CHAPTER 2

STUDY SITES AND SPECIES

2.1 Study sites

2.1.1 Venetia-Limpopo Nature Reserve

The Venetia-Limpopo Nature Reserve (Venetia) is situated in the Northern Province of South Africa (22°08_ – 27_S and 29°13_ – 28_E), slightly south of the meeting point of South Africa, Zimbabwe and Botswana (Fig. 2.1). It is a privately fenced park and is 34 500 ha in extent.

This semi-arid savanna is characterised by wet, hot summers (monthly mean maximum 32°C from October to December) and dry, mild winters (monthly mean maximum 24.7°C in June). The mean annual rainfall for Pontdrift, about 15 km from the reserve, is 366 mm (1967-1997) with a 36% coefficient of variation. The rainy season usually extends between October and March, with the probability of rain during January being higher than for other months (Smit & Rethman 1998a; Fig. 2.2 & 2.3). Rainfall occurs mainly in the form of thunder-showers.

The topography of the area is predominantly flat, with sandstone as the dominant underlying bedrock beneath deep (> 2 m) colluvial soils. The occasional rocky sandstone outcrop interrupts the landscape, together with two major seasonal rivers: the Kolope (flowing south to north) and the Setonki (west to north). Alluvial soils are found adjacent to rivers.

From the 1940s the land was used for livestock ranching. Farms were heavily stocked with cattle and goats, resulting in soil and vegetation degradation (MacGregor & O'Connor 2002). Livestock were removed when De Beers Consolidation Mines Ltd. purchased the land between 1981 and 1996 and the area was consolidated as a nature

