

## CHAPTER 7

### EFFECT OF TEMPERATURE ON TUBERISATION IN *PLECTRANTHUS ESCULENTUS*

#### 7.1 EFFECT OF LOW NIGHT TEMPERATURES ON TUBER INITIATION

##### 7.1.1 Introduction

Environmental factors greatly affect the growth and development of all living organisms. The response of plants to their environment is well documented, with almost all responses being influenced to a greater or lesser degree by temperature (Noggle & Fritz, 1976; von Denffer *et al.*, 1976; Salisbury & Ross, 1978). Night temperatures are particularly important in the growth of plants. Lowered night temperatures can lead to large improvements in quality of growth, or to the earliness and intensity of flowering or fruiting processes (Went, 1957). In the course of normal growth and development of plants there are short phases when special sensitivities to temperature occur (Leopold, 1964; von Denffer *et al.*, 1976). In many cases, temperature conditions will induce the formation of such underground storage organs as bulbs, corms, and tubers. Relatively low temperatures, particularly low night temperatures, promote the development of tuberous roots in the sweet potato (Kim, 1961; Edmond & Ammerman, 1971). A number of researchers have found that the response of different plant species to low night temperatures differ, with low night temperatures either reducing tuberisation, or having no effect (Davies, 1941; Alvey, 1965; Borah & Milthorpe, 1963; Moreno, 1970; Roca-Pizini, 1972).

In potato it has been shown that tubers can be induced by maintaining young plants at 7°C for a period of seven days (Burt, 1964). This effect has been confirmed in both the field and glasshouses when transferring plants from a warm to an appreciably cooler environment (Burt, 1965), as well as by treatment of isolated sprouts (Blanc, 1973). It is now a well-established fact that tuberisation of whole potato plants is hastened by short days and at low temperatures (Cutter, 1978).

A number of workers have concluded that low night temperatures have a greater effect on tuberisation in potato than day temperatures (Gregory, 1956; Went, 1959; Bodlaender, 1963; Menzel, 1982; Gopal, Minocha & Dhaliwal, 1998). Slater (1968) showed that tubers were formed earlier when the night temperature of the shoot was lowered, and earliest when the night temperature in both the shoot and root zone was lowered. Borah & Milthorpe (1963) reported that differences in temperature have a far greater effect on the number of tubers than on total yield, indicating that the main effect of low temperature appears to be on tuber initiation rather than on subsequent growth. Low night temperatures result in higher sugar (carbohydrate) contents in many plants, including potato and sugar beet (Leopold, 1964), a phenomenon believed to lead to tuberisation, but which is more likely to indicate the start of tuber growth (Hammes, 1972).

No information is available on the effect of night temperature on tuberisation in *Plectranthus esculentus*. The objective of this experiment was to determine the effect of low night temperature on tuber induction and growth.

### 7.1.2 Materials and Methods

Plants originating for the same tissue culture stock were used in this trial. The trial was carried out in Conviron controlled environment cabinets at the University of Pretoria's phytotron facility located on the experimental farm in Pretoria. The preparation of the material is detailed in **Chapter 4**. Four temperature treatments were used: 25/18°C, 25/15°C, 25/12°C and 25/9°C day/night temperature regimes. Lights were set to provide a 14 hour day and 10 hour dark period.

Twenty-one plants were placed in each temperature treatment on 18 August 2000, and exposed to the various treatments for a period of 21 days. Every third day three plants were removed from the controlled environment and three two-node cuttings made from two plants. The method of preparing the cuttings and the further treatment of both cuttings and intact plants are described in **Chapter 6.1**. After a period of three weeks in the glasshouse, intact plants and cuttings were harvested, and examined for signs of tuber formation.

### 7.1.3 Results and Discussion

The intact plants showed reduced growth due to exposure to low night temperatures. The most marked differences were between the highest and lowest temperatures (Figure 7.1), where plant height was reduced by approximately 60% at the lowest night temperature of 9°C when compared with that at the highest night temperature (18°C). This concurs with results obtained in potato, where stem elongation and haulm weight were found to be greater at higher temperatures, particularly under conditions of low irradiance such as occur in growth chambers (Menzel, 1985a).



