	10	D	406	9,3	0,045159	100	451	9,7	0,058931	0,013772	100	5	453	10,8	0,066512	0,007581	0,021353
			F	406	9,4	0,045825	100	454	10,6	0,065205	0,019380	0	0	494	12,2	0,088417	0,023212	0,042592
			H	406	9,8	0,047765	50	468	11,0	0,071270	0,023505	50	0	514	12,3	0,096332	0,025062	0,048567
			C	406	9,1	0,044578	0	476	10,6	0,071050	0,026472	0	0	522	12,5	0,101260	0,030210	0,056682
			C-D			-0,000581			0,012119	0,012700						0,034748	0,022629	0,035329
			C-F			-0,001247			0,005845	0,007092						0,012843	0,006998	0,014090
			C-H			-0,003187			0,000220	0,002967						0,004928	0,004708	0,008115
			H-D			0,002606			0,012339	0,010805						0,029820	0,017481	0,027214
			H-F			0,001931			0,006065	0,004125						0,007915	0,001850	0,005984
F-D			0,000666			0,006274	0,005608						0,021905	0,015631	0,021239			
3	1316	10	D	63	2,4	0,000287	100	157	3,7	0,002765	0,002478	100	2	196	4,2	0,008266	0,005788	0,007979
			C	63	2,4	0,000283	0	228	5,0	0,005723	0,005440	0	0	360	7,4	0,028577	0,022854	0,028294
			C-D			-0,000004			0,002958	0,002962						0,020311	0,017326	0,020315

Table 82: T values of data in Table 81 (D = Complete defoliation; F = First year complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Treatments compared	t November 1968	t November 1969	t July 1971
10	C & D	0,618	1,002	3,642**
7	C & D	0,370	4,486**	9,069**
	C & H	1,913	0,091	2,321*
	C & F	0,722	2,220*	3,748**
	H & D	1,568	4,507**	6,318**
	F & D	0,386	2,038	4,448**
	H & F	1,072	2,270*	2,041
	C & D	0,706	3,761**	8,410**

* Indicates significant differences

** Indicates highly significant differences

From Tables 81 and 82, it is clear that at the commencement of these experiments, the different groups in every age group did not differ statistically from each other (see t values for 1968). In addition, the following conclusions can be made:

a) **10 year old trees** (stand S.I. 70 and 1 287 stems per ha)

From the t value for 1969 it appears that 50 per cent defoliation had almost no influence on the volume increment of the trees. Complete defoliation which followed the next season had a considerably greater effect on the increment (see t value for 1971), the volume of the control trees being highly significantly higher than that of the eight experimental trees still alive ($t = 3,642$; $t_{16} (,01) = 2,921$). A further effect of the defoliation was therefore that 2 of the 10 experimental trees died during the spring of 1970. These trees can be regarded as a dead loss.

b) **7 year old trees** (stand S.I. 70 and 1 305 stems per ha)

In this case a comparison will be made between four treatments i.e. two consecutive complete defoliations (group D), a single complete defoliation (group F), two consecutive 50 per cent defoliations (group H) and the control (group C).

At the commencement of the experiment no significant differences were found (see t values, November, 1968). By October, 1969, the volume of wood of the control trees however was highly significantly, and significantly bigger than those of the groups of trees that were completely defoliated (C & D, $t = 4,486$; C & F, $t = 2,220$; $t_{18} (,01) = 2,878$, $t_{18} (,05) = 2,101$). The volumes of the trees that had been defoliated ^{by} 50 per cent, were highly significantly bigger than the one and significantly bigger than the other of the two groups that were completely defoliated (H & D, $t = 4,507$; H & F, $t = 2,270$; $t_{18} (,01) = 2,878$; $t_{18} (,05) = 2,101$).

After the second year's defoliation, the volumes of the trees completely defoliated twice, were highly significantly smaller than those of all other groups (July, 1971) (C & D, $t = 9,069$; H & D, $t = 6,318$; F & D, $t = 4,448$; $t_{13} (,01) = 3,012$). The volumes of the trees 50 per cent defoliated and completely defoliated for one year were respectively significantly and highly significantly smaller than those of the control trees, (C & H, $t = 2,321$; C & F, $t = 3,748$; $t_{18} (,05) = 2,101$; $t_{18} (,01) = 2,878$), but they did not differ significantly from each other.

Of the 10 trees which were defoliated twice, five died during the 1970/71 season. The loss due to mortality alone, was thus 50 per cent.

c) **3 year old trees** (stand S.I. 70 and 1 316 stems per ha)

At the commencement of the experiment no significant difference was found (see t values, November, 1968). However, by October, 1969, the volumes of the defoliated trees were highly significantly smaller than those of the control trees ($t = 3,761$; $t_{18} (,01) = 2,878$). After the second year's defoliation, the difference was even more noticeable and also highly significant ($t = 8,410$; $t_{16} (,01) = 2,921$). Of the 10 trees defoliated twice in succession, two died during the spring of 1970, representing a loss of 20 per cent.

The percentage wood loss, as a result of defoliation is provided in Table 83.

From this table it can be seen that smaller trees lose a larger percentage of wood increment than larger trees. The percentage wood loss per annum also

Table 83: The percentage wood loss per year as a result of defoliation, as calculated from Table 81

Commencing age	First year		Second year		Total % loss
	% defoliation	% wood loss	% defoliation	% wood loss	
10	50	28,1	100	67,5	50,1
7	100	48,0	100	74,9	62,3
	100	26,8	0	23,2	24,9
3	50	11,2	50	15,6	14,3
	100	54,4	100	75,8	71,8

increases after every defoliation. What is further noticeable is the fact that the wood increment of trees defoliated once was almost normal 12 – 30 months after defoliation.

During this experiment, 2 of the 10 year old, 5 of the 7 year old and 2 of the 3 year old trees died after 1,5;2 and 2 consecutive defoliations respectively. It therefore appears as if the three year old trees are not as readily killed as older trees. However, the percentage wood increment lost was the highest with young trees. Younger trees probably can recuperate more easily, and competition between younger trees probably also is less severe than between older trees.

The average usable volume of wood increment calculated for the different groups according to stem analysis, is indicated in Table 84.

The results in this table agree to a large extent with those calculated according to height and c.b.h. (Table 81).

On the assumptions that all live trees would grow normally 18 months after the last defoliation and that thinning is carried out as indicated previously, the loss can be calculated as summarized in Table 85.

Trees which died on account of defoliation will already be of no economical value during the next thinning. This fact was taken into consideration when the financial loss was determined. The recommended number of stems per ha was used.

From Table 85, it can be seen that the financial loss, as a result of defoliations, varies for different ages of trees. The discounted return of the financial

Table 84: Average volume wood increment of different ages of *P.patula* trees as calculated according to stem analysis (D = Complete defoliation for two consecutive years; F = Complete defoliation for one year; H = 50 per cent defoliation for two consecutive years; C = Control)

Commencing age in years	Tree group	Volume wood increment during the growing season		
		1968/69	1969/70	1970/71
10	D	0,026323	0,023180	0,023643
	C	0,026356	0,026953	0,035864
	C-D	0,000033	0,003773	0,012221
7	D	0,017819	0,014117	0,008092
	F	0,015902	0,013830	0,009949
	H	0,017428	0,017133	0,010524
	C	0,020479	0,019247	0,015824
	C-D	0,002660	0,005130	0,007732
	C-F	0,004577	0,005417	0,005875
	C-H	0,003051	0,002114	0,005300
3	D	0,001393	0,002423	0,002938
	C	0,004657	0,005208	0,008419
	C-D	0,003264	0,002785	0,005481

loss was calculated and the total discounted financial loss per ha thus obtained.

Spraying cost is estimated at R4,50 per ha for one application of the insecticide. As explained in the case of the pine emperor, insufficient data are available to predict defoliation. Until more information is available, decisions to spray can be made as follows:

Trees 10 years old: The chances that a partial defoliation of about 50 per cent or higher can be followed by a complete defoliation are relatively high. Therefore spraying can be recommended the year after a defoliation of more than 50 per cent. Four applications of the insecticide would still be economical.

Trees 7 years old: The probabilities of complete defoliation and the recommendation for spraying are as indicated above. To prevent two consecutive defoliations, up to 10 applications of the insecticide would still be economical.

Table 85: Calculation of financial loss per ha due to defoliation by poplar and pine-bark emperor larvae

Com-mencing age	Percentage and times of defoliation	Average loss of wood/tree in m ³	Normal number of stems /ha	Number of trees dead due to defoliation	Financial loss due to tree mortality at 69c/m ³ **	Discounted return in R/ha**	Trees felled at 10 yr			Trees felled at 15 yr			Trees felled at 20 yr			Trees felled at 25 yr			Trees felled at 30 yr			Total discounted financial loss in R/ha
							Number felled/ha	Financial loss at 69c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 93c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 127c/m ³ in R	Discounted return in R/ha*	Number felled/ha	Financial loss at 166c/m ³ in R	Discounted return in R/ha*	Clear felling	Financial loss at 194c/m ³ in R	Discounted return in R/ha*	
Poplar emperor																						
10	50x1	0,008060	642	0						271	2,03	1,52	124	1,27	0,71	99	1,32	0,55	148	2,31	0,72	3,50
	100x1,5	0,032763	642	128	15,91	12,60	-	-		143	4,36	3,26	124	5,16	2,88	99	5,38	2,25	148	9,41	2,94	23,93
7	100x1	0,012700	1334	0	-	-	692	6,06	5,09	271	3,20	1,98	124	2,00	0,94	99	2,09	0,73	148	3,65	0,96	9,70
	100x2	0,035329	1334	667	46,60	41,48	25	0,61	0,51	271	8,90	5,51	124	5,56	2,61	99	5,81	2,04	148	10,14	2,66	54,81
	50x1	0,002967	1334	0	-	-	692	1,42	1,19	271	0,75	0,46	124	0,47	0,22	99	0,49	0,17	148	0,85	0,22	2,26
3	50x2	0,008115	1334	0	-	-	692	3,87	3,30	271	2,05	1,27	124	1,28	0,60	99	1,33	0,47	148	2,33	0,61	6,25
	100x1	0,002962	1334	0	-	-	692	1,41	0,94	271	0,75	0,37	124	0,47	0,17	99	0,49	0,14	148	0,85	0,18	1,80
	100x2	0,020315	1334	267	5,26	3,71	425	5,96	3,96	271	5,12	2,55	124	3,20	1,19	99	3,34	0,93	148	6,65	1,38	13,72
Pine-bark emperor																						
6	100x2	0,013157	1334	0	-	-	692	6,28	4,98	271	3,32	1,97	124	2,07	0,92	99	2,16	0,71	148	3,78	0,93	9,51
4	100x2	0,012020	1334	667	7,57	5,34	25	0,21	0,15	271	3,03	1,60	124	1,89	0,74	99	1,97	0,58	148	3,45	0,76	9,17
	50x2	0,001465	1334	0	-	-	692	0,70	0,49	271	0,37	0,19	124	0,23	0,09	99	0,24	0,07	148	0,42	0,09	0,93

* Present value of return discounted at 6 per cent rate of interest

** The volumes used were that of the control trees (see Table 81)

Trees 3 years old: The probabilities are that these trees would be completely defoliated more than twice in succession. This should not be allowed to happen. These trees can be completely defoliated in one year without any previous indication of infestation. Since this is so, it is recommended that these trees be sprayed the year following complete defoliation.

Summarising, it can be said that total defoliation should be prevented. In cases especially prone to outbreaks, it might possibly not be economically justifiable to spray trees say every six years. In such cases resistant species will either have to be cultivated, or other control precautions such as, for example, pigs will have to be used.

E. Population density of *H. smilax*

Population density studies of the pine-bark emperor were undertaken in a block of 0,856 ha with 16 year old *P. patula* trees. In this case two successive generations were studied during the same season.

1) Pupal counts

Pupal counts were carried out during September and December, 1969 and during February, 1970. Pupation of the pine-bark emperor takes place in cracks against tree trunks. All pupae found lower than 4,5 m on 33 stems, were removed from their cocoons, counted and replaced in their cocoons. The pupae were removed to ensure that they were alive. This procedure was followed before the commencement of the season (September, 1969) and also subsequent to the pupation of each generation i.e. in January and April, 1970.

The number of pupae that were located is given in Table 86. The two sexes occur in more or less equal numbers, while the number of viable eggs is about 109 per female (see p.159). The descendents of the pupae could thus be calculated.

Table 86: Number of pine-bark emperor pupae found per tree during the 1969/70 season on the same 33 trees

Sampling date	Min	Max	Aver = a	Calculated number of pupae/100 m ² soil surface = 5a = b	Calculated number of viable eggs /100 m ² surface $\cong \frac{109}{2} \times b$
Sept, 1969	6	49	21,8	109	5 941
Jan, 1970	0	5	3,2	16	872
April, 1970	0	2	0,1	0,5	55

From Table 86 it can be seen that a drastic decrease in the population density occurred while this experiment was in progress.

2) Adult counts

Counting of adult insects was done once a week, between 1600 and 1700 hours, against the stems of trees in 10 plots (91 x 2,7 m each). As the adults emerge during the day and only fly away at dusk, these counts are regarded as a reasonably accurate estimate of the number of adults emerging in the plots during the days on which the counts were made. The results are indicated in Table 87.

Table 87: Total number of newly emerged pine-bark emperor adults counted once per week in 10 plots (91 x 2,7 m each)

Total for one day per week = a		Calculated total number per 100 m ² soil surface/season = $\frac{a \times 100 \times 7}{10 \times 91 \times 2,7}$	
First generation (October, 1969)	Second generation (January, 1970)	First generation	Second generation
75	23	21	7

According to this table, more were present during the first than the second generation. From the calculated number of adults per 100 m², it is clear that the number of emerging adults was much lower than the calculated number of pupae in the same area (Table 86). This reduction was most probably due mainly to predatism of pupae and moths by guinea-fowl (see below).

3) Larval counts

a) Counts of frass pellets

Forty-eight containers were placed out in the block as already described. The frass and severed needles were counted once a week and the frass of 10 containers individually compared with that of larvae of known instars.

The average number of frass pellets produced per instar as well as the average duration of each instar are summarized in Table 88.

The total numbers of frass pellets collected weekly in 48 containers are supplied in Table 89. The relative numbers of the different larval instars according to the size of frass pellets determined in 10 containers, are also supplied.

Table 88: Total number of frass pellets produced by the different larval instars of the pine-bark emperor

Instar	Number of frass pellets per instar	Average duration per instar in days	Average number of frass pellets per day per instar
1	171,1	8,7	19,7
2	225,6	9,1	24,8
3	282,9	9,7	29,2
4	540,6	17,3	31,2

Table 89: Total number of frass pellets produced by pine-bark emperor larvae collected weekly in 48 containers each with surface area of 1 811 cm² in the different blocks during 1969/70 and calculated number of larvae in the different instars as deduced from frass pellets (Is = Instar)

Week ending on	Total number frass pellets = a	Relative numbers of frass pellets of the different instars in 30 containers				Calculated number of larvae per 48 x 1 811 cm ² surface area = $\frac{a \times y}{Sx}$			
		Is 1 = x ₁	Is 2 = x ₂	Is 3 = x ₃	Is 4 = x ₄	Is 1	Is 2	Is 3	Is 4
1/11	72	25	0	0	0	4	0	0	0
8	317	78	23	6	0	12	3	1	0
15	972	135	90	20	0	27	14	3	0
22	2 471	418	324	139	7	59	36	13	1
29	1 541	166	235	148	41	22	25	13	4
6/12	799	54	146	172	57	5	11	11	3
13	1 170	30	52	191	95	5	7	21	10
20	588	4	18	89	131	0	2	7	10
27	432	0	9	21	70	0	2	3	10
3/1	211	0	0	15	61	0	0	1	5
10	37	0	0	0	8	0	0	0	1
17	8	0	0	0	2	0	0	0	0
Total						134	100	73	44
7/2	19	8	0	0	0	1	0	0	0
14	35	16	0	0	0	2	0	0	0
21	69	22	7	0	0	3	1	0	0
28	148	45	28	0	0	5	2	0	0
7/3	130	11	32	18	4	1	3	1	0
14	153	7	23	40	25	1	1	2	1
21	225	9	16	37	55	1	1	2	3
28	207	2	5	49	68	0	0	3	4
4/4	152	0	2	19	34	0	0	2	3
11	88	0	0	12	29	0	0	1	2
18	74	0	0	2	28	0	0	0	2
25	11	0	0	0	3	0	0	0	0
Total						14	8	11	15

According to this table, more frass pellets were produced during the first generation (November and December) than during the second generation.

If the average duration of the different instars is taken into consideration, and the fact that the sample surface was $48 \times 1\,811 \text{ cm}^2$ the number of larvae in the different instars can be calculated as indicated in Table 90.

Table 90: Calculated number of pine-bark emperor larvae per 100 m^2

Instar	Calculated total number of larvae per day ($48 \times 1\,811 \text{ cm}^2$) = a	Duration of instar in days = b	Calculated number of larvae per 100 m^2 during 1969/70 = $\frac{a}{b} \times \frac{100}{48 \times 0,1811}$
First generation			
1	134	8,7	177
2	100	9,1	126
3	73	9,7	87
4	44	17,3	29
Second generation			
1	14	8,7	19
2	8	9,1	10
3	11	9,7	13
4	15	17,3	10

From this table it is evident that there was a gradual reduction in the number of larvae from instar to instar.

If the number of first instar larvae calculated in Table 90 is compared with the numbers forecasted from pupal counts in Table 86, it is clear that the population as calculated from frass production was much lower than could have been expected from pupal counts. A very drastic reduction in the potential larval population is indicated. The pupal and/or adult stages of this insect appear to be especially vulnerable. The most important natural enemy of these stages is the guinea-fowl.

It is clear that the number of eggs predicted from the number of pupae and adults recorded for all three species of emperor moths, was much higher than the number of first instar larvae calculated from frass production. The following

are possible explanations for this. Firstly, predators may destroy a much greater proportion of pupae and adults than these studies revealed. Secondly, more eggs may be washed off by rain or destroyed by predators than found in these studies. Thirdly, the number of first instar larvae may be drastically decreased by predators shortly after emerging, or many may be unable to adapt themselves to prevailing ecological conditions. The last mentioned appears to be the most probable explanation because many dead first instar larvae were found.

b) Adult larval counts

The number of pupating larvae found against tree trunks in 10 lanes (2,7 x 91 m) was recorded once a week.

The results of these observations are supplied in Table 91.

As it takes about 2 hrs to construct a cocoon, and as pupation usually takes place during the day, probably about one sixth of the daily total was recorded once a week by the method employed.

Table 91: Total number of pupating pine-bark emperor, larvae observed once a week in 10 lanes of 91 x 2,7 m during the 1968/69 season and calculated number per 100 m²

Generation	Total number of pupating larvae observed once a week on trees in 10 lanes = a	Calculated number of pupating larvae in 100 m ² during the season = a x $\frac{100 \times 7 \times 6}{2,7 \times 91 \times 10}$
1	28	48
2	3	5

From Table 91, it can be seen that the number of pupating larvae was small after the first generation (i.e. about 10 per tree) and after the second generation very much smaller. If the number of final instar larvae which was determined by means of frass counts (Table 90) is compared with that of the pupating larvae (Table 91), it is obvious that the numbers agree fairly well.

F. Estimation of damage by *H. smilax*

Defoliation by the pine-bark emperor can occur twice during the same season while the trees are actively growing. After the first defoliation, new buds are formed, thereby providing food for the second generation.