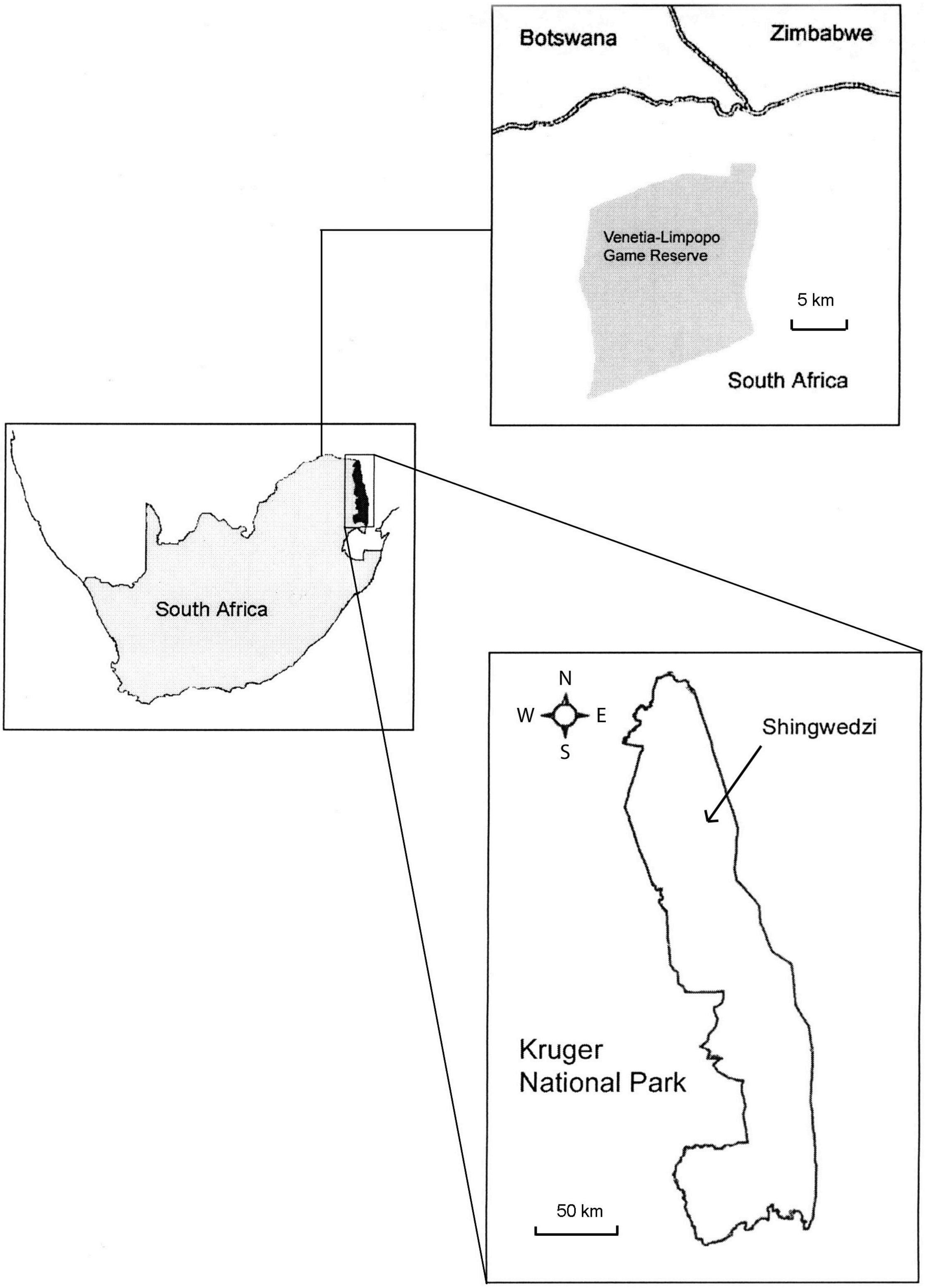

Figure 2.1 Maps showing the location of the two study sites used in this study, namely the Venetia-Limpopo Nature Reserve and Kruger National Park.

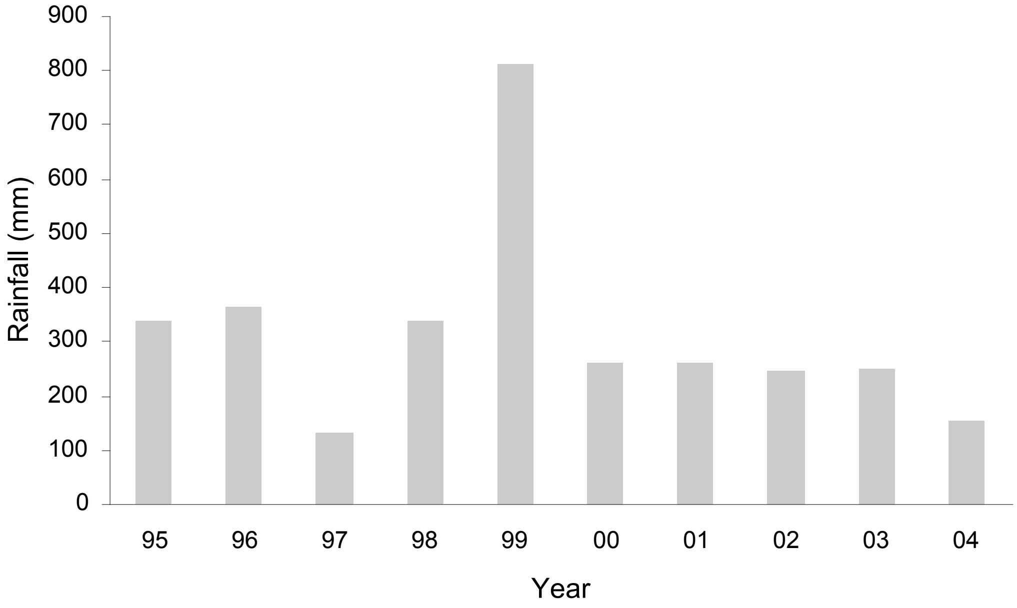

Figure 2.2 Annual seasonal rainfall (July- June) for Venetia from July 1995 to June 2005 (year indicates start of season).