**Figure 7.1** Effect of low night temperature on growth of *P. esculentus* plants (Left 25/18°C, Right 25/9°C)

#### Intact plants

No signs of tuber formation were exhibited by plants in any of the treatments, indicating that low night temperatures *per se* are not sufficient to induce tuber initiation in this species. Although the effect of photoperiod on tuber formation in *Plectranthus* was demonstrated in **Chapter 6**, the effect of radiation and external nitrogen supply was not investigated in

the course of this study. Other factors such as radiation, external nitrogen supply and photoperiod have been shown to influence tuber formation in both potatoes and sweet potatoes (Hahn & Hozyo, 1984; Menzel, 1985a), and it is possible that they could also play a role in tuber formation in this species. Irradiance could be of particular importance, as *Colocasia esculenta*, another tropical plant producing underground storage organs, is reported to have storage organ formation reduced by low irradiance. This is also an important factor affecting tuberisation in potato, but variation between genotypes occurs (Menzel, 1985a).

#### Cuttings

No signs of tuber formation or swollen bases on the underground shoots was noted for any treatment. All cuttings had both aerial shoots and subterranean shoots developing from the axillary buds in the leaf axils, but no differences were noted between the various treatments.

Generally, it appears as though low night temperatures increase tuber formation in potato, although different responses have been reported among different genotypes, with low night temperatures either reducing tuberisation, or else having no effect on it (Davis, 1941; Bodlaender, 1963; Borah & Milthorpe, 1963; Moreno, 1970; Menzel 1982). In *P. esculentus* the low night temperatures *per se* did not promote tuber formation. However, as photoperiod was not varied it is not possible to say if the low night temperatures used had an inhibitory effect on tuber induction, and this would need to be tested.

The effect of low night temperatures in conjunction with day neutral, or short day conditions still needs to be investigated, as well as the effect of changing day temperatures either on their own, or in conjunction with photoperiod changes. The effect of irradiance on this species should also be investigated in order to determine what effect it has on growth and development of the plants as this will enable comparisons to be made between growth chamber and field experiments.

### 7.1.4 Conclusions

Low night temperatures resulted in reduced vegetative growth of *Plectranthus*, with smaller plants under conditions of low night temperature. Up to 21 days exposure to low night temperatures under long day conditions did not result in tuber formation, unlike the situation encountered in potato.

## 7.2 INTERACTION BETWEEN TEMPERATURE AND PHOTOPERIOD

### 7.2.1 Introduction

A number of species show strong responses to both photoperiod and temperature, and it is not surprising that these factors should interact in their influence on the growth and development of plants. This interaction is particularly important in the initiation of reproductive growth and the formation of storage organs. Tuberisation in the potato is a complex process known to be influenced by genetic, environmental and physiological variables. A great deal of work has been carried out on the effect of various factors on tuberisation in potato, and available evidence indicates that the physiological age of the mother tuber, photoperiod, temperature, irradiance and nitrogen fertilisation all play a role in tuber formation, either directly or indirectly by mediating changes in hormone concentrations in the plant (Gregory, 1956; Went, 1959; Bodlaender, 1963; Moorby, 1978; Menzel, 1985a,b; van der Zaag & van Loon, 1987; Vreugdenhil & Struik, 1989; Ewing & Struik, 1992; Villafranca *et al.*, 1998). Miller & McGoldrick (1941) worked on field grown potatoes and stated that although both temperature and photoperiod influenced tuber yields, day length exerted the greater influence of the two factors. This view is shared by Charles, Rossignol & Rossignol (1992) who feel that photoperiod is the main factor controlling plant development, although other environmental factors interact with it.

Beaumont & Weaver (1931) indicated that very low temperature may induce potato cultivars to tuberise under long photoperiods. Werner (1934) obtained similar results, but also found that no tuberisation took place at high temperatures and long photoperiods. A number of researchers found that the effects of high temperatures (as high as 32°C) could

be overcome by exposing the plants to short photoperiods, although cultivar response varied greatly (Werner, 1935; Roberts & Struckmeyer, 1938; Gregory, 1954; Bodlaender, 1960; Bodlaender, 1963). High night temperatures, however, depressed tuber initiation (Gregory, 1954; Bodlaender, 1960; Schuster, Caliskan & Michael, 1978).

Went (1957) found that at nyctotemperatures of 10 or 14°C, almost as many tubers were formed under 8-h as under 16-h photoperiods, and that only at higher nyctotemperatures of 17-26°C was a 16-h photoperiod inhibitory. Even in continuous light, some tubers were formed at the low nyctotemperature. Schuster *et al.* (1978) found that some potato cultivars were unaffected by daylength, while others were unaffected by both daylength and temperature. Most cultivars, however, produced similar tuber yields under short and long day conditions at low temperatures, but yield was reduced under both photoperiods at high temperatures. Most cultivars produced no tubers under combined high temperatures and long days.