Large scale total defoliation has only been observed with 16 year old *P. patula* trees. As it was observed that larvae can develop normally on trees as young as four years, it is taken for granted that this insect can attain pest proportions on all trees from the age of three years onwards.

1) Partial defoliation in the population study plot

As described for the other two species, 36 trees in the population study block were chosen for normal defoliation, while 36 trees in four groups around the block served as controls.

The trees were subjected to normal defoliation for one year and were all dusted the following year to keep them free of larvae.

The percentage defoliation calculated from the crown depth of the trees and the total number of needles collected in 48 containers, are indicated in Table 92.

Table 92: Percentage defoliation by the pine-bark emperor during the 1969/70 season determined from the average crown depth of the trees, the average number of needles per metre crown depth (= c) and the number of severed needle tips in 48 containers (c = 54 453)

Generation	Total number of severed needle tips in $48 \times 1811 \text{ cm}^2 = a$	Average crown depth in m = b	Percentage defoliation $\frac{a \times 48 \times 0,1811}{2,7 \times 2,7} = \frac{a}{c(b-1)} \times 100$
1	6 124	7,6	2,03
2	1 446	7,9	0,46

From this table it can be seen that the degree of defoliation was low both in December, 1969 and February, 1970.

The average c.b.h., heights and volumes of the different groups and the statistical analysis are supplied in Table 93.

From this table it is clear that the volumes of the two groups of 36 trees did not differ statistically from each other before or after the experiment. It is therefore clear that these minimal defoliations did not have a noticeable effect on tree growth.

Table 93: Average wood increment of 36 partly defoliated *P. patula* trees and 36 control trees (495 stems per ha and 16 years old) (D = Defoliated trees; C = Control)

Tree group	October 1969			% defoliation	July 1971			Vol wood increment
	c.b.h. in mm	height in mm	vol in m ³		c.b.h. in mm	height in m	vol in m ³	
D	814	16,5	0,329290	2,03+0,46*	912	18,5	0,437420	0,108130
C	814	16,5	0,329300	0	887	18,7	0,441430	0,112130
C-D			0,000010				0,004010	0,004000
t value = 0,001				t value = 0,174				

* = Two successive defoliations of 2,03 and 0,46 respectively; $t_{70}(,05) = 1,994$

2) Complete defoliation by natural populations

In a plot where the trees were partly defoliated in the 1967/68 and twice completely in the 1968/69 season, the trees were inspected four times a year, and the number of dead and abnormal trees recorded.

The influence of total defoliation on crown mortality and death of trees, is given in Table 94.

Table 94: Effect of two consecutive complete defoliations by pine-bark emperor larvae on 16 year old *P. patula* trees (D = Completely defoliated trees, C = Control)

Tree group	Stems per ha	Number of dead trees	Crown mortality	Normal trees	Percentage abnormal trees
D	652	31	3	292	10,4
C	719	0	11	305	0,3

From this table it can be seen that two defoliations during the same year had a definite influence on the trees. Besides this effect, there must have been a great loss in wood increment.

3) Complete defoliation by artificial populations

Procedure

Six and four year old trees were used to determine the effect of two defoliations, during the same year, on the wood increment. Both groups were situated on stand S.I. 70, and 10 paired observations on c.b.h. were made. The heights

were directly determined with the aid of a measuring stick. A treatment of 50 per cent defoliation was included in the case of the four year old trees.

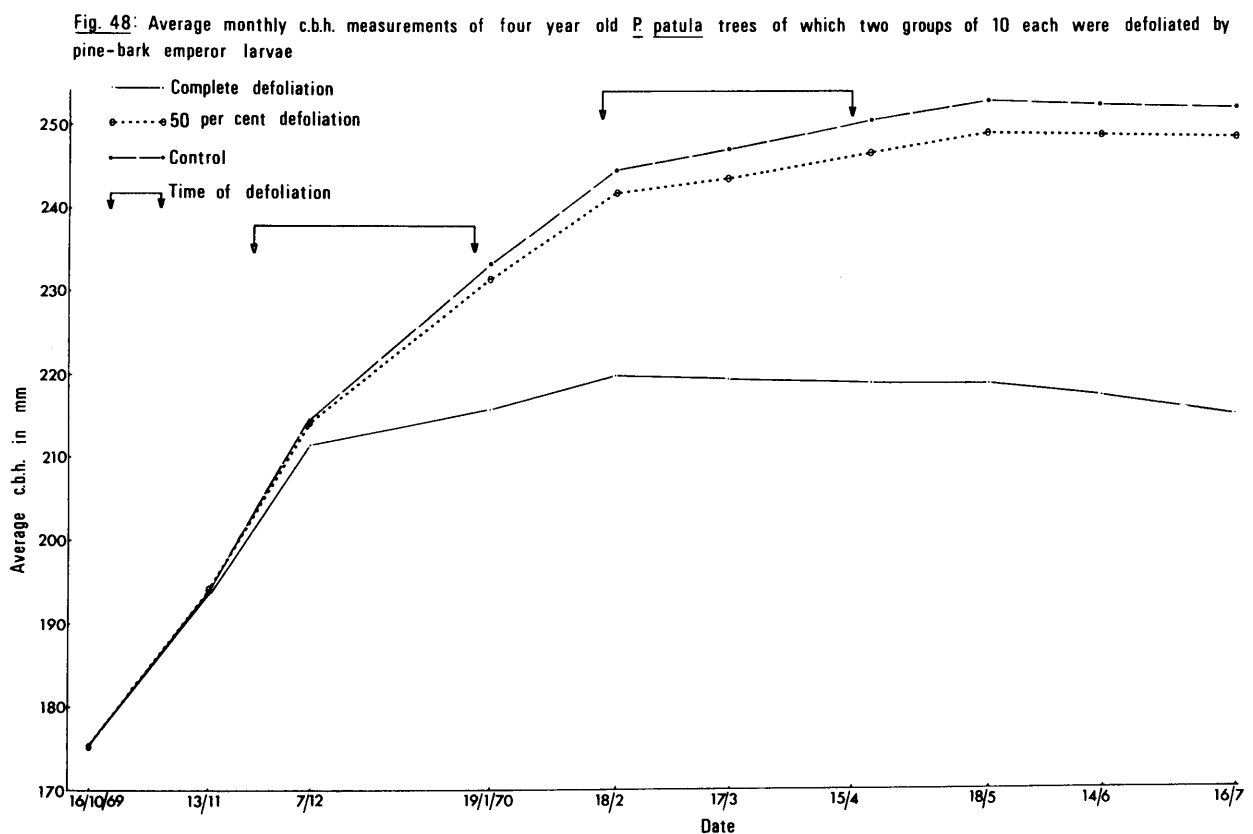
The treatment trees were defoliated during pine-bark emperor larval activity, namely, once during December, 1969, and once during March, 1970. All trees within 3,6 m from the experimental trees received the same treatment as these trees.

The desired degree of defoliation was obtained by removing the needles by hand during larval activity, and was spread over a period of about five weeks for for each tree.

The c.b.h. of the four year old trees was measured once a month while that of the six year old trees and all heights were determined a year later as well as at the end of the growing season of the next year. Note was also taken of dying trees.

Results

The average monthly c.b.h. of the three groups of trees in the four year age group is indicated in Fig. 48. From this fig. it is clear that the growing period is spread mainly over the months October to April.



The first defoliation takes place when approximately half of the yearly wood increment has already been added and the second at the commencement of the dormant period of the trees. The effect of the first complete defoliation is of such a nature that the growth of these trees is suppressed, whereas the growth is apparently little influenced by the initial 50 per cent defoliation. The effect of the second defoliation is that the growth of totally defoliated trees is completely inhibited and that the 50 per cent defoliated trees add very little wood. A further effect was that 4 of the 10 completely defoliated trees died during June to August, 1970.

Unfortunately part of the Kanonkop plantation was accidentally burnt down in August, 1970, with the result that 10 of the six year old, and 10 of the four year old trees were destroyed.

The average wood increment of the defoliated and control trees is indicated in Table 95 and the statistical analysis of the volumes in Table 96.

From Tables 95 and 96, the following conclusions can be made: At the commencement of this experiment, the different groups in each age group did not differ statistically from each other (see t values for 1969). Further conclusions are:

a) **6 year old trees** (stand S.I. 70 and 1 257 stems per ha)

After two complete defoliations in December, 1969 and March, 1970 the volumes of the defoliated trees were highly significantly smaller than those of the control trees ($t = 3,761$; $t_{18} (.01) = 2,878$). In the absence of further defoliation the previously defoliated trees grew more or less normally during the period October, 1970 to July, 1971, the volumes still being highly significantly smaller than those of the control trees. ($t = 3,641$; $t_8 (.01) = 3,355$). It is therefore clear that wood lost during one growing season can not be made up during the next.

b) **4 year old trees** (stand S.I. 70 and 1 193 stems per ha)

In this case a comparison will be made between three groups of trees i.e. two consecutive complete defoliations during one season (group D), two consecutive 50 per cent defoliations (group H) and the control (group C).

The 1970 t values indicate that after two defoliations during December,

Table 95: Average wood increment of four and six year old *P. patula* trees on stand S.I. 70 and level of defoliation during time of pine-bark emperor larval activity (D = Complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	No of trees/ha	n	Tree group	October 1969			% defoliation	October 1970				% defoliation	n	July 1971				Total vol wood increment in m ³ =c-a
				c.b.h. in mm	height in m	Vol in m ³ = a		c.b.h. in mm	height in m	Vol in m ³ = b	Vol wood increment in m ³ =b-a			c.b.h. in mm	height in m	Vol in m ³ = c	Vol wood increment in m ³ =c-b	
6	1257	10	D	30,3	7,6	0,020629	100	31,2	7,9	0,022930	0,002301	0	6	32,5	8,5	0,026704	0,003774	0,006075
			C	30,3	7,8	0,021331	0	33,4	8,4	0,028120	0,006789	0	4	38,1	9,4	0,040563	0,012443	0,019232
			C-D			0,000702				0,005190	0,004488					0,013857	0,008669	0,013157
4	1193	10	D	19,4	5,2	0,005764	100	21,9	5,4	0,007757	0,001993	0	5	23,3	6,3	0,010182	0,002425	0,004418
			H	19,4	5,2	0,005784	50	24,9	6,2	0,011409	0,005624	0	6	30,3	7,6	0,020757	0,010716	0,014973
			C	19,4	5,2	0,005772	0	25,3	6,6	0,012527	0,006755	0	4	31,4	7,6	0,022210	0,009683	0,016438
			C-D			0,000008				0,004770	0,004762					0,007258	0,012020	
			C-H			0,000012				0,001118	0,001131					0,001033	0,001465	
			H-D			0,000020				0,003652	0,003631					0,009291	0,010555	

Table 96: T values of data in Table 95 (t = t values during specific years; D = Complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Treatments compared	t 1969	t 1970	t 1971
6	C & D	0,706	3,761**	3,641**
4	C & D	0,034	9,902**	8,212**
	C & H	0,059	2,401*	1,100
	H & D	0,090	8,689**	7,107**

* Indicates significant differences

** Indicates highly significant differences

1969 and March, 1970 the volume of wood of the control trees was highly significantly bigger than that of the completely defoliated trees, and significantly bigger than that of the 50 per cent defoliated trees (C & D, $t = 9,902$; C & H, $t = 2,401$; $t_{18} (.01) = 2,878$ and $t_{18} (.05) = 2,101$). The volume of the 50 per cent defoliated trees was also highly significantly bigger than that of the completely defoliated trees ($t = 8,689$; $t_{18} (.01) = 2,878$). The 1971 t values indicate that, in the absence of further defoliations, the trees previously completely defoliated, that were still alive, grew more or less normally during the period October, 1970 to July, 1971, the differences remaining highly significant when the control or 50 per cent defoliated trees are compared to the completely defoliated trees, (C & D, $t = 8,212$; $t_7 (.01) = 3,499$, H & D, $t = 7,107$; $t_9 (.01) = 3,250$). The volume of the control trees was still bigger than that of the 50 per cent defoliated trees but the differences were not significant ($t = 1,100$; $t_8 (.05) = 2,306$).

The percentage increment loss as a result of defoliation is provided in Table 97.

Table 97: Percentage increment loss per year as a result of two consecutive defoliations during one year as calculated from Table 95

Commencing age in years	% defoliation	% wood loss		Total % loss
		October 1969- October 1970	October 1970 -July 1971	
6	100	66,1	69,7	68,4
4	100	70,5	75,0	73,1
	50	16,7	-10,7	8,9

From this table it can be seen that a slightly larger percentage of wood increment was lost by the four, than by the six year old trees. In the absence of further defoliations, the wood increment of previously defoliated trees was more or less normal during the period October, 1970 to July, 1971. Except for the 50 per cent defoliated four year old trees, the wood lost during one season can not be recovered during the next.

The average volume wood increment calculated according to stem-analysis is given in Table 98. The losses indicated are in fair agreement with those previously calculated (Table 95).

Table 98: Average volume wood increment of four and six year old *P.patula* trees as calculated according from stem analysis (D = Complete defoliation; H = 50 per cent defoliation; C = Control)

Commencing age in years	Tree group	Volume wood increment during the growing season	
		1969/70	1970/71
6	D	0,005686	0,004888
	C	0,007376	0,005564
	C-D	0,001690	0,000676
4	D	0,002706	0,001686
	H	0,002308	0,002055
	C	0,002861	0,002479
	C-D	0,000155	0,000793
	C-H	0,000553	0,000424

If thinning were done as indicated previously, the financial loss can be calculated as summarized in Table 85.

From Table 85 it can be seen that the financial loss is higher for the four than for the six year old trees. The discounted financial losses calculated for both age groups were higher than the cost of one application of the insecticide (R4,50/ha). The spraying cost is however higher than the calculated discounted financial loss in the case of four year old trees twice defoliated to an extent of 50 per cent.

Very little is known about the pine-bark emperor. It appears that two suc-

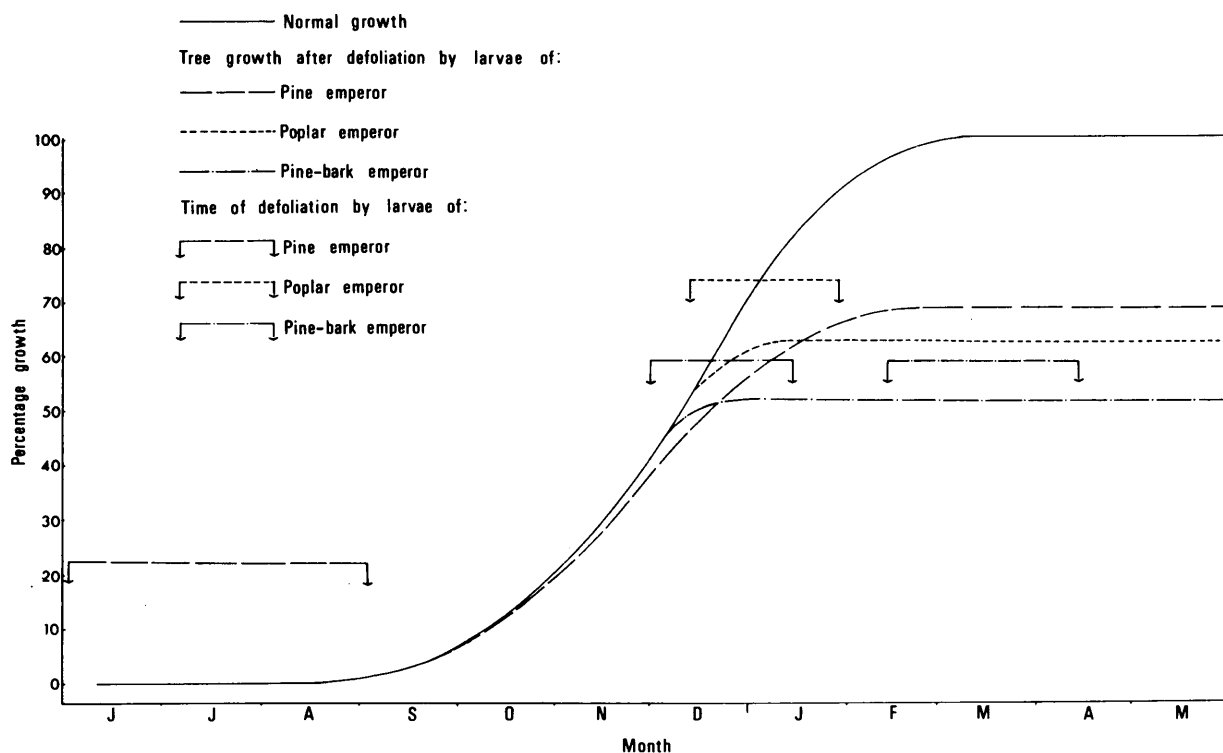
cessive defoliations are highly improbable. Spraying would thus only be aimed at preventing one or two defoliations. Since the trees die as a result of two successive defoliations, it is recommended that those up to six years old be sprayed the year following a complete defoliation. It is reasonably certain that the same holds good in the case of older trees although specific experiments with them have not yet been carried out. Trees older than six years suffering more than 50 per cent defoliation should also be sprayed during the next larval generation.

Summarising, it can be said that spraying would be economically justified if two consecutive complete defoliations can normally be expected.

G. Comparison of damage by three emperors

In Fig. 49 a comparison is made between normal growth of *P. patula* on the one hand and growth after defoliations by larvae of the three emperors studied.

Fig. 49: Growth of *P. patula* when defoliated by larvae of three species of emperor moths



From this fig. it can be seen that the trees grow mainly during the months

October to April. It is further clear that defoliation by the pine emperor larvae takes place during the resting period of the trees. Contrary to this, defoliation by the poplar emperor larvae occurs when the trees are actively growing, at a time when about a quarter of the yearly growth has been added. Defoliation by the pine-bark emperor larvae takes place when about half and again after about 90 per cent of the wood has been added. What is however important is the time of defoliation, and especially the fact that defoliation during the growing season inhibits growth to a greater extent than defoliation during the resting period.

These studies also indicate that trees defoliated during the resting period (pine emperor) do not die, while trees defoliated during the growing period may die if subjected to two defoliations during the same or consecutive growing seasons.

Kulman (1971), after summarising other publications, came to the conclusion that evergreen conifers usually survive a single complete defoliation in spring before the elongation of new foliage, and that later defoliation including the new foliage often causes mortality. He further states that pines usually show an immediate response to defoliation if it occurs before shoot or ring growth is completed. The findings of the present studies therefore agree with those of Kulman.

CHAPTER 6: NATURAL ENEMIES AND DISEASES

A. Natural enemies and diseases of *N. cytherea clarki*

1) Parasites

Parasites do not appear to be able to suppress the pine emperor in plantations. The following parasites however contribute towards some degree of its control.

a) Egg parasites

The egg parasites *Mesocomys pulchriceps* Cam., *Anastatus* sp. Ac. X. P24 (Eupelmidae) and *Pediobius* sp. Ac.X.P7 (Eulophidae) were reared from pine emperor eggs (Van den Berg, 1968). The biology and development of *M. pulchriceps* has been studied by Van den Berg (1970).

After most of the pine emperor eggs had hatched, counts were made of the number of eggs hatching and those failing to do so. Large numbers of the latter were collected and kept in honey jars to determine whether any parasites would emerge. The results of these studies can be found in Table 99.

During previous investigations, *Anastatus* sp. Ac.X.P12 was not found in pine emperor eggs, while the status of *Pediobius* sp. Ac.X.P7 was still uncertain (Van den Berg, 1968). *Pediobius* sp. Ac.X.P7 is however also a primary parasite, as it was reared on laboratory laid pine emperor eggs without any other parasites being present.