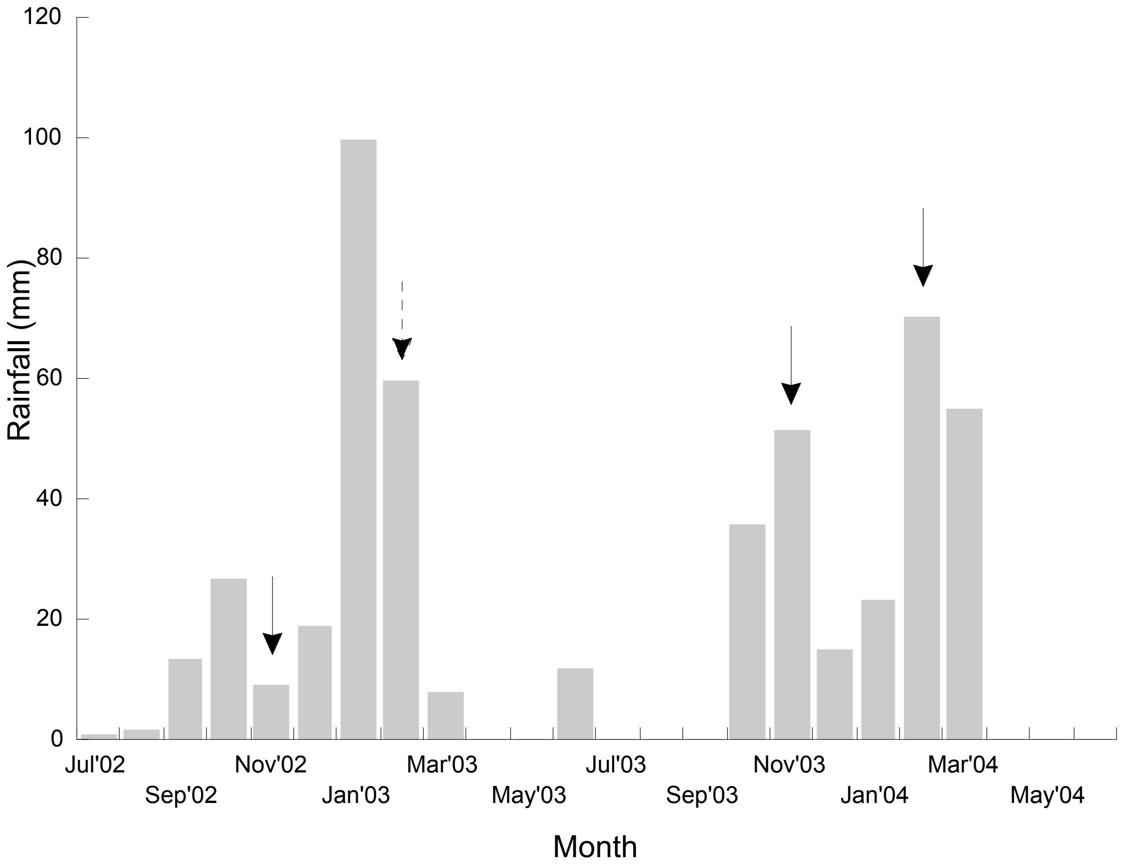

Figure 2.3 Monthly rainfall in Venetia over the two year period during which the study took place. Arrows indicate when oviposition by mopane moths took place (dashed arrow represents very few moths).

reserve. Indigenous herbivores were reintroduced in 1989 -1991, including 34 elephants in 1993 and 1994. The elephant population, which is now estimated to be at 60, is still at a relatively low density (0.17 animals/km^2) compared to other populations within mopane woodland (e.g. 1.1 elephants/km^2 in Luangwa Valley, Zambia; Lewis 1991).

Vegetation of the region is dominated by *Colophospermum mopane* (commonly known as 'mopane') and is classified as 'Mopane Veld' (Acocks 1953). Sixteen of the eighteen vegetation types in Venetia are dominated by this species, with short stature mopane woodland (average height of 1.5 m), found on colluvial soil, dominating (O'Connor 1992). These woodlands are dense, with > 70% cover. Within riverine vegetation, mopane trees reach up to 10 m in height. Other common tree species within Venetia include *Boscia foetida*, *Salvadora angustifolia* and *Lycium austrinum*.

2.1.2 Kruger National Park

The Kruger National Park (Kruger) is situated in the lowveld of northeastern South Africa, bordering Mozambique in the east and touching Zimbabwe in the North (Fig. 2.1). It is an elongated park extending about 350 km from north to south with an average width of 60 km, covering about two million hectares.

An aspect of this study was carried out in the north of Kruger, around Shingwedzi (23.10°S and 31.43°E). The topography of the area is flat, with basalt rock as the underlying bedrock in the east and granite in the west. Bands of alluvial soils following drainage lines run through the area. Shingwedzi falls within the northern arid bushveld zone and is also characterized by wet, hot summers (mean monthly maximum 34ºC in January) and dry, mild winters (mean monthly maximum 26ºC in June). The mean annual rainfall is 400 mm and is strongly seasonal, falling predominantly between October and May (Venter *et al*. 2003; Fig. 2.4). A number of seasonal rivers run through the

