THE INFLUENCE OF TREE THINNING AND SUBHABITAT DIFFERENTIATION ON THE REPRODUCTIVE DYNAMICS OF *ACACIA MELLIFERA* SUBSP. *DETINENS*

by

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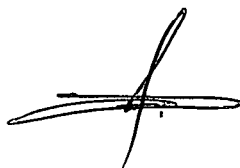University of the Free State
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DECLERATION

I declare the dissertation hereby submitted by me for the partial fulfilment of the requirement of the degree M. Sc. Agric. (Grassland Science) at the University of the Free State is my own independent work and has not previously been submitted by me at another university/faculty. I furthermore cede copyright of the dissertation in favour of the University of the Free State.

Mesghena Ghilay Hagos.

DEDICATION

I fully dedicate this thesis work to my mother Weizero Letekidan Teklai Gebremedhin and my late father Sheka Ghilay Hagos who played an incredibly significant role from the very beginning of my school attendance up to higher education, providing me with all the basic necessities and facilities for my study and their daily prayer and spiritual encouragement for the betterment and success of my life as a whole. I thank my GOD for He gave and blessed me with such enthusiastic parents.

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ABBREVIATIONS

BTE	Browse tree equivalent (g, kg ha^{-1})
BU	Browsing unit
CANVOL	Canopy volume
ETTE	Evapotranspiration tree equivalent (500 cm^3, ha^{-1})
LMAS	Leaf dry mass (g, kg ha^{-1})
LM_15	Estimated leaf dry mass below a browsing height of 1.5 m (g, kg ha^{-1})
LM_20	Estimated leaf dry mass below a browsing height of 2.0 m (g, ka ha^{-1})
LM_50	Estimated leaf dry mass below a browsing height of 5.0 m (g, kg ha^{-1})
LVOL	Estimated total leaf volume
PEG	PloyEthylene Glycol
TE	Tree equivalent

CHAPTER 1

INTRODUCTION

There are two subspecies of *Acacia mellifera* of which only subsp. *detinens* occurs in southern Africa. It may grow on a variety of soil types, ranging from Kalahari sands to heavy, clayey soils. In sandveld it often tends to be associated with more calcium-rich soils on drainage lines. It is usually found in arid areas where it is well adapted to dry conditions with its shallow, wide spreading root system. In South Africa *A. mellifera* is found widely distributed in the dryer western parts that includes the Northern Cape, North-West Province, Northern Province, western parts of the Free State and localized areas of Gauteng and Mpumalanga. It also occurs in Angola, Namibia and Botswana, extending northwards to Tanzania (Smit, 1999a). It is particularly common in the Kalahari Thornveld (Acocks, 1988), the vegetation veld type in which the current study was conducted.

The major economic uses of *A. mellifera* include its use as fuel and for making charcoal. It is an important source of nectar for honeybees and the production of honey (Palmer & Pitman, 1972; Bein *et al.*, 1996; Smit, 1999a). The pods, young twigs, leaves, and flowers of *A. mellifera* are nutritious and greedily eaten by stock, sheep and goats in particular as well as game (Palmer & Pitman, 1972; Bein *et al.,* 1996). During the 1966 drought, farmers in the Free State ground up small branches of the trees in hammermills, mixed this with molasses, and fed the mixture to their stock (Mostert *et al.,* 1969). As a leguminous tree, *A. mellifera* is also important for nitrogen fixation and soil enrichment (Bein *et al.*, 1996; Smit, 1999a).

Livestock farming and game ranching are the major activities in the Kalahari Thornveld (Van Rooyen & Bredenkamp, 1996; Meyer *et al.,* 2001). In these areas it is perceived that in recent history an increase in tree density occurred. This increase in woody plant density is commonly referred to as "bush encroachment" and involves the invasion of grasslands and the thickening of savanna (O'Connor & Crow, 1999). It is generally accepted that bush encroachment is encouraged by long-term overgrazing of the herbaceous layer, the elimination of browser herbivore species and the exclusion of sporadic hot fires (Smit *et al.,* 1999).

Most South African savanna ecosystems are water-limiting ecosystems and an increase in woody plant density (bush encroachment) invariably results in the suppression of

herbaceous plants (Donaldson & Kelk, 1970; Dye & Spear, 1982; Scholes, 1987; Belsky et al., 1989; Smit, 1994; Smit & Swart, 1994; Smit & Rethman, 1999). Bush encroachment is seen as the most important restrictive factor in realizing sustainable animal production in the savanna areas of the North-West Province (Meyer, 1998).

Ample evidence of the reduced productivity of the herbaceous layer as a result of the increase of A. mellifera exists for the Kalahari Thornveld (Richter, 1991). In an estimate of the degree of A. mellifera encroachment, Ebersohn et al. (1960) as cited by Donaldson (1969) maintain that, more than one million hectares of veld in the Molopo area are invaded by this species. This is considered to be a major problem reducing the grazing capacity of the Molopo area by as much as 50% (Donaldson, 1969). Though many control measures such as chemical bush control has been employed since the 1960's, encroachment of A. mellifera is still viewed as a serious problem (Richter, 1991).

While measures like tree thinning are often considered as an option to restore the herbaceous production potential of affected areas, little is known of the dynamics, and successional processes involved in savanna areas in general (Smit & Rethman, 1998a; Brown, 1999) and for A. mellifera in particular.

The growth and reproduction of the remaining trees following thinning are important for several reasons:

⊚ The reproductive dynamics of the remaining plants have direct consequences on the re-establishment of woody plants (Smit, 1994). This is important in estimating the effective time span of tree thinning operations (Scholes, 1990).

⊚ Trees are the main sources of food to browsers (Smit, 1994), and in addition, cattle may utilize a significant portion of browse during the dry season, even when abundant grass is available (Kelly, 1977), and this food source is being altered. The consequence of altering this feed sources need to be considered, especially for savanna areas in which game ranching is undertaken (Snyman, 1991).

● It is known that subhabitat differentiation result in differences between the nutrient status of soil under the canopy and those in the open areas (Smit & Swart, 1994). Tree thinning will influence the relative abundance of the canopied subhabitat.

The objectives of the study were to investigate the influence of different intensities of

tree thinning and the resultant tree density gradient on:

1. The seed production of *Acacia mellifera*.
2. The seed mass and seed dimensions of *A. mellifera*.
3. The seed distribution and soil seed bank of *A. mellifera*
4. The germination and survival of *A. mellifera* seeds
5. The degree of Bruchid beetle infestation of *A. mellifera*.
6. The germination and survival of *A. mellifera* seed in soil from under tree canopies and between tree canopies.

An additional objective was to determine the differences in soil nutrient status from under tree canopies and between tree canopies.

CHAPTER 2

LITERATURE REVIEW

2.1 GENERAL DESCRIPTION OF *ACACIA MELLIFERA* SUBSP. *DETINENS*

The family Mimosaceae, to which *Acacia mellifera* belongs, with several hundred genera and some 12 000 species, is one of the largest and most cosmopolitan of all the plant families. In South Africa and Namibia just over 100 species of trees belong to the family Mimosaceae, that is, nearly one ninth of the total number of species in the arid regions of the sub-continent (Palmer & Pitman, 1972).

Acacia mellifera was previously named *A. detinens* Burch., the specific name being based on the Latin "detinere" meaning "to detain" or "to hold". The tree has now been renamed *Acacia mellifera* subsp. *detinens*, which freely translated means, "the honey-bearing *Acacia* that holds one fast".

The name *Acacia* is derived from the Greek word "Acantha", meaning "thorn", and refers to the outstanding characteristics of this genus in Africa (Smit, 1999a). Most of the *Acacia* species have fine feathery foliage, composed of bipinately compound leaves. The leaflets are usually very small and often fold up against each other in sun or heat, or at night. The tiny fluffy flowers, bisexual or male, are borne in round balls or in spikes, usually with a heavy sweet scent (Palmer & Pitman, 1972). This is a vast genus with about 900 species, concentrated mainly in Africa and Australia. bout 40 species are native to South Africa.

Acacia mellifera is usually a multi–stemmed shrub up to 3 m high, or occasionally a tree that can grow to a height of 7 m. It has a spreading, rounded to flattened crown, which may reach down to ground level. As a tree it usually branches low down with a substantial horizontal spread that can well exceed its height. Its bluish-green foliage, when seen from a distance, is also distinctive (Smit, 1999a).

The bark on large mature trees is light to dark grey, roughish with longitudinal fissures that are generally darker (Smit, 1999a). More often, however, the main stem (trunk) is smooth green-yellow to grey (Palmer & Pitman, 1972), or light grey or grey-brown, with numerous pale grey raised, transversely-elongated lenticels (Smit, 1999a).
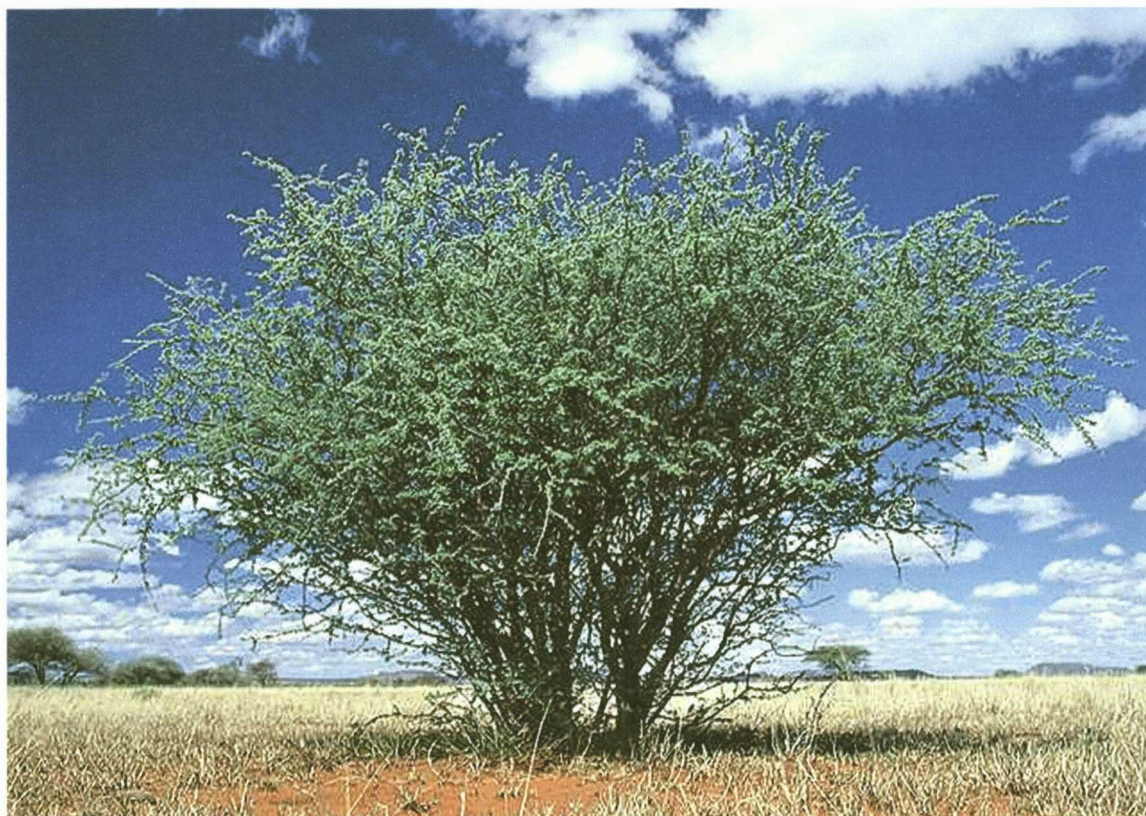
Figure 2.1 A typical *Acacia mellifera* subsp. *detinens* tree (Smit, 1999a).

Very young new season's shoots have a light green colour. They are smooth and are largely hairless. With maturation the colour of the shoots changes to a reddish-brown, greyish-green or light grey colour. On older shoots this light coloured layer splits longitudinally to reveal a smooth, green surface underneath (Smit, 1999a). Older, previous seasons' shoots are grey; grey-brown to dark olive green with numerous pale grey, raised, transversely elongated lenticels.

The stipules are unmodified and not spinescent. They do not persist and senesce early. Prickles are well developed, strongly recurved, sharp-pointed, paired and located at the nodes. They often occur closely spaced and there are thus more prickles per unit shoot length than with most other species. They may attain a length that ranges from 2.5 – 6 mm. Their colour on young, new season's shoot varies from green to yellowish with reddened tips and with a grey base. They are hairless. On older shoots and stems the prickles vary in colour form dark red to grey-black and in all cases the prickles base is lighter in shade than the prickle itself (Smit, 1999a).

The leaves are borne at the nodes, singly or up to 4 leaves per node (1-2 typical) (Smit, 1999a). The number of pinnae pairs ranges from 2-3 (Palmer & Pitman, 1972; Smit,

1999a). The number of leaflet pairs per pinnae varies from 1-4 (Smit, 1999a). Though the overall size of individual leaves is small, the leaflets are quite large. They are green when young, becoming bluish-green when older. The length of the leaflet is usually less than 10 mm (Palmer & Pitman, 1972; Smit, 1999a), however some times it can be up to 12 mm long and their width up to 6 mm.

The flowering spikes of *A. mellifera* subsp. *detinens* are borne at the nodes, singly or up to 5 per node on a previous season's shoot, often in great profusion before the appearance of the new foliage. The colour of developing buds varies from green to a characteristic reddish-purple prior to full bloom. The open, fully developed flowering spikes are very short with their length almost equal to their diameter, thus resembling globose flowering heads. They are scented and have a light cream to white colour with a mean length of 18 mm (range: 15 - 35 mm) (Smit, 1999a). In the winter and early spring, just before the leaves make their appearance, the shrub is covered with fragrant white, powder puff-like flowers (Van der Walt & Le Riche, 1999).

The pods of *Acacia mellifera*, which develop quickly and in abundance, are straight, sharply tapered at the base and bluntly pointed to rounded (oval-shaped) at the tip (Palmer & Pitman, 1972; Smit, 1999a). They are dehiscent, papery when dry and may attain a length of 70 mm and a width of 20 mm. They are flat, indistinctly venose, with a thin raised ending to the valves (Smit, 1999a). The colour of the young pods is green, sometimes with a reddish tinge, and they dry to a light brown or khaki colour (Smit, 1999a). The pods develop and ripen rapidly and the seeds are dispersed early in the season. The number of seeds per pod varies from 1 - 5 (Palmer & Pitman, 1972; Smit, 1999a) and they have an olive green to khaki colour.

As a shrub it may form large dominant stands, which can become so dense (mostly as a result of some disturbance) as to be almost impenetrable (Smit, 1999a). The occurrence of this shrub is a nightmare for many farmers in the North-West Province and in Namibia and overgrazing in these parts created a gap in which this shrub could increase (Van der Walt & Le Riche, 1999). The common and widespread *A. mellifera* subsp. *detinens* is known in South Africa by a variety of names, Swarthaak, Blackthorn, Blouhaak, Hakiesdoring, Hook thorn, Gnoibos and others.

2. 2 ECOLOGICAL AND SOCIAL VALUES OF *ACACIA MELLIFERA*

Soil conservation authorities have used *Acacia* species for many years for the

stabilization of shifting sand (Roux & Middlemiss, 1963a), and the landscape industry is becoming increasingly aware of the potential of these plants for the rapid establishment of woody ground cover by direct seeding techniques.

Acacia mellifera offers a perfect microhabitat for various animal species. Larks and Cape penduline tits enjoy nesting in the protection of its thorny branches. Rodents, especially *Thallomys peadulcus* (the tree rat), often gather small branches and stalks at the multi-stemmed base of this shrub to protect themselves against birds of prey (Van der Walt & Le Riche, 1999).

Kumar *et al.* (1997) reported that during a 24-hour observation period, 12 species of Lepidoptera, 9 species of Vespoidea, 2 of Formicidae and 4 of Coleoptera were observed feeding probably on the nectar and most certainly on the pollen of *A. mellifera*.

The Sapwood is thick and whitish. The heartwood is dark brown to greenish-black, and when oiled turns almost black. It is very tough and elastic, does not split, and is unsurpassed for axe and pike handles (Palmer & Pitman, 1972). The heartwood is termite- and borer-proof, and larger stems make excellent fencing posts. The tree produces an edible gum, which is sometimes mixed with clay to make floors.

In Botswana a decoction of the roots is used as a medicine for stomach pains. The poison with which Bushmen tip their arrows is often made from a powdered grub mixed with the sap of *Acacia mellifera* (Palmer & Pitman, 1972).

The cocoons of a brown, hairy caterpillar *Pachypasa capensis*, which sometimes occur in great abundance on *Acacia mellifera* and can defoliate the shrub entirely, is used by the Bushman males to make rustling ceremonial ankle bands (dance bands) (Van der Walt & Le Riche, 1999). Once the irritating hairs have been removed from the cocoon, they are filled with small stones or seeds, sown closed and threaded onto a thin leather thong.

In Griqualand West the Africans believe that this tree, like the Camel Thorn, attracts lightning. The hooked thorns are thought by them to have the power of enticing rain (Palmer & Pitman, 1972).

2.3 BUSH ENCROACHMENT

Imbalances in nature can manifest itself in various forms and one of the most conspicuous results of such an imbalance is the problem of 'bush encroachment'. Rangeland degradation, in the form of bush encroachment, remains one of the major structural problems handicapping optimal animal production (Bester & Reed, 1997). It is estimated that some 20 million hectares of South Africa are currently affected by bush encroachment (Ward, 2000). It is an ecological phenomenon that can render vast areas of land unusable for up to six decades. Grasses, being fast-growing plants with roots in the upper layer of the soil, out compete trees for water and nutrients and when overgrazing occurs, the grasses are removed, freeing up water and soil resources for the tree to exploit. Tree seeds are then able to germinate in masses, creating large areas to become virtually impenetrable thicket to stock (Ward, 2000).

Bush encroachment is an example of an agricultural problem that is also a bio-diversity problem (Ward, 2000): Reduced agricultural productivity occurs because of the low value of woody plants to livestock, while reduced bio-diversity occurs because a multi-species grass sward is replaced with a single tree species. However, Krestin (undated) suggested that, woody plants are an integral part of the savanna ecosystem that should be contained at its natural level but cannot and should not be eradicated completely. Hence savannas should be viewed as patch-dynamic systems composed of many patches in different states of transition between woody and grassy dominance.

The savannas of the world are characterized by having a continuous, well–developed layer of grasses and forbs and an open, discontinuous or scattered layer of shrubs or trees (Knoop & Walker, 1985), where the density of the woody components may vary both spatially and temporally (Skarpe, 1992).

In recent history trends towards increasing woody plant abundance in temperate and tropical grasslands and savannas have been reported world wide (Archer, 1994; McPherson, 1997). The reasons for an increase in the density of woody plants in any vegetation type are diverse and complex. In most situations the determinants of savanna systems have been modified by man, either directly or indirectly (Smit *et al.*, 1999). A widely prevalent assumption is that the historical range expansion and density of many woody species has been facilitated by the introduction of domestic livestock and subsequent "overgrazing" (Walker *et al.*, 1981), climatic change (Brown & Archer, 1989), exclusion of occasional hot fire, the restriction of movement of herbivores, poor

grazing management practices and the provision of artificial watering points (Smit *et al.*, 1999). It is also due to the elimination of mega herbivores, notably elephant, and the resultant increase and spread of seed by animals (Donaldson, 1966).

This increase in tree density, commonly referred to as bush encroachment, results in the suppression of herbaceous plants (Stuart–Hill & Tainton, 1989; Smit, 1999a), mainly due to severe competition for available soil water, nutrients, light as well as antagonistic chemical effects (Jameson, 1967). Furthermore, bush encroachment accentuates the effect of droughts and often gives rise to pseudo-droughts (fodder shortage during normal or dry years) (Richter, 1991; Meyer, 1998).

As early as 1964, Van der Schiff as cited by Stuart-Hill & Tainton (1999) estimated that, at least 13 million hectares of savanna had become encroached in South Africa and argued that a similar situation would be expected in most southern African countries. A host of woody species, like Acacias, is responsible for this. An estimation by Donaldson (1969) indicated that *Acacia mellifera* encroachment has already become a serious problem on approximately 1.25 million hectare in the Northern Cape. At least 50 percent of the natural pasture in the Molopo area, which embraces large parts of the Mafeking, Vryburg and Kuruman districts, has been invaded by *A. mellifera*. The increased grazing of the past decades has played an important role in encouraging *A. mellifera* encroachment in the Molopo area.

As a result of the absence of a dense grass cover under *Acacia mellifera* trees, soil losses due to water and wind erosion are also higher. This is a problem, which has assumed greater dimensions during the past 30 years in the Vryburg-Mafeking area (Mostert *et al.*, 1969). Bush encroachment is considered a major factor towards the low grazing capacity of savanna areas (Gammon, 1984), as cited by Smit & Rethman (1998a). However, observations made at Ferlo (280 mm rainfall per year) and Dahra (450 mm rainfall per year), Senegal, indicated that tree cover can also influence herbaceous vegetation by increased floristic richness, modified phenology, and higher production and nutrient cycling rates (Grouzis *et al.*, 1998). The main reason for these effects was increased water availability and soil fertility, which is related to tree density.

Finding a solution to the problem of bush encroachment, in such a way that "the natural balance" is taken into consideration, is of mutual importance to agriculture and conservation. The problem of bush encroachment is particularly acute in the communal

rangelands of South Africa where human and livestock population densities are very high and consequently overgrazing is common (Ward, 2000).

2.4 ECOLOGICAL CONSIDERATIONS (THINNING VERSUS CLEARING)

According to Smit (1999a), the reduction in grass production and grazing capacity attributed to an increase in woody plant density, appears to differ between savanna types, with the outcome determined by both negative and positive responses to tree removal. This is because in savanna vegetation the physical determinants, biological interactions and individual species properties are unique to each spatial and temporal situation (Smit et al., 1999). In addition, past management practices have added to the complexity by bringing about different kinds and degrees of modification (Teague & Smit, 1992).

2.4.1 Negative grass-tree interactions

In most savanna areas, grass yields decrease as tree density increases (Stuart-Hill et al., 1987), and this constitutes the main reason for tree thinning or clearing. Tree removal in these areas results in increased grass yields (Teague & Smit, 1992; Tiedemann & Klemmedson, 1977).

Clearing woody plants in mixed savanna dominated by Combretum apiculatum and Acacia tortillis resulted in an improvement in the grazing capacity from 9.1 ha AU^{-1} to only 7.3 ha AU^{-1} (Donaldson, 1978). In contrast a reduction in tree density in the Kalahari Thornveld improved the grazing capacity from 45.8 ha AU^{-1} (230 kg grass dry matter per hectare) to 8.7 ha AU^{-1} (1 200 kg grass dry matter per hectare) (Moore & Odendaal, 1987). These differences may be ascribed to the differences in soil type and soil fertility, which are considered important determinants of the magnitude of increased grass production after tree thinning (Richter, 1991).