Table 99: The development of egg parasites from field collected pine emperor eggs during the 1969 season.

Collection place	Number of eggs collected	Percentage eggs destroyed by parasite				Total % parasitism
		<i>Mesocomys pulchriceps</i>	<i>Anastatus</i> sp. Ac.X.P24	<i>Anastatus</i> sp. Ac.X.P12	<i>Pediobius</i> sp. Ac.X.P7	
<i>Welgelegen</i>						
i) Pine trees	1 792	6,9	0,4	0,2	0,9	8,4
ii) Indigenous trees next to pines	2 014	7,9	0,7	0,1	0,9	9,6
<i>Usutu</i>						
i) Pine trees	917	6,0	0,5	0,2	2,3	9,0
ii) Indigenous trees next to pines	836	7,3	1,1	0,8	3,9	13,1
iii) Indigenous trees about 50 m from pines	173	96,5	0,0	0,0	2,3	98,8

The high percentage of parasitism by *M. pulchriceps* on indigenous plant growth, situated about 50 m from pine trees, is very striking. As it has already been concluded that *M. pulchriceps* is as active on cultivated pine trees as on natural plant growth situated between these trees (Van den Berg, 1968), the pines apparently do not repel the parasite. The following may explain the difference in the percentage parasitism. Firstly, it has been found that the life cycles of the parasite and that of the pine emperor are not synchronized. Alternative host insects thus play an important role in the survival of egg parasites (Van den Berg, 1968). Most of these alternative host eggs can probably be found on indigenous plant growth. If eggs are laid on or near plants where parasites emerge from alternative host eggs, they will be subject to a greater degree of parasitism than eggs further away from the alternative host eggs. Secondly, a larger number of eggs appear close together on cultivated pines than on the sparsely distributed indigenous shrubs. If the egg parasites are distributed more or less evenly over a fairly wide region, fewer parasites for the same number of eggs will therefore be available in the case of pines than in that of indigenous shrubs, resulting in widely different degrees of parasitism.

The percentage parasitism by the four species of egg parasites agree fairly well with the results of previous investigations (Van den Berg, 1968).

b) Larval parasites

At least 200 larvae of each instar were collected, reared in cages of 30 x 30 x 45 cm and notes kept of all parasites making their appearance in these cages. Parasitised larvae were also looked for in plantations.

(i) *Ceromya luteicornis* Curr. (Tachinidae)

As far as could be determined, this parasite has not previously been bred from any of the subspecies of *N. cytherea*.

Usually two or three eggs are laid on pine emperor larvae in the first instar. The adult parasite emerges from pine emperor larvae during the second instar, frequently when the host is about to moult to the third instar. Of the collected larvae with eggs attached to them, only about one third were killed by the parasite. In all cases, one parasite emerged per host, the results of superparasitism, presumably brought about by larval competition. This species was found in the Usutu and Welgelegen plantations. The estimated percentage of parasitism on indigenous vegetation and on

P. patula is about 0,5 per cent.

(ii) *Apanteles maculitarsis* Cam. (Braconidae)

This is a well-known internal parasite of pine emperor larvae (Taylor, 1967).

The female lays a few eggs in quick succession in the same larva. The attacked larva often curls up and vomits a few drops of intestinal juice. Parasites trying to parasitise older larvae (fourth instar) are often injured by the larva curling up quickly and using its mandibles to defend itself against attack. The development of different larvae in the same host is very well synchronized as they all burrow their way out of the host at almost the same time, about three weeks after egg laying. The full-grown larvae then spin separate cocoons on the skin of the host larva, directly above their emergence holes. The prepupae take up a position with their heads away from the skin of the host larva. The prepupal stage occurs when the pine emperor larvae are in their third or fourth instar. The average number of parasite larvae developing per host is 11 (3–24 for 23 parasitized larvae) for third instar hosts and 27 (5–63 for 20 parasitized larvae) for fourth instar hosts.

Parasitized emperor larvae from which full-grown *A. maculitarsis* larvae have emerged a short while previously, stop feeding and crawl about for up to ten days, but eventually die. In nearly all cases, however, the adult parasites emerge after the host larvae have already died. A secondary parasite *Eurytoma* sp. Ac.X.P31 (Eurytomidae) developed in small numbers from *A. maculitarsis* cocoons. This secondary parasite presumably parasitises prepupae of *A. maculitarsis* in their cocoons. They emerge about a week later than *A. maculitarsis* adults. The emergence holes of *Eurytoma* sp. Ac.X.P31 differ from those of *A. maculitarsis*, a round hole being made dorso-laterally by the former, whereas a round lid is formed dorsally by the latter.

A. maculitarsis was also bred from *Nudaurelia wahlbergi* (Bsd.) larvae found near the Welgelegen plantation. *N. wahlbergi* thus serves as an alternate host for this parasite,

(iii) *Theronia* sp. Ac.X.P49 (Ichneumonidae)

As far as is known, this is the first record of this parasite being bred from both subspecies of *N. cytherea*

The full-grown parasite larva burrows out through the skin of the dead host

larva, and forms its cocoon between the dead larva and the object its host had been clinging to. The parasite larva emerges from pine emperor larvae when the latter are in their second or third instar. *Eurytoma* sp. Ac.X.P31 is also a secondary parasite emerging from the cocoons of this parasite.

Theronia sp. Ac.X.P49 contributes very little to the control of the pine emperor, as only six of them emerged from about 3 000 larvae kept under observation.

(iv) *Compsilura concinnata* Mgn. (Tachinidae)

According to Grobler (1957), this tachinid was imported from the U.S.A. in 1942 and released in the Jessievale and Spitzkop plantations with the object of controlling *Euproctis terminalis*.

This parasite has already been bred from pine emperor larvae collected from the Spitzkop area (Grobler, 1957). During the present study, it was recorded from the Usutu and Welgelegen plantations. Usutu is situated approximately 48 km East South East and Welgelegen 60 km North East of the Jessievale plantation respectively. This indicates that the species not only adapted itself well to these conditions, but also dispersed well.

It lays its eggs on any part of the body of the host larva. After hatching, the young maggot burrows through the host's skin and develops as an internal parasite. The full-grown maggot leaves the host after the host has died. This parasite also probably contributes very little to the control of the pest, since the degree of parasitism found in this study was only about one per cent.

(v) *Carcelia evolans* Wied. (Tachinidae)

Egg laying and development are more or less as described above for *C. concinnata*. The full-grown maggot emerges shortly after pupation of its host and forms a puparium in or near the host pupal cell. Percentage parasitism by this species was less than one per cent. Therefore its contribution towards control of the pest appears minimal.

A secondary parasite (parasite Ac.X.P60-Diapriidae) emerged from one of the puparia of this tachinid.

c) *Pupal parasites.*

More than 2 000 pupae were collected from the field, buried in soil at a depth of about 20 mm, and covered with a needle mat about 20 mm thick in cages of

1 x 1 x 2 m. Records were kept of the number of adults emerging and of any parasites making their appearance in these cages. Two months after the last adults had emerged, all remaining pupae were dissected

(i) Sp. Ac.X.P52 (Ichneumonidae)

This parasite emerges from pine emperor pupae, but at precisely what stage the host is parasitised is still uncertain. The percentage parasitism was about one per cent, therefore its contribution towards control of the pest is probably more important than the tachinid just mentioned.

2) Predators

Predators appear to be the most important biological agencies limiting the numbers of the pine emperor. All stages are preyed upon by some or other enemy. The stages particularly vulnerable are the larvae and adults. If certain of these predators appear in adequate numbers and are not disturbed, the pine emperor will probably cease to be a pest. In such areas the pest will usually be found in small numbers only, but sporadic outbreaks may occur, which will however again be suppressed by the predators.

a) Invertebrate predators

(i) Bloodsucking Hemiptera

In the case of certain lepidopterous larvae, distinct spots appear at the points where the piercing mouthparts of bloodsucking Hemiptera penetrate their bodies. Such marks, however, do not appear on pine emperor larvae or adults.

Glypsus conspicuus Westw. (Pentatomidae) was found to be the most important of these Hemiptera, attacking larvae as well as adults. Small numbers of two other species, i.e. *Dermatinus lugens* Stål. (Pyrrhocoridae) and *Rhinocoris pulvisculatus* Dist. (Reduviidae) were also observed attacking adults. The attacked larvae try to escape but apparently seldom succeed. All larval instars, and even adults, are preyed upon. Adults are sometimes attacked by groups of hemipterous nymphs. The mortality caused by *G. conspicuus* is estimated at between 5 and 10 per cent of the whole annual population. This species was very troublesome during field experiments, for instance where large numbers of larvae were employed to effect certain levels of defoliation.

(ii) **Mantids**

Two species, namely *Polyspilota aeruginosa* Goeze., and *Cilnia humeralis* Stål. were found to prey on pine emperor larvae and adults. Small larvae up to and including the third instar are easily caught by the adults of these mantids. Larvae in the fifth instar may be caught, but are able to wriggle themselves free and then drop to the ground. Frequently only part of an adult's abdomen is bitten off by a mantid. These injured adults may stay alive for a day or two and also fly about.

(iii) *Pteronemobius* sp. Ac.X.P54 (Gryllidae)

This cricket occasionally feeds on the expanding wings of freshly emerged moths with the result that the wings do not unfold normally, are damaged by holes or covered with blotches of tangled body fluids. These moths are hampered in their flight and in extreme cases such females may be unable to locate suitable oviposition sites.

(iv) **Spiders**

Olios sp. Ac.X.P53 (Sparassidae) preys on pine emperor larvae up to the fourth instar. Practically the whole larva is devoured. These spiders have been observed to ascend young *P. patula* trees (about 4 m high, pruned clean to a height of 1,5 m).

Caerostris sp. Ac.X.P47 (Argyropidae) was observed preying on adults. This spider spins a large web in which the moths are caught and sucked out.

b) **Vertebrate predators**(i) **Cape Chacma Baboon (*Papio ursinus* (Kerr))**

According to Tooke & Hubbard (1941) baboons appear to prey on all stages of the pine emperor, including the eggs. They are among the most important enemies of the pine emperor. They are, however, found only in hilly regions, and were not present in the Usutu plantation. In certain other areas they are considered a pest and are being eradicated. At Welgelegen, two troops, each consisting of more than 30 individuals, were present in 1969, each troop roaming over its own separate territory.

Eggs

A total of 1 000 eggs appearing on indigenous trees and shrubs less than 2 m

high were marked with cards (13 x 8 cm). These eggs were visited five times per week and counts made of remaining eggs as well as the number of larvae hatching from them.

From these observations it could be calculated that 43,1 per cent of the eggs disappeared during April, 1968. Baboons were active in this area and their faeces showed unmistakable signs that they had been actively preying on pine emperor eggs or gravid females. However, even with the aid of binoculars, it could not be determined whether baboons prey on the egg stage.

Larvae

Baboons have been observed to devour larvae, apparently swallowing them completely. Since nothing is left uneaten it was not possible to determine with certainty their contribution to the control of pine emperor larvae. Baboons are especially active in areas where young pine trees or indigenous trees are infested with larvae, as well as under large trees at the time that full-grown larvae descend the trees for pupation in the soil.

Pupae

Although it is believed that baboons dig out and devour pupae, this has not yet been directly observed in the field.

Adults

Baboons catch the inactive moths during the daytime. The wings are not eaten, but bitten off and dropped in a heap close together. Use was made of this fact to form an estimate of the roll played by baboons in destroying adults.

During the months February to May of the years 1968, 1969 and 1970, all moths, alive or dead, as well as all wings in 10 previously marked lanes (2,7 x 91 m) in two blocks, each 0,856 ha in extent, were counted weekly. All dead moths as well as all wings were buried after counting. Each group of four wings was recorded as one moth devoured by baboons.

From these counts it was calculated that of a total of 374 adults, 137 or 36,6 per cent were destroyed by baboons in 1968; in 1969, 179 adults or 65,6 per cent were devoured out of a total of 273; and during 1970, 51 adults or 48,1 per cent

were killed out of a total of 106.

The adults preyed upon are those sitting low down, many of them having emerged the previous night, and therefore before having laid any eggs. Moths dying of old age are apparently not eaten.

As more male moths can usually be located on the lower parts of stems during daytime, it is probable that more males than females are destroyed. Since a small proportion of gravid females can fall prey to baboons, not only the adult population but also the number of eggs to be laid may be affected.

(ii) **Vervet Monkey** (*Cercopithecus aethiops* (L.))

In contrast to baboons, monkeys feed not only low down but at all heights in the trees. It has been observed that freshly emerged, as well as older moths, are devoured and that the wings are also dropped, falling far apart and not in groups or heaps of 4 together. Since this is also the case with predation by birds, it was not possible to distinguish between the contribution made by these two groups of predators.

About five per cent of the adults were destroyed by either monkeys or birds in an area kept under observation in the Welgelegen Plantation during 1968. Monkeys were also active in trees harbouring larvae, but no direct proof that they do prey on larvae could be found.

(iii) **Bush Pig** (*Potamochoerus porcus* (L.))

There are strong indications that Bush Pigs dig up pupae. Signs of their diggings in infested areas have already been noticed by certain foresters. According to De Kock (personal communication), a herd of Bush Pigs was driven into an infested plantation to control the pine emperor. These pigs remained in the vicinity and reportedly kept this pest under control.

As the Bush Pig roots up the soil with its snout and obtains its food in this manner, it can be accepted with reasonable certainty that they will devour any pupae located by chance. It is also possible that they can locate pupae by smell as domestic pigs learn to do.

(iv) Birds

Larvae killed by birds are often not entirely devoured, leaving certain remnants behind from which the activity of bird predators can be recognized.

It was noticed that the Cape Raven (*Corvultur albicollis* (Latham)) preys on pine emperor larvae. Only four of these ravens were seen in the Welgelegen plantation during 1969, so that only a small contribution to the control of a large outbreak could be expected. Taylor (1967) states that the Cape Raven is probably a predator of *N. cytherea cytherea* adults in the Eastern Cape. It is therefore possible that pine emperor adults are also eaten.

The Steppe Buzzard (*Buteo buteo* (L.)) and the Cape Fiscal Shrike (*Lanius collaris* (L.)) are exceptionally active in infested areas in the Welgelegen and Usutu plantations, and may be predators of larvae and adults.

In the Mhlahlane and Bele plantations (Tsolo, Transkei), it was observed that Ground Hornbills (*Bucorvus leadbeateri* (Vigors)) are active predators of pine emperor larvae. These Hornbills apparently do not penetrate deep into the plantations and thus are only active along roads and on the outskirts of the plantations. Other birds that were also active in this infested area during the larval stage were the Black-headed Oriole (*Oriolus larvatus* Lichtenstein); the Fork-tailed Drongo (*Dicrurus adsimilis* (Bechstein)) and the Backbackiri (*Telophorus zeylonus* (L.)).

3.) Pathogens

Pathogens are of great importance in the biological control of both subspecies of *N. cytherea*. However, these pathogens do not exact their toll so regularly that they can be relied upon.

Tooke & Hubbard (1941) reported two types of pathogens, namely the polyhedral wilt disease and a mummifying disease.

The following examples concerning the pine emperor may be quoted: Hepburn (1961) mentioned that a large larval population was wiped out in the Barberton District in 1960 during an epidemic of some disease. Van den Berg (1964) states that a population in the Canaan plantation (Richmond, Natal) decreased by about 99 per cent due to an epidemic disease.

a) Viruses

Prinsloo (1967) could obtain no inclusion bodies from diseased pine emperor larvae.

Dr. A. Polson of the Virus Research Institute, Cape Town, found three types of viruses from larvae sent to him from the Welgelegen plantation during 1969. These viruses were named the β , ξ and β -related *Nudaurelia* viruses. It is surmised that larvae excreting a bright red paste-like faeces adhering to the anal plates, are infected with one or other of these viruses.

It appears that third, fourth and final instar larvae die more frequently due to viruses than the earlier instars. Kitajima (1926, according to Aruga in Steinhaus, 1963) found that general polyhedrosis could not be induced in second and third instar larvae of the silkworm while it could be done during the fourth and especially the fifth instar. This agrees with field observations on the pine emperor, namely that the more advanced larval stages appear to be more vulnerable to virus diseases.

During 1970, a strong wind from 3–9 mps blew continuously at Welgelegen for 22 hours. After about three weeks, many larvae died from “wilt-disease” virus. It would appear that wind has an influence on the susceptibility of the larvae to the virus, probably because feeding was interfered with, thus weakening their general resistance.

From 1967 to 1970 the infestation of the Welgelegen plantation spread from the same locality with a decline to the east; this took place annually. However, the plague was of economic importance only in this one locality. As the strongest winds usually blow from the west, this locality is better protected against winds. “Wilt-disease” also occurred here. The incidence of the disease was, according to general observations, lower than in the areas more exposed to the western winds. The strongest winds during the larval periods blew from the west during 1968 and 1969, and most probably also mainly from the west during the previous year as well. From these findings one is tempted to suggest that windy conditions may be responsible for stresses, making the larvae of the pine emperor more susceptible to virus and probably also to other diseases.

A stressor is an environmental factor or condition which causes deviation from the normal or preferred state in the animal (Jaques, 1961). There is ample evidence that chronic and latent infections commonly occur in insect populations (Kilgore &

Doutt, 1967). Aruga in Steinhaus (1963) proposes two main factors which are involved in the induction of occult insect viruses: (a) a genetic factor, (b) the physiological conditions which allow the insect to respond to the action of the inducing agent by the production of virus. Jaques (1961) fed larvae of *Trichoplusia ni* (Hübner) with low dosages of the nuclear-polyhedrosis virus. Larvae which were then placed under a constant physical stress of vibrations were up to four times as susceptible to the incidence of polyhedrosis as unstressed larvae. The stress could have acted by provoking an occult virus or by rendering the host more susceptible to the virus, or by a combination of both mechanisms (Jaques, 1961).

b) Bacteria

According to Prinsloo (1967), *Serratia marcescens* Bizio is an important mortality factor of the pine emperor. During tests undertaken during 1965 and 1966, 50 per cent of diseased larvae harboured *S. marcescens*. These larvae were exposed to food shortage and extreme cold and wandered on the ground for quite a time. It was assumed that these larvae became infected with this bacteria existing saprophytically on the decaying needle mat.

c) Fungi

Fungi play a less important role in the control of the pine emperor than found by Grobler (1957) for *Euproctis terminalis*.

(i) Larval fungus

The brown fungus, *Entomophthora* sp., also affects the wattle bagworm (*Kotochalia junodi*) (Hepburn, in press). It may be the same species as the one found on the pine emperor.

Although it often affects pine emperor larvae, no outbreaks of this disease have yet been noticed or recorded. Larvae killed by this fungus are covered with white spores, which can also be seen on the ground in the vicinity of the dead larvae. After a time the larvae dry up completely.