In sweet potatoes there appears to be conflicting evidence as to the effect of temperature and photoperiod on tuberous root formation. Kim (1961) states that low night temperatures combined with long days are the most critical factors for tuber formation. The interaction between these two factors also influences the formation of bulbs in onions. Day length is considered to be the major determinant of bulbing in this species (Heath, 1945), but in areas where only small changes in day length occur, temperature has been suggested as the more important factor (Abdalla, 1967; Robinson, 1971). Steer (1980) found that rapid bulbing took place at high temperatures under long day conditions, but ceased when plants were transferred to low temperatures under short day conditions.

Lewis (1953) and Naatsch & Runger (1955) reported that the promotive effects of short days on tuberisation in *Begonia tuber-hybrida* became more pronounced as temperatures decreased, results which were later confirmed by both Fonteno & Larson (1982) and Djurhuus (1985). Furthermore, tubers were formed in *Begonia evansiana* under non-inductive long days by exposing the plants to cold temperature at the end of the photoperiod (Esashi, 1961). *Begonia x hiernalis* on the other hand requires both long days and high

temperatures for proper development and flowering (Karlson & Werner, 1999).

### 7.2.1 Results and Discussion

No information on the effects of photoperiod and temperature on the tuberisation of *Plectranthus esculentus* could be found. An experiment was conducted in order to determine if there was an interaction between these two environmental factors on the tuberisation of *Plectranthus*.

### 7.2.2 Materials and Methods

This trial was conducted at the phytotron facility located at the University of Pretoria's experimental farm in Hatfield, Pretoria. The preparation of plants for the experiment are described in **Chapter 4**, while the facilities used are described in **Chapter 5**.

Four treatment combinations were used in this experiment, and each treatment combination was replicated 18 times, with one plant being a replicate. Treatments consisted of a combination of long days (14 hours daylength) at both a high (25/15°C day/night) and a low (20/10°C day/night) temperature regime, as well as short days (10 hours daylength) at the same two temperature regimes. The temperatures were set to run on a 12 hour cycle. The 14 hour daylength 25°/17°C treatment was considered the control treatment as experience had shown that plants maintained under these conditions would not induce tubers.

At the start of the trial period the plants were randomly allocated to each of the four treatment combinations and transferred to the applicable growth chamber. Treatments were continued for a period of 21 days to ensure good reactions from the plants, even though previous trials had indicated that a 14 day exposure period was more than sufficient to induce tuber formation in this species. At the conclusion of the treatment period the plants were removed from the growth chambers and 2-node cuttings made and planted as described in **Chapter 5**. The pots were laid out in a fully randomised design with 18 replicates. After a 28 day growing period in the glasshouse the cuttings were harvested, photographed, and the required data on tuberisation (swollen shoot bases and tubers) together with leaf area data collected for analyses.

### 7.2.3 Results and Discussion

#### Intact plants

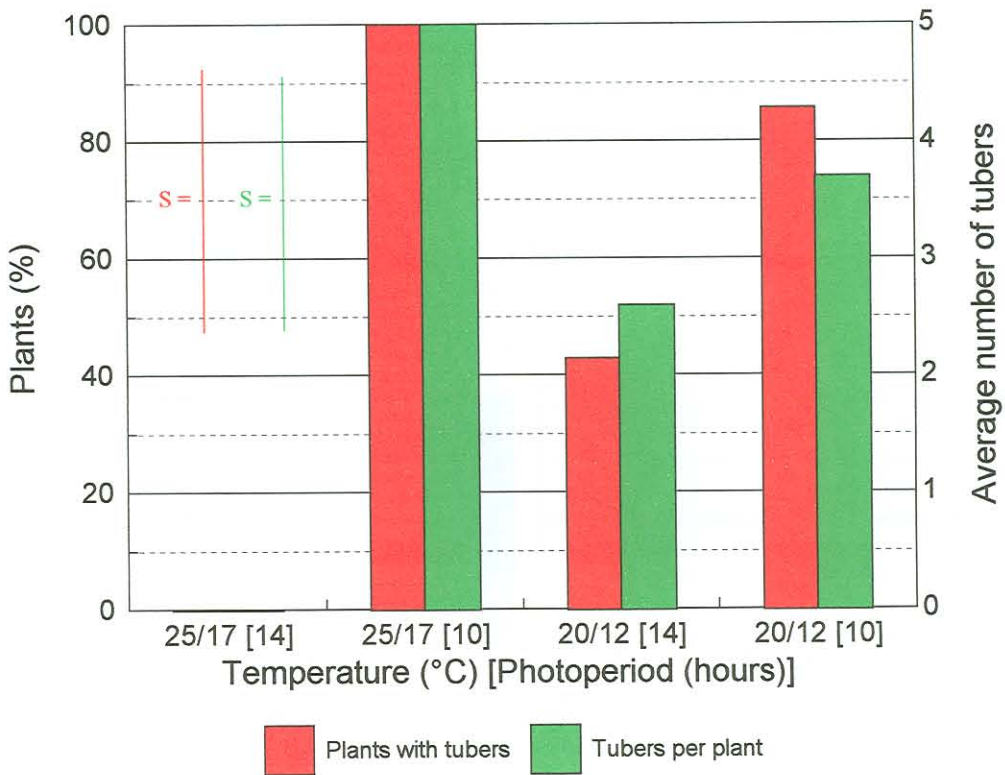
The intact plants were harvested at the same time as the cuttings. Tubers had formed on plants exposed to the short photoperiod (10 hours) treatments, irrespective of the temperature regime (25/17°C or 20/12°C). The degree of induction differed, with 100% of the plants at the high (25/17°C) temperature regime forming tubers, while 86% of plants at the low (20/12°C) temperature regime had tubers (Figure 7.2). Under long day (14 hours light) treatments 43% of the plants at the low temperature regime formed tubers, while no tubers were found on plants at the high temperature regime. There was a marked difference in the size of tubers produced under the various treatment regimes, with the largest tubers being formed on plants kept under short day / high temperature conditions. This was followed by those of plants kept under short day / low temperature conditions. The smallest tubers, not yet well developed and only visible as buds, were formed on plants kept under long day / low temperature conditions.