In areas with high tree densities a reduction in tree density, either mechanically or chemically, will result in an increase in grass production. In the Kalahari Thornveld increases of between 220% to 740% in grass production was measured after aerial application of an arboricide to a dense stand of A. mellifera and A. luederitzii (Moore et al., 1985).

According to Meyer (1998) thinning of A. mellifera had a positive effect on botanical composition and dry matter production of the herbaceous layer. The presence of A.

mellifera drastically affects both species composition and productivity of the area. He recommended a total or near total removal of this species.

Trials at different research stations in South Africa have clearly shown that the clearing of *Acacia karroo* (Sweet Thorn) is advantageous to the growth of grass, leading to doubling or trebling of the carrying capacity of the veld. Donaldson (1969) established in the Molopo area, that 6.8 ha of open grassveld could carry one head of cattle, while 13.6 ha of *A. mellifera* veld (at approximately 330 trees per hectare) are required for one animal. According to Trollope (1981), grass yield is affected by tree density only when the increase of trees is beyond a certain limit and the experiment in the False Thornveld of the Eastern Cape Province has shown this limit to be in the region of about 1 000 *A. karroo* trees per hectare.

Grass herbage yield data obtained over a three-year period from plots with different densities of *A. mellifera* (Figure 2.2) clearly illustrates the severe effects of encroaching *A. mellifera* on grass herbage production (Donaldson & Kelk, 1970). They found that grass yields decline linearly with increasing tree density. Yields declined rapidly as tree density increased to 350 mature *A. mellifera* trees per hectare, after which yields declined slowly. These findings confirm the general opinion held by farmers in the area that the control of encroaching *A. mellifera* must be regarded as a primary requirement before the production in the area can be increased.
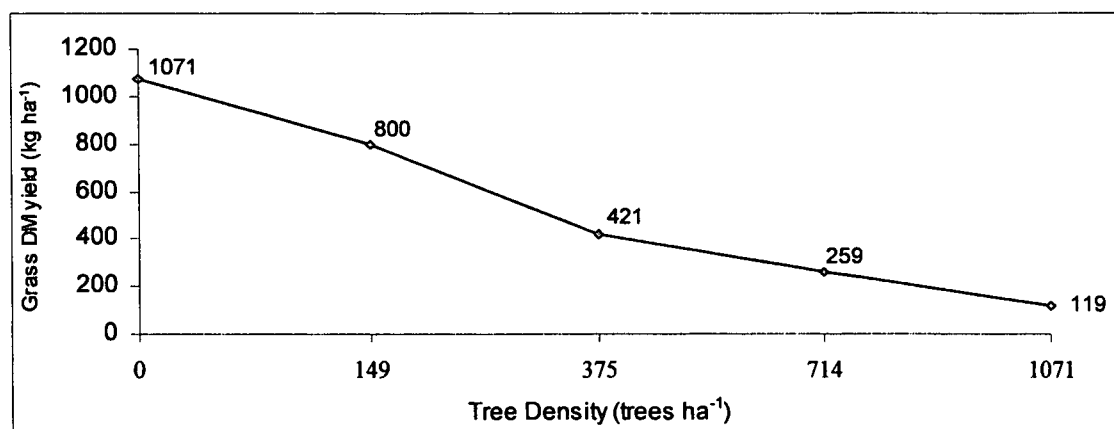
Figure 2.2 Decline in grass dry matter (DM) yield with increasing density of *A. mellifera* trees (Donaldson & Kelk, 1970).

The negative relation between tree basal area and herbaceous production has also been found to be curvilinear in the *Eucalyptus* savannas of Australia (Scanlan & Burrows, 1990) similar to that described by Donaldson & Kelk (1970). However, the

relation between tree biomass and herbaceous biomass in an *Eucalyptus* savanna in Australia has also been reported to be linear (Harrington & Johns, 1990).

2.4.2 Positive grass-tree interactions

The effect of trees on grasses may not always be negative and the net effect of favourable influences of woody plants on grass production depends on tree density (Stuart-Hill *et al.*, 1987; Smit, 1999a). Establishing trees create subhabitats, which differ from those in the open, with subsequent influences on the grasses. According to Stuart-Hill *et al.* (1987) a consistent pattern of grass production around isolated *A. karroo* was found to exist in the false Thornveld of the Eastern Cape. This pattern was characterized by high grass yields under and immediately south of the tree canopy, and low yields immediately to the north of the canopy. The former was attributed to favourable influences by the tree (e.g. shade and tree leaf litter), whereas the latter was attributed to reduced water input associated with the physical redistribution of rainfall by the tree and competition from the tree for soil water.

In Kenya, Belsky *et al.* (1989) recorded a significantly higher production of herbaceous plants beneath the canopies of both *A. tortillis* and *Adansonia digitata* than outside of their canopies. In the Mixed Bushveld of South Africa, higher dry matter yields have been recorded under the canopies of leguminous trees than either under non-leguminous trees or between the tree canopies (Smit & Swart, 1994). In contrast, Grossman *et al.* (1980) measured a significantly greater biomass in open veld than under *Burkea africana* and *Ochna pulchra* trees, although the canopied habitats did yield better quality forage.

The higher levels of soil nutrients in the soil under tree canopies may also be reflected in the herbaceous plants growing under the tree canopies. According to Smit & Swart (1994) differences between the total nutrient content under tree canopies compared to that in the open may often be ascribed to differences in the species composition and total dry matter yield between the various subhabitats.

In Mopane veld, Smit (1994) reported that subhabitat differentiation by *Colophospermum mopane* trees did provide some qualitative benefits. Some desirable forage grass species, which typically have high crude protein and *in vitro* digestibility values, prefer the canopied subhabitat to the open subhabitat and would probably be lost with the removal of all the *C. mopane* trees.

A possible contributing factor to the high production of forage from under-canopy subhabitats in southern Africa savannas is the well documented association between *Panicum maximum*, a palatable and potentially highly productive species (Jordaan, 1991; Smit & Rethman, 1992) and the under-canopy subhabitat of the larger trees in particular (Bosch & Van Wyk, 1970; Smit & Rethman, 1992; Smit & Swart, 1994). This species may develop into pure stands under, for example, *A. tortillis*, *A. karroo* and *Dichrostachys cinerea* trees taller than 2.0 m, 4.0 m and 4.5 m respectively (Smit & Van Romburgh, 1993).

Tree thinning results in drastic and immediate changes in the competition regime which had largely determined the growth and structure, on a temporal basis, of the plant community involved (Smit, 1994). The reaction of the herbaceous layer to tree thinning largely depends on rainfall (Smit, 1999a) and root biomass of the woody plants. In some *Acacia* species, like *A. mellifera*, the lateral roots can extend linearly up to seven times or more the extent of the canopy spread.

Measures like tree thinning are often considered as an option to restore the herbaceous production potential of areas affected by bush encroachment (Smit & Rethman, 1998a), however very little scientific information exists on the ecological impact of tree thinning, especially with regard to the reproductive dynamics of the remaining trees.

2.5 REPRODUCTION OF TREES AND ITS DETERMINANTS

An understanding of the problem of bush encroachment in southern Africa savanna requires an understanding of both the relationship between woody and grass components, and of the growth and dynamics of the woody species themselves (Smith & Walker, 1983). According to Smit (1994), tree thickening, or the increase of woody biomass, is primarily a function of two processes. Firstly, by the increase in biomass of already established plants (vegetative growth) and, secondly, by an increase in tree density, mainly from newly established seedlings (reproduction). This specific study will predominantly focus on the second one, that is, reproduction.

Reproduction encompasses the ability of mature trees to flower and produce viable seeds, and secondly the ability of these viable seeds to disperse, germinate and the newly established seedlings to survive (Smit, 1994).

2.5.1 Flowering and fruit production

Smit (1994) and Smit & Rethman (1998a) conducted a three year study in the South

African Mopani veld on the influence of tree thinning on the reproductive dynamics of *Colophospermum mopane,* including flowering and fruit bearing. They found that thinning of *C. mopane* reduced inter-tree competition, resulting in a significant increase in the flowering and fruit bearing of the remaining trees. They conclude that, although the percentage of reproductive trees was higher in the low tree density plots, the greater number of trees in the high tree density plots ensured that the total number of trees that flowered and produced fruits was of the same order than the number of trees that flowered in the low tree density plots.

Consumption of flowers by four browsing ruminant species was monitored in the Kruger National Park by Du Toit (1990). Flowers of *Acacia nigrescens* were important food sources to giraffes in the late dry season, and he suggested that this is not necessarily detrimental to the reproductive potential of the plant, since most African *Acacia* species bear high proportions of sterile flowers. Factors such as inflorescence structure and colour, pollen morphology and thorn structure suggests that some *Acacia* species could be pollinated by ungulates. Timing of flowering in *A. nigrescens*, and a close association between *A. nigrescens* and giraffes, indicates that giraffes could well be pollen vectors for this species (Du Toit, 1990).

Bowers & Dimmitt (1994) defined flowering triggers and developmental requirements for 6 woody plants by studying climatic and flowering data from a site in the Northern Sonoran Desert of Southern Arizona. They determined that flowering is triggered by rain in the shrubs *Acacia constricta, Ambrosia delfoidea, Encelia farinosa, Fouguieria splendens* and *Larrea tridentata,* but by photoperiod in the tree *Cercidium microphyllum.*

2.5.2 Seed germination

The influence of environmental conditions on the germination of many species is demonstrated by various laboratory experiments, showing the influence of varying temperature, light regimes, substrate salinity, pH, soaking in water and seed age on the germination of seeds (Donaldson, 1990; Cox *et al.,* 1993).

According to Mayer & Poljakoff-Mayber (1975), seeds are fairly resistant to extreme external conditions, provided they are in a state of desiccation. As a result seeds can retain their ability to germinate for considerable periods. Bein *et al.* (1996) recorded that the average number of *A. mellifera* seeds per kg is about 20 000 and seeds germinate in 2 to 14 days with a germination percentage of 50 - 80%. Story (1952), found that the

germination of *A. karroo* seed during the growing season is low (6.6% to 11.4%) and highly erratic. This is apparently caused by a highly impermeable seed coat. This physical barrier may cause the seed to lie dormant for many years unless some form of treatment is carried out to improve permeability (Clemens *et al.,* 1977), damaging the seed coat can reduce this physical dormancy. Seeds of some plants have a seasonal dormancy, which prevents the seed from germinating under unfavorable environmental conditions (Meyer & Monsen, 1992). Du Toit (1972a) found that *A. karroo* seed germinated over a wide range of temperatures but requires a moist environment for germination because of the presence of water-soluble germination-inhibiting substances in the outer coat of the seed, which must be leached from the seed before it will germinate.

It was shown by Choinski & Tuohy (1991) as cited by Smit (1994) that seeds of *Colophospermum mopane* germinated under a wide range of temperature and water potential but best at water stress conditions of –0.14 MPa. They conclude that *C. mopane* seems physiologically well adapted to water stress conditions. Burrowing of seeds by rodents may also contribute to the spread of some woody species (Cox *et al.,* 1993).

The germination responses of seeds from the African tree species *Colophospermum mopane, Combretum apiculatum, Acacia tortillis* and *A. karroo* under varying regimes of temperature and water stress (indicated by incubation in PolyEthylene Glycol (PEG) 8000) were reported by Choinski & Tuohy (1991). *Combretum* and *Colophospermum* were found to germinate under the widest range of temperatures and water potentials, for example, as strongly negative as –1.0 MPa at 20°C and 30°C, respectively. However, *Acacia* species showed progressive reduction in germination rates and radicle elongation in response to decreasing water potential. Experiments giving pre-imbibition treatment in water prior to transfer to PEG solutions showed that both *Acacia* species germinated at approximately 90% if given such pre-treatment and less than 10% if transferred directly to PEG. They conclude that *Colophospermum mopane* and *Combretum apiculatum* are the most stress-adapted species. Berkat *et al.* (1996) tested the imbibition of four *Acacia* species at water potentials of –0.03, -0.3, -0.6, -0.9 and – 1.3 MPa and found that *Acacia meamsii* imbibed more water and germinated better over a broader range of water potential.

Coughenour & Detling (1986) also examined the relation between seed germination of *A. tortillis* and differing concentrations of PEG 8000 or Hoagland's solution. They found

that both maximum germination percentage and radicle growth was affected by altering the water potential (with PEG) of the imbibition medium. They noted that germination of *Acacia tortillis* occurred most successfully at water potentials less negative than −0.6 MPa, although under field conditions these seeds would probably be subjected to a drying period unless buried in dung.

Palma *et al*. (1995b) also conducted a study to determine optimal temperature for seed germination, seed tolerance to water stress and the effect of light on germination using normal and scarified *Acacia senegal* seeds and naked embryos. In their study, optimal germination temperature for normal seeds was 25°C. Naked embryo and scarified seeds germinated best at 30°C. A slight positive photoblasty was detected when the integument remained intact. At osmotic potentials of 0.7 and 0.9 MPa there was still seed germination of up to 70%, with a considerable increase in 24 and 50 hours respectively. From these results, they concluded that the seed of *A. senegal* is tolerant to high water potentials and resistant to dry conditions. Similar to this Cox *et al*. (1993) found that optimal temperature for germination of *Acacia constricta* and *Prosopis velutina* shrubs ranged from 26 to 31°C.

In Australia Clemens *et al*. (1977) conducted a study on the germination of seeds of five *Acacia* species (*A. falcata, A. myrtifolia, A. longifolia* var. *longifolia, A. terminalis*, and *A. suaveolens*), following a manual chipping treatment or exposure to water held at different temperatures for discrete time periods. The response was evaluated on the basis of the final percentage germination, and estimates of rate of germination and time taken for germination to commence. The differences in response to soaking in hot water were insufficiently to be of practical significance. No single treatment gave optimum germination in all species. Increasing severity of treatments improved the germination rate and percentage germination up to a point where seed mortality became apparent. Manual chipping of the seed improved the germination rate, and the seeds began to germinate faster than those given any of the hot water treatments. However, in some species the germination percentage were lower in chipped seeds than in those treated with hot water. From these findings they conclude that, because of the sensitivity of some seed to high temperature, application of hot water treatments must be strictly controlled and methods employed which ensure uniform treatment for all seeds. A treatment at 100°C may be too hot for some species even at very short soakings. Manual chipping or scarification cannot be guaranteed to promote the germination of all viable seeds, although the rate of germination is greatly increased and the lag phase shortened considerably.

Srimath *et al.* (1991) carried out a study on seeds collected from a 9-year-old woodlot of *Acacia mellifera* at Mettupalay, Tamil Nudu, India. They found that among the various acid scarification treatments (5, 10, 15, 20, 25 & 30 min.), a duration of 10 minutes gave the best germination. Among the three size grades separated in BSS sieves, medium sized seeds germinated the best with the highest vigour in terms of root growth and a vigour index. The larger seeds gave poorer results, and small seeds the poorest.

Germination tests on *Acacia farnesiana* were conducted by Gill *et al.* (1986) in Nigeria. During these tests seeds were scarified by various treatments which include: incubation at 60 - 70°C for 6 - 12 hours; soaking in boiling water for 1 - 2 minutes; con. Sulfuric, nitric or hydrochloric acids for 10 minutes; moistening with seed extract; electric shock application (0.5 - 1.75 amp.); soaking and drying cycles; and scarification with sandpaper. The best germination (98%) was achieved after the sand paper treatment. The acid treatment also increased germination with 65 - 66% compared with a value of approximately 30 - 40% for untreated (control) seeds. Other effective treatments were soaking and drying (64% germination) and electric shock (53% germination with the 1.75 amp. treatment). Hashim (1990) reported that seeds of *Acacia nilotica* and *Albizia anthelmintica* germinated only after soaking in a large volume of water and concluded that the seeds may contain chemical inhibitors that restricted germination. Undamaged seeds of other tree species such as *Acacia seyal, A. gerrardii* and *Prosopis africana* required scarification with concentrated sulfuric acid for 5 to 150 minutes to give optimum germination in 2 to 9 days (Hashim, 1990)

Reproduction of *Acacia senegal* was studied by Palma *et al.* (1995a) to determine whether there are inherent seed characteristics that limit germination. The age, role of teguments and capacity of imbibition were analyzed using three types of seeds: Normal, scarified and naked embryos. They observed that in seeds three or more years old the germination percentage diminished, latency increased and imbibition time was shortened (4 to 5 hours). Germination of scarified seeds, however, was homogeneous even at low temperatures and they concluded that there are no obstacles to seed germination at the embryo level.

Seeds of some woody plants have dormancy, which prevents the seed from germinating under unfavourable conditions (Zietsman & Botha, 1987; Meyer & Monsen, 1992). Dormancy can be due to the seed coat preventing or interfering with water uptake, mechanical restraint or prevention of leaching of inhibitors (Zietsman & Botha, 1987). In addition, seeds of some tree species may not be dormant on dispersal but could be

forced into a seasonal dormancy by unfavourable conditions on the germination of the seeds. Despite or perhaps because of the dormancy of some tree species, it remains viable for extended periods, and seeds over 57 years old have germinated under laboratory conditions, and such extended viability of seed is apparently characteristics of many *Acacia* species (Trollope, 1981).

Jerlin & Vadivelu (1994) conducted a study on *A. mellifera* seed, using two scarification methods, viz. hot water treatment, Sulfuric acid (200ml kg^{-1} seed) treatment. Among the treatments tried the acid treatment for 10 minutes was the best, giving a higher germination (84.5%) compared with untreated seeds (22.6%), as well as increased root length, shoot length and vigour. They recommended sand scarification for 15 minutes as a slightly less effective method for softening the seed coat.

Magnani *et al.* (1993) tested seeds of *Acacia boormani, A. implexa, A. kybeanensis, A. myrtifolia, A. rubida* and *A. terminalis* for germination. In all cases it was low (<9%) due to the high proportion of hard seeds. The seeds were then treated at 100^{0}C with dry heat or boiling water for 1, 2, 4, 8, & 16 minutes. They found that treatments were most effective in breaking primary dormancy in *A. myrtifolia, A. implexa* and *A. terminalis*, but had no dormancy braking effect on *A. boormani*. In this specific study Magnani *et al.* (1993) generalized that the boiling water treatment was more effective than the dry heat treatment and the latter treatments also increased the proportion of non-viable seeds, particularly when applied for longer durations.

Thermotolerance is another survival strategy of seeds, which enables them to survive periods of post-imbibitional heat stress. This thermotolerance has been demonstrated to exist in seeds of *Combretum apiculatum* from lower altitude area, whereas seeds from high altitude areas did not exhibit the same tolerance (Chikono & Choinski, 1992).

The sexual reproduction in some *Acacia* species will be further suppressed when animals eat flowers, pods and seeds. In passing through the gut of large herbivores, these seeds may be digested or killed (Cox *et al.*, 1993), although many seeds are reported to survive the alimentary process (Stuart-Hill, 1999). The survival rate apparently depends on the presence or absence of hard impermeable seed coats (Gwynne, 1969), type and maturity of the seed and on the type of animal consuming the seed (Stuart-Hill, 1999). The alimentary process of sheep and cattle can actually stimulate germination in those seeds, which survive (Story, 1952; Du Toit, 1972b). Germination of these seeds are often improved from scarification by digestive fluids,

while being dispersed when defecated (Coe & Coe, 1987), but large seeds, like those of *Colophospermum mopane*, rarely escape mastication and are either destroyed or they suffer extensive structural damage (Styles, 1993).

According to Miller (1996b), the number of *Acacia* seeds surviving passage through the gut usually, but not always increased with large mammal body mass, and ingested seeds exhibited greater germination than uningested seeds when germinated on filter paper or in dung and soil media. Seed germination in soil exceeded that in dung. Cox *et al.* (1993) observed that, after passage by sheep, about 6% of the *Acacia constricta* and 13% of the *Prosopis velutina* seeds germinated. While after passage by cattle, only 1% of the *A. constricta* and 3% of the *P. velutina* seeds germinated and they concluded that seed consumption and passage by sheep and cattle appear to adversely affect seed germination.

Fire may also destroy seeds of some tree species (Holmes *et al.*, 1987), but incidents of enhanced germination of seeds of some woody species by fire, have been reported (Hodgkinson, 1991). According to Trollope (1981), burning is one way of stimulating germination, presumably because of the damage it causes to the seed coat. However, Cox *et al.* (1993) noted that a prescribed fire killed 100% of seeds of *Acacia constricta* and *Prosopis velutina* placed on the soil surface but had no measurable effect on the germination of seeds sown at 2 cm.

Knoop (1982) as cited by Smit *et al.* (1999), observed that on a site dominated by *Acacia* species, large number of seeds germinated and survived when cleared of herbaceous vegetation, but few were found in an uncleared area.

Swaminathan *et al.* (1991) evaluated the germination of *A. mellifera* seeds that were collected in a 9-year-old woodlot from two aspects (east and west) and three crown heights (top, middle and bottom). The aspect had no effect on percentage germination but germination energy was higher in seeds gathered from the western aspect than from the east and also seeds collected from the top of the crown gave superior germination.

2.5.3 Seed predation

Insect damage is one of the factors influencing seed germination of *Acacia* species. Bruchid beetles are amongst the predominant predators of seeds of *Acacia* species and quite common in Africa (Sabiiti *et al.*, 1991). Seed predation by beetles provides a good

system for the study of interactions between seed beetles and the seeds of *Acacia* species (Mucunguzi, 1995b). Seed predation by insects may be critically important in plant dynamics. The damage caused is due to the eating of the cotyledons and/or embryos of the seeds, which eventually reduces their viability (Auld & Myerscough, 1986). High seed-beetle infestation of 95.6% and 99.0% was reported in *Acacia tortillis spirocarpa* from fresh seeds and those stored for a year, respectively (Lamprey *et al.*, 1974). Sabiiti & Wein (1987) reported a high rate of infestation (96%) of seed beetles in *Acacia sieberiana* in Uganda.

Bruchid larvae infestation starts early in the seed development stage before maturation and dispersal. The larvae grow inside the seeds and may pupate and emerge as adults, unless the seeds are either destroyed or ingested by mammals (Mucunguzi, 1995b). Southgate (1978) indicated that the level of certain aminoacids, notably pipe colic acid and some heteropolysaccharides is the factor determining the exploitation of *Acacia* seed resource by bruchid larvae.

Ernst *et al.* (1990) conducted a laboratory study on the life history of *Bruchidius aberatus*, its impact on the quality and germination of seeds of *Acacia nilotica* (seeds were collected in south-eastern Botswana) and food plant specificity. According to Ernst *et al.* (1990), rearing experiments showed that only a small part of the *Bruchidius* population that emerges between February and March is multivoltine- having several generations in one. Feeding experiments showed that the reproductive activity of *Bruchidius* females is not stimulated by pollen. The minimum life span of adult beetles varied between 4 and 40 days (Ernst *et al.*, 1990), but did not differ between univoltine, having only one generation in one year, and multivoltine beetles. Hatching of the first instra larvae took 22 days at a temperature regime of 20/15^{0}C and it took 3 to 11 months for development from larvae to adult. The results of their study show that during dry storage of seeds, *Bruchidius ubertus* can destroy the total amount of stored seeds within a few years. In stored seed pools, food plant specificity of the bruchid larvae was shown to be low. A field experiment conducted by Johnson & Siemens (1991) in Venezuela indicated that female bruchids use non seed cues associated with *Acacia* (pod valves, cow dung and horse dung) to locate *Acacia* seeds, and when seeds of both hosts are encountered, females oviposit equally on seeds of both species (*Acacia* seeds and non host *Parkonsonia aculeata*).