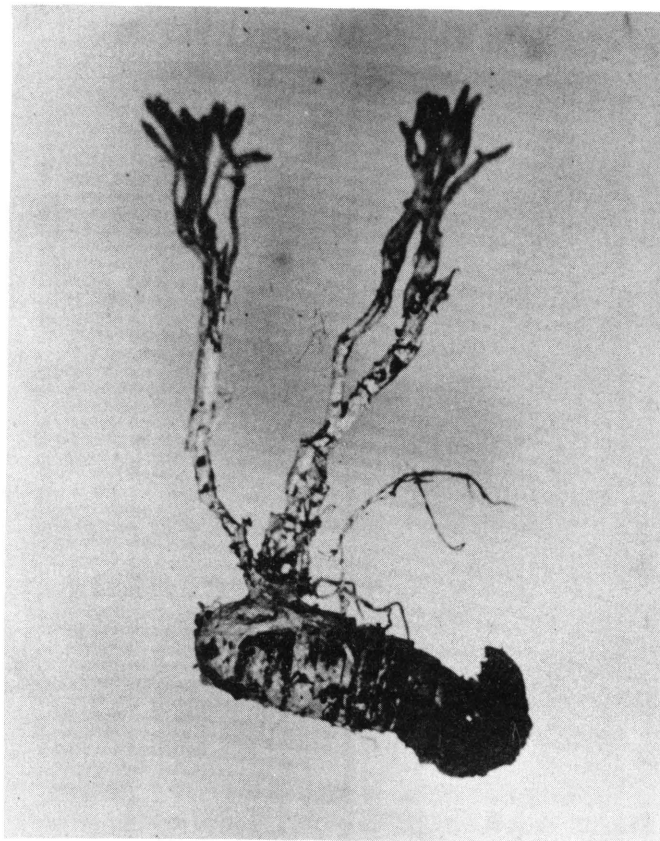
Cladosporium cladosporioides (Fresen.) De Vries, was obtained from dead pine emperor larvae. Although the group to which this fungus belongs, is often saprophytic, Dr. W.F.O. Marasas of the Pretoria herbarium is of the opinion that it is probably parasitic on pine emperor larvae.

(ii) **Pupal fungus**

During 1968, fungus infected pupae were found in the Welgelegen plantation. The same fungus was also found the following year at the Usutu plantation.

Dr. C. Booth of the Mycological Institute, London, identified the fungus as *Cordyceps taylori* Saccardo (Plate 18).

Plate 18: Pine emperor pupa infected with the fungus *Cordyceps taylori*



According to Dr. Marasas, the species has not yet been recorded in the Republic. The only publication that could be traced in the literature on this fungus, is that by Saccardo (1883) who provides a short description of the species and mentions that it was discovered in Australia in 1843.

Larvae wandering about on the soil before pupation probably come into contact with the spores present on the needle mat. They pupate normally, but the fungus then attacks and kills the pupae, later filling them completely with mycelium.

The fertile hyphae grow through the needle mat during February to April, their tips at first turning slightly orange-red, and later white when new spores are produced. The spores can be dispersed by wind and rain and can make contact with larvae of the following or a later generation crawling about on the substrate.

In the Barberton district where fungal activity causes the death of pupae, the percentage of pupae infected with the fungal growth was determined in 10 randomly chosen plots each measuring 2,7 x 2,7 m. All pupae that could be located were thoroughly inspected and classified as either healthy or infected with a fungal growth. From these studies it was found that 4,9 per cent of the pupae were killed by this fungus during 1967/68 and 3,7 per cent during 1968/69.

4) Life tables

Procedure

Pine emperor adults busy copulating were collected and placed in gauze cages containing pine branches. Eggs laid on these branches were tied to small *P. patula* trees (four years old) the following morning – about thirty per tree, until a total of 1 000 eggs was reached. These eggs were marked with small white cards, (13 x 8 cm), on which the number of eggs was written. Of eggs occurring naturally on indigenous trees and shrubs (0,5 – 2 m high), a further 1 000 were marked. All other eggs on these trees as well as all on the vegetation occurring underneath them, were removed.

The two groups of 1 000 eggs and larvae hatching from them were examined and counted at least five times a week. The number of individuals and, where known, the cause of death of each individual, were recorded on these cards. Unhatched eggs were collected and placed in honey jars in the laboratory, for parasite development.

Final instar larvae nearing the prepupal stage were transferred to trees with cloth funnels around them, so that all pupating larvae could be collected and placed in fruit jars half filled with damp earth. These pupae were then removed and buried separately at a depth of about 50 mm in the soil underneath the trees and marked with pegs driven in the soil about 30 cm away from each pupa. Once a month the pupae were dug out, examined and reburied in the same position.

From the two life tables compiled according to this method, an estimated life table was constructed for large trees (15 years old). The numbers in this estimated

life table were obtained by averaging the other two. In cases where eggs and larvae were lost from young trees, probably due to predation by baboons, these losses were reduced in the life table for the older trees, as baboons could not have reached all of them. However, larvae descending taller trees can fall prey to baboons, which explains the smaller role of this mortality factor in older trees. The number indicated for the older trees reflects the probable degree of predation by baboons at the time of pupation. For the purpose of life table studies, 100 pupae were buried under 15 year old trees as indicated above. Of the diseases, those due to viruses are regarded as the most important. No distinction could be made between stinkbug predation and death due to diseases. For this reason these two factors have been grouped together. It is however highly probable that stinkbugs were the more important of the two during these experiments, as they were often observed together with the larvae on which they had been preying.

For the older trees, the calculated percentage predation by baboons on adults for the year 1969 was used (65,6 per cent). Baboons will most probably concentrate more on areas with high, than on those with low populations. Furthermore, the chance of detecting a moth on the bare stem of a 15 year old tree is much greater than that of finding it between young unpruned trees. It was therefore decided to accept a figure of 32,8 per cent as more realistic for predation by baboons in the case of unpruned young trees.

Results

Life tables for the pine emperor in the three ecologically different areas in the Welgelegen plantation for the period February, 1968 to May, 1969 are indicated in Table 100. In all three cases the probable fate of 1 000 newly laid eggs is reflected from the time they were laid until the adult stage was reached.

Many of the eggs simply disappeared, probably due to predation by baboons. During the egg stage this could be regarded as one of the most important mortality factors, especially on indigenous trees and shrubs. Parasitism and inviability were also important factors for reducing the egg population.

The larval stages were especially prone to attack by stinkbugs and/or viruses. Snow and predation by baboons and birds, also proved to be of considerable im-

Table 100: Life tables of the pine emperor in three ecologically different areas from February, 1968 to May, 1969.

Stage and mortality factor	Four year old <i>P. patula</i> trees		Indigenous trees and shrubs		Estimated table for 15 years old <i>P. patula</i>	
	Number of individuals		Number of individuals		Number of individuals	
	Commence-ment of stage	Destroyed during stage	Commence-ment of stage	Destroyed during stage	Commence-ment of stage	Destroyed during stage
Egg stage	1 000		1 000		1 000	
(a) Inviability		86		71		79
(b) Inability to hatch (dead in shell)		35		27		31
(c) Parasitism by						
(i) <i>Mesocomys pulchriceps</i>		95		83		89
(ii) <i>Anastatus</i> sp Ac.X.P. 24		28		31		30
(iii) <i>Anastatus</i> sp Ac.X.P.12		9		0		5
(iv) <i>Pediobius</i> sp Ac.X.P7		58		52		55
(d) Predation by ? baboons or birds (disappeared)		67		337		0
Total destroyed		378		601		289
Larval stage	622		399		712	
(a) Snow		156		73		176
(b) Predation						
(i) Stinkbugs and/or virus		256		202		293
(ii) Mantids		4		26		5
(iii) Baboons or birds (disappeared)		195		93		20
(c) Diseases						
(i) <i>Entomophthera</i> sp..		1		0		1
(d) Parasitism						
(i) <i>Apanteles maculitarsis</i>		3		5		3
Total destroyed		616		399		498
Pupal stage	6		0		214	
(a) Parasitism						
(i) <i>Carcelia evolans</i>		0		—		3
(ii) Sp Ac.X.P52		0		—		1
(b) Diseases						
(i) <i>Cordyceps taylori</i>		0		—		9
Total destroyed		0		—		13
Adult stage	6		0		201	
(a) Predation						
(i) Baboons		2		—		132
(ii) Monkeys and/or birds		0		—		10
Total destroyed		2		—		142
Number of adults able to mate and lay eggs	4		0		59	

portance in reducing larval populations.

On indigenous trees and shrubs practically all the larvae disappeared during one day. It may be taken for granted that even a much higher population would have suffered the same fate. Predation by baboons is the most likely explanation.

The pupal stage appeared to be the least vulnerable. A fungus disease, *Cordyceps taylori*, appeared to be the most important pupal mortality factor. No evidence of predation on pupae was found.

Newly emerged adults underneath tall trees were considerably reduced by baboons.

Although all mortality factors could not be identified, it appears that baboons were by far the most effective natural enemies. Of the parasites, those of the egg stage were most important.

Of the 1 000 eggs with which the experiment was commenced, not a single individual reached maturity on indigenous trees and shrubs. On 4 and 15 year old *P. patula* trees, respectively 4 and 59 adults reached maturity and were able to mate and lay eggs. On the assumption that a female lays an average of 182 eggs, about six females, and therefore six pairs of males and females would be required to lay 1 000 eggs. The population in the case of the 15 year old trees could therefore have increased five fold, while in the four year old trees it would have been reduced to a third of that of the previous season. It is clear that the ecological processes prohibiting this species from multiplying excessively in the undisturbed natural ecosystems occurring in its area of distribution, have been drastically curtailed in the artificially created ecosystem of the pine plantation. Of the processes impaired, predation by baboons is strongly indicated.

Although no adults resulted from eggs laid on indigenous trees and shrubs and only very few from those laid on young *P. patula* during 1968/69, eggs were again laid on these same shrubs and trees during 1969. All of these 1970 eggs on indigenous vegetation, and many of those on young *P. patula* trees, must therefore have been derived from adults originating elsewhere.

B. Natural enemies and diseases of *P. irius*

The procedure used was the same as indicated for the pine emperor except where stated otherwise.

1) Parasites

Parasites do not play a sufficiently important role to suppress the poplar emperor effectively.

a) Egg parasites

Anastatus sp. Ac.X.P12 was the only egg parasite reared from poplar emperor eggs from the Pan–Rietvlei area. Both *Anastatus* sp. Ac.X.P12 and *M. pulchriceps* were bred from eggs from the Piet Retief District (Van den Berg, 1968).

Of 2 104 eggs collected on *P. patula* in the Rietvlei plantation during 1968/69, only 12 were parasitised, seven by *Anastatus* sp. Ac.X.P12 and five by *M. pulchriceps*, the total parasitism being 0,6 per cent. On young bluegum and peach leaves, 15,3 per cent of a total of 343 eggs were parasitised, 33 eggs by *Anastatus* sp. Ac.X.P12, 12 eggs by *M. pulchriceps* and 9 eggs by *Pediobius* sp. Ac.X.P7.

During a previous investigation in 1964 and 1965, no egg parasites were obtained from this area (Hepburn *et al*, 1966). Somewhat later only *Anastatus* sp. Ac.X.P12 was recorded (Van den Berg, 1968). It seems probable that these parasites have spread to these areas only fairly recently. This is the first known record of *Pediobius* sp. Ac.X.P7 from poplar emperor eggs. As pointed out earlier, this species is a primary parasite.

b) Larval parasites

(i) *Apanteles maculitarsis*

Although the poplar emperor was studied since 1965 in the Rietvlei and Pan plantations, *A. maculitarsis* was bred from larvae for the first time during the 1969/70 season. From 5–27 adults developed per larva in the case of three larvae in the third and eight larvae in the fourth instar. *A. maculitarsis* is not considered an important parasite of the poplar emperor.

Larvae from which *A. maculitarsis* have recently emerged, can stay alive for quite a long time. The adult parasite frequently emerges before the larva dies.

A. maculitarsis was also bred from *Pachypasa capensis* found in the Rietvlei plantation.

(ii) *Exorista fasciata* Mgn. (Tachinidae)

Hepburn *et al* (1966) make mention of unidentified tachinids developing from larvae. Most probably the tachinid recorded by them was *E. fasciata*, small numbers of which were found in the present investigations.

(iii) *Carcelia evolvans*

When eggs of this parasite are laid on sclerotized pupal structures, the area directly surrounding the egg usually turns black after a few days, probably as a result of the parasite larva working its way through the host integument. The parasite larva crawls out of the pupa shortly after becoming full-grown and forms a puparium in the vicinity of the pupa. One or two larvae have been observed to emerge from the same poplar emperor pupa.

c) Pupal parasites

(i) *Enicospilini* sp. Ac.X.P43 & Ac.X.P44 (Ichneumonidae)

Parasite Ac.X.P43 was found in the Sheepmoor as well as the Rietvlei and Pan plantations, while Parasite Ac.X.P44 was only bred from pupae from Sheepmoor. Both these parasites emerge from pupae after all moths have emerged from unparasitised pupae (about mid December). In the Rietvlei plantation, 3,1 per cent of the 1 200 collected pupae were killed by Parasite Ac.X.P43 during 1968.

2) Predators.

Predators are the most important enemies of the poplar emperor and usually contribute most to their control.

a) Invertebrate predators

(i) Bloodsucking Hemiptera

Hepburn *et al* (1966) found that *Glypsus conspicuus* attacked larvae and adults of the poplar emperor.

During the present observations, three species of stinkbugs were found attacking larvae and adults, namely *G. conspicuus*, *Pantoleistes princeps* Stål. (Reduviidae) and *Dermatinus lugens*.

Larvae of the poplar emperor killed by the bloodsucking Hemiptera could be

recognized from the fact that distinct black spots appear at the points where the piercing mouth parts penetrated their bodies. Young larvae turn completely brown-black.

In order to gather some information on larval mortality due to these predators, 30 plots each measuring 2,7 x 2,7 m were laid out in a 10 year old *P. patula* plantation. All dead larvae or their remnants were collected and carefully examined twice a week for seven weeks. After all larvae had pupated, the number of pupae formed in these plots was determined. The results can be found in Table 101.

Table 101: The total number of poplar emperor larvae killed by predators, collected in 30 blocks of 2,7 x 2,7 m during 1968/69 and total number of pupae formed subsequently

	Mortality factor	Date during 1971							Total	%
		2-8/1	9-15/1	16-24/1	25-31/1	1-7/2	8-14/2	15-21/2		
Number of larvae killed	Stinkbugs	32	108	162	147	70	3	0	522	24,7
	Hawks	0	347	379	297	153	3	1	1 180	55,8
	Unknown predators or diseases	4	11	23	14	16	1	0	69	3,3
Total number of pupae formed									342	16,2
Grand total									2 113	100,0

From this table it is evident that stinkbugs are very important enemies of the poplar emperor.

These bloodsucking Hemiptera do attack adults, but their effect on the population is difficult to ascertain.

(ii) Spiders

In young bluegum trees, a spider, *Synaema imitator* ... (Thomisidae) was observed to attack first and second instar larvae. This spider however appears in such small numbers that its contribution towards control can be regarded as negligible.

b) **Vertebrate predators**

(i) **Birds**

Hepburn *et al* (1966) mention that a hawk of the genus *Milvus* was noticed to prey on larvae in the plantations.

Large flocks of hawks, namely *Buteo buteo* (L.) and *Milvus migrans* (Boddaert) often visit areas where dense populations of poplar emperor larvae occur. Larvae are caught and devoured in the trees as well as on the ground underneath the trees.

Larvae killed by birds are usually not entirely devoured, and may be recognized from the remnants left behind. Some idea of the probable number of larvae killed by these birds could be formed by examining the remnants found in the 30 plots mentioned above. The data can be found in Table 101.

From this table it is clear that hawks are exceptionally valuable enemies of the poplar emperor. Unfortunately they sometimes locate severely infested areas too late, with the result that many larvae have already pupated by the time of their arrival. During the 1968/69 season hawks were first noticed on 7.i.1969 at which time about 10 per cent of the larvae had already pupated.

At times the white stork *Ciconia ciconia* (L.) is also active under infested *P. patula* trees at the time of pupation. According to general observations, larvae crawling on the ground are devoured, whereas prepupae and newly formed pupae are possibly dug up and devoured.

Guinea-fowls, *Numida meleagris* (L.), are sometimes also active during pupation and also when adults emerge. It is believed that larvae, pupae and adults are preyed upon.

The fiscal shrike *Lanius collaris* (L.) preys on third to fifth instar poplar emperor larvae. During field experiments it was noticed that larvae sometimes vanish from trees. At first it was believed to be due to hawks and the experimental trees were enclosed with 10 cm gauze wire. However, larvae continued to vanish and rat traps were set with larvae as bait. On two occasions fiscal shrikes were caught in these traps. This shrike however does not appear in sufficient numbers to contribute much towards the control of this insect.

(ii) **Cape Wild Cat** (*Felis lybica cafra* Desmarest)

During observations at night time on emergence and mating of adults, it was noticed that some moths disappeared or were damaged. A wild cat was seen leaving an adult of which the abdomen was missing. These wild cats live in abandoned meercat holes in the Rietvlei and Pan plantations.

(iii) **Yellow Mongoose** (*Cynictis penicillata* (G. Cuvier))

The Yellow Mongoose definitely preys on pupae and adults of the poplar emperor. It is uncertain whether single pupae are dug up, but during experiments with large numbers of pupae in cages, great difficulty was experienced in preventing mongooses from entering the cages. If pupae are in fact dug up on a large scale by mongooses, a reasonable degree of control can be expected, since pupae are present in the field for such a long period.

3) Pathogens

As far as is known, pathogens are not of as much importance in the biological control of the poplar as in that of the pine emperor.

a) Viruses

Large numbers of mature larvae were found to be dying of a suspected wilt disease during 1960 at Sheepmoor (Hepburn *et al*, 1966).

Extra nuclear viruses were isolated from poplar emperor larvae sent to Dr. A. Polson. As no signs of an epidemic could be found in this area before or after these larvae were collected, these viruses seemed to be of little importance.

b) Bacteria

The bacterium *Vibrio leonardi* Metalnikov & Chorine, a well-known insect pathogen, was isolated from diseased larvae of the second generation of 1959/60 at Sheepmoor (Hepburn, 1961; Prinsloo, 1962). Hepburn *et al* (1966) mention that a few pathogenic organisms had been cultured from the intestines of larvae. *Serratia marcescens* was also isolated from poplar emperor larvae and may be regarded as an important mortality factor of this species (Prinsloo, 1967).

The exact contribution towards control by these bacteria is not known, but

it is believed that it would usually be of little importance.

c) **Fungi**

No larvae infected with fungi have been noticed.

The fungus *Cordyceps taylori* has been obtained from only one pupa in the Rietvlei plantation. Infection, the formation of fertile hyphae and dispersion appear to be as described for the pine emperor.

C. **Natural enemies and diseases of *H. smilax***

1) **Parasites**

Parasites are of great importance, especially during the second and third generation of the season. A large number of parasite species have been obtained from larvae and pupae of the pine-bark emperor.

a) **Egg parasites**

Although egg parasites have been found in the vicinity of the two plantations, no egg parasites have yet been obtained from field collected eggs. As the eggs appear during the early spring, mid summer and early autumn, it is rather surprising that no parasites were found.

b) **Larval parasites**

It has been observed in the field that *Apanteles* spp. as well as 1–3 Tachinid parasites emerge from the same dead larva. It thus seems as if these two parasites do not compete very severely with each other in the same host.

(i) *Apanteles aethiopicus* Wlkn. (Braconidae)

A large number (about 300) of this parasite develop from the same larva. This parasite destroys larvae in the third and fourth instars.

(ii) *A. maculitarsis*

This braconid was bred from one larva to which 33 cocoons of this parasite were attached.

(iii) *Exorista fasciata*

From 1–3 individuals of this tachinid have been obtained from the same third instar larva.

(iv) *Carcelia evolans*

This parasite lays its eggs on almost any part of the larva, frequently on the head of the fourth instar. From 1–3 parasites have been obtained from the same pupa. As many as 15 have been counted on one larva during both the second and third larval generations of this emperor.

c) **Pupal parasites**

Pupal parasites appear to be more important than larval parasites.