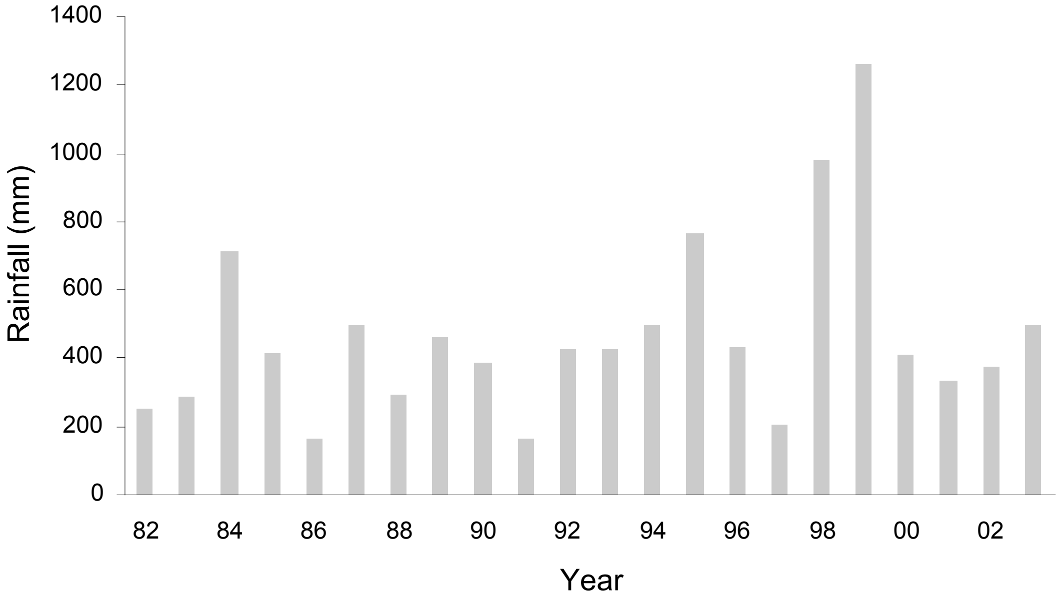

Figure 2.4 Annual seasonal rainfall (July- June) for Shingwedzi in the Kruger National Park from July 1982 to June 2003 (year indicates start of season).

Shingwedzi area, and permanent surface water is available through numerous artificial water points (boreholes and dams) constructed in 1933 and in the 1950s and 1960s (Gaylard *et al*. 2003). As in Venetia, the vegetation is dominated by mopane trees, which range in height from short scrub mopane to taller riverine trees. The alluvial plains are more species-rich, however, with tree species such as jackal-berry (*Diospyros mespiliformis*), leadwood (*Combretum imberbe*) and the common cluster fig (*Ficus sycamorus*).

Between 1836 and 1902, uncontrolled hunting and the rinderpest epizootic outbreak in 1896 decimated game populations within the Kruger area. By 1903 most of the area became a game sanctuary where until 1926, when it was officially proclaimed the Kruger National Park, the emphasis was on the protection and rebuilding of game populations (Mabunda *et al*. 2003).

Historically, elephant numbers are believed to have been low in the area (Whyte 2001), but by 1896 they were extinct. The first subsequent elephant sighting in Kruger was in 1905 in the southern region, from where they spread north and were first sighted around Shingwedzi in 1933. Their numbers increased rapidly until 1967, when 6, 586 individuals were counted, after which culling began. Between 1967 and 1994 (when culling was suspended), a total of 16, 201 elephant had been killed or removed from the park, and between 1994-2001 a further 465 individuals were removed. By 2002 the population had reached about 10, 459 (Whyte *et al*. 2003).

2.2 Mopane trees

2.2.1 Distribution and ecology

Colophospermum mopane (Caesalpinioideae, Leguminosae), a xeric savanna woodland species, is the dominant tree over vast areas of land in southern Africa with an altitude range of 300-1,000 m. Occurring over approximately 550, 000 km^2, it's range includes Mozambique, Zimbabwe, Angola, Botswana, Namibia, South Africa and southern Malawi (Fig. 2.5; Mapaure 1994). Factors determining the distribution of mopane are thought to vary in different parts of its range, but generally include frost, soil type, minimum rainfall and length of the growing season (Timberlake 1995).

Physiologically, the species is well adapted to dry conditions, with the annual (unimodal) rainfall over mopane veld averaging 300-700 mm, with a long dry season. There is also an association with comparatively clay-rich soils with a high pH (Timberlake 1995). According to Gertenbach (1987) mopane trees do not favour alkaline soils *per se*, as they will grow better on fertile, slightly acid permeable soil. They are, however, most often excluded from these soils by deep-rooted *Acacia* species (Cole 1986). Mopane tend to thrive on soil where the exchangeable calcium in the B-horizon is high, and where the B-horizon is shallow (Gertenbach 1987). The ability to grow so well under such soil conditions, and resist drought (O'Connor 1999), is mainly due to the root system that is markedly shallow and extensive (usually 300-1200 mm deep), extending deeper in deep soils (Smit 1994; Timberlake 1995). Additionally, the root biomass is exceptionally high (mean: 17 354 kg ha^{-1}), exceeding the leaf biomass (mean: 1 023 kg ha^{-1}; Smit & Rethman 1998b), and the roots of mopane are also able to utilize soil water at a low metric potential (below –15.2 bar, Henning & White 1974). This gives them a competitive advantage over grasses and may explain the poor grass layer in most mopane woodland (O'Connor 1999). The large underground biomass also enables mopane to