Siemens *et al.* (1991) conducted a field study in Arizona to determine which factors kept the bruchids *Stator limbatus* and *S. pruininus* restricted to different species of *Acacia* in

sympatry. The factors assessed were plant micro-environment, interspecific competition, the suitability of seeds for food, and the impact of natural enemies. They observed that female bruchids selectively oviposited on seeds of their normal host when given a choice of Acacia seeds in their normal host micro-environment. It is concluded that the proximate determinant of locality restricted use of hosts was oviposition behaviour, which was suggested to best relate to differences in the suitability of hosts for larvae (Siemens et al., 1991).

Traveset (1991) investigated the patterns of resource utilization by the seed predators Mimosetes nubigens and M. mimosae on Acacia farnesiana in Costa Rica. The intensity of seed predation was dependent on plant size, fecundity or relative isolation. He found that the hymenoptera parasitoid Urosigalphus species accounted for about 40% and 30% of insect emergence from fruits in the two years, respectively. Bruchid eggs were more likely to be attacked by Urosigalphus species in green than in mature fruits. He suggests that the parasitoid activity select against oviposition by Mimosetes species at an early stage of fruit maturation. He also observed that heat and desiccation results in considerable pre-emergence bruchid mortality.

Ecological interactions between the bruchid seed predators and the vertebrate seed dispersers of the legume Acacia farnesiana in Santa Rosa National Park, Costa Rica were investigated by Traveset (1992). The variables compared were number of insects "ingested" and number of insects escaped before fruit removal. He found a high pre-emergence mortality, mainly due to environmental agents such as high temperature and desiccation. It was concluded that the dynamics of the insect seed predator populations cannot be easily predicted based on changes in the seed disperser's population densities. Traveset (1991) also observed that, survival from egg to adult in fallen fruits was about 18%. Beneath A. farnesiana, females of the bruchids preferred fruits in the shade to those in the sun. He suggested that the natural enemies and abiotic factors are more likely to limit bruchid populations than intra-or inter-specific competition.

Mucunguzi (1995a) investigated the effect of bruchid beetles on seed germination and seedling establishment of Acacia gerrardii and A. sieberiana. In his experiment, infested and non-infested seeds from each of the Acacia species were divided into two groups. One group was used in germination trials in petri dishes fixed with moist filter paper at about 25°C in the laboratory. The second group was planted in soil in wooden boxes for the monitoring of seedling emergence, growth and establishment. He found that bruchid beetles significantly reduced (P < 0.05) germination and seedling establishment of A.

gerrardii, while they promoted early germination and establishment in A. sieberiana. He concluded that bruchid beetles caused the removal of many seedlings of A. gerrardii, while A. sieberiana has adapted itself to survive bruchid beetle infestation. Hashim (1990) also reported that seeds damaged by bruchid beetles failed to germinate if their embryos were eaten, but germination of damaged seeds whose embryos were not eaten was sometimes as high as that of controls and bores made by the bruchids in seeds may have facilitated moisture imbibition.

Mucunguzi (1995b) also carried out a study on seed predation by bruchid beetles to understand the interactions between seed beetles and Acacia seeds in Queen Elizabeth National Park, Uganda. Seed infestation was assessed using cutting tests. Four seed beetles, the cerambycid Enartha castelnaudi, and the bruchids Tuberculobruchus natelensis and Bruchidius species were found in two large seeds of Acacia sieberiana, while Caryedon serratus and Bruchidius submaculatus were found in small seeds of A. gerrardii. The small seeds of the latter species had a higher rate of infestation than the larger seeded A. sieberiana in spite of the latter species having more seed predators than the former. The intensity of seed predation on A. sieberiana showed negligible differences within and between study sites. The intensity of seed predation was only significant with A. gerrardii at one study site. He concluded that the possible compensatory response by A. sieberiana to seed predation by beetles is characteristic of many large seeds with adequate resources to accommodate a guild of seed predators.

According to Abdullah & Abulfatih (1994), the distribution of Acacia trees and their bruchid seed pests in south-western Saudi Arabia revealed that each of the host-insect pairs occupied a specific range along the altitudinal gradient from sea level to 2 500m. They found that at low to intermediate altitudes, between sea level and 1 750m, in hot to warm environments, the following host-insect pairs were recorded: Acacia aska - Bruchidius spp., A. ehrenbergiana - B. saudicus, A. hamulosa - Bruchidius spp., A. oerfota - Bruchidius spp., A. seyal - Bruchidius spp., A. tortillis - B. aurivilli and A. tortillis - B. sahelicus. At high altitudes between 1 750 and 2 500 m, in a cool environment the following host-insect pairs were also recorded: A. negrii - B. arabicus and A. gerrardii-B. arabicus. Abdullah & Abulfatih (1995) also found that the rates of seed predation varied among Acacia species, but the greatest were recorded in A. tortillis and A. ehrenbergiana (50.5 and 54.4% seeds attacked, respectively on average).

According to Miller & Coe (1993), seeds infected with bruchid beetle larvae and which

have been eaten have greater germination (0 -13.6%) than uneaten infested seeds (0.8 - 4.4%). They suggested that in the presence of bruchid beetles, it may be beneficial for *Acacia* seeds to be eaten by ungulates.

Miller (1994b) conducted a study to test the hypothesis that "in the presence of bruchid beetles, it is advantageous for *Acacia* seeds to be eaten by ungulates". The study was conducted on pods of *Acacia nilotica* and *A. tortillis* on trees and on the ground from May to November 1992 in a nature reserve in the Northern Province, South Africa. In his study the pods on trees were eaten by giraffe (*Giraffa camelopardalis*), attacked by bruchid beetles, fell to the ground or disappeared to unknown causes. Pods on the ground were eaten by ungulates (mainly *Tragelaphus strepsiceros* and *Aepyceros melampus*) and rodents, attacked by bruchids, buried by termites and ants, lost to decomposition, and a few disappeared to unknown causes. In the presence of ungulates, pods were consumed shortly after maturity, and their seeds were freed from the pod and disappeared some distance from the parent. He found that ingested and defecated seeds exhibited a greater potential germination than uneaten seeds.

Miller (1994a) also conducted a study on the interaction of large African herbivores and bruchid beetles with seeds of *Acacia* species. The germination of bruchid-infested seeds was also compared. He found that bruchid-infested seeds germinated and the germination of bruchid-infested and uninfested *A. tortillis*, *A. nilotica* and *A. hebeclada* seeds did not differ. Pods ingested by large herbivores lowered bruchid infestation of consumed and defecated seeds compared to uningested seeds. Uninfested, ingested and voided seeds of *A. tortillis* germinated significantly better than uninfested, uningested seeds. He concluded that pod ingestion by large herbivores may reduce bruchid infestation, increase *Acacia* seed germination and, therefore, increase potential *Acacia* seedling recruitment.

Seed removal rates, relative to seed availability in the litter layer of *Acacia* infested vegetation, were studied by Holmes (1990) to determine the importance of indigenous ants and vertebrates as dispersers and predators respectively. He recorded a relative loss to the annual seed fall of 50% and 80.95% in dense *Acacia saligna* and *A. cyclops* stands, respectively. Ants and rodents removed significant quantities of seeds, but a large proportion may have rotted (Holmes, 1990). In dense *A. saligna* stands, ants usually removed all seeds presented to them within 7 days, compared with only 36% of seeds in dense *A. cyclops* stands. However, in dense stands of both species, rodents were relatively slow to take seeds, removing 31% within 7 days. The results of Holmes

(1990) indicate that indigenous ants have played a critical role in maintaining and accumulating *Acacia* seed banks and thus may have facilitated the development of dense *Acacia* stands.

2.5.4 Seedling establishment

Woody plant seedlings require sufficient light and water if they are to establish successfully. According to Trollope (1981), favourable water conditions are necessary during the establishment period because the seedlings of *Acacia karroo* are extremely sensitive to desiccation. Growth analysis has also revealed that the seedlings of *Acacia* species have a low growth rate and slow root development.

Seedling establishment of many woody plants, including *Acacia*, can also be influenced by irradiance (Smith & Shackleton, 1988). Environments with high inter-annual rainfall variability are often only suitable for seedling establishment in the wetter years (Chesterfield & Parsons, 1985). Most *Acacia* species are thought to be heliophytic and require high irradiance levels for optimal growth (Du Toit, 1967). Sustained heavy grazing of grasses can reduce their above- and below-ground biomass, and thus their use of resources. This may promote the establishment of woody seedlings because of increased irradiance at ground level and increased availability of below-ground resources (Caldwell *et al.*, 1987) as cited by O'Connor (1995).

A further possible effect of domestic livestock is to consume and disperse seeds of woody species, with dung pats acting as a suitable environment for seedling germination and establishment (Brown & Archer, 1989). This advantage of seedling establishment within a dung pat may be due in part to the aversion of livestock to grazing near dung.

In contrast to this, O'Connor (1995), who conducted a study on sites above and below the natural altitudinal tree line of *Acacia karroo* in grassland of the Eastern Cape, found no seedlings emerged from dung pats. Shading dramatically increased the density of surviving *A. karroo* seedlings. In the open, only 3 and 1.5 seedlings m^{-2} remained respectively at the end of the growing season, compared to 23.3 and 19.5 seedling m^{-2} under shading for these respective times. This was attributed to the effect of shade on moisture availability in a season, which received only 54% of the normal rainfall. O'Connor (1995) concluded that the survival of *A. karroo* seedlings were related to moisture availability, with no or poor survival below 500 mm rainfall, indicating that *A. karroo* can only establish in certain rainfall areas. In addition, treatments affected seedling size, in particular seedlings growing under shade and within a dense grass

canopy were etiolated. He also concluded that *A. karroo* seedlings are capable of establishing and surviving within a dense grass sward for at least a year, tolerant of low irradiance and of interference. He suggests that this species predominantly forms a seedling bank, which has implications for the invasion of grassland by woody species.

An important determinant of woody seedling recruitment competition from other plants, either from other woody plants (Smith & Walker, 1983), or herbaceous plants (Brown & Archer, 1989). During the initial stages of growth following germination, woody plants are normally in direct competition with the grasses for the resources in the topsoil layers (Hurt & Tainton, 1999). Trollope (1981) is of the opinion that grasses, because of their shallow root system, are more competitive for moisture in the topsoil than woody plants during germination and seedling establishment.

Smit & Rethman (1998a) found low seedling numbers along a density gradient of *Colophospermum mopane*, and no specific pattern of seedling establishment was observed. They suggested that at higher tree densities the severe competition from established *C. mopane* trees could account for the low seedling establishment, while in the low tree density plots competition from newly established herbaceous plants may account for tree seedling absence.

As the root systems of tree seedlings have to penetrate the shallow soil layer, the seedlings must actively compete with the herbaceous plants for the water contained in the shallow soil layer. Therefore, the weaker the herbaceous community, the greater the success for the establishing of tree seedlings (Hardy *et al.*, 1999). Shallow rooted tree species, like *Acacia mellifera* and *Grewia flava*, increase in abundance following overgrazing of the grass layer, which suggests that they are favoured by an increase in water availability in the upper soil layer (Skarpe, 1990).

Deans *et al.* (1993) reported that supplementary nutrition and inoculation with compatible *Rhizobium* bacteria had no significant effect on nodulation of the roots of *Acacia mellifera*, although nutrition increased seedling growth of *A. mellifera*. It was concluded that the inoculum potential of the soil was high, but the nodulation in the field was inhibited by a lack of water. In a separate study, seedlings of *A. mellifera, A. senegal* and *A. seyal* grown in a tree nursery, in Sudan, produced substantial numbers of nodules when peat was added to the Nile silt/sand medium and they suggested that improved aeration seemed the most likely reason for the stimulation of nodule production.

In a green house experiment conducted by Franco *et al.* (1996), seeds of *A. farnesiana* and *Celtis pallida* were planted in pots filled with soil from under *Prosopis glandulosa* canopies and in adjacent interspaces. They found that seedling mass of both species was greater in canopied soils than in interspace soil in sunlight. The mass, however, of the two species did not differ between soil sources in the shade. Successful establishment of tree and shrub seedlings occurs mainly during above average rainfall seasons when competition for surface soil moisture is moderately low (Trollope, 1999).

Heavy grazing would, therefore, by reducing competition from the grass, have a positive effect on the establishment of woody seedlings. On the other hand, a vigorous herbaceous community would compete strongly with the seedlings of the woody plants (Hurt & Tainton, 1999). These plants may either be stunted by such competition, or may not be able to survive such competition in a very vigorous grassland sward, particularly when combined with different fire and browsing regimes.

Van Vegten (1983) identified overgrazing of grasses as the main cause of woody plant increase, in savanna areas of eastern Botswana. Skarpe (1990) also observed that in areas with no and moderate grazing, shrub densities fluctuated but showed no consistent change, while density increased with heavy grazing.

Thompson (1960) as cited by Smit *et al.* (1999) reported that *C. mopane* seedlings could not establish where the grass cover was dense. In contrast to these reports, Brown & Archer (1989) recorded high rates of emergence and establishment of *Prosopis* seedlings on long-term protected plots that carried a good grass cover. Similarly in the Eastern Cape, resting veld did not prevent the establishment of *Acacia karroo* seedlings after the eradication of mature trees (Du Toit, 1972a).

In their natural habitat in Australia and Africa, there is very little *Acacia* seedlings regeneration beneath the canopy of mature *Acacia* trees. There is also little or no regeneration under thickets or plantations of *Acacia* growing as exotics and *Acacia* seedlings rarely survive under closed canopies of grasses (Brown & Booysen, 1967), or trees and shrubs (Roux & Middlemiss, 1963b).

Reader *et al.* (1995) found that a regression model, which uses tree density as the independent variable accounted for between 93% and 98% of inter-specific variation in seedling establishment. This result provides empirical support for models of tree dynamics in gaps that assume seedling establishment depends on canopy tree density.

Denslow (1995) studied the effect of tree density on seedling establishment and found that both tree density and diversity are likely to be greater in areas of high stand turnover rates (replacement/decomposition). Thinning and non-catastrophic mortality reduced both the density and diversity in areas of low gap frequency, and gaps are often sites of high species diversity. Hence, seedling establishment and sapling (young tree) density increase flowering canopy opening.

Smith & Goodman (1986) examined seedling establishment relative to canopy cover in both *Acacia nilotica* and *A. tortillis* communities. They identified two types of species: those whose establishments are associated with or unaffected by tree canopy cover, and those whose establishment are limited to between-canopy or open environments. Of the latter type the *Acacia* seedlings are distinctive as they fail to establish under the canopy of any established individual, regardless of species. *Euclea divinorum*, as an example of the first group, does have the ability to establish under canopies. Both *A. nilotica* and *E. divinorum* were found to be regularly dispersed, but there was no significant correlation between nearest-neighbour distance and combined size for mixed species nearest-neighbour pairs of *A. nilotica* and *E. divinorum* (Smith & Goodman, 1987) as cited by Smit (1994).

Ben-Shahar (1991) has demonstrated that tree species of communities dominated by *Acacia senegal-Acacia tortillis* and *Euclea divinorum-Acacia nilotica* had characteristic dispersal strategies. These were manifested through intra- and inter-specific competition among the dominant tree species. *Acacia senegal* become dominant in areas previously dominated by *A. tortillis*, while *E. divinorum* was replacing previous dominance by *A. nilotica*.

Scholes (1990) estimated that recovery of cleared *Colophospermum mopane* thicket in the eastern lowveld, to a level where its effect on grass production is comparable to that in the pre-cleared state, occurs within 14 years. He has indicated that the recovery period is shortened by higher rainfall and lengthened by drought. Based on an establishment rate of 4 seedlings $ha^{-1} y^{-1}$, he estimated that the *C. mopane* trees would re-grow to the original pre-cleared state within 40 years.

In *Burkea* - savanna, Lubke & Thatcher (1983) reported that following a burn the number of *Ochna pulchra* plants between 1m and 3.5 m dropped, but that the number of those less than 1m increased dramatically. Likewise, Sabiiti & Wein (1988) observed high emergence of *Acacia sieberiana* seedlings (172 seedlings m^{-2}) in Uganda after a fire of high intensity (3 200 kw m^{-2}) compared to unburned areas (6 seedlings m^{-2}). Du Toit

(1972a) reported that fire, while not preventing establishment, retarded seedling development of *Acacia karroo* in the Eastern Cape.

2.6 SOIL NUTRIENT STATUS IN RELATION TO TREE DENSITY AND SUBHABITAT DIFFERENTIATION

Nutrients, such as nitrates, phosphorous, a series of anions and cations and various trace elements are essential to the nutrition of plants, and act as determinants of the composition, structure and productivity of vegetation. While the base-richness of the parent material is initially important in determining soil fertility, biological activities are important in the creation and maintenance of localized areas of enhanced soil fertility, often on base-poor substrates. Trees, and more specifically leguminous trees like the *Acacia* species, are important in establishing areas of enhanced soil fertility (Smit, 1999a).

Nitrogen is one of the key elements in ecosystem functioning and productivity (Du Preez *et al.*, 1983; Tietema *et al.*, 1992). The occurrence of N-fixation due to microbial activities under leguminous trees is a possible source of N enrichment (Felker & Clark, 1982; Hogberg & Kvarnstrom, 1982; Virginia & Delwiche, 1982; Shearer *et al.*, 1983; Hogberg, 1986). The annual N fixation by *Leucaena leucocephala* in a semi-arid site in Tanzania was estimated at 110 kg ha^{-1} (Hogberg & Kvarnstrom, 1982). Most comparative studies, which have involved *Acacia* species, have shown that soil enrichment under their canopies was higher than under non-leguminous tree species. Soil under tree canopies has higher concentrations of nitrogen, soil organic matter, phosphate and exchangeable cations like potassium, magnesium and calcium compared to soil from the open areas (Smit, 1999a).

A pattern of nutrient-enriched soil patches is often associated with the distribution of woody species in the savanna landscape. Higher nutrient levels under trees are related to greater organic matter contents in the soil under trees (Dunham, 1991). This is due to greater litter inputs by trees compared to grasses and importation of organic matter by birds, insects and other animals, which rest, live and eat in or under trees (Belsky *et al.*, 1989; Teague & Smit, 1992). This is an example of what Scholes (1991) termed "nutrient import".

Moyo *et al.* (1998) conducted a study in semi-arid rangelands to establish whether differences in soil nutrient status and microclimate exists between understorey and open

areas. He found that the created micro-habitat had an improved soil physical and nutrient status and reduced evaporation. The reason was ascribed to the higher volume of litter-fall (Kennard & Walker, 1973; Moyo et al., 1998), and associated increased content of soil organic matter which improves soil physical properties such as water infiltration, water holding capacity, aeration and bulk density (Elwell, 1986).

Woody plants can act as nutrient pumps. Nutrients are extracted at depth in the soil profile and deposited on the surface through, for example, leaf drop. This allows for higher soil fertility often associated with palatable species such as Panicum maximum to occupy the sub-canopy habitats, where they can contribute to the grazing value of savanna areas (Bosch & Van Wyk, 1970).

Contrary to reports of higher pH under tree canopies (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Palmer et al., 1988; Young 1989), Belsky et al. (1989) recorded a lower pH (5.4) at the base of Acacia trees than further from trunk (pH 6.3). However, based on the positive association between increases in exchangeable cations and soil pH (high base saturation) (Barnard & Folscher, 1972; Kennard & Walker 1973; Hatton & Smart, 1984), a higher pH under canopies of savanna trees conforms more logically with the higher content of exchangeable cations in this subhabitat.

The tree canopy is principally responsible for the creation of a distinct sub-canopy habitat characterized by a low light intensity, a relatively high soil moisture level and generally higher fertility levels (Smit & Van Romburgh, 1993). Grass species, such as Panicum maximum, which grow beneath tree canopies, contribute significant amounts of forage, and therefore, bush control measures should not simply involve a complete removal of woody plants (Smit & Swart, 1994). In savanna ecosystems that have suffered little disturbance, grass species composition has often been found to differ between the understorey areas and areas away from the influence of tree crowns, with understorey areas dominated by mesic, high yielding, palatable, perennial grass species. In contrasts, low yielding and less palatable perennial or annual grasses dominate areas away from the influence of tree crowns (open areas) (Belsky et al., 1989). Grass yield and quality has consequently been higher in areas directly below tree crowns compared to surrounding open areas (Stuart-Hill et al., 1987). These differences have occurred in spite of overhead tree crowns that intercept and reduce precipitation and despite competition for water and nutrients between tree and grass roots in the understorey areas (Amundson et al., 1995). However, data from a study carried out in Zimbabwe indicated that the soil nutrient status under canopies of Acacia sieberiana

and *Parinari curatellifolia* was not significantly different despite better litter quality and fast decomposition rates of *A. sieberiana* (Chivaura *et al.*, 1998)

According to Roberts & Gillman (1995) soil nutrient resources typically are assumed to change following forest disturbances, usually with nutrient availability increasing initially and subsequently decreasing through later stages of succession. The effect of forest disturbances on soil organic matter, pH and extractable soil nutrients were examined by Roberts & Gillman (1995) to determine the relationship of these variables to changes brought about in the herbaceous layer. Extractable nutrient concentrations were 1.5 - 3 times higher in the A1 horizons of mesic sites than dry mesic sites. Soil pH and cations increased after disturbance on mesic sites, but not on dry mesic sites. They also observed that herbaceous species diversity increased after disturbance on mesic sites, but with decreases in the importance of shade-tolerant tree species. These results suggest that soil nutrient resources do not always change through secondary succession and that pattern change can be distinctly site dependent.

With increasing tree density, soil nutrient status can be expected to change. There is evidence that soil organic matter increases on a landscape scale, when tree density increases. Both the disappearance of fertile islands and an increase in organic matter input associated with increases in tree density have implications for future vegetation productivity for savannas. According to Roos & Allsopp (1997), we need a greater understanding of the long term effects of both the influence of increasing tree density and of tree thinning on nutrient distribution in order to manage savanna rangelands in a sustainable manner. We also need to know more about soil processes, which influence productivity, such as nutrient cycling and which will control uptake of many plant species. The results of their work indicated that, at low-density sites the organic matter content and, total and mineralisable nitrogen were significantly higher in soil collected under trees, while the OM / N ratio was significantly lower under trees compared to soil from open positions and the available total and mineralisable phosphorus and pH showed no significant difference. Temporary increases in woody plant density therefore promote long-term ecosystem productivity by increasing nutrient and organic matter concentrations in the surface soils in some savanna ecosystem.