(i) **Pupal parasite Ac.X.P45**

This parasite apparently parasitises the pupa and not the larva. As the parasites are very small (about 3 mm long), they crawl into holes in the cocoon of the pine-bark emperor to lay their eggs. During the 1969/70 season a larger percentage of pupae on *P. radiata* was parasitised than on *P. patula*. This may be due to a thicker cocoon being spun on *P. patula* than on *P. radiata*. A large number of parasites emerge from the same pupa. About one third of the pupae was killed by this parasite.

(ii) *Coccygomimus* sp. Ac.X P44 (Ichneumonidae)

This parasite parasitises the pupa and probably also the larva. The parasites emerge from the pupae during November and December.

2) **Predators**

Where birds are present, such as in the Kanonkop-Keerom plantations, predators probably are responsible for a higher mortality than parasites, but the opposite is probably true for areas where birds have been eradicated.

a) **Invertebrate predators**(i) **Bloodsucking Hemiptera**

Three species, namely *Glypsus conspicuus*, *Pantoleistes princeps* and *Rhinocoris*

pulvisculatus were found attacking larvae and adults.

(ii) **Spiders**

A spider *Synaema imitator* was observed to attack first and second instar larvae.

b) **Vertebrate predators**

(i) **Guinea-fowls (*Numida meleagris*)**

Guinea-fowls are among the most important enemies of pupae and adults. A considerable number of guinea-fowls appeared in the Middelburg area and also in the plantations during 1969/70.

Crop analysis of one female on the night of 23.x.1969, revealed that 26 pupae and 20 adults of the poplar emperor had been devoured by this bird, together with other items of food, a short time previously. Many adults contained eggs indicating that especially freshly emerged adults are caught. It is however highly improbable that prey more than 60 cm above ground level would be reached. Since pupae are present for about seven months of the year, guinea-fowls can be of great assistance in reducing the population.

(ii) **Owls and hawks**

Owls and hawks appear in the plantation in small numbers. It is however uncertain whether larvae and adults are regularly preyed upon. Remains of larval skin had been noticed in an owl pellet, indicating that larvae may sometimes be eaten.

(iii) **Bats**

Bats are active in the plantation at the same time that moths are actively flying about, and it seems probable that moths are caught. Janse (1946) is also of the opinion that bats prey on different species of moths.

3) **Pathogens**

So far no pathogens have been obtained from the pine-bark emperor. Larvae seldom succumb to diseases during laboratory rearings and appear to be quite resistant to pathogens.

CHAPTER 7: CONTROL

A. Control of *N. cytherea clarki*

A number of different methods have been used to control this insect. Nothing has yet been published about some of these methods; they are shortly dealt with to serve as historical background.

1) Hand collection

a) Collection of larvae

According to Hepburn (1961), hand collecting of larvae was carried out at Schagen on 40,5 ha of *P. patula* trees 3,6–4,5 m high. Complete defoliation was prevented, but during the following season, the infestation spread and became heavier.

During 1964, larvae were collected from young trees (2–3,5 m high) at Enon Estates (Richmond, Natal), and buried. For two collections (June and August), the cost amounted to about R3,20 per ha. The mortality in the area concerned was close on 100 per cent, but this did not prevent re-infestation.

During 1970 it was concluded that hand collection from trees about 4,5 m high was completely ineffective in the Mhlahlane plantation (Tsolo, Transkei), as sufficient larvae remained to ensure a fairly heavy re-infestation.

b) Collection and marketing of larvae

Although the closely related mopane worm (*Nudaurelia belina* (Westw.)) is dried and sold on a large scale for human consumption (Palmer & Pitman, 1961; Van den Berg, 1968) and pine emperor larvae are readily eaten by certain Bantu tribes, this method has hardly ever been attempted.

During 1965, Mr. A.G. Cumming of Weltevreden, Schagen (personal communication) adopted the following procedure: From June to September young Bantu labourers were employed to collect larvae which had descended to the ground to pupate, and remunerated at 20c per 4,5 l container full of larvae.

The method of preparing larvae for sale and human consumption consists of squeezing out the gut contents, and then salting and frying the larvae in their own fat until almost dry. Hereafter, the larvae were left on sheets to dry. The final product

which can be stored for a considerable period was sold at R5 per grain bag. The demand substantially exceeded the supply. In large heavily infested trees, about 70–80 per cent control was achieved at a cost of less than R1,20 per ha, after the income from the sale of dried larvae had been taken into account.

During 1971 Bantu were allowed, under supervision, to collect larvae from small infested trees in the Usutu plantation for their own benefit. These Bantu went so far as to hire buses for this purpose and removed grain bags full of larvae. The results were the achievement of fairly good control.

c) Collection of pupae

Pupae were gathered in the Weltevreden (Schagen) and Edenvale (Pietermaritzburg) plantations during 1963 and 1964 for sexual attraction experiments. The cost amounted to about R3,50 per ha between rows without brushwood. To obtain adequate riddance of the pest, the cost was estimated to be at least R6,00 per ha.

d) Collection of adults

At the recommendation of Dr. H.E. Prinsloo, adults were collected at Weltevreden (Schagen) during 1965. They were knocked off the trees in the morning, collected and destroyed. The total cost was about R4,80 per ha. Although many were destroyed, the results were poor. This may have been due to the following facts: About two thirds of the moths that emerged during the night move higher up in trees at dawn with the result that many of them can not be reached to be killed. No collections were made either early or late during the adult period or on Sundays. There was also nothing to prevent moths from other areas infiltrating and laying their eggs in the area from which the adults had been collected.

2) Control by fire

a) Larvae

Mr. J.P. Kleynhans (personal communication) recounted the following experience in a *P. patula* plantation at Ameide (Barberton) during 1956. During the summer following complete defoliation, a hailstorm severely damaged the trees and *Diplodia* fungus caused the crowns of many to die. Although the trees recovered to some extent, an exception-

ally heavy infestation again occurred. In June 1957 all the larvae and eggs were destroyed when the entire section, 16 ha in extent and containing trees of about 3–4 m high, was deliberately burnt down.

When making fire-breaks, the grass in lanes surrounding the plantation is burnt. When indigenous shrubs are burnt down during this process, many larvae and eggs are frequently destroyed.

b) Pupae

During December, 1964, the effect of burning the dead needle mat and brushwood that covered the pupae was determined at Enon Estates, Richmond, Natal in a block containing trees 9–12 m high which had been pruned clear up to about 4 m from the ground.

Prior to the commencement of the experiment, the brushwood was evenly scattered between the rows, and the pine mat raked away from the tree trunks. The area was set alight on a hot, dry day, seven days after 28 mm of rain. Damage to the crowns of the trees did not occur as the fire was confined to well below the growing foliage.

Counts of live and dead pupae were done before and after the fire in 20 randomly taken plots of 4,86 m² each (1,8 x 2,7 m), 10 blocks before and 10 blocks 48 hours after the fire. The results can be found in Table 102, and the statistical analysis in Tables 103 and 104.

Table 102: Number of pine emperor pupae per 2,7 x 1,8 m plots before and after burning the brushwood to control them

Plot	Before fire			After fire		
	Alive	Dead	Total	Alive	Dead	Total
1	15	0	15	8	6	14
2	9	0	9	5	7	12
3	8	1	9	9	10	19
4	21	1	22	2	6	8
5	13	0	13	4	4	8
6	15	0	15	6	4	10
7	9	1	10	1	8	9
8	17	2	19	3	7	10
9	14	0	14	6	9	15
10	8	2	10	2	10	12
Grand Total	129	7	136	46	71	117

Table 103: Analysis of variance of data in Table 102 on the total number of pupae per plot

Source of variation	SS	d.f.	MS	F
Between group totals before and after fire	45,35	1	45,35	3,20 ⁻
Within group totals	255,20	18	14,18	
Total	300,55	19		

⁻Do not differ significantly at the 5% level ($F_{1,18} = 4,41$)

Table 104: Analysis of variance of data in Table 102 on the number of live pupae before and after the fire

Source of variation	SS	d.f.	MS	F
Between groups before and after the fire	344,45	1	344,45	26,35**
Within groups	235,30	18	13,07	
Total	579,75	19		

**Differs highly significantly at the 1% level ($F_{1,18} = 8,28$)

From Table 103 it follows that the total number of pupae in the plots before and after the fire did not differ significantly. The statistical analysis in Table 104, indicates that the live pupal population after the fire was highly significantly lower than before. A pupal mortality of 55 per cent was noted. The actual mortality could have been higher as some of the remaining pupae could later have dried out, as a result of the removal of the protecting pine needle mat, or could have been parasitised more easily. The pine roots as well as low hanging pine needles were slightly scorched. The cost of this experiment amounted to R3,66 per ha.

3) Control of adults with the aid of ultra-violet light

An ultra-violet light was mounted about 1,5 m above the ground and 30 cm from a white vertical sheet in the Weltevreden (Schagen) plantation one night during March, 1966. The moths attracted to the light were mechanically killed shortly before dawn. The results indicated that out of approximately 10 000 moths destroyed only 10 per cent were females, and furthermore, most of them had very few eggs in their bodies. The only benefit which may be gained from this method

would be the reducing of the males to such a level that many females would not be able to mate. According to Van den Berg (1968), adults are not attracted to the light from much more than 100 m. Evidently many lamps will be required if the area involved is large. These would also have to function every night for three consecutive months to obtain adequate control. Because of the high cost of power and equipment, this method will definitely be too expensive.

4) **Attracting and destroying males**

Towards the end of 1967, pupae were collected at Usutu, Swaziland, sexed and kept in cages. Female moths emerging from these pupae were used to attract males. Thousands of males which were found near the cages were mechanically killed shortly before dawn. This method was ineffective as most of the eggs, examined in close proximity of the cages and up to 50 m away, were viable.

Bosman (1970) is of the opinion that a pheromone-based control programme would probably succeed against the pine emperor moth.

5) **Control by thinning and pruning**

During normal forestry practice, cultivated pine trees are pruned to eliminate dry knots in the wood. They are also thinned out a number of times, thus allowing the best trees to grow more vigorously.

The following methods can be applied to decrease the population. Firstly, pruning and thinning out of infested areas can be carried out when egg laying has been completed. Larvae emerging from eggs on dead branches usually succumb. Secondly, in areas where spraying is either impossible or not desirable, and where complete defoliation can be expected, pruning and thinning can be carried out two months before defoliation is expected. The larvae then quickly consume the only available needles and many die of starvation. Thirdly, when timber is hauled out of the plantation during the pupal stage of the insect, many pupae are crushed to death.

6) **Control by wild bushpigs**

According to Mr. M.P.S. de Kock (personal communication), formerly of the Mamre plantation, Carolina District, a herd of bushpigs was chased into an infested

area with the aid of a few horsemen during 1962. These pigs were introduced during the pupal season, remained in the infested area, and kept the pest under control. From then until 1971 no further damage was reported.

7) Control by domesticated pigs

Hardenberg (1912) first mentioned the fact that pigs could dig up and destroy pupae of *Nudaurelia tyrreha* (Cram.) under pine trees. Since about 1926, *N. cytherea cytherea* has been controlled by this method (Brain, 1929; Tooke, 1935).

According to Webb (1958), aerial spraying was much cheaper than enclosing pigs in an infested area by means of fences at Kluitjieskraal, Wolseley in 1956. The calculated cost was R18,53 per ha for control by pigs and R3,71 to R7,86 per ha for aerial spraying. Most of the expense was incurred in moving the fences to new positions.

Pigs have already been used occasionally to control the pine emperor. Detailed data were obtained for the first time in 1964–65 when pigs were introduced into an infested *P. patula* plantation at Enon Estates (Richmond).

Twenty pigs were obtained by the forester and introduced into the plantation towards mid December, 1964. The pigs were herded into a small camp (33 x 39 m constructed from dead tree trunks), which was situated centrally in the infested area and through which a stream of water flowed. Two swineherds were appointed to look after them.

At first the pigs were fed oats at night, while they had to look for food in the camp during the day. Pupae were dug out and placed on their food, but were avoided. At this early stage it seemed as if the experiment would be a failure as pupae were being pushed aside by the pigs.

After the pigs had been in the camp for about a week, a few of them began to show an interest in the pupae. After approximately another week, all pigs eagerly dug up and devoured pupae. At this stage the pigs were herded out of the sty in the mornings and forced to graze systematically and at a slow pace, up the one lane and down the other. They were herded into the sty at night and supplied with food which was daily decreased so that three weeks after introduction no more food

was provided. After the whole infested area (32,3 ha) had been covered once, the procedure was repeated for a second and third time.

Within the first two weeks, three pigs died from unknown causes, but apparently not as a result of hunger or poisoning from pupae.

Sows with sucklings were kept in separate camps and fed oats at night. When the piglets were old enough to locate their own food, they were herded with their mothers and the other pigs.

Countings of live and dead pupae were done in 10 plots before and 10 plots after the pigs were introduced. The experimental plots were taken at random and each plot was 5,02 m² (1,83 x 2,74 m).

Pupal counts before and after the introduction of pigs are provided in Table 105 and the statistical analysis in Table 106.

Table 105: Number of pupae in 20 experimental plots 5 m², 10 before and 10 after pigs were introduced

Plot	Number of pupae before			Number of pupae after		
	Alive	Dead	Total	Alive	Dead	Total
1	15	0	15	0	0	0
2	9	0	9	0	0	0
3	8	1	9	1*	0	1
4	21	1	22	0	0	0
5	13	0	13	1	0	1
6	15	0	15	1	0	1
7	9	1	10	0	0	0
8	17	2	19	0	0	0
9	14	0	14	0	0	0
10	8	2	10	0	0	0
Grand Total	129	7	136	3	0	3

*Moth already emerged

Table 106: Analysis of variance of data in Table 105 on the total number of pupae per plot

Source of variation	SS	d.f.	MS	F
Between groups before and after	884,4	1	884,4	91,18**
Within groups	174,5	18	9,7	
Total	1 058,9	19		

**Differs highly significantly at the 1% level ($F_{1,18} = 8,28$)

The statistical analysis indicates that the number of pupae that could be located after the experiment was highly significantly smaller than before it was started. From the data it can also be calculated that 97,8 per cent of the pupae had disappeared. Unfortunately no control plots were protected against the action of the pigs. From other studies it was found that very few, if any, pine emperor pupae disappeared due to other predators (in the absence of wild bushpigs). The mortality observed was thus probably due solely to pigs.

It was also noticed that the pigs devour adults and even chase them if they do not fly too high. It is believed that pigs will also devour caterpillars crawling on the ground in search of a suitable locality for pupation.

Calculation of cost of control by pigs

Gross expenditure

Price of 20 pigs	R 311,60
Erection of a camp	5,00
Bran (10 bags)	32,50
Wages of two swineherds for 3,5 months	49,00
	<hr/>
	R 398,10

Assets

Value of pigs as at March, 1965	
Large pigs (17) at cost price	R 264,86
Small pigs (18) at R3,00 each	54,00
	<hr/>
	R 318,86

Net expenditure to obtain 98 per cent control in 32,3 ha R 79,24

Net expenditure per ha R 2,45

Pigs possess a highly developed sense of smell which enables them to locate pupae buried in the soil. As soon as a pupa has been located by smell, the pig starts to root up the soil more or less exactly where the pupa occurs. There is therefore nothing haphazard or random about their digging behaviour as may be the case with their sniffing. Even their sniffing may not be totally executed at random as

one might judge it to be, but may somehow be orientated by the presence of a pupa or other food some short distance away. Consequently, very little or no time is wasted by digging up soil where no food will be found. They certainly do not have to dig up virtually all the soil in order to unearth almost all the pupae in the infested area. They seem to be able to sniff out pupae up to 7,5 cm deep with great ease (i.e. as deep as the deepest pupae found).

During pupation, the soil in the summer rainfall regions is relatively hard (July to September), resulting in the larvae not penetrating deep into the soil. If the pigs are introduced after the first spring rains, the soil will be soft and the pupae easy to root out. In the winter rainfall regions, however, it is moist during pupation, enabling the pupae of *N. cytherea cytherea* to burrow deeper into the soil. According to Geertsema (1970) they pupate as deep as 10 cm below the soil surface. When the pigs start to root up the pupae (October to January), the soil is, although still moist, a bit harder, and pupae are not so easily reached. Consequently, pigs will probably be more effective against *N. cytherea clarki* in summer rainfall regions than against *N. cytherea cytherea* in the winter rainfall areas.

8) Chemical control

a) Hand spraying

According to Mr. J.U. Spies (personal communication), of Oosterbeek plantation (Barberton), pine emperor larvae were sprayed by hand during 1958. The trees (*P. patula*) were 1,5–3,5 m high and unpruned. Spraying was carried out with 50 per cent BHC diluted in water to a concentration of about 0,08 per cent, at a total cost of R1,73 per ha. The pest was almost entirely eradicated.

b) Aerial spraying

A summary of chemical control precautions applied against *N. cytherea cytherea* larvae before 1958 is supplied by Webb (1958). Webb (1958, 1961) found that nendrin gave excellent results. Since that time, Donald (1963), tested sevin, but found this to be less effective than nendrin. Nendrin is still generally used at present.

To control larvae, aerial spraying was carried out during 1961 at Weltevreden

(Schagen) using 211 ml nendrin active ingredient (a.i.) and 749 ml triona oil adhesive in 33,7 l water per ha. The mortality was approximately 92 per cent (Hepburn, 1961).

During 1963 the pine emperor completely defoliated about 121 ha of *P. patula* trees on the farm Canaan (Richmond, Natal). Canaan occupies 283 ha of undulating scenery. Although the topography rendered flying at low heights difficult, aerial spraying was considered possible except for a few small areas. As a heavy outbreak was expected the next season, it was decided to conduct an aerial spraying experiment in this plantation in 1964.

Timing of spray application

To ascertain when spraying should take place, the proportion of eggs already hatched was determined weekly. On the assumption that only about 75 per cent of the eggs would eventually hatch, it was decided to spray about a week after 70 per cent larval emergence.

Ten trees of about 4 m high were taken at random, at weekly intervals, to determine the percentage hatch. All branches which could be reached from the ground, were pulled down and all eggs that could be located (hatched as well as unhatched), were collected. These egg masses were kept in the laboratory in numbered petri-dishes and examined daily. From these observations it appeared that more than 70 per cent of the eggs had hatched by the 16th May, 1964; spraying was thus planned to take place about a week later.

Spraying date and other details

Two blocks totalling 121 ha were sprayed on the 26th May, 1964, while the rest (162 ha) was deliberately left unsprayed with the view of obtaining large numbers of pupae for sexual attraction experiments that were planned for the following spring. Consequently, this unsprayed area was available as a control.

Spraying was done without any assistance from the ground, the pilot depending on his own resources to decide where successive runs should be made.

The Piper Pawnee 235 used, flew at a speed of 161 km p h, the spray pressure being 0,28 kg per cm². The spray mixture consisted of 10,23 l Endrex (19,5% nendrin EC) diluted in 440,96 l diesoline (i.e. 152 ml a.i./ha). The swath

width was approximately 18 m and the height of the aircraft about 1,5–3 m above the tree-tops.

Penetration of spray

In order to study the penetration of the spray at different heights in the trees, the following method was employed. Deposit cards, as described by Davis & Elliot (1953), were spaced at 0,91 m intervals, starting from the tops of the trees. The cards (8 x 12 cm) were fastened with drawing pins onto a piece of cardboard and a branch at the correct height. This was done in 30 *P. patula* trees (12 of them 8 years old, 12 in the 9 year old class and 6 of them 11 years old), as well as in 5 new offshoots of felled bluegum trees.