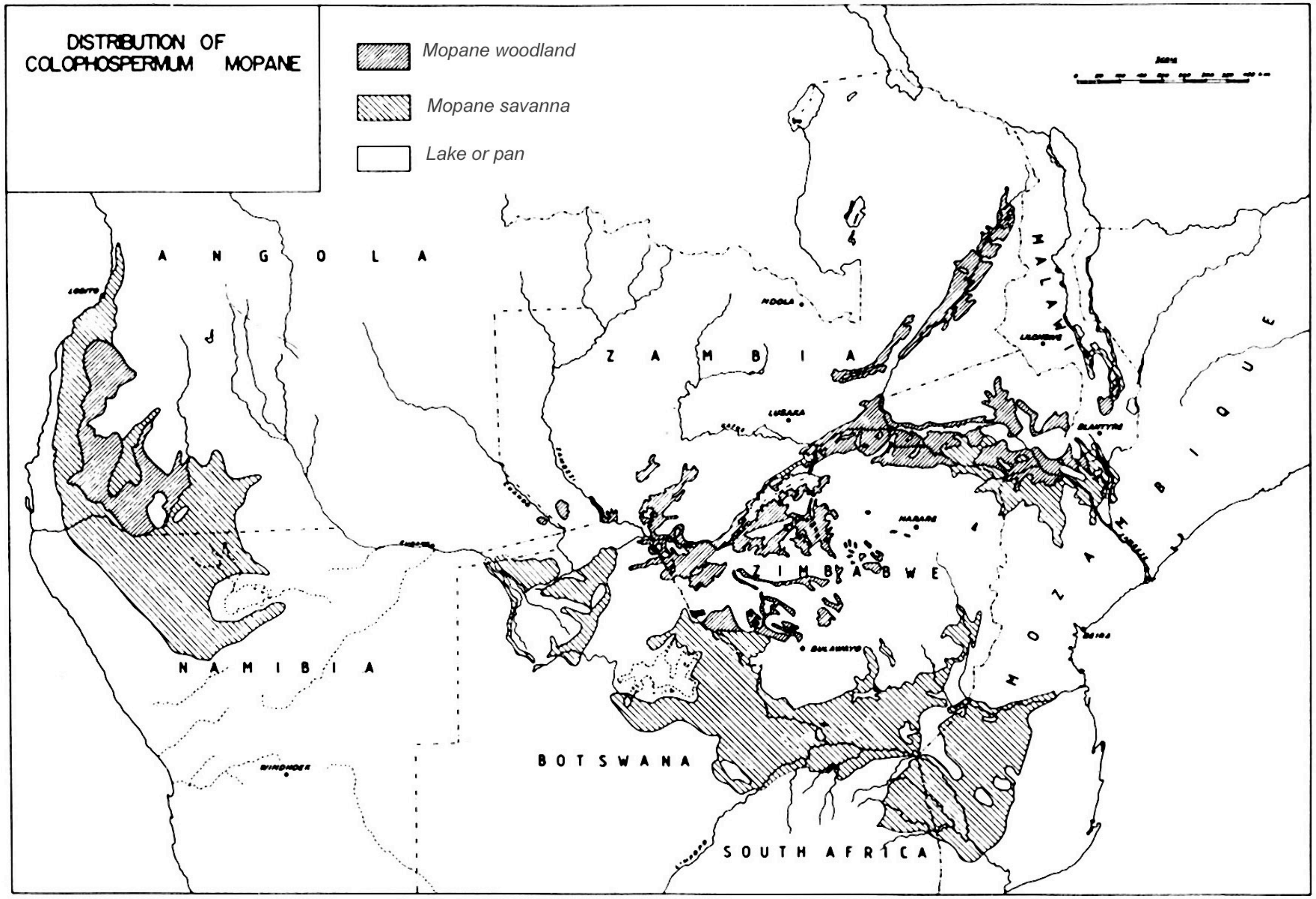

Figure 2.5 Distribution of *Colophospermum mopane* in Southern Africa (from Mapaure 1994).

readily produce shoots from the rootstock when the plant is damaged by fire, drought or herbivory.

It is common for mopane to out-compete most other woody species within its range (O'Connor 1999) and generally occurs in monospecific stands with comparatively low alpha and gamma diversities (Timberlake 1995). There is, however, a high degree of variability within mopane woodlands. While mopane usually ranges from about 10 m in height, with large areas of low scrub of 1-2 m, stands of trees up to 20 m high exists and are termed "cathedral mopane" (Van Wyk 1993). O'Connor (1992) identified the principle cause of these variations in tree height to be variations in the soil, particularly depth and pH. In the Kruger National Park, mopane growing on soils derived from basic material i.e. basalt, dolerite and gabbro are multi-stemmed shrubs of 1-2 m in height, while trees growing on sandy soils are usually single-stemmed and up to 5 m tall (Fraser *et al.* 1987). Mopane woodlands of stunted growth are generally found on soil with a high clay content, relatively impenetrable B-horizon, sodic soil conditions and a shallow A-horizon (Dye & Walker 1980). Densities of mature mopane woodland also vary, ranging from a few trees per hectare in arid northwestern Namibia (Viljoen 1989) to 481 trees ha^{-1} in southeastern Zimbabwe (Kelly & Walker 1976) and 2,740 trees ha^{-1} in northern South Africa (this study). An additional factor known to influence tree density and structure in mopane woodlands is fire. Tree density and tree height can be significantly reduced in frequently burnt areas, while the number of stems per tree tends to increase due to coppicing (Kennedy & Potgieter 2003).