CHAPTER 3

STUDY AREA AND TRIAL LAYOUT

3.1 STUDY AREA

3.1.1 Location

The study was conducted on the farm "Wilzenau", situated approximately 35 km south-west of the town Bray and approximately 25 km north-west of the town Pomfret in the North-West Province of the Republic of South Africa. It is located at $23^{0}27"48'E$, $25^{0}33"15'$ S, at an altitude of ± 1 000 m above sea level (Figure 3.1).

This area is located in the Savanna Biome (Rutherford & Westfall, 1986), characterized by a herbaceous ground layer and a distinct upper layer of woody plants.

3.1.2 Climate

The climate of the area is hot and semi-arid. The rainy season usually extends from October to March inclusive, but rainfall is irregularly distributed and erratic. The mean long-term seasonal rainfall for the period 1954/1955 to 1999/2000 (55 years) was 347. 3 mm (CV = 37.0 %, range = 137.6 - 623.7 mm) (Meyer *et al.*, 2001).

The area is characterized by very high day temperatures of up to 42°C during the summer months, while the winter months are much cooler with very low minimum temperatures of up to -9°C (Van Rooyen & Bredenkamp, 1996), with an average annual temperature of 18°C. The adverse effect, which the high maximum temperatures may have on the plants and animals, is reduced by the much lower temperatures experienced during night time (Donaldson, 1969). Typical of the semi-arid western part of South Africa this area experiences dry and desiccating north-westerly winds, which mainly occur during the spring and summer months (Donaldson, 1969).

3.1.3 Vegetation

The study area is located in the Kalahari Plains Thorn Bushveld (Van Rooyen & Bredenkamp, 1996). Acocks (1988) described the area as Kalahari Thornveld Proper (16a).

FIG. 1 - Molopo Area (—.—.—.—.—.—.—)   (Scale 1 inch = 2.5 miles)
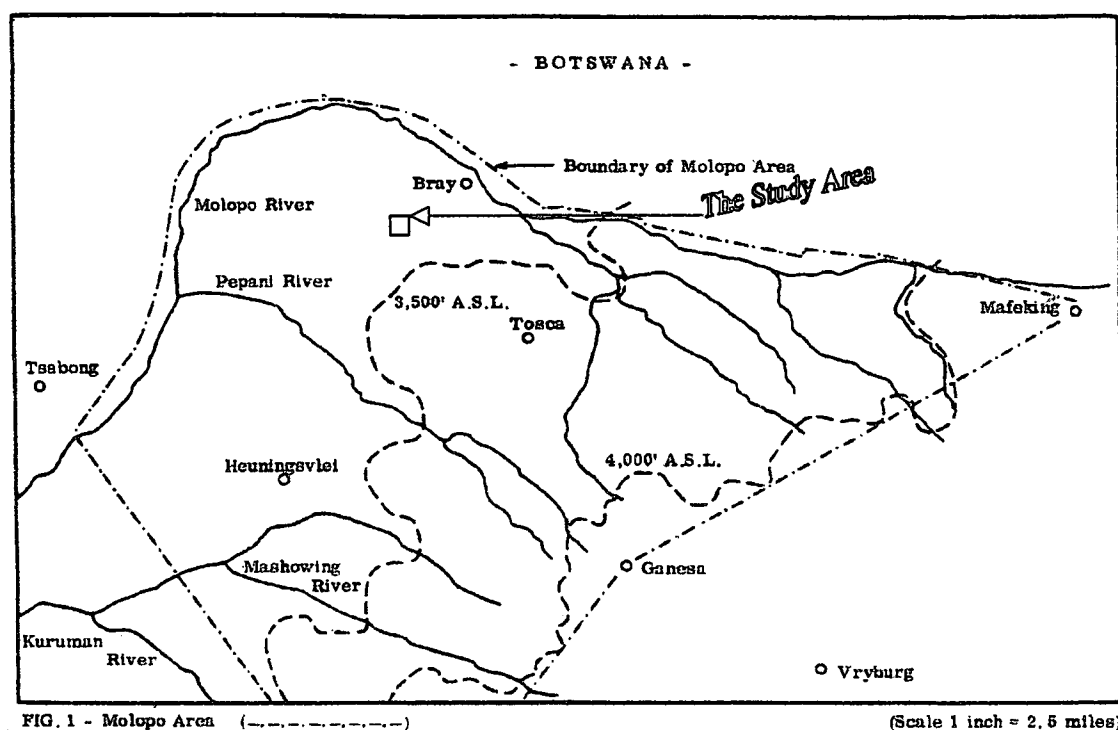
Figure 3.1 Map of the Molopo area, illustrating the location of the study area (Donaldson, 1969).

This veld type is characterized by a fairly well-developed tree stratum with *Acacia erioloba* (Camel Thorn) and *Boscia albitrunca* (Shepherd's Tree) as the dominant trees, along with scattered individuals of *Acacia luederitzii* var. *luederitzii* (False Umbrella Thorn) and *Terminalia sericea* (Silver clusterleaf), which may be locally conspicuous. The shrub layer is moderately developed and individuals of *Acacia millifera* subsp. *detinens* (Black Thorn), *Acacia hebeclada* (Weeping Candle Thorn), *Lycium hirsitum*, *Grewia flava* and *Acacia haematoxylon* (Grey Camel Thorn) dominate this layer (Van Rooyen & Bredenkamp, 1996). The study area is dominated by *Acacia mellifera* subsp. *detinens*.

The grass cover depends on the amount of rainfall during the growing season. The climax and most useful grass species of the area is *Antephora pubescens* (Wool grass). Grasses such as *Eragrostis lehmaniana* (Lehman's Love grass), *Schimidtia pappophoroides* (Kalahari sand quick) and *Stipagrostis uniplumis* (Silky Bushman grass) are conspicuous (Van Rooyen & Bredenkamp, 1996).

3.1.4 Geology and Soil

The soil of the area are deep sandy to loamy of aeolian origin, underlain by calcrete and

is described as Kalahari sand (Van Rooyen & Bredenkamp, 1996). These sands are extremely low in organic matter and mineral elements (Donaldson, 1969). The chemical analysis of soil samples of red and grey sandy soils, obtained from the farm "Buttermere", indicated the percentages of P, Ca, K and N to be 0.0009, (0.0091), 0.127, (1.059), 0.006, (0.011) and 0.163, (0.400) respectively, with pH values of 5.6 and (7.5) (Donaldson, 1969). The figures in brackets are those for the relatively rare grey pan soils.

The sand is deep in most areas, especially in the northern parts of the area in the vicinity of the Molopo River. The deep sandy soils of the Molopo area may also explain the susceptibility of the area to encroachment by deep-rooted woody plants, since these soils are (due to their low field capacity) more likely to be moistened to greater depths than clay or loam soils (Donaldson, 1969). Although the soils vary in colour, the texture appears to be the same, consisting mainly of coarse and fine sand particles and the colour of the sand varies in tint from deep red - especially in the drier western and south-western areas - through pinkish and yellowish to pale grey (Donaldson, 1969).

Soil samples were collected from the experimental site and analyzed (see Chapter 8 for more detail). The soil is acidic with an average pH of 5.12. The average phosphorus and nitrogen contents are 2.98 and 242 mg kg^{-1}, respectively. The average exchangeable cations, that is, calcium, magnesium, potassium and sodium present in the soil are 380, 78, 66, and 31 mg kg^{-1}, respectively. The organic matter content of the soil was very low and the average of all sample soils accounts only 0.693%.

The results from the soil physical analysis of the experimental site are presented in Table 3.1. It indicated that more than 93% of the soil is made up of sand with very little clay and silt.

TABLE 3.1 Analysis of the soil texture of soil from the experimental site.

No	Soil texture	Diameter (mm)	% in soil
1	Coarse sand	> 0.5 – 2	3.206
2	Medium sand	> 0.25 - 0.5	28.206
3	Fine & very fine sand	> 0.05 - 0.25	61.704
4	Coarse & fine silt	> 0.002 0.05	1.967
5	Clay	< 0.002	4.917
	TOTAL		**100**

3.2 TRIAL LAYOUT

The study was conducted on plots on which the *Acacia mellifera* trees were thinned approximately 11 years prior to the current study. The initial thinning treatments as described below were conducted by C. G. F. Richter [1].

3.2.1 Treatments

The study area consists of six, 0.5 ha plots (50 m x 100 m), thinned to different tree densities. One of the plots was left undisturbed with 2 000 Tree equivalents (TE) ha^{-1} (referred to as the 100% plot) and the others thinned to approximately 1 000 TE ha^{-1} (50%), 600 TE ha^{-1} (30%), 400 TE ha^{-1} (20%), 200 TE ha^{-1} (10%) and totally cleared with 0 TE ha^{-1} (0%) (1 TE = a tree of 1.5 m in height). The latter treatment (0 TE ha^{-1}) was not used in this specific study as the scope of this study is related with the reproductive dynamics of the remaining *Acacia mellifera* trees.

The plots were located adjacently on a homogeneous area of 3.0 ha. Treatments were allocated randomly to the plots and not in a numerical order. Bush density was determined by categorizing woody individuals into one of six height classes (>0 – 0.5 m; >0.5 m – 1.0 m; >1.0 m – 2.0 m; >2.0 m – 3.0 m; > 3.0 m – 4.0 m; >4.0 m height) (Teague *et al.*, 1981). All individual woody plants below 1.0 m were removed and the remainder proportionally thinned according to the height class distribution of the plants in the control plot.

In order to ensure that the stands of *Acacia mellifera* were as homogeneous as possible, all trees and shrubs of individual woody species other than *A. mellifera* were removed before *A. mellifera* plants were thinned. The removal of the other woody species avoided an unnecessary and non-ecologically important source of variance.

3.2.2 Methods of thinning woody plants

Thinning of the woody plants to establish the tree density gradient commenced during November 1989. Since then, thinning to maintain the prior determined tree density took place during June of each year until 1997. Since 1997 no further thinning took place.

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[1] Mr. C. G. F. Richter, Free State Department of Agriculture, Private Bag X01, Glen 9360.

Trees were cut at a height of 4 cm and the stumps sprayed with a 2% concentration of Picloram and Triclopir (Tordon Super) mixed in diesel. All top growths were removed from the plots. None of the remaining woody plants were affected by this chemical treatment.

Thinning was controlled to ensure a similar relative abundance of woody plants of various sizes between treatments.

3.2.3 Transects and measuring zones

In each 50m x 100m plot a permanent transect of 20 m x 100 m was established in the center of each plot and marked by permanent wires and poles. These transect lines were used for the phenological observations and harvesting of seeds (see chapter 4). The remainder of the experimental plots were used for soil sample collection and seed distribution determination within defined subhabitats (see chapter 5).

3.3 RAINFALL DURING TRIAL PERIOD

Table 3.2: Monthly rainfall data (mm) of the experimental site and the surrounding towns for the study period (* = data not available).

Months	Rainfall (mm)		
	Experimental Site	Bray	Pomfret
January 2000	124.0	46.1	129.4
February	77.0	59.5	110.4
March	35.0	18.7	69.8
April	29.0	14.0	30.4
May	22.0	0	22.6
June	4.0	0	0
July	0	0	0
August	0	0	0
September	0	0	6.0
October	*	0	10.0
November	*	88.55	90.2
December	*	0	85.4
TOTAL	291.0	226.85	554.2
January 2001	*	10.0	10.8
February	*	0	14.2
March	*	0	63.6
April	*	0	45.8
May	*	70.0	31.0
June	*	0	0
TOTAL	*	80.0	165.4

Rainfall is an important determinant of the growth and development of the remaining woody plants in the area. For this specific study, daily rainfall data from January 2000 – June 2001 were recorded by a standard rain gauge placed at the experimental area. In addition, daily rainfall data for 18 months, starting from January 2000 – June. 2001, of the surrounding towns of Bray and Pomfret was obtained from the South African Weather Bureau.

3.4 TREE BIOMASS MEASUREMENTS

3.4.1 Introduction

The evaluation and interpretation of the ecological dynamics of tree thinning requires a quantitative description of tree populations. The number and structure of the remaining woody plants are the fundamental characteristics of the net result of any particular thinning operation. An accurate description of these populations is thus a logical prerequisite for the study of the effect of such operations. The purpose of the survey was aimed at obtaining some quantitative data on the remaining trees to relate to some aspects of the reproductive dynamics along the tree density gradient. This quantification should not be confused with the approximate number of Tree Equivalents (TE) ha^{-1} that was used to name the various treatments (see section 3.2.1).

3.4.2 Procedure

The spatial canopy of all rooted live *A. mellifera* trees encountered in fixed transects (5 m x 100 m) located in the middle of each of the experimental plots, was measured during November 2000. The measurements consisted of the following: (I) maximum height, (ii) height where the maximum canopy diameter occurs, (iii) height of first leaves or potential leaf bearing stems, (iv) maximum canopy diameter, and (v) base diameter of the foliage at the height of the first leaves. The spatial canopy volume of each tree was calculated from these measurements (Smit 1989a, 1989b).

Leaf dry mass and leaf volume estimates were calculated using a modified version of the quantitative description technique of Smit (1989a, 1989b) as described by (Smit, 1994). This technique provides estimates of the leaf dry mass and leaf volume at peak biomass, based on the relationship between the tree's spatial canopy volume and its leaf dry mass and leaf volume. This technique was compiled into the BECVOL-model (Biomass Estimates from Canopy VOLume) (Smit, 1994), and it incorporates regression

equations, developed from harvested trees, which relates spatial volume (independent variable) to leaf volume (dependant variable): ln y = -3.880 + 0.708x, r = 0.941, P<0.001, and leaf volume (dependant variable): ln y + -2.933 + 0.697x, r + 0.948, P<0.001. Spatial tree canopy volume (x) was transformed to its normal logarithmic value, while y represents the estimated leaf dry mass (g) and leaf volume (cm^3) respectively. The number of Evapotranspiration tree equivalents (ETTE) ha^{-1} was subsequently calculated from the leaf volume estimates (1 ETTE = mean leaf volume of a single-stemmed tree with a height of 1.5 m = 500 cm^3 leaf volume) (Smit, 1989a).

In addition the total leaf DM ha^{-1}, stratified estimates of the leaf DM ha^{-1} below 1.5 m, 2.0 m and 5.0 m, respectively, were also calculated, using the BECVOL-model (Smit, 1994). The height of 1.5 m represent the mean browsing height of the goat (Aucamp, 1976) and impala (*Aepyceros melampus*) (Dayton, 1978), while 2.0 m and 5.0 m represents the mean browsing heights of the kudu (*Tragelaphus strepsiceros*) (Wentzel, 1990) and giraffe (*Giraffe camelopardalis*) (Skinner & Smithers, 1990), respectively. These browsing heights are mean heights and not maximum browsing heights, and were only used to draw comparisons. It is known that large individuals are able to reach higher than those mean heights, e.g. 2.5 m and 5.5 m for kudu and giraffe respectively (Dayton, 1978), while breaking of branches may enable some browsers to utilize browse at even higher stratums (Styles, 1993).

Estimates of the browsing capacity were made from the leaf DM estimate, using the following formula proposed by Smit (1999b).

$$y = \frac{DM^{(1.5)} \times f \times p}{r}$$

Where, y =   browsing capacity (ha GU^{-1})

DM$^{(1.5)}$ =   total leaf DM yield ha^{-1} up to a height of 1.5 m

f =   utilization factor (see below)

p =   phenology (0 = no leaves, 1.0 = peak biomass)

r =   daily browse DM required per BU (3.5 kg day^{-1})

BU =   Browser unit defined as the metabolic equivalent of an average kudu with a mass of 140 kg (Dekker, 1997).

From the stratified BECVOL estimates of leaf dry mass below 1.5 m (LM - 15) and leaf dry mass below 2.0 m (LM - 20) approximate browsing capacity was calculated for three

seasons. The available dry mass of the two strata was calculated by multiplying the total dry mass with a utilization factor (f) of 0.15 and phenology (p) of the *A. mellifera* in different seasons, that is, 1.0 from December - July, 0.4 for the month of November and 0.0 for the months of August - October when 100% of the *A. mellifera* leaves are shed (Smit, 1999a).

3.4.3 Results

3.4.3.1 Total leaf biomass estimations of the experimental plot

From the BECVOL-measurements the actual number of *A. mellifera* trees ha^{-1} and ETTE ha^{-1} were calculated (Figures 3.2 and 3.3 respectively).

As a result of the differences in the size and leaf volume of individual trees, the number of ETTE ha^{-1} calculate were more or less similar in the 20%, 30% and 50% plots (Figure 3.3), though the actual number of trees differed between these plots (Figure 3.2).
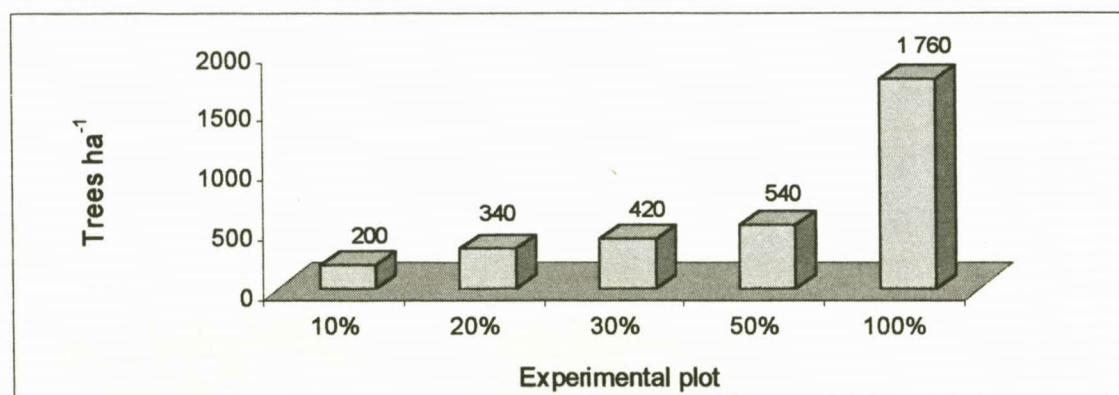
Figure 3. 2 Actual number of *A. mellifera* trees along the tree density gradient.
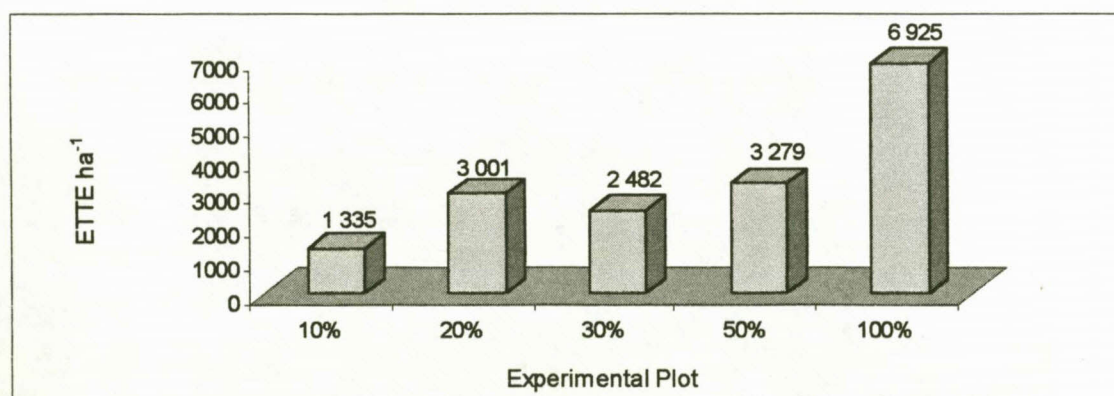
Figure 3.3 Total ETTE ha^{-1} along the tree density gradient.

3.4.3.2 Browsing Capacity for different seasons

The estimated total leaf dry mass of the experimental plot is presented in Figure 3.4. Since *Acacia mellifera* is a deciduous plant, the browsing capacity of the area differs from season to season in accordance with leaf flushing and leaf senescens. As a result, the phenology (p) of *A. mellifera* leaves from August to October is zero (Smit, 1999a) and the browsing capacity during these periods is zero. The phenology of leaves during November is 0.4 with very low browsing capacity as compared to December – July with a leaf phenology of 1.0 (Smit, 1999a).
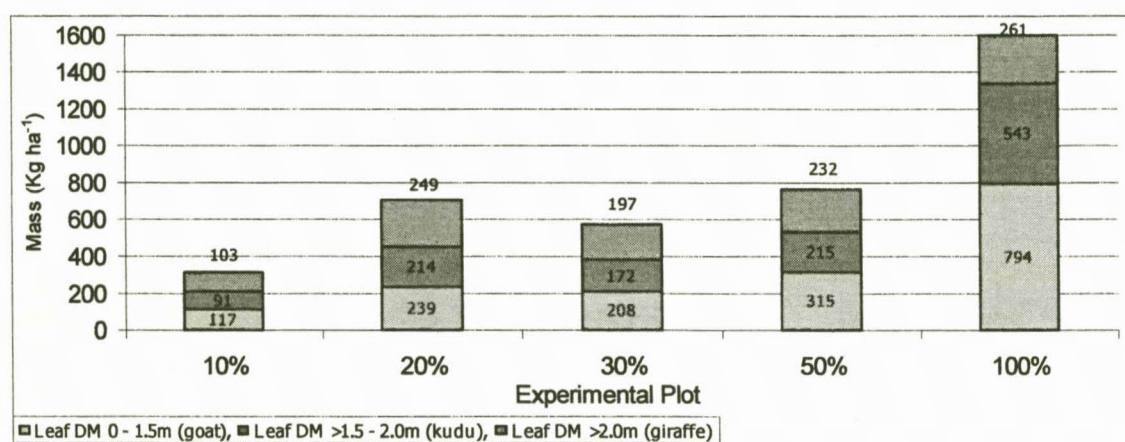
Figure 3.4 Estimated total leaf dry mass within the limits of mean browsing heights of the goat, kudu & giraffe respectively along the tree density gradient.

The available leaf dry matter of trees in the various experimental plots as calculated from the BECVOL survey, corrected for utilization (f) and phenology (p) is presented in Table 3.3.

TABLE 3.3 Available leaf dry matter of trees in the various experimental plots during different seasons.