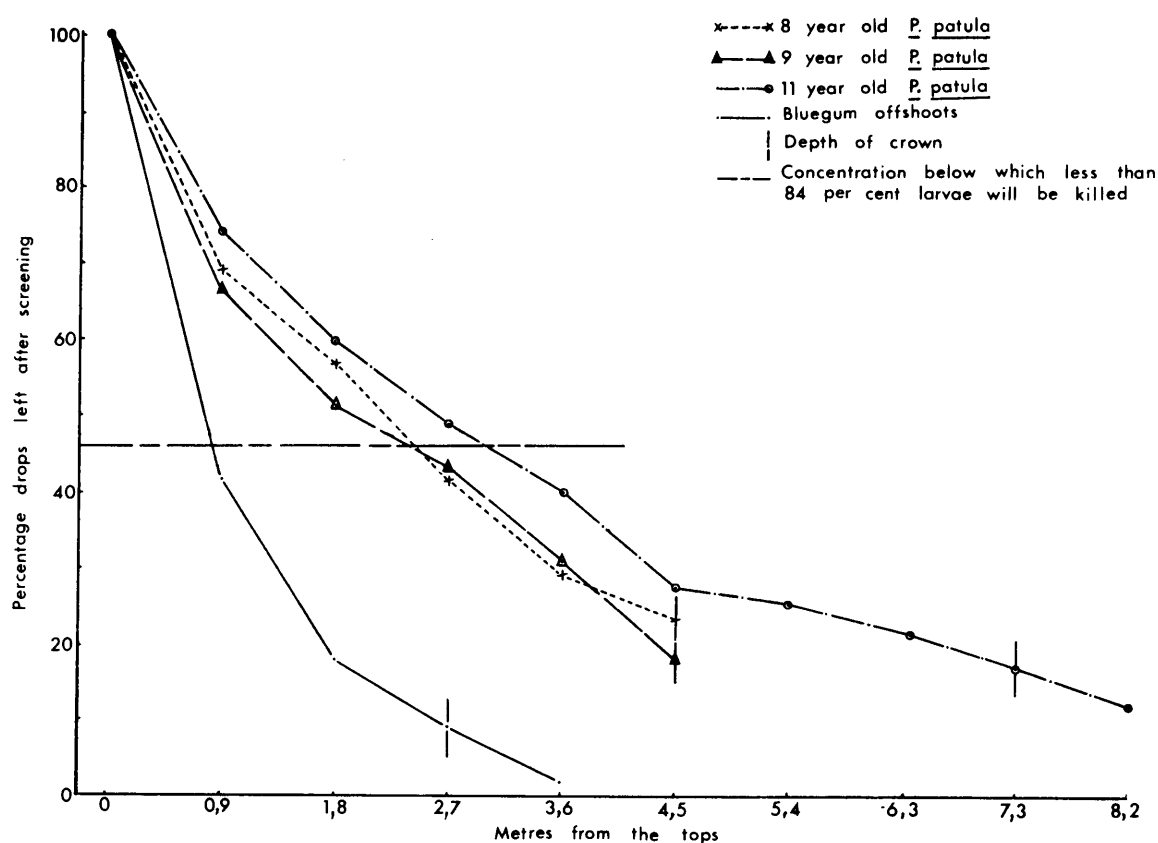
The deposit marks in the different size ranges (1,5 mm and larger for large, 1–1,5 mm for medium and smaller than 1 mm for small) were recorded for the different positions in these trees. Counting of the droplets on each card was done by actual countings in four randomly taken areas of 40,96 mm² each. According to Davis & Elliot (1953), the diameters of the deposit marks are on the average about 6,5 times larger than those of the drops causing them. The total volumes due to large, medium and small drops, i.e. 10,22; 3,72 and 0,24 μ l, could hereby be calculated. By using the volume of small drops as the standard of comparison, the number of drops for the different cards could be calculated and compared with each other.

The penetration of the insecticide into the crowns of different ages of *P. patula* and new offshoots of bluegum is given in Fig. 50.

From this fig. it can be seen that the screening effect of foliage is such, that more than 50 per cent of the insecticide is deposited in the top 2,7 m of the trees in the case of *P. patula* and in the top 0,9 m in the case of new bluegum offshoots.

The total number of drops recorded on the top cards was 41 763. This would represent the full dosage of 152 ml a.i. nendrin per ha. According to Webb (1961), 70,15 ml a.i. nendrin per ha destroyed 83,8 per cent of *N. cytherea cytherea* larvae. From this it may be assumed that this concentration (which would represent 19 274 drops or 46 per cent of the applied dosage) will also kill about

Fig. 50: Percentage screening of spray deposit at different heights in trees



84 per cent of *N. cytherea clarki* larvae. It may therefore be concluded that the mortality of larvae occurring lower than about 2,7 m from the tops of *P. patula* trees (receiving 23 per cent of the applied dosage) would be less than 84 per cent. The same applies to larvae lower down than about 0,8 m from the tops of young bluegum offshoots. It is therefore clear that *P. patula* trees with crown depths of more than 4,5 m and young bluegum offshoots more than 1,6 m should receive higher dosages.

Deposit cards were also placed at random on the soil in the areas to be sprayed. The purpose of this was to determine how evenly the spray was distributed over the sprayed area. From a study of these deposit cards it was concluded that the spray was fairly evenly distributed, and, taking into account that no ground assistance was given, the method used was considered to be fairly satisfactory.

Mortality

Larval mortality was determined by two methods, which will be treated separately.

Method (a): Drench-spraying to kill all surviving larvae

In the sprayed area, 20 plots were taken at random as well as four plots in the unsprayed area, each 2,7 x 2,7 m and situated between four trees. Immediately after spraying, a canvas was spread over each plot to detect dead larvae more easily. The plots were inspected daily, the dead larvae removed and counted, and the live ones left on the cloth.

These mortality counts were continued until the mortality under the control trees and that under the sprayed trees was about the same (after 4 weeks). Hereafter, all four trees surrounding each plot were drench-sprayed with a 13 per cent stock formulation of BHC emulsifiable concentrate diluted in water to 0,15 per cent BHC. The idea behind this drench-spraying was to kill virtually all larvae remaining in the trees. The dosage used was considered sufficient to almost certainly kill all larvae in these trees. A power spray-pump (Holder 1,5 metric hp.) was used and the trees were sprayed by climbing into them in order to reach the tops. Hereafter, all larvae dropping on the canvas were collected and counted daily for five days.

Results

The number of larvae killed per 2,7 x 2,7 m plot after spraying with nendrin on 26th May and with BHC on 22nd June is given in Table 107.

From this table it can be seen that the mortality per sprayed plot varied between 74,8 and 99,6 per cent, which indicates that spraying was done fairly evenly. In the unsprayed control plots, the natural mortality amounted to an average of 12,5 larvae per plot, while the result of the drench-spraying with BHC indicated that an average of 101,0 larvae per plot had survived up to that stage. The natural mortality during the four weeks before drench-spraying with BHC was therefore about 11 per cent. Unfortunately the average total population on the control trees at the beginning of the experiment (26th May) amounted to only about 114 larvae per plot, in contrast to

Table 107: Total number of larvae killed per plot of 2,7 x 2,7 m at Canaan after spraying with nendrin on the 26th May, and after drench-spraying with BHC on the 22nd June, 1964

Plot no.	Age in years	Total number of larvae killed after spraying with			Percentage kill after spraying with nendrin
		Nendrin	BHC	Total per plot	
1	11	400	22	422	94,8
2	11	595	15	610	97,5
3	11	622	20	642	96,9
4	11	360	13	373	96,5
5	11	153	14	167	91,6
6	9	326	17	343	95,0
7	9	229	12	241	95,0
8	9	119	40	159	74,8
9	9	149	1	150	99,3
10	9	92	6	98	93,9
11	8	227	21	248	91,5
12	8	161	6	167	96,4
13	8	161	21	182	88,5
14	8	219	15	234	93,6
15	8	233	1	234	99,6
16	8	109	2	111	98,2
17	8	271	11	282	96,1
18	8	192	17	209	91,9
19	8	248	36	284	87,3
20	8	124	9	133	93,2
Total		4 990	299	5 289	
Average		249,5	15,0	264,5	94,3
Control		Unsprayed	Drench-sprayed with BHC	Total	Percentage natural mortality
1	8	16	102	118	13,6
2	8	9	97	106	8,5
3	8	10	116	126	7,9
4	8	15	89	104	14,4
Total		50	404	454	
Average		12,5	101,0	113,5	11,0

Mortality according to the formula of Abbott* (1925) = 93,6%

$$* \% \text{ mortality} = \left(\frac{\% \text{ mortality obtained} - \% \text{ mortality control}}{100 - \% \text{ mortality control}} \right) \times 100$$

about 195 larvae per plot in the sprayed eight year old trees, the difference being highly significant (Table 108).

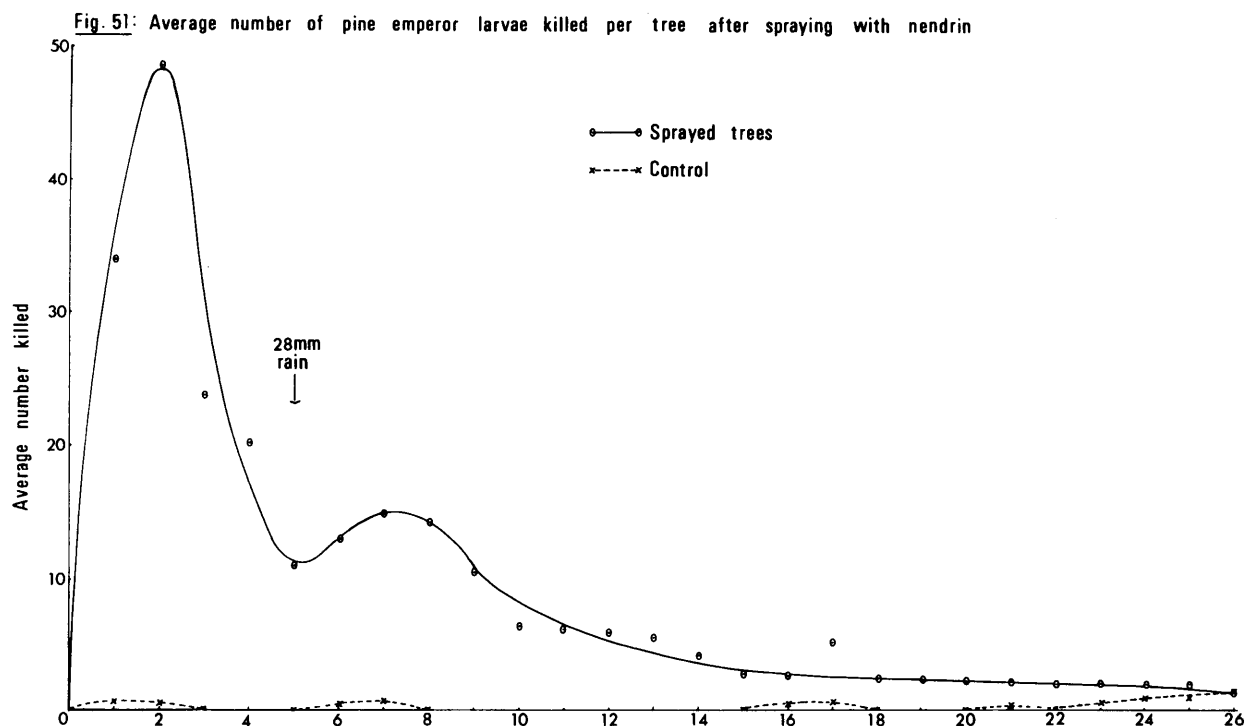
Table 108: Analysis of variance of data in Table 107 of the total number of larvae in sprayed eight year old trees and the control

Source of variation	SS	d.f.	MS	F
Between sprayed and control groups	25 504,71	1	25 504,71	9,52**
Within groups	32 144,15	12	2 678,68	
Total	57 648,86	13		

**Differs highly significantly at the 1% level ($F_{1,12} = 9,33$)

It is highly probable that with the denser population in the sprayed area, the natural mortality would have been higher than the 11 per cent found for the control trees. This figure was nevertheless used as the correction factor in Abbott's formula.

The mortality curve as determined by picking up dead larvae in sprayed and unsprayed plots is shown in Fig. 51. From the points plotted a free-hand curve was drawn.



From this fig. it can be concluded that the largest mortality occurred within the first four days after spraying, which was probably due to the contact action of nendrin. The gradually declining mortalities observed later on were probably due to a combination of contact and stomach poison effects. After about 24 days, there was very little difference between mortalities in the sprayed and unsprayed areas. Fewer larvae die during rainy weather than a day or two before or after the rain. This may be due to the fact that the larvae feed and move about less during cool and wet conditions than during hot dry weather.

Method (b): Chopping down trees to collect all surviving larvae

Before spraying, ten trees considered to be representative of the area to be sprayed were taken at random. Sheets of canvas were spread open on the ground around the trunks of the trees and the trees chopped down. Larvae dropping from the trees during the chopping process, were collected from the sheets. After the trees had been felled, larvae were collected from all branches and recorded for each tree. The same procedure was followed five weeks after spraying, on ten other trees also taken at random in the sprayed area. The results of these investigations are provided in Table 109 and statistical analysis in Table 110.

Table 109: Total number of larvae per tree before and after spraying of the trees as determined by felling the trees

Tree no	Number of larvae before spraying	Number of larvae after spraying	Total
1	306	8	314
2	177	25	202
3	242	80	322
4	254	56	310
5	178	22	200
6	124	50	174
7	416	24	440
8	196	5	201
9	271	38	309
10	950	27	977
Total for 10 trees	3 114	335	3 449
Percentage	90,3	9,7	100

Table 110: Analysis of variance of data in Table 109

Source of variation	SS	d.f.	MS	F
Between groups before and after spraying	386 140,0	1	386 142,0	13,43**
Within groups	517 578,9	18	28 754,4	
Total	903 718,9	19		

**Differs highly significantly $F_{1,18}(,01) = 8,28$

From the totals for the 20 trees in Table 109, it can be calculated that 90,3 per cent of the larvae were killed during the four weeks after spraying. Using the same correction factor of 11,0 per cent in Abbott's formula, the mortality obtained by spraying can be estimated at 89,1 per cent.

The statistical analysis in Table 110 indicates that a highly significantly smaller number of larvae could be found on 10 trees after spraying than on 10 trees before.

The two estimates of mortality obtained by the two methods, i.e. 93,7 and 89,1 per cent, may be regarded as being of the same order, from which it may be concluded that any one of the two methods could be used in estimating the mortality obtained.

The cost of spraying amounted to R6,18 per ha.

The mortality obtained is almost the same as that found by Hepburn (1961) at Schagen, namely about 92 per cent.

c) Comparison of insecticides

This aerial spraying experiment, involving five different insecticides, was conducted in the Usutu plantation (Swaziland) in blocks C6 and C22, where six year old *P. patula* trees were about 6–8 m in height.

The area to be sprayed was divided into four blocks, each about 10 ha in extent. In each block, six plots of 19,2 m (swath width) by 91,4 m (length of run) separated by strips 41,1 m wide, were marked off. The plots in each block were allotted to the five insecticides and the control by drawing numbers from a hat. There were therefore four replications of each treatment as well as of the control.

Four similarly coloured flags (markers) were placed at the corners of each plot to be sprayed, different colours being used for the different treatments. The pilot

was given a flag with the colour corresponding with that of the insecticide in his tank, thereby enabling him to identify all four plots to be sprayed with that particular insecticide.

The tank contained a small quantity more of the insecticide than would be needed to spray five run lengths. Before spraying the first plot, the spray pump was put into operation for a marked run length a small distance away from the experimental area, to ensure that the booms were filled to capacity with spray liquid. The spray delivered during this run length amounted to about 1,5 times boom capacity. Directly afterwards, the specific four plots were sprayed. After spraying with each of the insecticides, the tank and booms were drained, rinsed with 90 l clean water and another 90 l clean water sprayed out before pouring the next insecticide into the tank.

The insecticides used were: nendrin (Endrex 19,5% EC) at 275 ml a.i. in 33,7 l of diesel oil per ha; all other insecticides were administered in 33,7 l of water per ha: DDT (25% EC) 2 200 ml a.i.; cidal (85% EC) at 1 190 ml a.i.; endosulfan (Thiodan 35% EC) at 735 ml a.i.; and Thuricide (15 billion *Bacillus thuringiensis* spores per g (EC) at 2 100 ml a.i. plus 8,8 ml Triton B. There were therefore five insecticidal treatments and one untreated control giving six treatments in all, each replicated four times.

The spraying took place from 0600 to 0900 hours on the 11th June, 1969. The Piper Super Cub aircraft sprayed at a speed of 144 km p h at a height of about 0,3 to 1,5 m above the tops of the trees. The nozzles were of the 45 W D8 type and spraying was done at a pressure of 0,32 kg per cm².

There was no wind at the beginning of the experiment, but towards the end there was a very light breeze. According to deposit cards located in different positions in the plots, the wind had no visible effect on the spray deposit.

Mortality

The larval mortality was determined by two methods.

Method (a): Massive overdusting to kill all surviving larvae

A day before spraying, three observation areas of 8,2 x 2,7 m each were raked clean in the central three lanes of each plot. They were numbered and all dead larvae found within these areas collected and recorded daily. After 22 days the mortality under the sprayed trees was lower than that under the con-

trol trees. From this it was concluded that all larvae remaining on the trees can be considered as having survived the different treatments. The numbers of dead larvae collected up to that stage were recorded as the numbers that succumbed due to the different treatments. In order to establish the numbers surviving at that stage, the trees in and adjoining all observation areas were massively overdusted with a five per cent mercaptothion dust. This was done 23 days after the date of spraying, by means of a power duster and at such a dosage that virtually all larvae in the vicinity of the observation areas would certainly be killed within a few days. The larvae that died during the first week after this massive overdusting were collected daily from the observation areas and recorded as the numbers surviving the different spray treatments applied 23 days before overdusting. From these figures the percentage mortality was calculated for each replication of the different spray treatments.

Results

The results of this experiment can be found in Table 111. These results have been summarized as shown in Table 112 for the purpose of the statistical analysis appearing in Table 113.

From Table 113 it can be concluded that the mortalities obtained with endosulfan, Thuricide, nendrin and DDT did not differ significantly from each other, while they differed highly significantly from that of control. The mortality of all treatments differed highly significantly from that of the control.

For chemical control, endosulfan is recommended at 735 ml a.i. in 33,7 l of water per ha for trees about 6-8 m tall. Although Thuricide killed 91,1 per cent of the larvae in this experiment, and is of great value for the protection afforded to parasites, predators and other forms of animal life, it can not be recommended. During a further experiment on a mixed population of *N. cytherea clarki* and *Euproctis terminalis*, Thuricide killed about 25 and 22 per cent of the larvae respectively. During another experiment carried out on *N. cytherea cytherea* during 1969 in Knysna, about 30 per cent of the larvae were killed by Thuricide. From these experiments it may be concluded that the results obtained with Thuricide are dependent on conditions not yet fully understood. Until the time that these conditions are known, Thuricide can not be recommended for spraying on a large scale.