2.2.2 Phenology

Mopane is a slow-growing deciduous species with pinnate leaves, consisting of two large leaflets that together resemble the wings of a butterfly. Leaf size may vary considerably on the same tree (Wiggins 1997; Potgieter & Wessels 1998) and under hot, dry conditions, the leaflets fold closed and hang down, thereby casting very little shade. Trees are generally leafless from August to October, after dropping their leaves from the onset of the dry season. This is, however, dependant on rainfall (amount and distribution), as leaves may be retained between successive rainy seasons under favourable conditions, which can then be an important source of browse at a time when resources are most limited (Oates 1972). Leaf flush may occur after the first summer rains in October and November (in South Africa) or independently of rain (Styles & Skinner 1997a).

Flowers are small, greenish in colour and inconspicuous (Krüger *et al*. 1999), emerging after the leaf flush, from December to March. Their emergence is, however, highly irregular with some trees not flowering for several years at a time. Fruits of mopane are indehiscent, flat and kidney-shaped with a single yellowish and wrinkled seed within the pod (Coates Palgrave 1983). The seed is covered with resinous glands, making it sticky, yet fruits are dispersed by rainwater and wind (not by epizoochory; Styles & Skinner 1997b).

2.2.3 Uses

Mopane woodland is of great economic importance in the areas where it occurs. Large parts of mopane woodland are used for game and livestock farming (cattle and goats), by both commercial and rural farmers. Here, mopane forms a crucial role, as its foliage is an important browse for many herbivores such as elephant (*Loxodonta africana*), eland (*Taurotagus oryx*), kudu (*Tragelaphus strepsiceros*), and impala (*Aepyceros melampus*; Lewis 1986; Styles 1993; Ben-Shahar 1998; Styles & Skinner 2000). Leaves have a high crude protein content, varying from 9,3% in winter to 15.9% in summer. Considering the crude protein content of the diet of kudu, a highly selective feeder, is about 12-14% in the late wet season and 9% at the end of the dry season (Owen-Smith & Cooper 1989), the crude protein content of mopane clearly exceeds the requirements of even such a selective feeder. The total phenolic content of its leaves is also comparatively low, as Styles and Skinner (1997a) found young leaves to have a mean total phenolic content of 147.7 mg C./g dry material, which is significantly lower than that of *Acacia nilotica* (373,3 mg C./g), a palatable woody species (du Toit *et al.* 1990). Additionally, senescing leaves were found to be at their most palatable in late winter/early spring, thus providing a valuable resource for herbivores before the spring flush (Styles & Skinner 1997a). Seedpods are also eaten during the dry season, and in some areas, mopane has been known to prevent large-scale livestock and game losses from drought.

Within rural communities the tree is valued for its timber, which is used in the construction of huts, fencing and kraals (Madzibane & Potgieter 1999; Mashabane *et al.* 2001). Mopane is also extensively used as firewood, as the wood burns slowly and produces good coals (Tietema *et al.* 1991), and charcoal produced from mopane is widely utilized in countries like Zambia (Chidumayo 2000). Another valuable resource obtained from mopane woodlands is the mopane caterpillar (*Imbrasia belina*), which forms an important food source for rural communities. This edible caterpillar, which feeds almost exclusively on mopane and displays outbreak dynamics, is harvested in large numbers and has become an important trading commodity (Makhosandile 1999). The larvae are collected during the summer and are then gutted and dried for consumption. In Botswana, the mopane trade brings in about R46 million annually (Potgieter *et al.* 2001).

2.3 Mopane moths and caterpillars

Mopane caterpillars are of the emperor moth *Imbrasia belina*, a Saturnid. The species is widespread in southern Africa, tropical and East Africa, occurring from semi-desert to savanna and thick bush. The larvae feed on a number of tree species, including *Colophospermum mopane*, *Carrissa grandifola*, *Sclerocarya birrea*, *Commiphora glandulosa*, *Acacia tortilis*, *Cassia abreviata*, *Diospyros* spp., *Ficus* spp., *Rhus* spp., *Terminalia* spp. and *Trema bracteolate* (Pinhey 1972). However, large outbreak populations only follow that of their main host plant, mopane.

The life cycle of *I. belina* has been well documented (Ditlhogo 1996). Throughout most of its distribution, the species has two generations emerging in a summer season (bivoltine), with the first generation emerging from pupation in November to December and the second in February to March. In more arid areas, however, there is usually only one generation (univoltine). The first generation population is also considerably larger than the second one (Ditlhogo 1996), possibly due to the first generation feeding on more nutritional young leaves (Klok & Chown 1999).