Plots	LM - 15 (kg ha^{-1})	Available DM (Kg ha^{-1}) Dec. - July	November	LM - 20 (kg ha^{-1})	Available DM (Kg ha^{-1}) Dec. - July	November
10%	117	17.55	7.2	208	31.2	12.48
20%	239	35.85	14.34	453	67.95	27.18
30%	208	31.2	12.48	380	57	22.8
50%	315	47.25	18.9	530	79.5	31.8
100%	794	119.1	47.64	1 337	200.55	80.22
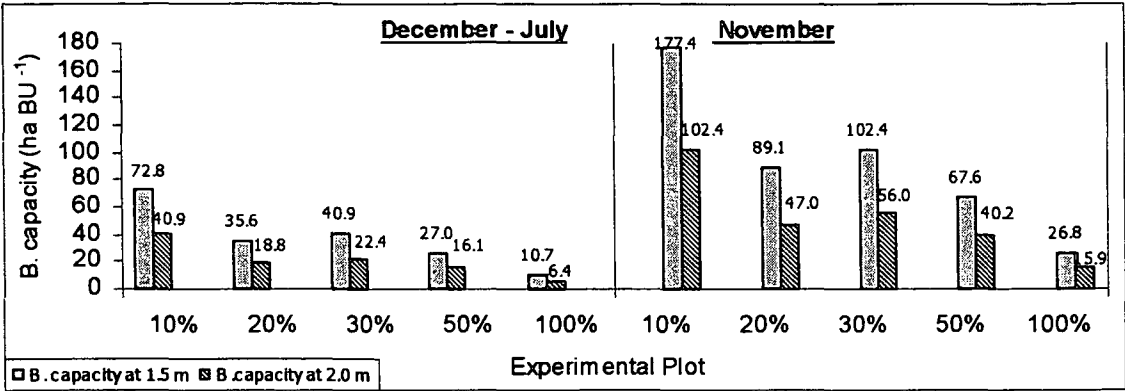
Figure 3.5 Browsing capacity (ha BU^{-1}) at different seasons.
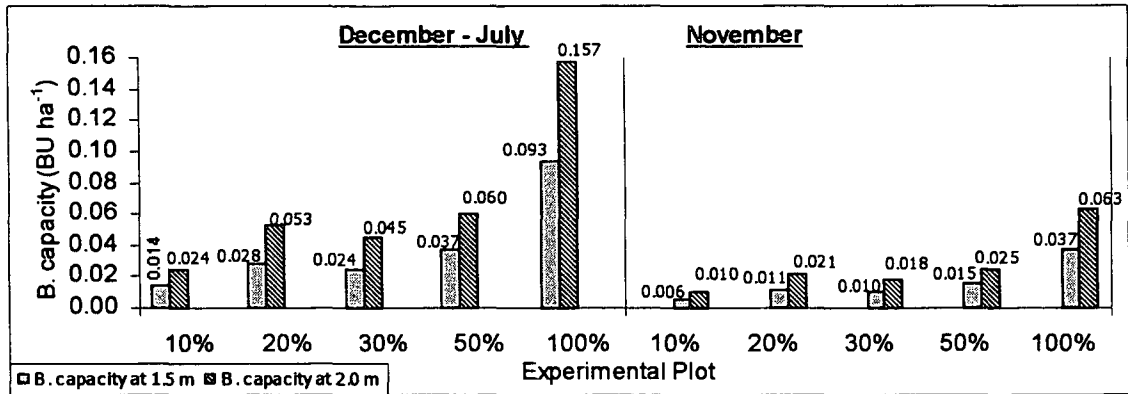
Figure 3.6 Browsing capacity (BU ha^{-1}) at different seasons.

The Browsing capacity of the area increased with the increase in the tree density, but in general, proved to be low (Figures 3.5 & 3.6).

3.5 TERMINOLOGY

The terminology used in this thesis is in accordance with Trollope *et al.* (1990), unless referenced or described.

ANIMAL UNIT (AU): An animal with a mass of 450 kg and which gains 0.5 kg per day on forage with a digestible energy percentage of 55%.

AVAILABLE BROWSE: The browse material determined on the basis of maximum height above ground to which a specified animal can utilize it (Smit, 1996).

BIOMASS: Total amount of living plant material present above and below ground in a particular area at any given time - kg ha^{-1}.

BROWSE: The sum total of that material of woody species that is potentially edible to a specific set of animals, and browse is commonly regarded as the current season growth of both leaves and twigs (Rutherford, 1979).

BROWSER UNIT (BU): Metabolic equivalent of a Kudu (100% browser) with a mean body mass of 140 kg (Dekker, 1997).

BUSH ENCROACHMENT: The phenomenon of increasing tree and shrub density in savanna (Smit et al., 1996).

CANOPY: Cover of leaves and branches formed by the tops or crowns of plants.

CANOPY COVER: Proportion of the ground area covered by the vertical projection of the canopy - %.

CARRYING CAPACITY: Potential of an area to support livestock through grazing and/or browsing and/or fodder production over an extended number of years without deterioration to the overall ecosystem (ha AU^{-1}).

DECIDUOUS: The seasonal senescens and shedding of leaves (Smit, 1999a).

DEHISCENT: The splitting open of ripe pods to release the seed (Smit, 1999a).

GRAZER UNIT (GU): A metabolic equivalent of a Blue wildebeest (100% grazer), with a mean body mass of 180 kg (Dekker, 1997).

GRAZING/BROWSING CAPACITY: Productivity of the grazeable/browseable portion of a homogeneous unit of vegetation expressed as the area of land required to maintain a single animal unit over an extended number of years without deterioration to vegetation or soil – ha AU^{-1} or AU ha^{-1}.

MULTIVOLTINE: Having several generations in one year (Gullan & Cranston, 2000).

PHENOLOGY: Study of the time of appearance of characteristic periodic events in the life cycles of organisms in nature and how these events are influenced by environmental factors.

QUADRAT: A small clearly demarcated plot or sample area of a known size on which ecological observations and measurements are made.

SAVANNA: A physiognomic type of vegetation comprising a tree or shrub overstory and herbaceous understory.

SHRUB: A perennial woody plant with two or more stems arising from or near ground level (Smit, 1999a).

TRANSECT: An imaginary or real line along which measurements or surveys of ecological observations are made (Vorster, 2000).

TREE EQUIVALENT: Tree or shrub that is 1.5 m tall.

UNIVOLTINE: Having only one generation in one year (Gullan & Cranston, 2000).

CHAPTER 4

SEED PRODUCTION OF *ACACIA MELLIFERA*

4. 1 INTRODUCTION

The seed is the product of the fertilized ovule formed within an ovary in the angiosperms. In seed production, plants may be regarded as achieving up to four main objectives, namely, re-sorting of their genetic material, a dispersal mechanism, multiplication mechanism and survival (Bradbeer, 1988).

Acacia mellifera propagates essentially from seed. Unlike most of the other woody plants growing in the Molopo area, *A. mellifera* flowers only during spring (September – October) (Donaldson, 1969). Only relatively few plants flower during abnormally dry seasons and out of season flowering has not yet been observed (Donaldson, 1969). The seed ripens towards the middle of November or beginning of December.

The pods are flat, predominantly straight with only occasional constrictions between seeds and tapered at both ends (Smit, 1999a). They are dehiscent and hairless with a narrow, but distinct raised edging to the valves with transverse venation radiating inwards. There is a great variation in the yield of seeds from year to year and the yield of individual plants is also irregular. Donaldson (1969) estimated that the average number of seeds produced per tree annually equaled 12 246 seeds.

The objectives of this study were:

(i)   To investigate the influence of tree thinning on the seed production of *Acacia mellifera*.

(ii)   To compare and evaluate the relations of leaf biomass with seed production of *A. mellifera*.

4.2 PROCEDURE

For the purpose of phenological observations, seed harvesting and leaf biomass estimates, fifty (50) *Acacia mellifera* trees (10 sample trees/plot) were randomly selected. The selection procedure accounted for a proportional sampling of all represented sizes of the represented *A. mellifera* trees. The sample trees were marked

accordingly. All sample trees were located within the middle 20 m x 100 m transect lines (0.2 ha) of each tree density plot.

On August 09, 2000 the first stage of flowering of the *Acacia mellifera* trees were recorded. The measured criteria were:
  (i)   Percentage of sample trees not flowered.
  (ii)   Percentage of sample trees bearing flowering buds.
  (iii) Percentage of sample trees flowered.

Unfortunately only one observation on the phenology of the *Acacia mellifera* trees was possible.

Actual seed harvesting of the ripened *A. mellifera* trees was conducted on 20 November, 2000 when ripening was at its peak (Donaldson, 1969; Smit, 1999a). All the pods and seed from the 50 marked trees were harvested. A large plastic sheet was put on the ground under the circumference of each tree canopy. The pods with their seeds were harvested by hand directly from the individual trees. Those that could not be reached by hand were knocked with a long stick so as to drop the seed on the plastic sheet. In some cases seed already dislodged from the dehiscent pods were picked from the ground underneath the tree canopy. All 50 sample trees of the experimental plots within the 20 m x 100 m transect lines were also measured and analysed according to the BECVOL procedure (Smit, 1989a; Smit, 1989b) to estimate their leaf biomass in relation to seed production along with the tree density gradients. The measurements were conducted during February 2001 when the *A. mellifera* trees were full of leaves.

Seeds and pods of each individual sample tree were put in labeled paper bags for further processing. All seeds and pods were wind dried in the sun and all seeds removed from the pods and counted by hand.

4.3 DATA ANALYSIS

The relation between ETTE as an index of potential tree competitiveness (independent variable) and the number of seeds (dependent variable) was established using regression analyses (Draper & Smith, 1981; Mstat-C, 1991; Microsoft Excel, 1997). Similarly, the relations between leaf dry mass (independent variable) and the number of seeds (dependent variable) was established using regression analyses. Other data are presented graphically (Microsoft Excel, 1997).

4.4 RESULTS AND DISCUSSION

4.4 .1 Flowering

Due to the non-parametric nature of the phenological data, subjective judgement was used to evaluate the sample trees in the experimental plot. During the first observation, a higher percentage of flowering occurred in the lower density plot (10%) with a decline in flowering with an increase in tree density (Figure 4.1). The reason for this early flowering in the thinned plots may be ascribed to reduced inter-tree competition resulting in a higher resource availability in the lower tree density plots. Similar to this result, Smit & Rethman (1998a) and Smit (1994) reported that *Colophospermum mopane* trees in low-density plots flowered more profusely than those in densely wooded plots
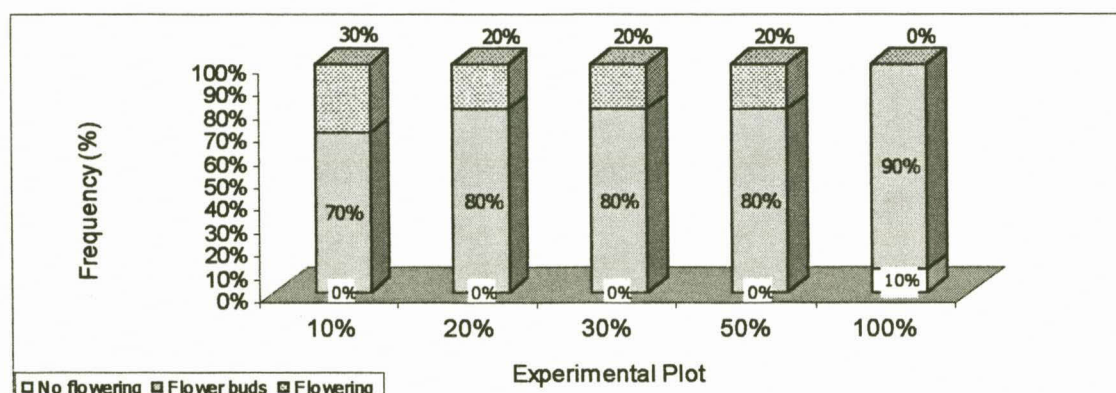
Figure 4.1 Percentage of *A. mellifera* trees that has not flowered, those with flower buds and those that flowered during August 2000.

Smit (1994) and Smit & Rethman (1998a) found that thinning of *Colophospermum mopane* reduced inter-tree competition, resulting in significant increases in the flowering and fruit bearing of the remaining trees. It was concluded that, although the percentage of reproductive trees were higher in the low tree density plots, the greater number of trees in the high tree density plots ensured that, the total number of trees that flowered and produced fruit were of the same order than the number of trees that flowered in the low tree density plots.

No flowering was observed in the control plot (100%), but most of the sample trees were full of flowering buds. According to Donaldson (1969) unlike most other woody plants growing in the Molopo area, *Acacia millifera* flowers only during spring (August to October).

4.4.2 Seed production

The mean seed production per tree of the harvested *A. mellifera* trees is presented in Figure 4.2 and the estimated total seed production ha^{-1} for the various tree density plots in Figure 4.3.
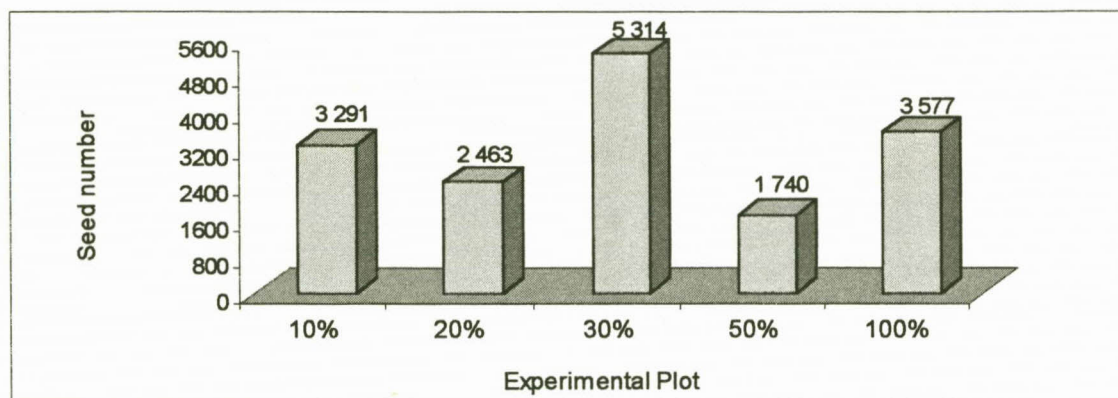
Figure 4.2 Mean seed production tree^{-1} (n = 10 trees/plot). of *A. mellifera* along the tree density gradient
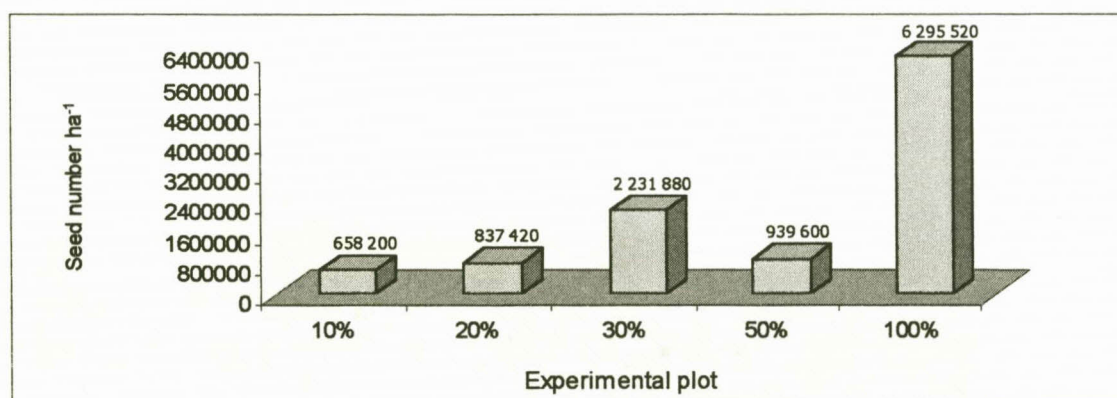
Figure 4.3 Estimated total seed production ha^{-1} of *A. mellifera* in the various tree density plots (mean seed production tree^{-1} x plants ha^{-1}).

A large variation in seed production per tree within the tree density gradient occurred (Figure 4.2). Both Smit (1994) and Smit & Rethman (1998a) reported a substantially higher seed production of *Colophospermum mopane* trees in low tree density plots. In contrast to their findings, the mean seed production of *A. mellifera* trees over the tree density gradient did not follow a specific trend, with the highest production obtained from trees in the 30% plot (Figure 4.2). However the large number of trees ha^{-1} in the high-density plot (100%) ensured a substantially higher seed production in comparison of the thinned plots (Figure 4.3).

Donaldson (1969) recorded a mean seed production of 12 246 seeds tree^{-1} on four average-sized (2.5 – 3.0m) *Acacia mellifera* trees. The mean number of seeds produced tree^{-1} in this study (all plots combined) equalled 3 277 (n = 50, range = 301 – 16 657, SE ±3 232). The reason for this large difference in potential seed bearing of *A. mellifera* can be ascribed to seasonal variation in production due to variations in determinants such as soil water status, predation of flowers and seed, and possible losses due to the early release of some seeds from the pods.

4.4.3 Total tree biomass of individual trees

The results of the biomass estimates (BECVOL – model) of the 10 sample trees in each tree density plot are presented in Table 4.1.

TABLE 4.1 Mean biomass estimates of the individual trees (n = 10) within the various tree density plots (CANVOL = canopy volume (m^3), LVOL = Estimated total leaf volume (cm^3), ETTE = total evapotranspiration tree equivalents, LMAS = estimated total leaf dry mass (g)).

Plot	CANVOL (m^3)	LVOL (cm^3)	ETTE (1 ETTE = 500 cm^3)	Leaf dry mass (tree^{-1})			
				LM_15 (g)	LM_20 (g)	LM_50 (g)	LMAS (g)
10%	10.0	3980	7.96	590	1174	1855	3619
20%	10.2	3821	7.64	492	1015	1784	3291
30%	11.5	4333	8.67	644	1159	2024	3827
50%	7.6	3257	6.51	554	1074	1514	3142
100%	7.0	3070	6.14	620	1052	1427	3099

From Table 4.1 it is evident that in general the mean canopy volume of the *A. mellifera* trees decreased with an increase in tree density. The lower the tree density, the larger the tree's canopy diameter. The trends in canopy volume (CANVOL), leaf volume (LVOL), the Evapotranspiration tree equivalent (ETTE), and leaf dry mass (LMAS) are similar with trees from the 30% plot the exception, being the highest of all the plots. The largest mean vertical measurements of tree height (L_A), height at maximum canopy diameter (L_B) and shortest height of first leaves (L_C) were 2.93 m, 2.13 m & 0.39 m, respectively, all recorded from plants in the 30% plot.

4.4.4 Relations between ETTE, Leaf dry mass (g) and seed production

4.4.4.1 ETTE plant^{-1} versus seed production plant^{-1}

The relationship between ETTE plant^{-1} and seeds plant^{-1} was non-significant (P = 0.063)

with a low correlation r = 0.265, n = 50), and a low coefficient of determination (r^2 = 0.070) (Figure 4.4). However, the general trend indicates an increase in seed production tree^{-1} with an increase in ETTE.
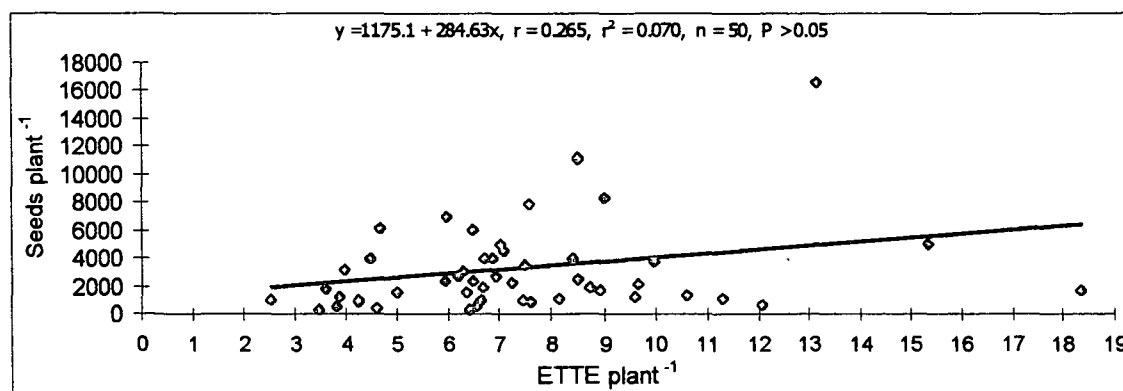
Figure 4.4 Regression analysis for the relations between ETTE plant^{-1} (independent variable) and seeds plant^{-1} (dependent variable) of the individual sample trees in the experimental plots.

4.4.4.2 Leaf dry mass plant $^{-1}$ versus seed production plant $^{-1}$

The relationship between leaf dry mass plant $^{-1}$ (g) and seeds plant $^{-1}$ of the individual *A. mellifera* trees were non-significant (P = 0.064) with a low correlation (r = 0.264, n = 50). The calculated coefficient of determination was also very low (r^2 = 0.070) (Figure 4.5).
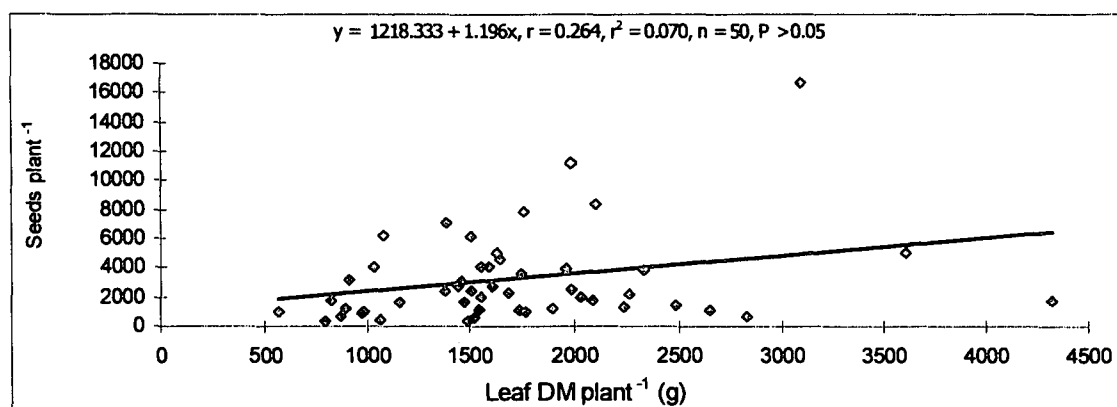
Figure 4.5 Regression analysis for the relations between Leaf DM plant^{-1} (independent variable) and seeds plant $^{-1}$ (dependent variable) of the individual sample trees in the experimental plots.

In correspondence with the higher tree densities, the plots with high number of Evapotranspiration Tree Equivalents (ETTE) and high leaf dry mass (LMAS) (g) produced more seeds than the corresponding plots with low ETTE and LMAS values

(See Table 4.1). Although individual trees in the control (100%) plot were smaller with lower ETTE and LMAS values, a relatively large number of seeds were harvested.

4.4 5 Relations between ETTE ha⁻¹, Leaf DM ha⁻¹ and seed production ha⁻¹.