Table 111: Numbers and percentages of pine emperor larvae that died after different treatments, and the numbers surviving 22 days later in each of the three observation areas (2,7 x 8,1 m each) in each of four replications

Treatments	Replication	Observation area						Totals for each treatment		Percentage mortality	Percentage mortality Abbott* formula
		a		b		c					
		Number of larvae		Number of larvae		Number of larvae		Dead	Surviving		
		Dead	Surviving	Dead	Surviving	Dead	Surviving				
Nendrin (275 ml a.i./ha)	1	22	3	23	4	29	3	74	10	88,1	
	2	88	1	11	1	12	1	111	3	97,4	
	3	24	3	29	1	33	4	86	8	91,5	
	4	22	4	21	2	25	3	68	9	88,3	
									339	30	91,9
DDT (2 200 ml a.i./ha)	1	21	5	19	2	24	2	64	9	87,7	
	2	16	5	17	2	14	1	47	8	85,5	
	3	20	0	23	2	35	2	78	4	95,1	
	4	24	7	20	2	23	3	67	12	84,8	
									256	33	88,6
Cidial (1 190 ml a.i./ha)	1	12	17	15	11	17	14	44	42	51,2	
	2	3	8	8	7	9	5	20	20	50,0	
	3	11	13	11	10	9	7	31	30	50,8	
	4	10	11	11	8	11	16	32	35	47,8	
									127	127	50,0
Endo: sulfan (735 ml a.i./ha)	1	31	2	30	1	23	0	84	3	96,6	
	2	20	2	13	1	12	1	45	4	91,8	
	3	21	1	30	3	28	1	79	5	94,0	
	4	23	2	26	0	16	0	65	2	97,0	
									273	14	95,1
Thuricide (2 100 ml a.i. + 8,8 ml Triton, B/ ha)	1	32	3	26	3	29	4	87	10	89,7	
	2	8	0	12	1	11	2	31	3	91,2	
	3	26	2	23	1	29	2	78	5	94,0	
	4	22	2	23	1	18	1	63	4	94,0	
									259	22	92,2
Control	1	6	26	4	27	5	32	15	85	15,0	
	2	2	18	0	16	3	19	5	53	8,6	
	3	5	32	4	29	2	25	11	86	11,3	
	4	4	21	2	23	3	34	9	78	10,3	
									40	302	11,7

$$* \% \text{ mortality} = \left(\frac{\% \text{ mortality treatment} - \% \text{ mortality control}}{100 - \% \text{ mortality control}} \right) \times 100$$

Table 112: Summary of the percentage mortalities appearing in Table 111 randomized block

Treat- ment \ Block	B1 Nendrin	B2 DDT	B3 Cidial	B4 Endosul- fan	B5 Thuricide	B6 Control	Total
R1	88,1	87,7	51,2	96,6	89,7	15,0	428,3
R2	97,4	85,5	50,0	91,8	91,2	8,6	424,5
R3	91,5	95,1	50,8	94,0	94,0	11,3	436,7
R4	88,3	84,8	47,8	97,0	94,0	10,3	422,2
Total	365,3	353,1	199,8	379,4	368,9	45,2	1 711,7
Aver	91,325	88,275	49,950	94,850	92,225	11,300	

Table 113: Analysis of variance of data in Table 112

Source of variation	SS	d.f.	MS	F
Blocks	20,28	3	6,76	
Treatments	22 949,72	5	4 589,94	421,87**
Error	163,22	15	10,88	
Total	23 133,22	23		

**Differs highly significantly at the 1% level ($F_{5,15} = 4,56$)

S.S.D. = 7,585 (5%) and 9,564 (1%)

endosulfan	Thuricide	nendrin	DDT	cidial	control
94,850	92,225	91,325	88,275	49,950	11,300

Percentages underlined by a continuous line do not differ significantly. Percentages underlined by a dotted line do not differ highly significantly.

Method (b): Reduction in the numbers of needles severed and frass pellets produced

As previously mentioned, there were six treatments each replicated four times. A day before spraying, four containers (each 48,1 x 37,7 cm and 20 cm deep) were placed at random in the middle three lanes of each plot. The number of severed needles and frass pellets dropping in these containers were recorded daily for four weeks after spraying. The numbers of needles and frass pellets collected in the four containers in the same replication on the same day, were added together. The total

for each replication before treatment could thus be compared with the totals on any day for a period of four weeks after treatment. It was decided to compare the totals recorded one day before treatment with those on the same day of each of the following three weeks; thus three comparisons were made, spaced at weekly intervals. From these figures, the percentage reduction in needles and frass pellets collected were calculated for each replication at intervals of one, two and three weeks after spraying.

Results

The results of these studies can be found in Table 114. The negative values in this table are due to increases instead of decreases in the numbers of needles or frass pellets collected, thus indicating negative rather than positive results. The results obtained with the five insecticidal treatments were all positive with only one exception, namely the needle count after one week in the first replication of cidial.

As judged from needle drop and frass reduction for each week, endosulfan and nendrin appeared to be quick acting, while DDT, cidial and Thuricide seemed to be slow acting.

The percentage by which the numbers of needles severed had been reduced three weeks after treatment (see lines W3 in Table 114) have been summarized, as shown in Table 115, and statistically analysed in Table 116.

From Table 115 it can be seen that all insecticidal treatments yielded positive results, in contrast to some negative results of the control. The control therefore indicates that older larvae waste more needles than younger larvae, thus stressing the effectiveness of all insecticidal treatments.

From Table 116 it is clear that there were no significant differences between the reductions of needle fall obtained with endosulfan, nendrin, Thuricide and DDT. These four treatments were, however, all significantly more effective than cidial. All insecticidal treatments differed significantly from the control.

The percentage reductions in the number of frass pellets collected three weeks after treatment (see lines W3 in Table 114) have been summarized in Table 117 and statistically analysed in Table 118.

Table 114: The number of and the percentage reduction in severed needles and frass pellets collected one day before and on three days at weekly intervals after the different treatments, as determined in four containers per treatment (B = before; W1, W2 & W3 = Three weekly intervals after treatment; R% = Percentage reduction)

Treatment	Time	Replication																Treatment totals		Treatment mean % reduction		% reduction Abbott's formula	
		1				2				3				4									
		Needles		Frass		Needles		Frass		Needles		Frass		Needles		Frass		Needles	Frass	Needles	Frass	Needles	Frass
		n	R %	n	R %	n	R %	n	R %	n	R %	n	R %	n	R %	n	R %						
Nendrin	B	226		214		105		102		149		134		75		29		555	479				
	W1	75	66,8	66	69,2	32	69,5	25	75,5	33	77,9	24	82,1	22	70,7	17	41,4	162	132	70,8	72,4	73,9	77,3
	W2	47	79,2	16	92,5	8	92,4	24	76,5	45	69,8	11	91,8	20	73,3	8	72,4	120	59	78,4	87,7	81,4	88,1
	W3	31	86,3	11	94,9	2	98,1	9	91,2	32	78,5	18	86,6	4	94,7	0	100,0	69	38	87,6	92,1	87,6	90,9
DDT	B	234		156		163		78		111		81		103		80		611	395				
	W1	58	75,2	44	71,8	62	62,0	50	35,9	78	29,7	71	12,3	29	71,8	38	52,5	227	203	62,9	48,6	66,8	57,6
	W2	73	68,8	50	67,9	52	68,1	14	82,1	21	81,1	23	69,1	32	68,9	7	91,3	178	96	70,9	75,7	75,0	76,5
	W3	32	86,3	12	92,3	29	82,2	3	96,2	13	88,3	16	79,0	11	89,3	2	97,5	85	33	86,1	91,6	86,1	90,3
Cidial	B	108		136		130		52		146		74		141		86		525	348				
	W1	140	29,6	125	8,1	76	41,5	35	32,7	96	34,2	53	28,4	63	55,3	55	36,0	375	268	28,6	23,0	36,1	44,2
	W2	89	17,6	55	59,6	85	34,6	43	17,3	72	50,7	49	33,8	52	63,1	38	55,8	298	185	43,2	46,8	51,2	48,5
	W3	64	40,7	36	73,4	68	47,7	21	59,6	75	48,6	30	59,5	59	58,2	48	44,2	266	135	49,3	61,2	49,1	55,4
Endosulfan	B	120		134		112		148		37		34		92		80		361	396				
	W1	39	67,5	11	91,8	13	88,4	33	77,7	11	70,3	8	76,5	25	72,8	31	61,3	88	83	75,6	79,0	78,2	82,7
	W2	13	89,2	2	98,5	7	93,8	4	97,3	4	89,2	5	85,3	14	84,8	7	91,3	38	18	89,5	95,4	91,0	95,6
	W3	0	100,0	1	99,3	16	85,7	3	98,0	3	91,9	1	97,1	9	90,2	9	88,8	28	14	92,2	96,5	92,2	96,0
Thuricide	B	78		126		51		54		75		112		31		49		235	341				
	W1	34	56,4	28	77,8	29	62,7	21	61,1	29	61,3	52	53,6	11	64,5	18	63,3	103	119	56,2	65,1	60,8	71,2
	W2	11	85,9	4	96,8	17	66,7	10	81,5	33	56,0	17	84,8	5	83,9	1	98,2	66	32	71,9	90,6	75,9	90,9
	W3	5	93,6	3	97,6	9	82,4	3	94,4	8	89,3	14	87,5	3	90,3	2	95,9	25	22	89,4	93,6	89,4	92,6
Control	B	41		67		30		34		64		40		163		67		298	208				
	W1	34	17,1	56	16,4	27	10,0	19	44,1	58	9,4	52	-30,0	214	-31,3	125	-46,4	333	252	-11,7	-21,2		
	W2	71	73,1	49	26,9	44	-46,7	26	23,5	74	-15,6	46	-15,0	158	3,1	94	-40,3	347	215	-16,4	-3,4		
	W3	44	-7,3	48	28,4	30	0,0	20	41,2	81	-26,6	59	-47,5	142	12,9	54	19,4	297	181	0,3	13,0		

Table 115: Percentage reductions in severed needles collected three weeks after treatment

Treatment Block	B1 Nendrin	B2 DDT	B3 Cidial	B4 Endosulfan	B5 Thuricide	B6 Control	Total
R1	86,3	86,3	40,7	100,0	93,6	- 7,3	399,6
R2	98,1	82,2	47,7	85,7	82,4	0,0	396,1
R3	78,5	88,3	48,6	91,9	89,3	- 26,6	370,0
R4	94,7	89,3	58,2	90,2	90,3	12,9	435,6
Total	357,6	346,1	195,2	367,8	355,6	- 21,0	1 601,3
Aver	89,400	86,525	48,800	91,950	88,900	- 5,250	

Table 116: Analysis of variance of data in Table 115

Source of variation	SS	d.f.	MS	F
Blocks	363,51	3	121,17	
Treatments	30 143,52	5	6 028,70	4,42*
Error	2 043,92	15	136,261	
Total	32 550,95	23		

*Differs significantly at the 5% level ($F_{5,15} = 2,90$)

S.S.D. = 26,841 (5%)

endosulfan	nendrin	Thuricide	DDT	cidial	control
<u>91,950</u>	<u>89,400</u>	<u>88,900</u>	<u>86,525</u>	<u>48,800</u>	- 5,250

Percentages underlined by a continuous line do not differ significantly.

Table 117: Percentage reductions in frass pellets collected three weeks after treatment

Randomized block

Treatment Block	B1 Nendrin	B2 DDT	B3 Cidial	B4 Endosulfan	B5 Thuricide	B6 Control	Total
R1	94,9	92,3	73,4	99,3	97,6	28,4	485,9
R2	91,2	96,2	59,6	98,0	94,4	41,2	480,6
R3	86,6	79,0	59,5	97,1	87,5	- 47,5	362,2
R4	100,0	97,5	44,2	88,8	95,9	19,4	445,8
Total	372,7	365,0	236,7	383,2	375,4	41,5	1 774,5
Aver	93,175	91,250	59,175	95,800	93,850	10,375	

From Table 117 it can also be seen that all results concerning the percentage reduction of frass pellets were positive, except for the third replication of the control. The average value for the control was however positive, indicating that either some of the larvae disappeared, or that older larvae produce fewer frass pellets per day than younger larvae. Although single larvae could have pupated, the decrease is probably due to less frass being produced by older larvae.

Table 118: Analysis of variance of data in Table 117

Source of variation	SS	d.f.	MS	F
Blocks	1 744,23	3	581,41	
Treatments	22 999,95	5	4 599,99	16,90**
Error	4 082,30	15	272,15	
Total	28 826,48	23		

**Differs highly significantly at the 1% level ($F_{5,15} = 4,56$)

SS D. = 37,945 (5%) and 47,844 (1 %).

endosulfan	Thuricide	nendrin	DDT	cidial	control
95,800	93,850	93,175	91,250	59,175	10,375

Percentages underlined by a continuous line do not differ significantly. Percentages underlined by a dotted line do not differ highly significantly.

The analysis in Table 118 indicates that the percentage reductions in frass pellets obtained with the different insecticidal treatments after three weeks did not differ significantly from one another. All treatments did however differ highly significantly from the control.

Counting of dead larvae is considered the most accurate method of determining percentage mortality. The other methods based on needle fall and the production of frass, indicated mortalities in close agreement with those based on larval counts. Of the other two methods, the average reduction based on frass pellets was closer to that based on larval counts. Van Dyk, Prinsloo & Pretorius (1969) who compared frass production with larval counts for assessing the results obtained in an aerial spraying experiment against *Euproctis terminalis*, came to the same conclusions. The method based on frass production and needle fall is however much more economical and practical than that based on larval counts and may therefore be strongly recommended for use by foresters.

9) Discussion of control precautions

In practice control methods are usually applied too late, i.e. after pupation has already commenced and the trees already seriously damaged. All that can then be achieved is the lowering of the potential population of the next generation.

Hand collecting and the collecting and marketing of larvae can only be recommended if the trees are less than 3m high. If infestations however, occur in taller trees, they will have to be controlled by other methods to prevent reinfestation.

Collecting pupae and adults can not be recommended. Fire can only be used in exceptional cases or for destruction of larvae on indigenous shrubs.

No success was achieved in the experiment using live females to attract the males. It therefore appears that synthetic attractants will not necessarily give satisfactory results, especially in plantations where relatively large areas are severely infested. If the population can however be decreased beforehand in some other way, this control method may be useful; sexual attractants may also be useful for confusing the males. This would however probably be very expensive.

Thinning out and pruning can be an important control method. If carried out after egg laying, the hatching larvae will die of starvation. If it is done about two

months before defoliation is expected, it would also result in larval starvation. When timber is pulled out of a plantation during the pupal period, many pupae are crushed to death.

The introduction of wild bushpigs can be very effective and if they occur naturally in the vicinity, it can be recommended. Domesticated pigs are regarded as one of the cheapest and best methods of biological control and can be very strongly recommended. The herding of pigs, ensuring that they feed systematically throughout the plantation, seems to be a great improvement on allowing them a free run within a relatively extensive fenced off area.

Hand spraying can be recommended in areas where the population is limited to young trees. Aerial spraying has proved to be very effective and possesses the additional advantage of being completed in a short time, thus limiting the damage done to the trees.

B. Control of *P. irius*

In comparison with the pine emperor, fewer control precautions have been tried against the poplar emperor.

1) Thinning and pruning

As mentioned with the pine emperor, thinning and pruning can be applied to decrease the population.

2) Birds

Hepburn *et al* (1966) experimented with peacocks and turkeys to determine whether they would dig up and devour pupae. Since these birds showed no interest in either exposed or buried pupae, the experiments were terminated.

3) Pigs

a) In poplar plantations

According to Hepburn *et al* (1966), a number of pigs were introduced in an infested area of the Sheepmoor plantation during May to September, 1960. Although many pupae were destroyed, heavy reinfestation was not prevented the next generation. The inability of the pigs to wipe out the pest was attributed to the ex-

ceptionally dense root system of *P. deltoides*, sheltering many of the pupae. As the pupal stage occurs during the dry season, the hard soil probably also protected many of the pupae. It may be worthwhile to modify and then repeat this experiment, introducing the pigs from the middle of January at the height of the rainy season.

b) **In pine plantations**

An experiment was conducted during 1969 to test the ability of pigs in controlling the pupal stage.

A sty (11 x 11 m) was constructed from dead tree trunks, situated centrally in an area of 34,4 ha.

As the forester of Rietvlei was in possession of pigs, it was decided to regard their mass as criterion of their value. The mass of the 13 pigs available was determined before being introduced into the plantation on the 14th February, 1969.

During the day, the pigs were forced by a swineherd to graze systematically over the whole area. During the night they were kept in the sty and provided with water but no extra food. Contrary to previous experience with the pine emperor, the pigs devoured poplar emperor pupae offered them from the first day. After a few days, pupae were eagerly dug up and devoured.

Pupal counts were made in 20 randomly taken plots before and another 20 plots after completion of the experiment, each plot being 2,7 x 2,7 m. The results of these counts can be found in Table 119 and the statistical analysis in Table 120.

The number of pupae that could be located after the experiment was highly significantly lower than those located before the experiment (Table 120). No control plots were used where pigs were not allowed to graze. From other studies it was found that few poplar emperor pupae disappeared from this plantation due to other predators. The mortality observed was thus apparently brought about chiefly by the pigs.

Three months after introduction, the mass of the pigs was again obtained. The mass of the 13 pigs before and three months afterwards is provided with the statistical analysis in Table 121.

Table 119: Number of poplar emperor pupae in 40 plots of 2,7 x 2,7 m, 20 before and 20 after 13 pigs had been herded in an infested area.

Plot	Number of pupae	
	Before	After
1	24	1
2	35	1
3	30	3
4	16	2
5	15	0
6	25	1
7	24	3
8	17	5
9	21	1
10	5	5
11	8	1
12	8	0
13	17	3
14	19	2
15	21	1
16	22	6
17	23	2
18	28	0
19	31	4
20	18	0
Total	407	41
% pupae destroyed = 89,9		

Table 120: Analysis of variance of data in Table 119 (of the number of pupae per plot before and after herding pigs)

Source of variation	SS	d.f.	MS	F
Between groups before and after	3 348,9	1	3 348,9	67,75**
Within groups	1 219,5	18		
Total	4 568,4	19		

**Differs highly significantly at the 1% level ($F_{1,18} = 8,28$)

Table 121: Mass of pigs in kg before and three months after they had fed exclusively on poplar emperor pupae

Pig no	Mass before = a	Mass after = b	Increase in mass = b-a	Relative increase in mass = $\frac{b-a}{a}$
1	8,6	22,2	13,6	1,58
2	9,1	25,0	15,9	1,75
3	12,3	29,4	17,1	1,40
4	12,3	29,6	17,3	1,41
5	12,7	28,6	15,9	1,25
6	12,7	34,1	21,4	1,69
7	15,9	31,8	15,9	1,00
8	21,3	49,9	28,6	1,34
9	40,4	72,6	32,2	0,80
10	43,6	65,8	22,2	0,51
11	44,0	72,6	28,6	0,65
12	61,7	78,5	16,8	0,27
13	99,9	109,0	9,1	0,09
Total	394,5	649,1	254,6	13,74
Average	30,35	49,93	19,58	1,06
$S_{\frac{x}{x}} \frac{A-B}{A-B} = 1,86; t = 68,59^{**}; t_{,01} (12) = 3,06$				

From this table it can be seen that all the pigs had a greater mass after the three months during which they had fed exclusively on poplar emperor pupae. The smaller the pigs, the bigger the relative increase in mass. This means that if the pigs are bought for the purpose of controlling pupae and are sold afterwards, young pigs would be more economical than older ones.

According to the statistical analysis in Table 121 it is clear that the pigs weighed highly significantly more after than before feeding on poplar emperor pupae.

In order to calculate the cost of biological control by herding pigs, it was decided to credit the account with the increase in value of the pigs due to their growth.