Adult moths have rudimentary mouth parts and do not feed, harvesting all their water and nutrient resources while they are caterpillars (Holm & de Villiers 1983). They live for two to three days, during which time their only function is to find receptive mates and to oviposit. Female moths lay a single cluster of 30-335 eggs on the upper or lower surface of leaves (Fig. 2.6a) and on twigs or branches of mopane trees (Ditlhogo 1996; personal observation). The larvae emerge after approximately ten days and pass through five instars before pupation (Klok & Chown 1999). The larval stage lasts approximately six weeks, during which time the caterpillars’ body mass increases by about 4000 fold and the fifth instars reach a length of about 80 mm (Gaston *et al.* 1997; Fig. 2.6b). At the end of the larval stage, the fifth instar climbs down to the ground and burrows into the soil, where it pupates. Depending on the generation, eclosion occurs either six to seven months after pupation.

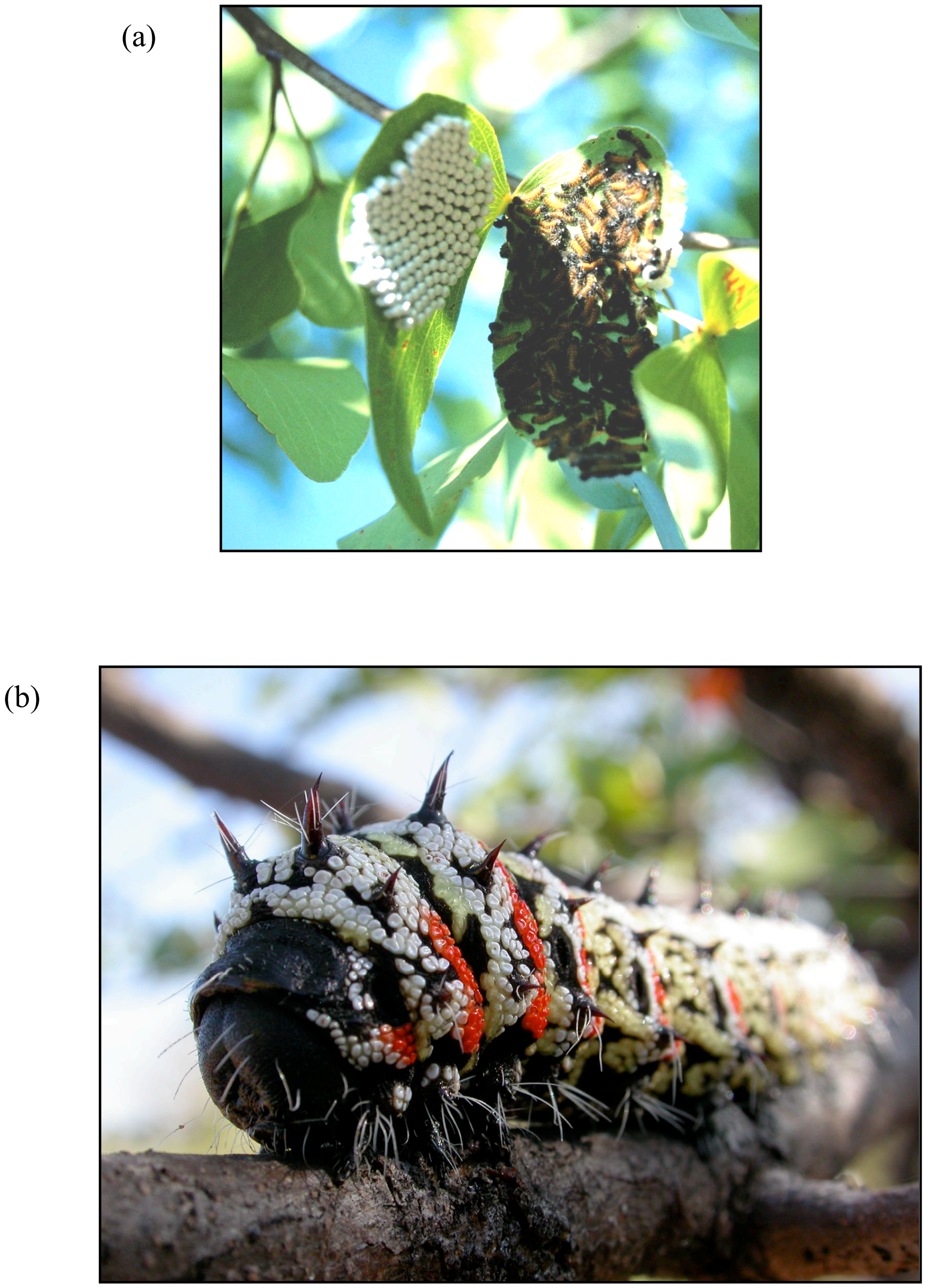

Figure 2.6 (a) An egg mass and newly hatched mopane caterpillars on a mopane leaf, and (b) a fully grown mopane caterpillar.