4.4.5.1 ETTE ha⁻¹ versus seed production ha⁻¹

A significant (P = 0.041) correlation (r = 0.894, n = 5) with a reasonable coefficient of determination (r^2 = 799) was established for the relation between ETTE ha⁻¹ and total number of seeds ha⁻¹ (Figure 4.6).
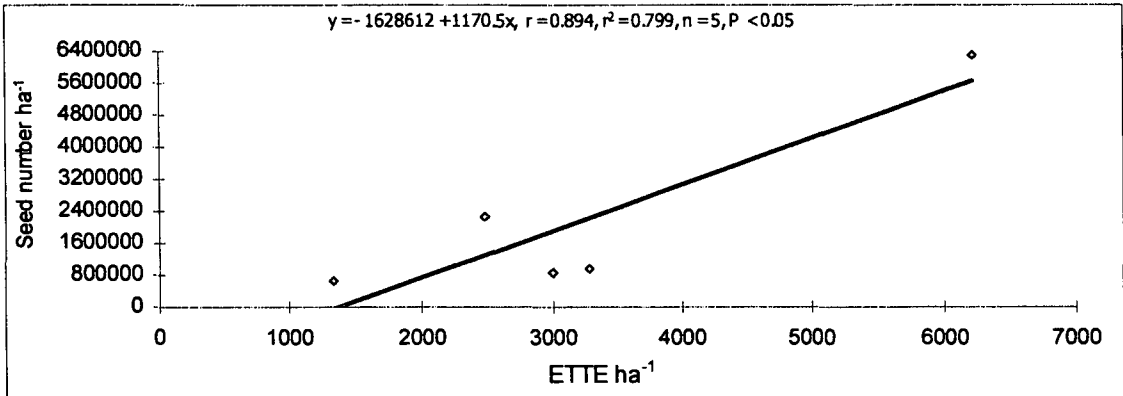
Figure 4.6 Regression analysis for the relation between ETTE ha⁻¹ and seed number ha⁻¹ of the experimental plots.

4.4.5.2 Leaf dry mass (kg ha⁻¹) versus seed production ha⁻¹
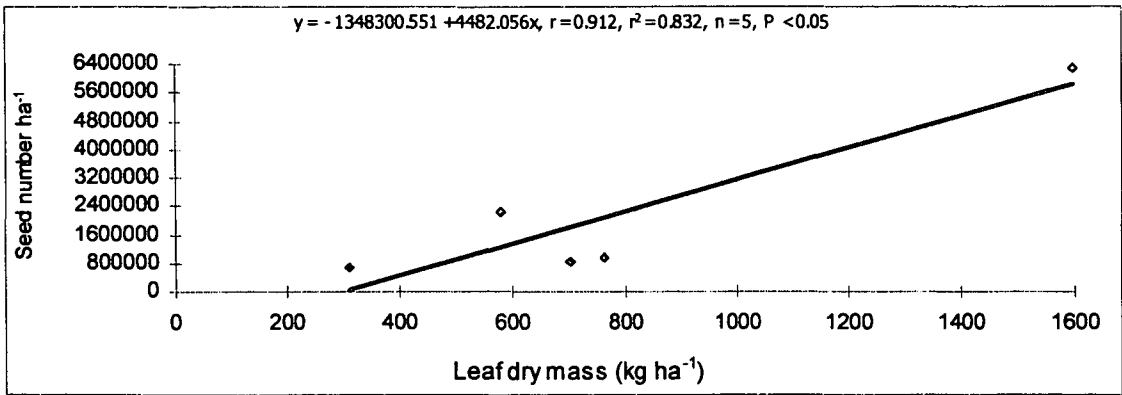
Figure 4.7 Regression analysis for the relation between Leaf dry mass (kg ha⁻¹) and seed number ha⁻¹ of the experimental plots.

As can be expected a significant (P = 0.03) correlation (r = 0.912, n = 5) with a high coefficient of determination (r^2 = 0.832) was also established between leaf dry mass (kg ha^{-1}) and total number of seeds ha^{-1} (Figure 4.7).

Since the average seed production tree^{-1} did not decline notably with an increase in tree density (Figure 4.2) the significant correlation between ETTE ha^{-1} versus seed number ha^{-1} and leaf dry mass (kg ha^{-1}) versus seed number ha^{-1} can simply be ascribed to the differences in the number of trees ha^{-1} in the different experimental plots.

4.5 CONCLUSIONS

The following general conclusions can be drawn from this investigation:

(i) Tree thinning brought about early flowering of *A. mellifera* in the lower tree density plots as a result of reduced inter-tree competition. With an increase in the intensity of thinning, the flowering percentage at a specific date increased.

(ii) Mean seed production tree^{-1} of the *A. mellifera* trees over the tree density gradient did not follow a specific trend, not influenced by the tree thinning. Differences were observed between the seed production of individual trees, but these differences could not be related to the tree density gradient.

(iii) Despite low correlation coefficients there are indications that seed production of individual trees increase with an increase in ETTE and leaf dry mass tree^{-1}, that is, bigger plants produce more seeds.

(iv) Statistical significant negative correlations between ETTE ha^{-1} and leaf dry mass (kg ha^{-1}) and total seed production ha^{-1} were established.

CHAPTER 5

SEED MASS AND SEED DIMENSIONS

5.1 INTRODUCTION

Based on some physical measurements, seeds may fall in various size ranges. Large seeds have the capacity to contain large embryos and substantial food reserves, which would enable a seedling to achieve considerable growth of both roots and shoots before it become dependant on its own photosynthesis. Salisbury (1942) as cited by (Bradbeer, 1988) points out that, in the extreme development of this strategy, the large size of the fruits is often associated with a low rate of fruit production. He concludes that for most species at least the seed production is considerably in excess of that required for mere replacement of losses by death and sufficiently so to bear no obvious relation to normal seedling mortality. The size of the seed production, or more precisely the reproductive capacity, is regarded as a positive asset in the competitive ability of a species, which tends to insure occupancy of the available ecological niches and so to increase the species' frequency and distribution (Bradbeer, 1988).

Seed size and shape have long been thought to influence the burial and persistence of seeds in the soil, with seed buried in the soil showing greater persistence than those exposed on the soil surface for long periods of time (Thompson & Girme, 1979). Smaller and spherical seeds, which tend to become buried in the soil, were more persistent than larger and more flattened or elongated seeds (Thompson et al., 1993) as cited by Garner & Witkowski (1997). More specifically all species with both more spherical seeds (<0.14 mm variance in seed dimension) and weighing <3 mg form long-term persistent seed banks in the soil. However, some of the species tested with long-term persistent seed bank had seeds >10 mg in size.

Another factor, which may be associated with variation in seed size and shape within species, is pre-dispersal seed predation. Szentesi & Jermy (1995) found that at the species level seed predation by bruchid beetles was higher in larger seeded species and in more spherical seeds within European leguminosae. This contradicts Jansen's (1969) findings for Central American legumes that smaller seeded species showed higher levels of predation. However, seed size and shape also vary within species and may influence levels of predation, depth of burial and persistence in the soil.

Garner & Witkowski (1997) determined seed mass, seed shape ratio and the variance in seed dimensions in relation to depth of burial for three common spinescent savanna trees, *Acacia nilotica, A. tortillis* and *Dichrostachys cinerea.* These species are hard seeded and form at least short-term persistent (1 - 5 years) soil seed banks. They found a consistent tendency for seed size within species to increase with depth of burial, which is interpreted as showing that larger seeds may have greater longevities in the soil than smaller seeds.

The seeds of *Acacia mellifera* are flattened, circular and quite large with a diameter of 8.0 – 12.0 mm (Smit, 1999a) and an average thickness of 1.8 mm (Donaldson, 1969). Smit & Rethman (1998a) indicated that the mass of seeds of the same woody species can differ along tree density gradients. The mass of *Colophospermum mopane* seeds collected in low tree density plots were found to be higher than those from the densely wooded plots, however, they appear to have the same germination potential.

Tossell (1960) observed that seed weight has an important effect on seedling establishment and vigour during the first 4-week period of development. This period is an extremely critical one in stand establishment. He suggested that early seedling vigour was associated with seed weight and he recommended those strains of low seed weight be discarded and the remainder screen for seedling vigour in the green house. Rogler (1954), working with crested wheatgrass, reported highly significant correlation between seed weight and emergence, and two years later, Kneebone (1956) reported that selection for seedling vigour was effective in side-oats and that seed weight was correlated with seedling vigour.

Kittock & Patterson (1962) observed that the higher seedling vigour from heavy seed was only short-lived and that moisture stress tended to equalize the growth from seed of different sizes. According to Twamley (1967), seedlings from large seeds show greater seedling vigour. It has been shown that seedlings from larger seeds survive longer when grown in the absence of any mineral nutrients other than those in the seed, and they are also able to emerge from greater depths in the soil (Jurado & Westoby, 1992).

The objectives of the study were:

(i)   To determine the influence of tree density on the seed mass of *Acacia mellifera.*

(ii)   To determine the influence of tree density on the seed dimensions of *Acacia mellifera.*

(iii)   To compare and evaluate the relationship between seed mass and leaf biomass estimations.

5.2 PROCEDURE

A total of 300 ripe, dry *Acacia mellifera* seeds were randomly selected from each marked sample tree (see chapter 4) and their combined mass determined with an electronic digital scale. The mean seed mass of each sample tree was multiplied by the total seed count of the corresponding sample (see chapter 4) to obtain the actual mass of the total seed produced by the sample trees.

A total of 100 seeds from each plot of the tree density gradient (10 seeds/sample tree) were randomly selected for mass determination of individual seed. Seeds infested by bruchid beetles were excluded and only undamaged seed were selected. Individual seeds were weighed on an electronic digital scale (accurate to 0.0001 g). In addition, 200 pairs of seedpod covers were randomly selected from all sample trees to determine the average pod mass encapsulating the seed.

For the determination of the dimensions of the seed, 500 seeds (50seeds/sample tree) from each plot of the tree density gradient were randomly selected. The Bruchid beetle infested seeds were discarded and replaced by undamaged seeds. Three dimensions (length, width and thickness) of the individual seed were measured with a calliper (accurate to 0.01 mm).

5.3 DATA ANALYSIS

The seed mass and seed dimensions were analyzed according to the procedure described by Smit (1994) and Smit & Rethman (1998a). The frequency distributions of the *A. mellifera* seeds from trees of the different tree density plots were analyzed with division in the following classes:

- Mass: 9 classes with a class interval of 0.01 g (0.03–0,039, 0.04–0.049, 0.05–0.059, 0.06–0.069, 0.07–0.079, 0.08–0.089, 0.09–0.99, 1.0–1.09 and 0.11–0.19).
- Length: 7 classes with a class interval of 1.0 mm (4.0–4.99, 5.0–5.99, 6.0–6.99, 7.0–7.99, 8.0–8.99, 9.0–9.99 and 10.0–10.99).
- Width: 6 classes with a class interval of 1.0 mm (4.0–4.99, 5.0–5.99, 6.0–6.99, 7.0–7.99, 8.0–8.99 and 9.0–9.99).

o   Thickness: 8 classes with a class interval of 0.02 mm (0.8–0.99, 1.0–1.19, 1.20–1.39, 1.4–1.59, 1.6–1.79, 1.8–1.99, 2.0–2.19 and 2.2–2.39).

In addition, regression and correlation analysis (Mstat-C, 1991), and Microsoft Excel graphics (Microsoft Excel, 1997) were used to analyze the seed mass and seed dimension data in relation to the estimated tree biomass (ETTE ha^{-1} and leaf DM ha^{-1}) (Smit, 1989a).

5.4 RESULTS AND DISCUSSION

5.4.1 Seed dry mass

5.4.1.1 Individual seed dry mass

The frequency distributions of *Acacia mellifera* seeds from trees of the different tree density plots within the nine dry mass classes are presented in Figure 5.1. In contrast to the findings of Smit (1994) and Smit & Rethman (1998a) on *Colophospermum mopane*, the mass of the *A. mellifera* seeds collected from the low tree density plots were lower than those from the high tree density plots.

In the 10% and 20% plots, the largest percentage of seeds fell within the classes of 0.06 - 0.069 g and 0.07 - 0.079 g classes, respectively. In the high tree density plots (50% and 100%) the largest percentage of seeds fell within the classes of 0.08 - 0.089 g and 0.09 - 0.099 g classes, respectively (Figure 5.1).

An average (all plots combined) *Acacia mellifera* seed dry mass of 0.0748 g (n = 500) was obtained. From Figure 5.2 it is clear that the average seed mass (n = 100) of *A. mellifera* increased linearly from 0.699 g seed^{-1} in the 10% plot to 0.0811 g seed^{-1} in the 100% plot.

The negative effect of tree clearing on the seed mass of *Acacia mellifera* is evident from these results. With the increase in the intensity of tree thinning, the seed mass of *A. mellifera* trees was decreased. A possible reason could be the depletion of soil nutrients with the decrease in tree density. This will be discussed in Chapter 8.

5.4.1.2 Total seed dry mass of the experimental plots

The average total seed dry mass (plots combined) of the sample trees was 214.26 g tree^{-1} (n = 50). Comparison of the average seed dry mass production (n = 10) of trees

from the different tree density plots showed no distinct pattern (Figure 5.3). The highest average production (349.06 g tree⁻¹) was recorded from trees in the 30% plot, with the lowest average production (113.63 g tree⁻¹) recorded from trees in the 50% plot.
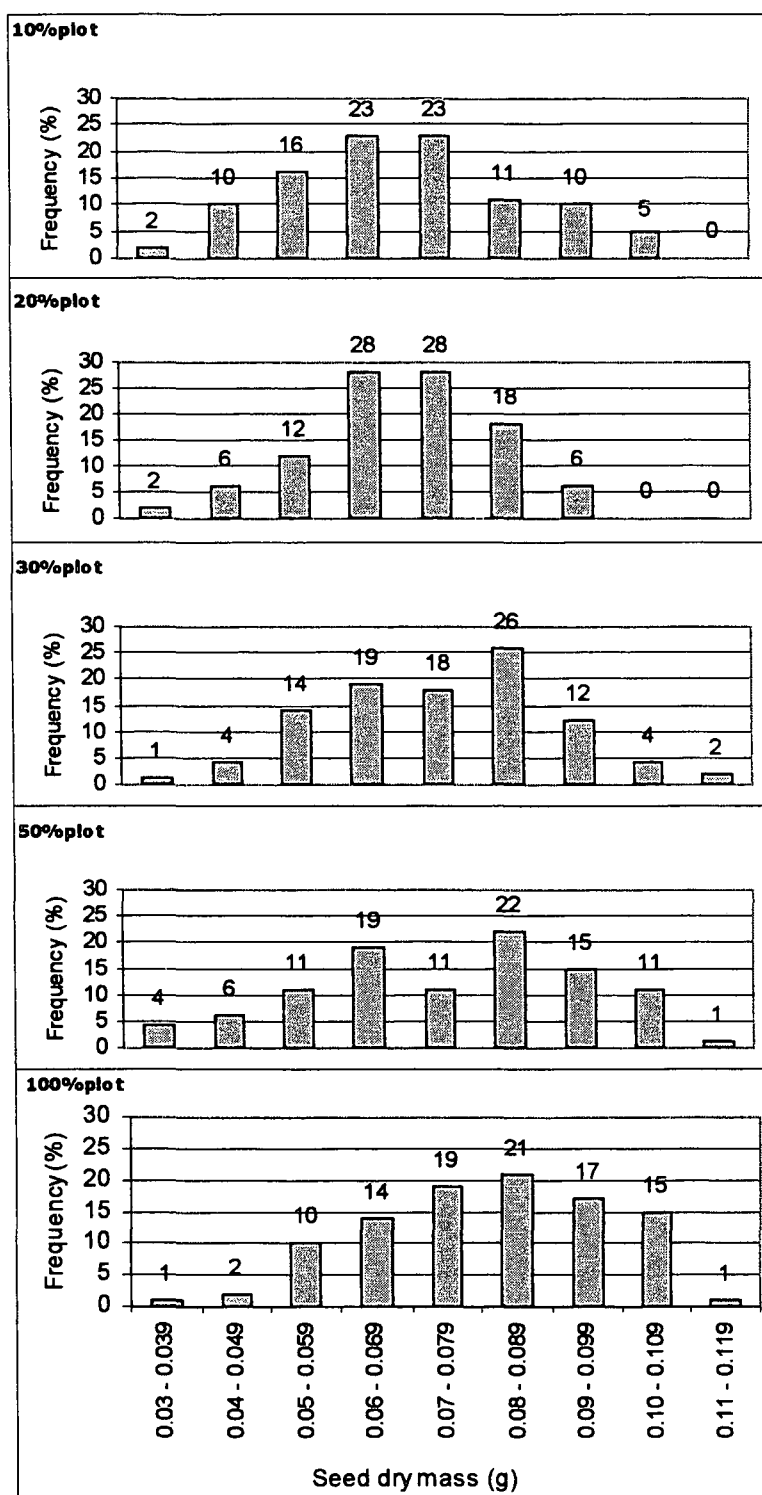
Figure 5.1 The frequency distributions of *A. mellifera* seeds from trees of the different tree density plots within nine dry mass classes.

The average seed dry mass ha^{-1}, based on the average seed production per tree multiplied with the total number of plants ha^{-1}, of the combined plots was estimated to be 149.43 kg ha^{-1} (n = 3 260, actual number of *A. mellifera* trees of the experimental plot as indicated in Figure 3.2). The estimated total seed dry mass ha^{-1} of the different experimental plots is presented in Figure 5.4. As expected, with an increase in tree density a marked increase in total seed dry mass ha^{-1} occurred.
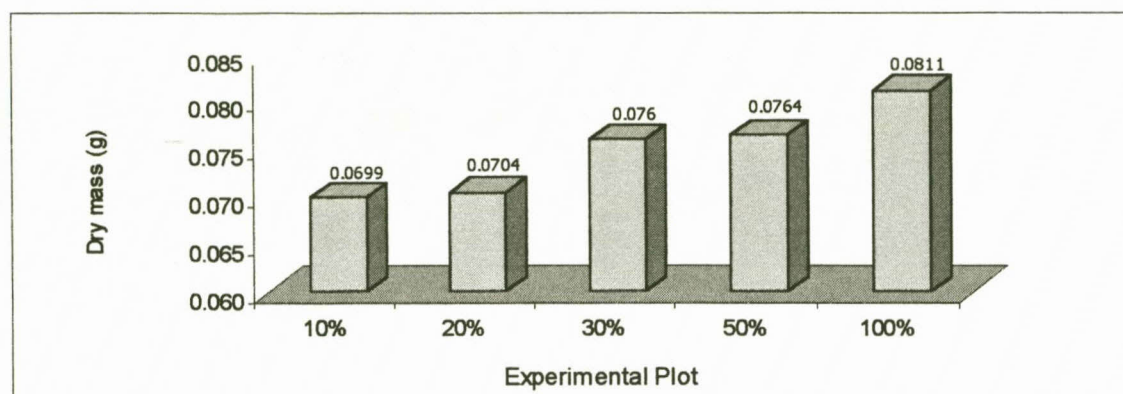
Figure 5.2 Mean seed mass (n = 100) of *A. mellifera* along the tree density gradient.
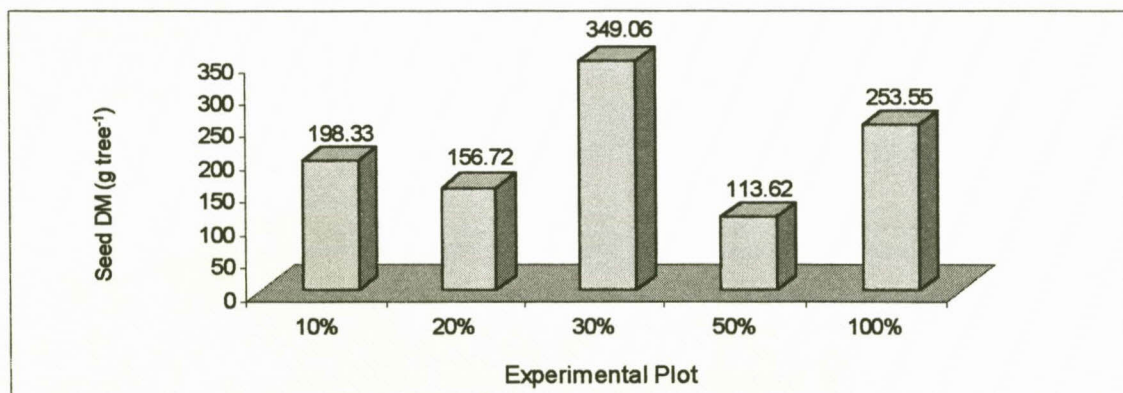
Figure 5.3 Mean seed dry mass per tree (n = 10) of *A. mellifera* trees from the different tree density plots.
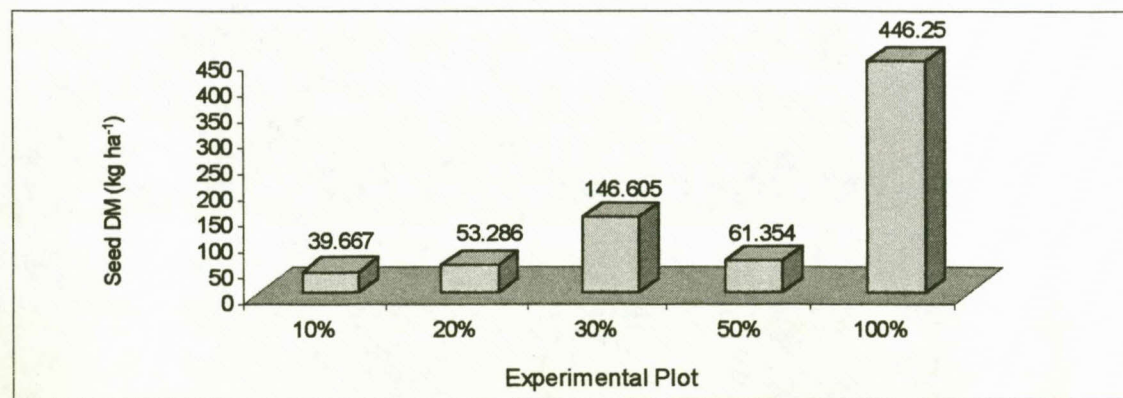
Figure 5.4 Estimated seed dry mass ha^{-1} of the different tree density plots.

5.4.2 Relations between leaf biomass (ETTE and leaf dry mass) and seed dry mass

5.4.2.1 ETTE versus seed dry mass

The relation between ETTE tree^{-1} and the average dry mass seed^{-1} (g) was non-significant (P = 0.646) with a low correlation coefficient (r = 0.067, n = 50). The calculated coefficient of determination was also very low (r^2 = 0.004) (Figure 5.5).
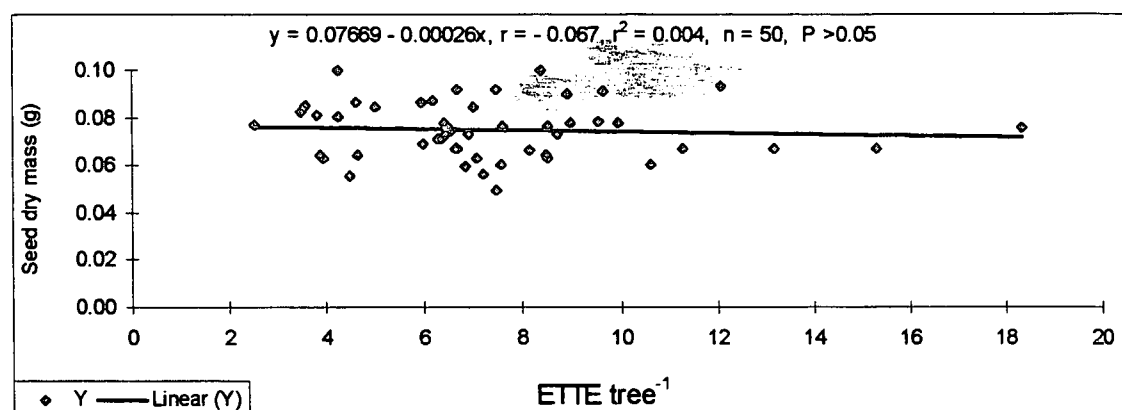
Figure 5.5 Regression analysis of the relation between ETTE tree^{-1} and the average seed dry mass (g seed^{-1}) of individual *A. mellifera* trees.