The number of tubers formed on the plants also differed between the treatments, with more tubers being found at the high temperature treatment than at the low temperature treatments (Figure 7.2). At the low temperature regime treatments a greater number of tubers were found on plants kept under short day conditions than on those under long day conditions (Figure 7.2). An average of 5.0 tubers per plant were found at the 27/17°C[10h] treatment, while 3.7 tubers per plant occurred at the 20/12°C[10h] treatment, and only 2.6 tubers were found on plants treated at 20/12°C[14h].

#### Cuttings

The average tuber size, as indicated by tuber mass differed between these treatments, with larger tubers being found on plants at the lower temperature treatment. The dry mass of tubers at the lower temperature regime was almost double (0.59g) that of tubers at the higher temperature (0.35g). This negative correlation between tuber numbers and tuber size appears to be fairly common in potatoes as well (Ewing, 1981).



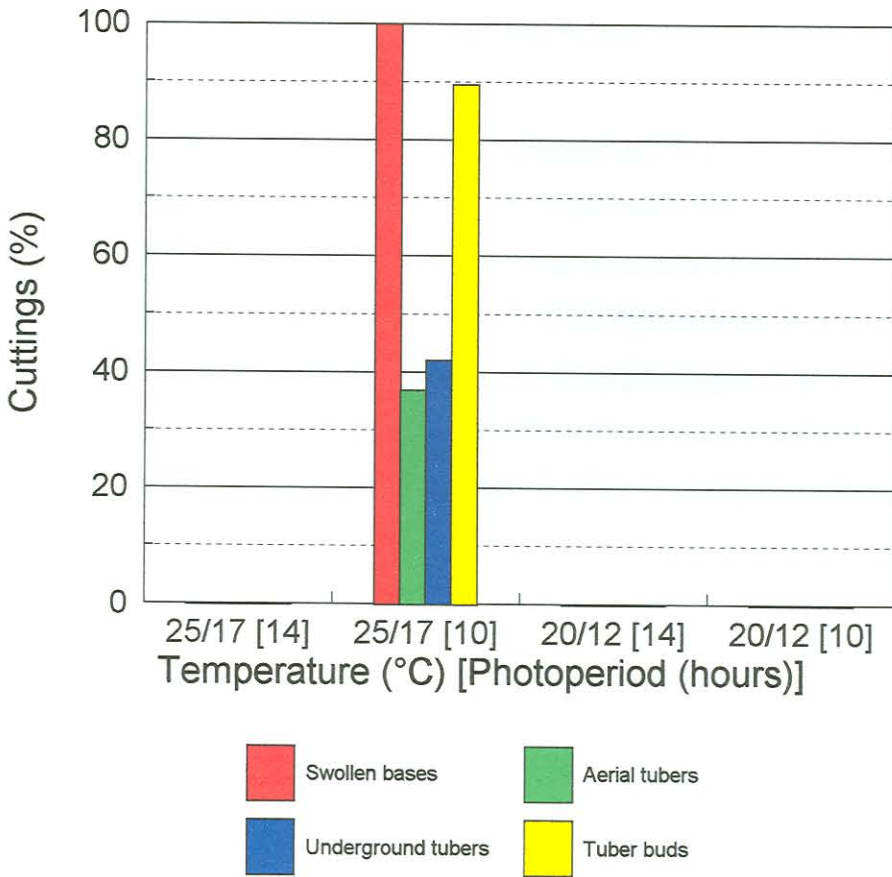


**Figure 7.2** Effect of temperature and photoperiod on tuberisation of intact plants

Large tubers were only found on plants exposed to the short photoperiod, with all of the plants at the higher temperature regime having large tubers, while only 43% of those at the low temperature regime had these large tubers.

### Cuttings

Tuberisation on the cuttings differed from that of intact plants. Swollen bases of underground shoots, tuber buds and tubers, were limited to those cuttings taken from plants at the 25/17°C [10h] treatment (Figure 7.3). In this case 100% of the cuttings exhibited swollen bases on the underground shoots, while no cuttings from plants exposed to any of the other treatments exhibited this phenomenon. The same tendency was noted with tuber occurrence. The absence of any sign of tuber induction on cuttings at the lower temperatures, especially in the case of the 20/12°C [10h] treatment can not be explained.



**Figure 7.3** Tuber induction on cuttings of *Plectranthus esculentus* as affected by photoperiod and temperature

The leaf area of cuttings from plants exposed to the 20/12°C [10h] treatment was significantly lower than that on cuttings from plants exposed to the 14 hour photoperiod at the same temperature regime. The leaf area of plants exposed to light for 14 hours at the 25/17°C temperature regime were smaller than those exposed to 10 hours of light, while the opposite tendency occurred with plants at the 20/12°C temperatures (data not presented).

The leaf area of the cuttings was not significantly affected by temperature differences at the

10 hour photoperiod, but there was a significant difference in leaf area noted between temperatures at the 14 hour photoperiod. The leaf area at the 20/12°C temperatures was found to be significantly higher than that at the 25/17°C temperatures.