Mopane caterpillars are well known for their population outbreaks, which may result in large stands of trees being completely defoliated. Population numbers may vary quite considerably from year to year in any single locality however, and the cause of these variations in time and space is not yet properly understood. Factors proposed to be important in the population dynamics of mopane caterpillars include browse quality, soil type and rainfall, but recent attention has focused on the role of disease (Dwyer *et al.* 2000) and parasitoids (predominantly *Mesocomys pulchriceps*; van den Berg 1971; Berryman 1996; Maron & Harrison 1997).

The overall abundance of mopane caterpillars, which is apparently declining (Roberts 1998), may also be affected by an increase in harvesting by people, as moths are reported to have disappeared from parts of Botswana after heavy harvesting (Bartlett 1996). In addition to over-harvesting, suggested threats to mopane caterpillar abundance include deforestation of mopane woodland and increasing drought. Deforestation may be caused by the felling of trees to facilitate harvesting of the caterpillar, or through heavy elephant utilization (Styles & Skinner 1996).

Apart from humans, *I. belina* provide food for numerous other predators. Pupae are readily dug up by jackals (*Canis mesmelas*), bat-eared foxes (*Otocyon megalotis*), warthogs (*Phacochoerus aethiopicus*) and aardvarks (*Orycteropus afer*); larvae are eaten by mammals (mainly baboons, *Papio ursinus* and vervet monkeys, *Cercopithecus aethiops*), birds (34 species were documented by Styles 1995), and invertebrates (e.g. spiders, ants, and mantids; Styles & Skinner 1996); and moths are taken by birds, spiders and bats (Hill & Smith 1984).

2.4 African elephants in mopane woodlands

Mopane woodland is found extensively within conservation areas in southern Africa and within these areas, mopane often forms the principle food source in the diet of African elephants (*Loxodonta africana*, order: Proboscidea, family: elephantidae; De Villiers *et al.* 1991; Lewis 1991). Despite its abundance, mopane is selected for by elephants (Viljoen 1989; Smallie & O'Connor 2000), thereby making these woodlands susceptible to elephant induced damage (Ben-Shahar 1993).

Elephants utilise mainly branches, foliage and the main stem of mopane trees, but the type of utilisation is dependant on tree height (Smallie & O' Connor 2000). Most branch, foliage and stem utilisation occurs on trees < 4 m high and most bark utilisation on trees > 4 m in height. Pushing over of mopane trees is very rare. Elephants also tend to prefer branches from a relatively low height (< 1 m, Smallie & O'Connor 2000; 1-2 m, Caughley 1976) and therefore utilise more biomass of shrub mopane than of mature trees (Ben-Shahar 1993). Additionally, previously damaged trees of < 2 m in height are preferred to unutilised trees, as the damage-induced coppicing provides a greater availability of their preferred stem size. Consequently, elephants tend to have a greater impact on smaller mopane trees, thereby preventing the recruitment of taller trees. In northern Botswana, for example, Ben-Shahar (1998) found that even though 43% of mopane trees were affected by elephants, the density of large trees remained largely unchanged. As a result, the woodland structure is often double-tiered, comprised of coppicing shrubs and tall trees (Timberlake 1995).

While individual trees are generally only lightly utilised, breakage of the main stem can result in a 51-75% loss of biomass (Smallie & O'Connor 2000). When smaller size classes are depleted (e.g. due to drought or concentrated feeding around water holes), larger trees are also utilised more than normal, and new elephant damage to mopane increases significantly with increasing elephant densities (Ben-Shahar 1996a). Elephants can therefore have a significant impact on mopane woodland structure, sometimes reducing woodland to shrubland (Ben-Shahar 1998). However, due to the type of damage inflicted on the trees (predominantly branch and stem breakage rather than the pushing over of trees), elephant browsing tends to have little impact on tree density, even when elephant densities are high. On a regional scale, there is also no evidence that elephants reduce biomass of mopane woodlands below a sustainable level. Ben-Shahar (1996a), for example, showed that in the absence of fire, mopane woodland would only begin to decline if elephant densities exceeded 10.5 animals/km^2. This is considerably higher than current mean elephant densities within mopane woodland (e.g. 1.1 elephants/km^2 in Luangwa Valley, Zambia; Lewis 1991), but is comparable to localised densities around water sources at the end of the dry season (7 –10 animals/km^2 in northern Botswana; Ben-Shahar 1996b).

While the modification of mopane woodland structure tends to have little impact on the elephant population, it can, however, have either a positive or a negative effect on many associated species, such as birds, insects and other mammals (Cumming *et al.* 1997; Mills & Hes 1997). At high densities, they can therefore have a significant impact on the dynamics and functioning of systems, and are hence considered as keystone species in the ecology of mopane woodlands (Timberlake 1995).

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