5.4.2.2 Leaf dry mass (g tree^{-1}) versus seed dry mass

The relations between leaf dry mass (g tree^{-1}) and the average dry mass seed^{-1} (g) of the *Acacia mellifera* trees was also non-significant (P = 0.648) with a low correlation coefficient (r = 0.066, n = 50). The calculated coefficient of determination was also very low (r^2 = 0.004) (Figure 5.6). This result is as expected since ETTE and leaf dry mass is correlated variables (Smit, 1989a).
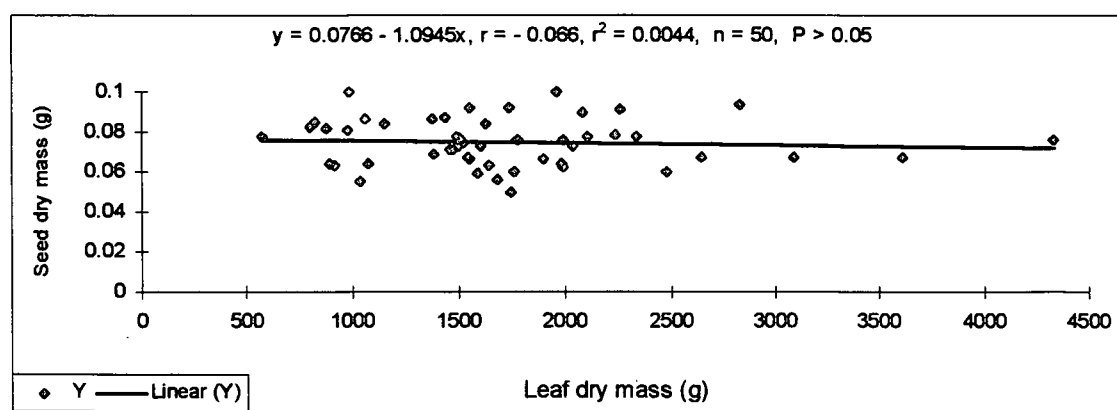
Figure 5.6 Regression analysis for the relation between leaf dry mass (g tree^{-1}) and the average seed dry mass (g seed^{-1}) of individual *A. mellifera* trees.

5.4.3 Relations between ETTE ha^{-1} and leaf dry mass (kg ha^{-1}) with seed dry mass (kg ha^{-1})

5.4.3.1 ETTE ha^{-1} versus seed dry mass (kg ha^{-1})

The relation between ETTE ha^{-1} and seed mass (kg ha^{-1}) was significant (P = 0.027) with a high correlation coefficient (r = 0.920, n = 5). The calculated coefficient of determina-tion was also high (r^2 = 0.0846) (Figure 5.7).
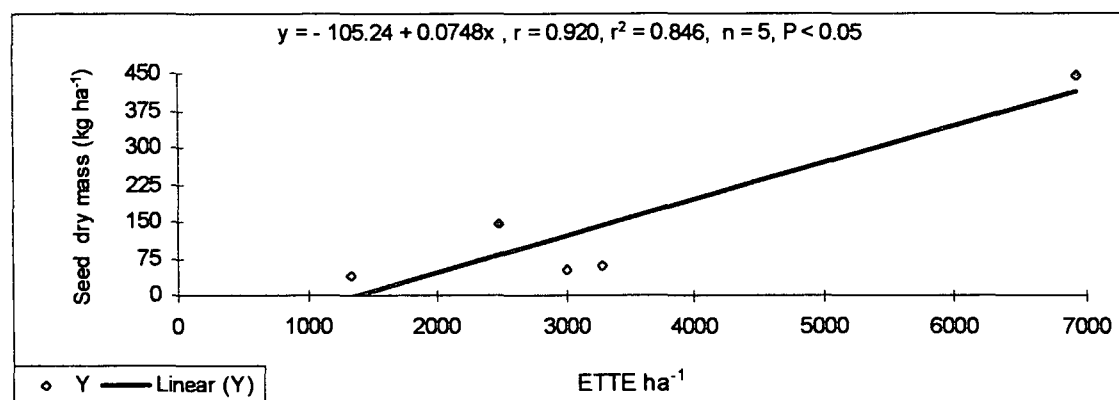
Figure 5.7 Regression analysis of the relation between ETTE ha^{-1} and seed dry mass (kg ha^{-1}) of the *A. mellifera* trees from the different tree density plots.

5.4.3.2 Leaf dry mass (kg ha^{-1}) versus seed dry mass (kg ha^{-1})

Similar to ETTE ha^{-1}, a significant (P = 0.028) relation between the leaf dry mass (kg ha^{-1}) and seed dry mass was established with a high correlation coefficient (r = 0.918, n = 5). The calculated coefficient of determination was also high (r^2 = 0.842) (Figure 5.8).
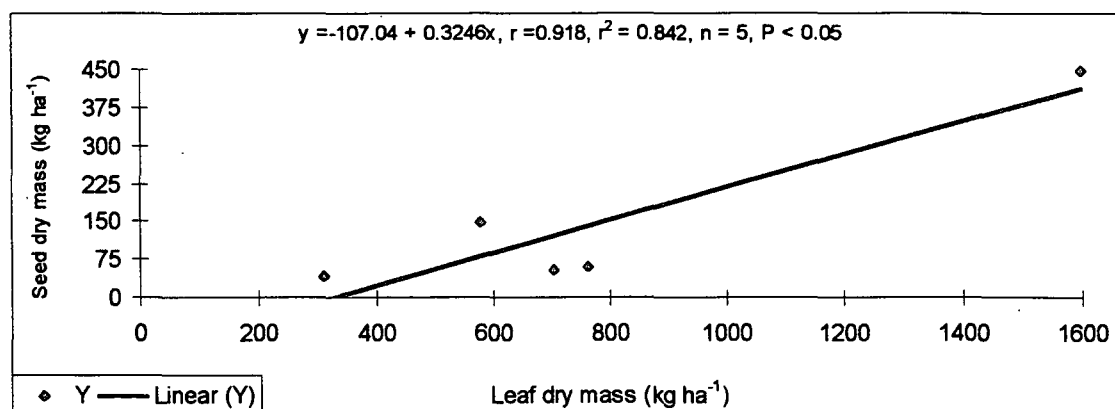
Figure 5.8 Regression analysis of the relation between leaf dry mass (kg ha^{-1}) and seed dry mass (kg ha^{-1}) of the *A. mellifera* trees from the different tree density plots.

The positive relations between ETTE ha^{-1} and leaf dry mass (kg ha^{-1}) with the dry mass ha^{-1} of the produced seed confirmed the logical conclusion that more seeds are produced in the high tree density plots as a result of the greater number of trees present in these plots.

5.4.4 Pod mass

The term "pod", as used here, refers to the pod covers without the enclosed seeds. The mean pod dry mass of the *A. mellifera* trees in the different tree density plots is presented in Figure 5.9 and the estimated pod dry mass ha^{-1} presented in Figure 5.10.
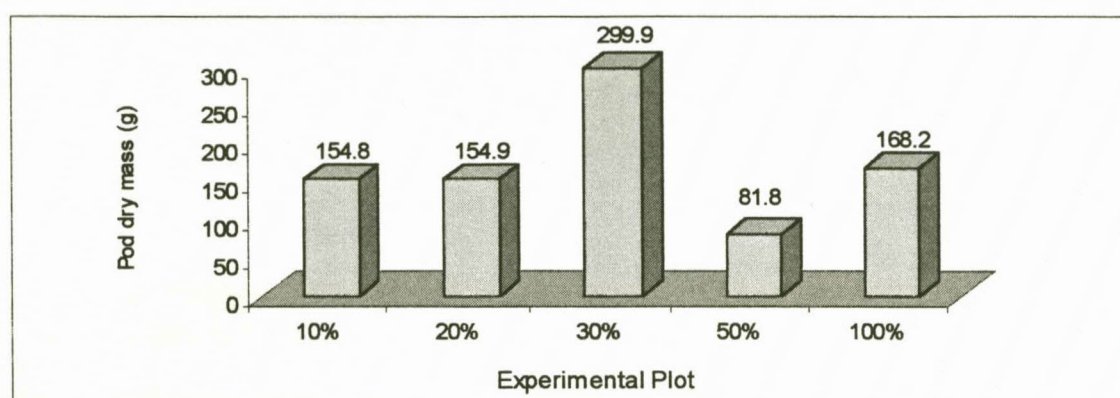
Figure 5.9 Mean pod dry mass (g pod^{-1}) (n = 10) of trees in the different tree density plots.
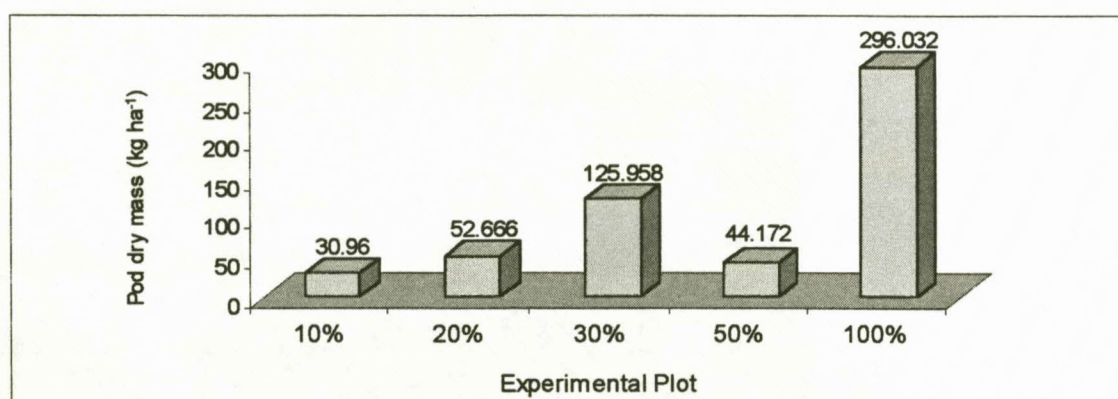
Figure 5.10 Estimated pod dry mass ha^{-1} produced in the different tree density plots.

The mean pod mass of a single *Acacia mellifera* seedpod (without seed) was 0.0941g (n = 200 pairs). According to Smit (1999a), the number of seeds per pod of the *Acacia mellifera* trees varies from 1 – 5, and Donaldson (1969) reported 2 – 3 seeds per pod. An average of two seeds per pod was established in this study.

As in the case of the seed dry mass discussed in the previous section, the higher total pod mass ha^{-1} in the high tree density plot (100% plot) is a direct result of the greater number of trees in this plot.

5.4.5 Seed Dimensions of *Acacia mellifera* seed

5.4.5.1 Seed length

The average seed length of 2 500 measured *A. mellifera* seeds was 8.05 mm (range, 4.48 – 10.94 mm). Smit (1999a) reported a range of 7.0 – 10.0 mm seed length. The frequency distribution of *A. mellifera* seed length from trees of the different experimental plots within seven length classes is presented in Figure 5.11. More than 75% of the seeds from all plots fell within two class intervals (7.0 – 7.99 and 8.0 – 8.99 mm). However, a larger number of seeds (18%) in the high tree density plot fell within the 9.0 – 9.99 mm class as compared to the lower tree density plots.

5.4.5.2 Seed width

The average seed width of 2 500 measured *A. mellifera* seeds was 7.45 mm (range, 4.04 – 9.78 mm) Smit (1999a) reported a range of 6.0 – 8.0 mm. The frequency distribution of *A. mellifera* seed widths from trees of the different tree density plots within six width classes is presented in Figure 5.12. About 50% of the seeds in all plots fell within the 7.0 – 7.99 mm class interval. In the high density plot (100%) more than 30% of seeds fell within the class interval 8.0 – 9.99 mm and 9.0 mm – 9.99 mm respectively, but in the low density plot (10%) more than 28 % fell within the 6.0 – 6.99 mm class interval.

5.4.5.3 Seed thickness

The average seed thickness of 2 500 *A. mellifera* seeds was 1.59 mm (range, 0.81 – 2.34 mm). Donaldson (1969) reported an average thickness of 1.8 mm.

The frequency distribution regarding the thickness of *A. mellifera* seed from trees of the different tree density plots within eight thickness classes is presented in Figure 5.13. Seeds collected from trees in the high-density plot (100%) were thicker than those of the lower tree density plot. More than 50% of the seeds in the control plot fell within the 1.6 – 1.79 mm and 1.8 – 1.99 mm classes, compared to the low density plots except for the

30% plot. More than 60% of the seeds collected from the low tree density plot (10%) fell within the 1.2 – 1.39 mm and 1.4 – 1.59 mm classes.
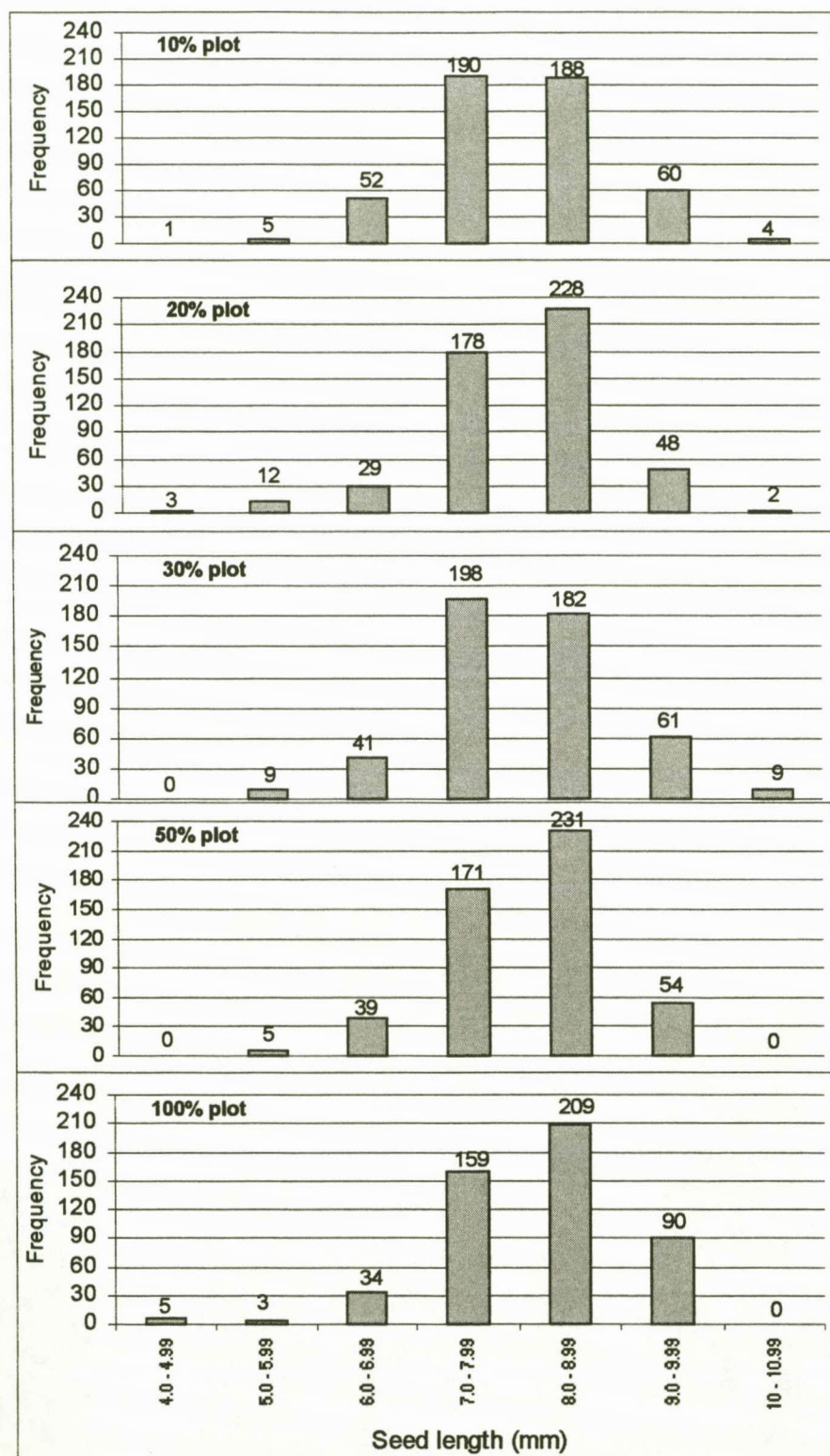
Figure 5.11 Frequency distribution, in seven length classes, of *A. mellifera* seed lengths from trees of the different experimental plots.
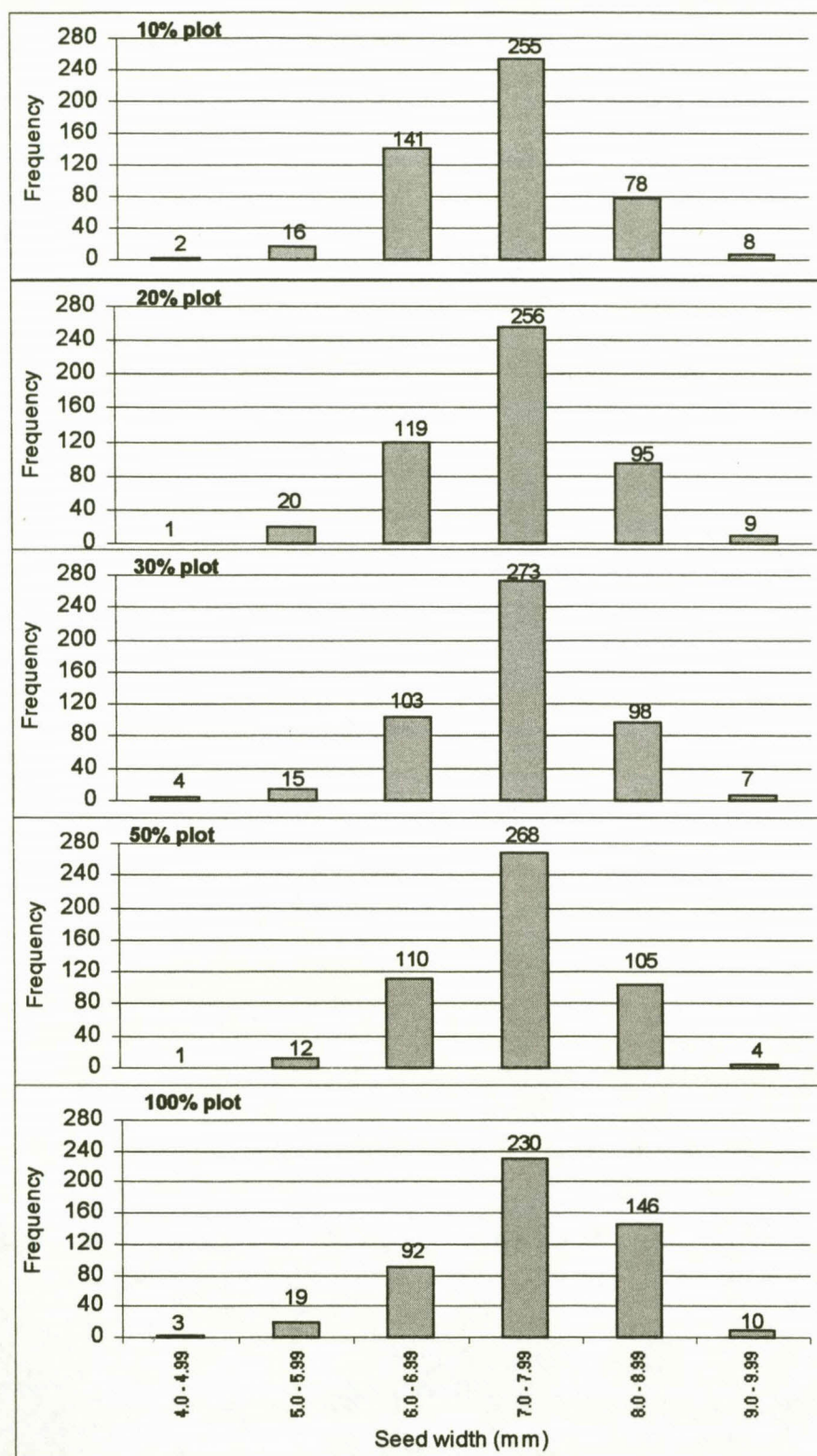
Figure 5.12 Frequency distribution, in six width classes, of *A. mellifera* seed widths from trees of the different experimental plots.
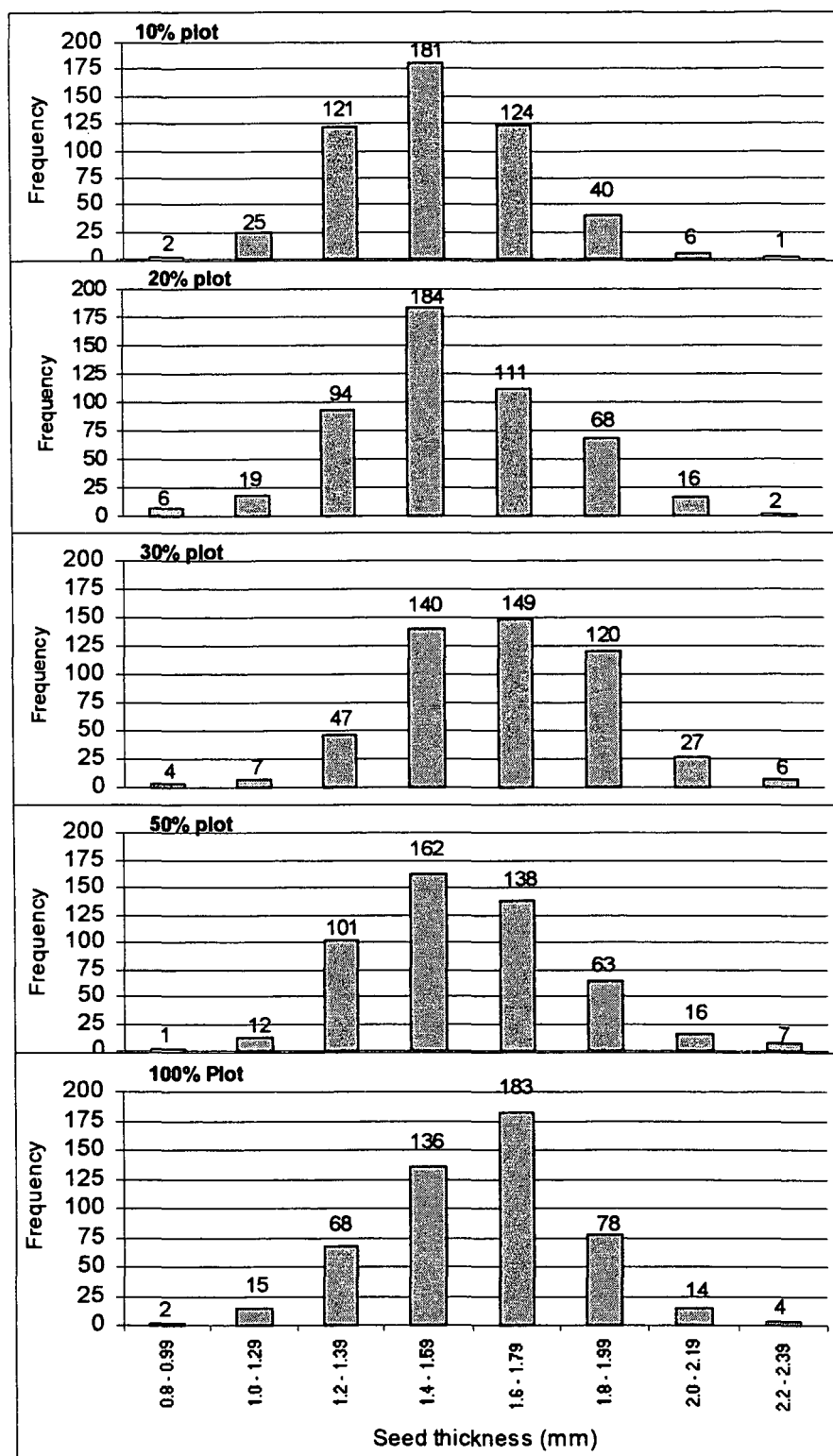
Figure 5.13 Frequency distribution, in eight thickness classes, of *A. mellifera* seed thicknesses from trees of the different experimental plots.