It appears as though leaf senescence played an important role in the determination of this factor, with leaves declining faster at the 25/17°C treatments. The cuttings from plants exposed to the 20/12° [14h] treatment retained the largest number of leaves compared with all other treatments. Leaves on cuttings at the 25/17°C [14h] treatment showed some signs of die-back before harvest. It is possible that leaves from plants grown at 25/17°C [14h] could age faster than those at 20/12° [10h]. The effect of temperature and photoperiod on the growth and aging of leaves needs to be studied in order to clarify this effect.

#### 7.2.4 Conclusions

Photoperiod was the major factor affecting tuber induction and temperature played a minor role in inducing tuberisation in intact plants. Research on the effect of other environmental factors on tuberisation is still required to quantify the effects of temperature and photoperiod on tuberisation.

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## 1.1 EFFECT OF LEAF NUMBER / AREA

### 1.1.1 Introduction

Under appropriate environmental conditions plants such as potato, sweet potato and other tuber crops convert most of the assimilates being produced into reproductive storage organs. It is generally believed to be true that the larger the leaf area on the plant at that stage the greater the amount of assimilates available for transport to the storage organs, and so the greater the yield. This is consistent with the general principle of the conservation of assimilates.

It is generally accepted that leaf area of plants has been increased to advantage in various crops. In the case of potato, this has been done by Kato (1953), Kato & Swain (1954), DeGuzo, Ogata & Nishii (1961), Cruzado *et al.* (1961). Contrary to expectations, tuber formation in some varieties of *Dioscorea* (*Dioscorea eschscholzi*) and in *Solanum tuberosum* (*Solanum tuberosum*) has been increased by discoloration, while the effect of this practice on *Solanum tuberosum* (*Solanum tuberosum*) has proved inconsistent (Seaman & Khatun-Ghannam 1972, Khatun-Ghannam 1971, Das Gupta, 1972, Arik & Akbar, 1979).

As early as the middle of the 20<sup>th</sup> century it was assumed to be possible to increase the yields of both sugar beet and main crop potatoes by planting earlier in order to obtain a greater leaf area at the time tuber bulking commenced (Watson, 1952). However, it is not only assimilate production that is affected by leaf area, but also the production of the so-called "tuberization stimulus". One of the major problems in using plants to investigate the tuberization response in potato has been the effect of plant size, as it can be expected that a plant with many leaves will manufacture and transport much more of this stimulus than a smaller plant will (Swing, 1961; Kato, Swain & Senesac, 1963). This effect was