Calculation of cost of biological control by herding pigs

Expenditure

Wages of swineherd at 80c per day	R72,00
Erection of sty	5,00
Transporting water	3,00
	<hr/>
Gross expenditure	R80,00
Estimated increase in value of pigs	
(254,6 kg at 22c per kg)	R56,01
Net expenditure to obtain 90 per cent control in	
34,4 ha	<hr/>
	R23,99
Net expenditure per ha	70c

All the indications are that pigs can effectively and economically be used in the biological control of the pupal stage of the poplar emperor. It was however noticed that after digging at a specific spot for some time, the pig seems to lose interest and to wander off, although a pupa was definitely present where it had been digging. This happened where the soil was very hard and dry and may have been due to the fact that the pupae were too deep to be unearthed.

The total number of pupae in the area must have been about a million. The pigs devoured 90 per cent, thus about 900 000. Each pig must therefore have accounted for something like 770 pupae per day, amounting to roughly 4 l, a volume that an average pig of 40 kg might well be able to manage. It must however be borne in mind that other predators, such as the Yellow Mongoose, were present in the plantation, so that the number of pupae devoured by pigs could have been slightly smaller than calculated.

In a second experiment, the same 13 pigs were allowed to roam about in an area of 11 ha for 30 days from the 15th of May. As in the first experiment only water was supplied. Pupal counts were made in 10 randomly taken plots before the introduction of pigs and 10 plots 30 days later. The results can be found in Table 122, and the statistical analysis in Table 123.

Table 122: Number of poplar emperor pupae in 20 plots of 2,7 x 2,7 m, 10 before and 10 after pigs were left to roam in an area of 11 ha

Plot	Number of pupae	
	Before	After
1	25	4
2	18	6
3	15	3
4	20	7
5	14	11
6	12	6
7	31	7
8	27	13
9	30	5
10	26	10
Total	218	72
% pupae destroyed = 67,0		

Table 123: Analysis of variance of data in Table 122 (the number of pupae per plot before and 30 days after 13 pigs were introduced in an area of 11 ha and left unherded)

Source of variation	SS	d.f.	MS	F
Between groups before and after	1 065,8	1	1 065,8	36,96**
Within groups	519,2	18	28,84	
Total	1 585,0	19		

**Differs highly significantly at the 1% level ($F_{1,18} = 8,28$)

From Table 123 it can be seen that highly significantly less pupae could be located after than before this experiment.

In Tables 124 and 125 the number of pupae before and after the two experiments are compared with each other.

Table 124: Analysis of variance of data in Tables 119 & 122 before the experiment

Source of variation	SS	d.f.	MS	F
Between groups before and after	14,02	1	14,02	0,25 ⁻
Within groups	1 584,15	28	56,58	
Total	1 598,17	29		

⁻Do not differ significantly at the 5% level ($F_{1,28} = 4,20$)

Table 125: Analysis of variance of data in Tables 119 & 122 after the experiment

Source of variation	SS	d.f.	MS	F
Between groups before and after	176,82	1	176,82	32,03**
Within groups	154,55	28	5,52	
Total	331,37	29		

**Differs highly significantly at the 1% level ($F_{1,28} = 7,64$)

From Table 124 it can be concluded that the pupal populations of the two areas were the same before the introduction of the pigs. From Table 125 it however follows that this was not the case after the experiments, the pupal population being significantly higher in the area where the pigs had not been herded.

From the data it can further be calculated that the number of pupae destroyed per unherded pig was about 565 in comparison with 770 destroyed daily per pig when herded. However, since the same 13 pigs were used, they were older and more were nearly full-grown when they were not herded. Since the more full-grown pigs gained less in mass, they probably require less food than younger pigs. Further-

more the soil was considerably drier at this time of the year (mid May to mid June) than during the time when pigs were herded (mid February to mid May). This may explain the apparent greater effectiveness of the herded pigs. Further research is necessary before definite conclusions can be reached on the value of herding the pigs.

4) Control by insecticidal sprays

The only other insecticidal spraying yet applied against poplar emperor larvae was done by Hepburn *et al* (1966). As the results were influenced by rain no definite conclusions could be made. However, it was thought that mortalities obtained by nendrin, DDT and chlorfenvinphos were probably more than 95 per cent, while that by carbaryl was weak.

On 1st January, 1969, an experiment was conducted at Rietvlei on 10 year old *P. patula* trees (average height 9,5 m), in order to compare the effectiveness of five different insecticides, one of which was a bacterium.

It was done in part of a plantation 34,4 ha in extent which was divided into four blocks. In each block six plots 19,2 x 91,4 m were laid out, separated by strips of 41,1 m wide. In each block five plots were to be sprayed with the different insecticides while one was to serve as a control. There were therefore six treatments, each replicated four times. The insecticides used were all administered in 33,7 l of water per ha, i.e. nendrin (Endrex 19,5% EC) 275 ml a.i.; DDT (25% EC) 2 200 ml a.i.; phosphamidon (Dimecron 51,7% EC) 346 ml a.i.; mevinphos (Phosdrin 25,4% EC) 1 245 ml a.i. and Thuricide (15 billion *B. thuringiensis* spores per g EC) at 2 100 ml a.i. plus 8,8 ml Triton B.

Four similarly coloured flags (markers) were placed at the corners of each plot (as mentioned for the pine emperor), and the pilot was given a flag with the colour corresponding to that of the insecticide in the tank. There was no wind at the beginning of spraying, but towards the end there was a very slight breeze. From deposit cards on the ground underneath the trees, it was concluded that a reasonably uniform cover was obtained throughout the experiment.

Two methods were employed to estimate the results obtained as indicated below.

Method (a) : Massive overdusting to kill all surviving larvae

The mortality was determined by the same methods as used for the pine emperor.

A day before spraying, three observation areas, each 2,7 x 2,7 m, were raked clean in the central three lanes of each plot. Daily records were kept of dead larvae in these observation areas. Severed needles and frass pellets were noted daily in four containers in each plot. After 14 days, the natural mortality under the control trees was about the same as that under the sprayed trees. The trees surrounding each observation area were dusted as described for the pine emperor.

Results

The total number of dead larvae collected up to 14 days after spraying were considered as having died due to the different treatments, while the numbers that died during the first week after the massive overdusting were taken as the numbers surviving these treatments. From these figures the percentage mortality was calculated for each replication of each treatment. The results of this experiment can be found in Table 126. These results have been summarized as shown in Table 127 for the purpose of the statistical analysis appearing in Table 128.

From Table 128 it can be seen that the mortalities obtained with DDT and nendrin do not differ significantly from one another; they do however differ significantly from all other treatments. Thuricide differs highly significantly from DDT, phosphamidon, mevinphos and the control. Phosphamidon and mevinphos did not differ significantly from each other but highly significantly from the control.

For chemical control DDT may be recommended at 2 200 ml a.i. in 33,7 l of water per ha, or nendrin at 275 ml a.i. in 33,7 l of water (or diesolien) per ha for trees about 10 m tall.

Method (b): Reduction in the numbers of needles severed and frass pellets produced

Four containers each 48,1 x 37,7 cm were placed in the central three lanes of each plot a day before spraying. The numbers of severed needles and frass pellets in these containers were recorded daily for two weeks after spraying. The daily total number of needles and frass pellets for the same replication before treatment could therefore be compared with any daily total of the same replication after treatment.

Table 126: Numbers and percentages of poplar emperor larvae that died after different treatments and the numbers surviving 14 days later in each of the three observation areas (2,7 x 2,7 m each) in each of four replications

Treatment	Replication	Observation area						Totals for each treatment		Percentage mortality	% mortality (Abbott* formula)
		a		b		c					
		Number of larvae		Number of larvae		Number of larvae		Dead	Surviving		
		Dead	Surviving	Dead	Surviving	Dead	Surviving				
DDT (2 200 ml a.i./ha)	1	117	3	113	1	101	2	341	6	98,3	
	2	89	0	97	1	68	0	254	1	99,6	
	3	63	1	60	0	87	0	212	1	99,5	
	4	38	0	31	1	40	0	109	1	99,1	
								916	9	99,0	99,0
Nendrin (275 ml a.i./ha)	1	75	1	91	1	111	5	277	7	97,5	
	2	51	0	93	3	73	2	179	5	97,3	
	3	24	2	33	2	23	0	80	4	95,2	
	4	20	3	26	1	16	1	62	5	92,5	
								598	21	96,6	96,5
Phospha- midon (346 ml a.i./ha)	1	7	9	8	10	11	4	26	23	53,0	
	2	17	14	10	9	13	9	40	32	55,6	
	3	9	4	11	7	5	3	25	14	64,1	
	4	2	4	7	5	3	6	12	15	44,4	
								103	84	55,1	54,1
Mevin- phos (1 245 ml a.i./ha)	1	15	16	18	18	20	17	53	51	51,0	
	2	17	16	17	13	22	21	56	50	52,8	
	3	10	8	20	16	12	11	42	35	54,5	
	4	3	4	6	5	6	2	15	11	57,7	
								166	147	53,0	52,0
Thuri- cide (2 100 ml a.i. + 8,8 ml Triton B/ha)	1	62	20	84	14	59	15	305	49	86,2	
	2	16	2	31	5	20	1	67	8	89,3	
	3	41	5	48	6	53	9	142	20	87,7	
	4	9	1	8	3	15	3	32	7	82,1	
								546	84	86,7	86,3
Control	1	3	73	4	107	2	65	9	245	3,5	
	2	0	24	1	31	0	23	1	78	1,3	
	3	0	19	0	47	0	24	0	90	0,0	
	4	0	6	0	17	0	10	0	33	0,0	
								10	446	2,2	

$$* \% \text{ mortality} = \left\{ \frac{\% \text{ mortality of insecticide} - \% \text{ mortality of control}}{100 - \% \text{ mortality of control}} \right\} \times 100$$

Table 127: Summary of the percentage mortalities appearing in Table 126**Randomized block**

Treatment Block	B1 DDT	B2 Nendrin	B3 Phosphami- don	B4 Mevinphos	B5 Thuricide	B6 Control	Total
R1	98,3	97,5	53,0	51,0	86,2	3,5	389,5
R2	99,6	97,3	55,6	52,8	89,3	1,3	395,9
R3	99,5	95,2	64,1	54,5	87,7	0,0	401,0
R4	99,1	92,5	44,4	57,7	82,1	0,0	375,8
Total	396,5	382,5	217,1	216,0	345,3	4,8	1 562,2
Aver	99,125	95,625	54,275	54,000	86,325	1,200	

Table 128: Analysis of variance of data in Table 127

Source of variation	SS	d.f.	MS	F
Blocks	59,42	3	19,81	
Treatments	27 454,31	5	5 490,86	381,52**
Error	216,49	15	14,43	
Total	27 730,22	23		

**Differs highly significantly at the 1% level ($F_{5,15} = 4,56$)

S.S.D. = 8,737 (5%) and 11,016 (1%)

DDT	nendrin	Thuricide	phosphamidon	mevinphos	control
99,125	95,625	86,325	54,275	54,000	1,200

Percentages underlined by a continuous line do not differ significantly. Percentages underlined by a dotted line do not differ highly significantly.

Results

The results of the needle and frass studies before and after the spraying experiment are given in Table 129. The negative values in this table are due to increases in the numbers of needles. The result obtained with the five insecticidal treatments were all positive with two exceptions, namely, the needle counts after one week in the first and fourth replication of mevinphos.

Table 129: Number of and the percentage reduction in severed needles and frass pellets collected one day before, and on two days at weekly intervals after the different treatments, as determined in four containers per treatment (B = before, W1 = After one week, W2 = After two weeks, R% = Percentage reduction)

Treatment	Time	Replication																Treatment totals		Treatment mean % reduction		% reduction Abbott formula	
		1		2		3		4															
		Needles	Frass	Needles	Frass	Needles	Frass	Needles	Frass	Needles	Frass	Needles	Frass	Needles	Frass	Needles	Frass						
n	R%	n	R%	n	R%	n	R%	n	R%	n	R%	n	R%	n	R%	n	R%	Needles	Frass	Needles	Frass	Needles	Frass
DDT	B	364		135		283		83		294		97		147		42		1 088	357				
	W1	122	66,5	14	89,6	112	60,4	7	91,5	96	67,3	5	94,8	83	77,6	5	88,1	413	31	62,0	91,3	57,9	89,9
	W2	37	89,8	8	94,1	36	87,3	4	95,2	21	92,9	4	95,9	19	87,1	6	85,7	113	22	89,6	93,8	89,0	92,1
Nendrin	B	343		86		309		60		208		69		169		38		1 029	253				
	W1	136	60,3	16	81,4	83	73,1	10	83,3	133	36,1	14	79,7	50	70,4	11	71,1	402	51	60,9	79,8	51,2	76,6
	W2	71	79,3	19	77,9	70	77,3	7	88,3	52	75,0	6	91,3	27	84,0	3	92,1	220	35	78,6	86,1	77,4	82,2
Phospha-midon	B	164		67		539		142		276		68		171		37		1 150	314				
	W1	112	31,7	21	68,7	338	37,3	60	57,7	169	38,8	24	64,7	148	13,5	21	43,2	767	126	33,3	59,9	23,6	53,6
	W2	134	18,3	21	68,7	226	58,1	56	60,6	131	52,5	22	67,6	94	45,0	10	73,0	585	109	49,1	65,3	46,3	55,5
Mevinphos	B	305		156		231		72		263		79		182		59		981	366				
	W1	342	- 12,1	52	66,7	230	0,4	25	65,3	215	18,3	31	60,8	195	- 7,1	26	55,9	882	134	10,1	63,4	0,4	57,6
	W2	171	40,7	37	76,3	137	40,7	19	73,6	144	45,2	27	65,8	154	15,4	33	44,1	606	116	38,2	68,3	34,8	59,4
Thuricide	B	438		186		422		101		235		94		295		76		1 390	407				
	W1	152	65,3	38	79,6	209	50,5	36	64,4	139	40,9	26	72,3	178	39,7	39	48,7	678	139	51,2	65,8	41,5	60,4
	W2	94	78,5	28	84,9	156	63,0	26	74,3	64	72,8	17	81,9	82	72,2	26	65,8	396	97	71,5	76,2	69,9	69,5
Control	B	356		101		305		78		278		90		225		53		1 164	322				
	W1	320	10,1	89	11,9	272	10,8	57	26,9	251	1,0	87	3,3	208	7,6	45	15,1	1 051	278	9,7	13,6		
	W2	338	5,1	82	18,8	291	4,6	49	37,2	288	- 3,6	76	15,6	186	17,3	44	17,0	1 103	251	5,2	22,0		

As judged from needle drop and frass: reduction for the two weeks, nendrin appeared to be more quick acting than the other four treatments.

The percentages by which the numbers of needles severed had been reduced two weeks after treatment (see lines W2 in Table 129) have been summarized as shown in Table 130, and statistically analysed in Table 131.

Table 130: Percentage reductions in severed needles collected two weeks after treatment

Randomized block

Treatment Block	B1 DDT	B2 Nendrin	B3 Phosphami- don	B4 Mevinphos	B5 Thuricide	B6 Control	Total
R1	89,8	79,3	18,3	40,7	78,5	5,1	311,7
R2	87,3	77,3	58,1	40,7	63,0	4,6	331,0
R3	92,9	75,0	52,5	45,2	72,8	- 3,6	334,8
R4	87,1	84,0	45,0	15,4	72,2	17,3	321,0
Total	357,1	315,6	173,9	142,0	286,5	23,4	1 298,5
Aver	89,275	78,900	43,475	35,500	71,625	5,850	

Table 131: Analysis of variance of data in Table 130

Source of variation	SS	d.f.	MS	F
Blocks	54,06	3	18,02	
Treatments	19 785,44	5	3 957,09	32,23**
Error	1 841,45	15	122,76	
Total	21 680,95	23		

**Differs highly significantly at the 1% level ($F_{5,15} = 4,56$)

S.S.D. = 25,484 (5%) and 32,132 (1%)

DDT	nendrin	Thuricide	phosphamidon	mevinphos	control
89,275	78,900	71,625	43,475	35,500	5,850

Percentages underlined by a continuous line do not differ significantly. Percentages underlined by a dotted line do not differ highly significantly.

From Table 131 it is clear that no significant difference in the reduction of

needle fall could be found between DDT, nendrin and Thuricide, while DDT and nendrin did differ highly significantly from phosphamidon, mevinphos and the control. Phosphamidon did not differ significantly from mevinphos but both differed highly significantly from the control. Thuricide and phosphamidon, phosphamidon and mevinphos as well as mevinphos and the control did not differ highly significantly from one another.

The percentage reduction of frass pellets two weeks after treatment has been summarized in Table 132. For the analysis see Table 133.

Table 132: Percentage reductions in frass pellets collected two weeks after treatment
Randomized block

Treatment Block	B1 DDT	B2 Nendrin	B3 Phosphamidon	B4 Mevinphos	B5 Thuricide	B6 Control	Total
R1	94,1	77,9	68,7	76,3	84,9	18,8	420,7
R2	95,2	88,3	60,6	73,6	74,3	37,2	429,2
R3	95,9	91,3	67,6	65,8	81,9	15,6	418,1
R4	85,7	92,1	73,0	44,1	65,8	17,0	377,7
Total	370,9	349,6	269,9	259,8	306,9	88,6	1 645,7
Aver	92,725	87,400	67,475	64,950	76,725	22,150	

Table 133: Analysis of variance of data in Table 132

Source of variation	SS	d.f.	MS	F
Blocks	263,99	3	88,0	
Treatments	12 694,63	5	2 538,93	32,38**
Error	1 176,21	15	78,41	
Total	14 134,83	23		

**Differs highly significantly at the 1% level ($F_{5,15} = 4,56$)

S.S.D. = 20,364 (5%) and 25,677 (1%)

DDT	nendrin	Thuricide	phosphamidon	mevinphos	control
92,725	87,400	76,725	67,475	64,950	22,150

Percentages underlined by a continuous line do not differ significantly. Percentages underlined by a dotted line do not differ highly significantly.

From the analysis of the reduction of frass pellet countings in Table 133, it can be seen that no significant differences could be found between DDT, nendrin and Thuricide. DDT and nendrin did differ significantly from phosphamidon, mevinphos and the control, while DDT differed highly significantly from phosphamidon, mevinphos and the control. Thuricide did not differ significantly from phosphamidon and mevinphos. All treatments differed highly significantly from the control.

The percentage mortality based on the reduction of frass was, on the average, closer to the figure based on larval counts, than that based on the reduction of needles severed. As described for the pine emperor, the counting of dead larvae is considered to be the most accurate method of obtaining the percentage mortality. The methods of counting needles and frass, however, gave approximately the same results. The last two mentioned methods are much more economical and practical than that based on larval counts, and are recommended for use by foresters.

5) Discussion of control precautions

Although the collecting and marketing of larvae of the poplar emperor as well as handspraying have not yet been attempted, both can be recommended because these methods have been applied successfully against the pine emperor.

Thinning out and pruning, as described for the pine emperor, may be effective.

Since the whole poplar emperor larval population is present during the last week in December, aerial spraying will probably be more practical and effective against this insect than against the pine emperor.

Control of pupae by pigs, though very promising, is not quite as effective as found for the pine emperor. This may be attributable to the fact that pupae are formed during months when the soil is moist, allowing full-grown larvae to burrow quite deeply into the soil. If the soil dries out afterwards, pigs may experience some difficulty in unearthing them. Nevertheless, pigs are undoubtedly one of the cheapest and best control measures.

C. Control of *H. smilax*

Although no control methods have been attempted, it is surmised that the following insecticides should give effective control whether applied from the ground

or the air, at the same concentrations that proved to be effective against the other two species of emperor moths, i.e. endosulfan, DDT and nendrin.

As this species pupates in cracks in the bark of the trees, pigs will not be able to control them. Thinning out and pruning might also be ineffective as the larvae are very active.

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