The mean dimensions of 2 500 *A. mellifera* seeds harvested from the different experimental plots (500 seeds plot^{-1}) are presented in Figure 5.14. The trend indicates that there is a slight increase in seed dimensions with an increase in tree density.

All the results obtained from the seed dimensions in the different experimental plots showed similar relationships with the decrease/increase in tree density. In general, seeds harvested from the control (100%) plot were longer, wider and thicker than those of the lower tree density plots.
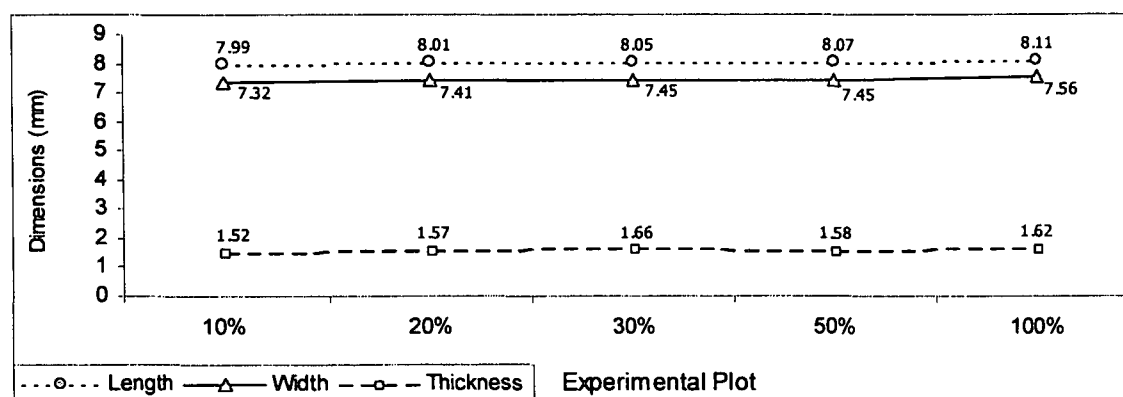
Figure 5.14 Mean dimensions (n = 500) of *A. mellifera* seeds harvested from the different tree density plots.

5.5 CONCLUSIONS

The following general conclusions can be drawn from this investigation:

(i). Seeds harvested from the lower tree density plots were lighter than seeds harvested from the high tree density plot. The average seed mass of *A. mellifera* increased linearly over the tree density gradient from 0.0699 g seed^{-1} (10% plot) to 0.0811 g seed^{-1} (100% plot).

(ii). The average seed dry mass production tree^{-1} showed no distinct pattern and was not correlated with the tree density. Despite this variable seed production of individual trees, the total seed dry mass ha^{-1} increased in relation to an increase in tree density.

(iii). Leaf biomass of individual trees, expressed as ETTE and leaf dry mass, was not correlated with the average dry mass of individual seed.

(iv). Leaf biomass of the *A. mellifera* trees per unit area, expressed as ETTE ha^{-1} and leaf dry mass ha^{-1}, was highly correlated with the seed dry mass ha^{-1}. These significant relations were a direct consequence of the greater number of trees present in the high tree density plots.

(v). Seeds harvested from the high tree density plot were longer, wider and thicker than those from the lower tree density plots.

CHAPTER 6

SEED DISTRIBUTION AND SOIL SEED BANK IN RELATION TO TREE DENSITY AND SOIL SUBHABITAT

6.1 INTRODUCTION

The ability of viable seeds to disperse and to survive until such time that they can germinate is an important strategy in the reproductive dynamics of woody plants (Smit *et al.*, 1996). The release of *A. mellifera* seeds from the parent plant normally results in their dispersal over a comparatively small radius. The spread of *A. mellifera* into the surrounding area is characterized by a concentration of a number of plants in clumps, which appear to be contagiously distributed. In the initial stages of its spread, these thickets generally consist of one or more large mother plants surrounded by younger plants of two or more age groups. The greater portion of the shedded seeds fall within the leaf canopy of the mother plant. Despite this potential source of seed, the presence of seedlings or juvenile plants underneath the tree canopy is the exception rather than the rule (Donaldson, 1969).

The presence of relatively large numbers of plants of various age groups in the area around the mother plant is a typical characteristic of *A. mellifera* and various other woody plants. Seeds of *A. mellifera*, while still attached to the papery pods are blown into this zone by winds (Donaldson, 1969). From observations in the field of the seeds laying scattered on the soil underneath and around the mother plant, it was noticed that after good rains all the seeds absorbed moisture, increased in size and, on drying, shrivelled and ultimately disintegrated. Only 0.5% of the seeds may initially survive (Donaldson, 1969).

Sabiiti & Wein (1987) stated that for all plant population, recruitment of seedlings is necessary to maintain the population size over the long-term. However, little is known about the persistence of seeds of spinescent *Acacia* woody species that are often involved in bush encroachment in savanna areas of South Africa. According to Thompson *et al.* (1993) as cited by Garner & Witkowski (1997), soil seed bank dynamics may provide an explanation, at least in part, to seedling establishment. He classified the soil seed bank persistence into three types: transient seed bank (persist for <1 year), short-term persistent (>1 year and <5 years) and long-term persistence (>5 years).

According to Leck *et al.* (1989), all the viable seeds present on or in the soil or associated litter constitute the soil seed bank. Each has spatial and temporal dimensions. Seeds display both horizontal and vertical dispersion, reflecting initial dispersal onto the soil and subsequent movement. Seed bank may be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than one year.

Owens *et al.* (1995) reported that persistence of *Acacia berlandieri* seeds in the soil seed bank varied with depth. In their study, after 42 days, viable seed population of *A. berlandieri* seeds was reduced by 10% and 80% for surface and buried seeds, respectively, and no viable seeds were present after 3.5 months of burial. In a related study on persistence Berkat *et al.* (1996) reported that *Acacia mearnsii* had the best survival of buried intact seeds over 8 months.

According to Leckie *et al.* (2000), the variation in seed bank richness among habitats was positively correlated with canopy cover, soil moisture, and soil nutrients, but not with the seed bank density or total number of species in the above-ground vegetation. Seed bank density increased with soil moisture. Woody species predominated in the seed bank of plots with richer soils, deeper litter, and more closed canopies. Herbaceous species predominated in the seed bank of plots with more open canopies, more mesic water regimes, and greater species richness in the aboveground vegetation (Leckie *et al.*, 2000).

Olivares *et al.* (1996) studied the amount, composition and quality of the seed bank in relation to the presence or absence of an *Acacia caven* canopy and to continuous grazing (CG) and rotational deferred grazing (RDG) of natural grassland. Their results indicated that CG increased the abundance of seeds but reduced the occurrence of valuable forage species and in both grazing systems *A. caven* increased the seed bank and the proportion of dormant seeds in RDG.

Since the seed distribution and soil seed bank of *A. mellifera* are important determinants of its spread and reproduction, the study of these aspects is essential in understanding its reproductive dynamics.

The objectives of this study were:

(i)   To establish the existence and magnitude of a soil seed bank of *A. mellifera* in relation to the tree densities.

(ii)   To investigate the seed re-distribution of *A. mellifera* within defined subhabitats and at varying tree densities.

(iii)   To determine the relationship between the leaf biomass (ETTE ha^{-1}) and seed distribution within subhabitats.

6.2 PROCEDURE

Six *A. mellifera* trees were randomly selected from each plot and labelled accordingly. During August 09, 2000, one tree density plot was randomly selected to determine if a soil seed bank (seed from previous seasons) exists for *A. mellifera* in three identified subhabitats.

According to the procedures of Smit & Swart (1994), a 0.5 m x 0.5 m quadrat was used to excavate a soil monolith of 0.5 m x 0.5 m x 0.20 m from: (i) under the tree canopy close to the stem base, (ii) under the tree canopy at the edge of the canopy, and (iii) in the open area adjacent to the tree canopy. In the latter case two samples were taken in two opposing wind directions (in the direction of the wind and opposite the wind direction). Samples were taken from the six marked trees. The excavated soils were sieved manually using a 3 mm x 3 mm wire mesh to collect any seeds present in the soil.

In order to determine the distribution of seeds of the current season, rectangular plastic containers (0.21 m x 0.14 m x 0.07 m) were inserted along the three defined subhabitats in both wind directions of the 5 x 6 sample trees in each of the experimental plots (Figure 6.1).
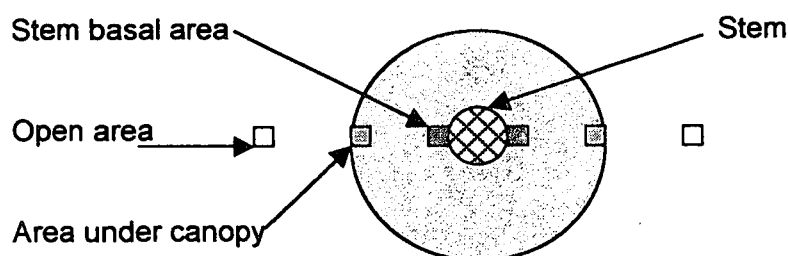
Figure 6.1 Schematic diagram showing the location of rectangular plastic containers inserted along the subhabitats in the wind direction and opposing the wind direction.

During March 2001, the contents (seed + pod) of the plastic containers were collected

and emptied into labelled paper bags to determine the pattern of seed distribution along the two directional subhabitat gradients. The contents of the plastic containers were transported to the facilities of the University of the Free State, where all the seeds were counted by hand.

6.3 DATA ANALYSIS

Microsoft Excel graphics (Microsoft Excel, 1997) was used to present the data of seed distribution frequency along the two directional subhabitat gradients. The data were compared according to frequency distribution along the tree density gradient. Regression and correlation analysis (Mstat-C, 1991) was implemented to determine the relations between ETTE ha^{-1} and the estimated seed distribution per unit area of the five tree density plots and the two directional subhabitat gradients.

6.4 RESULTS AND DISCUSSION

6.4.1 Soil seed bank

6.4.1.1 Seeds of the previous season

The randomly selected plot for the assessment of the possible soil seed bank of the previous season was the 30% plot. Donaldson (1969) reported that about 99.5% of *Acacia mellifera* seeds initially disintegrate and are destroyed by moisture. Not a single *A. mellifera* seed was found within the collected soil samples, confirming the claim by Donaldson (1969) that there is no carry over of seed from one season to another (no seed bank). Environmental factors like the fluctuations and extremes of the alternating day and night temperatures as well as the susceptibility of the seeds to rotting, after exposure to moisture, are the most likely reasons for the inability of *A. mellifera* seeds to survive in the soil. In addition, some seeds also suffer ingestion and damage by small mammals and insects.

6.4.1.2 Seeds of the present season

During early February 2001 (about 75 days after the seed harvesting), a visual assessment was done to investigate the soil seed bank of the *A. mellifera* trees that produced fresh seed in the present season. It was observed that more than 80% of the

fresh seeds were already disintegrated and destroyed with only a black circular spot of seed coat without any endospermic content remaining. Some of the seeds also suffered damage from insects (this will be discussed in Chapter 7).

During a second visual assessment done early March 2001 (approximately 105 days after seed harvesting), it was observed that almost all the current season's *A. mellifera* seeds in the experimental plot were decomposed as a result of the very high summer temperature (about 42°C) and exposure to fluctuating moisture. Similar to this result, Owens *et al.* (1995) found no viable *Acacia berlandieri* seeds after 3.5 months of burial. In contrast to these findings it is reported that there are other *Acacia* species that do form persisting soil seed banks. Because of the hard-seededness, species like *A. nilotica* and *A. tortillis* may form persistent soil seed banks that can remain viable for a period of at least 1-5 years. Such seed banks may number several hundred to several thousand seeds m^{-2} (Smit 1999a).

In general, the persistence of *A. mellifera* seeds in the soil within the three defined subhabitats and along the tree density gradients showed no difference and it can be concluded that a soil seed bank do not exist in the case of *A. mellifera*.

6.4.2 Seed re-distribution within the defined subhabitats

Most of the seeds collected in the plastic containers were in an advanced state of decomposition, but the pod covers remained largely unaffected. Because of the decomposition of the seeds, difficulty was experienced in counting the individual seeds. As a compromise it was decided to count the pod cover pairs and multiply the number of pod cover pairs with the average number of seeds per pod (two seeds in this case) to get some estimate of the actual number of seeds. Donaldson (1969) reported an average of 2 – 3 *A. mellifera* seeds per pod. The area covered by each container was 0.0294 m^2 and this area was converted to 1 m^2 to estimate the distribution of seeds per m^2 within the defined subhabitats.

The estimated seed distribution of *A. mellifera* for the five experimental plots and two directional subhabitats is presented in Figure 6.2. The numbers of *A. mellifera* seeds distributed per unit area were higher in the higher tree density plots (100%, 50% and 30%) as compared to the lower tree density plots (20% and 10%). In almost all the plots the number of seeds distributed per unit area were higher in the direction of the wind as

compared to the opposite wind direction, except in the 30% plot. This, however, could be the result of the close proximity of neighbouring trees.
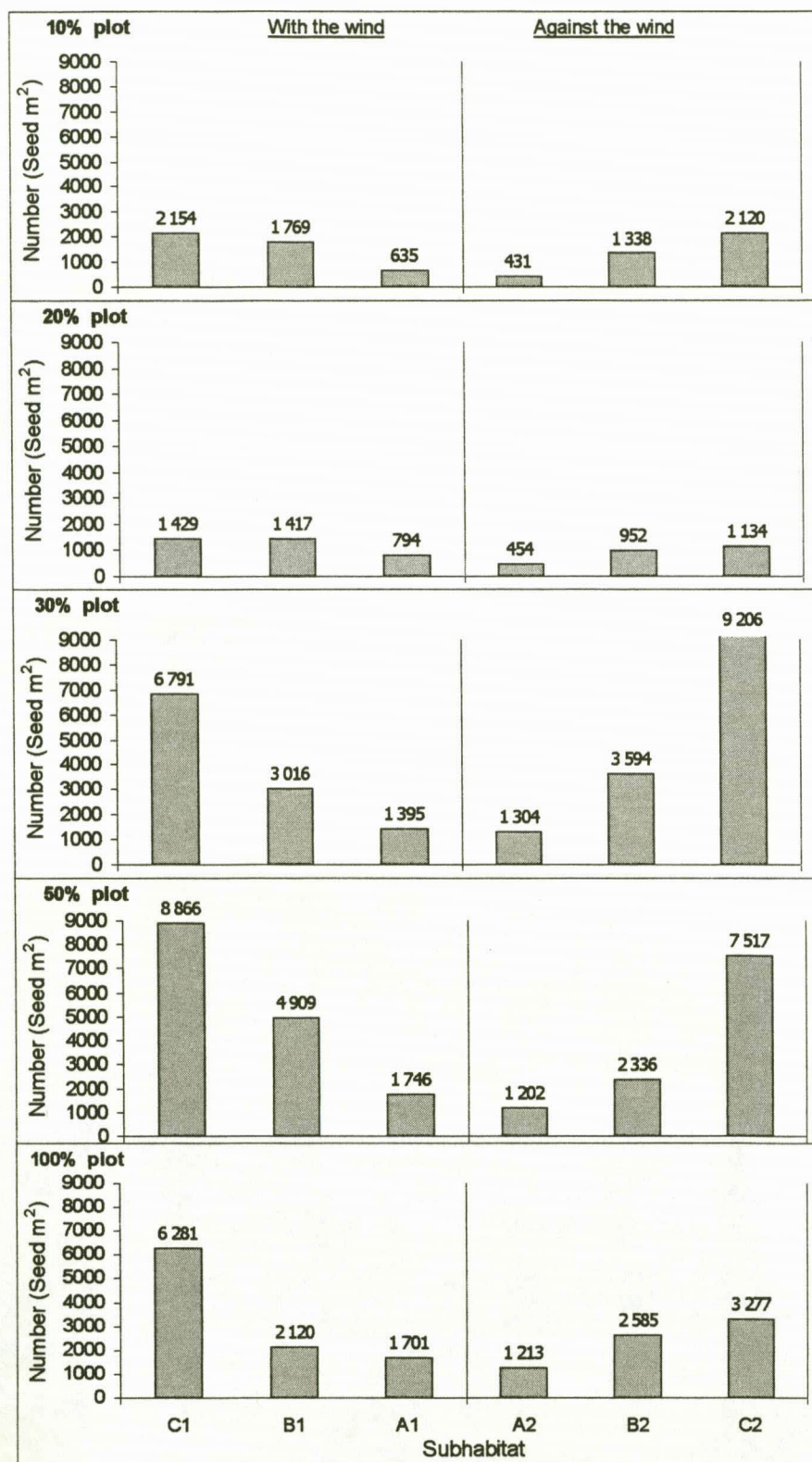
Figure 6.2 Mean *A. mellifera* seed distribution (n = 6) within two directional subhabitats along the tree density gradient (A = around stem, B = under canopy, C =open area).

It was observed that, in both wind directions, a greater number of shedded seeds fell in the open area as compared to the seeds that fell under the tree canopy spread and around the stem base area. In both wind directions, the number of seeds that fell around the stem area was much lower in comparison to the other subhabitats. In all cases the portion of seeds that fell in the direction of the wind of all three subhabitats were higher than those in the comparable subhabitats against the wind. This result applies to trees from individual plots (Figure 6.2) as well as for all the trees and plots combined (Figure 6.3). Similar to this result, Donaldson (1969) reported that the greater portion of seeds shed, fell within the leaf canopy of the mother plant rather than the stem base area, but, he did not consider the distribution of seeds in open areas.
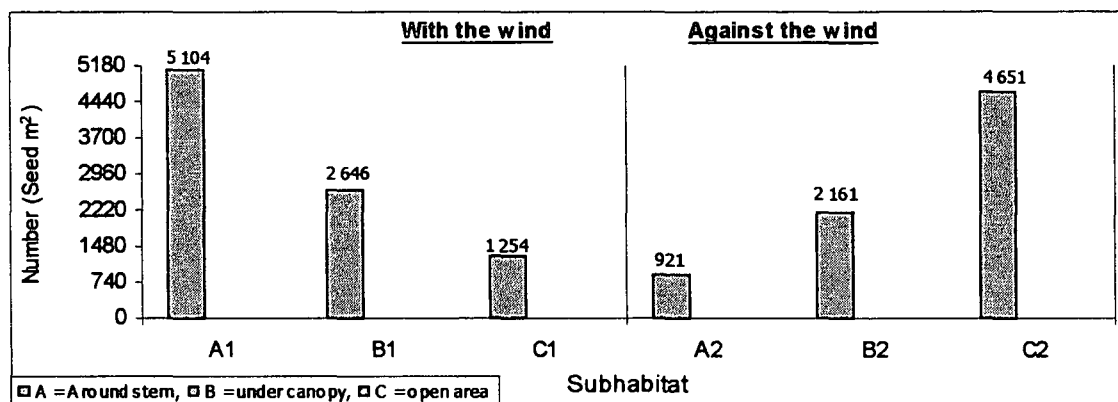
Figure 6.3 Mean seed distribution pattern (n = 30) in relation to the defined subhabitats of all the sample trees (experimental plots combined).

In general, it was observed that the pattern of seed distribution markedly increased from the stem basal area to the open area in both wind directions. This increase in the number of shedded seeds that fell in open area could, in part, also be attributed to the fact that the distance between neighbouring trees decreased with an increase in tree density. This phenomenon was clearly observed in the control plot and plots with a relatively high tree density such as the 50% and 30% plots. Hence seeds of trees other than the sample trees may have been collected in the sampled, open areas. For this reason the number of seeds counted in the open areas of the high tree density plots (100%, 50% & 30%) were higher than those counted in the low tree density plots.

6.4.3 Relations between ETTE ha^{-1} and seed distribution within subhabitats.

The results of the regression analysis of the relations between ETTE ha^{-1} and the

number of seeds distributed per m^{-2} around the stem base area, in both directions, are presented in Figures 6.4a and 6.4b.
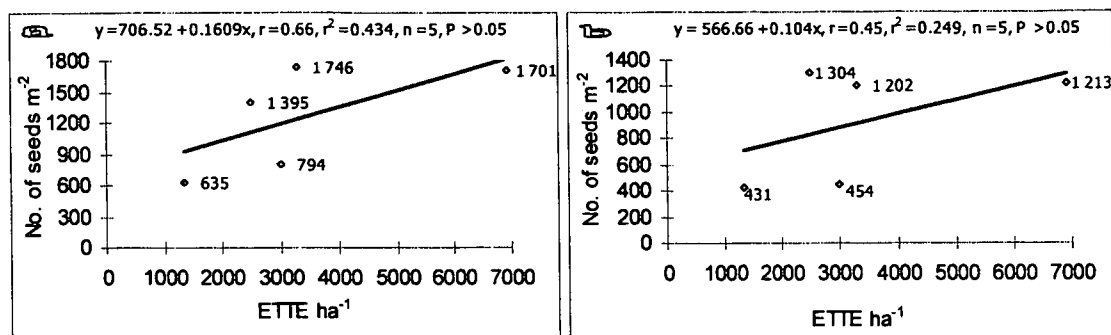
Figure 6.4 Regression analysis between ETTE ha^{-1} and seed distribution around the stem base area ("a" the direction with the wind and "b" the direction against the wind).

The correlation between ETTE ha^{-1} and seed distribution m^{-2} of the seeds collected from the stem base area was non-significant (P = 0.23 for "a" and 0.39 for "b", respectively), with low correlation coefficients.

No marked differences in the number of seeds distributed between plots were observed in this subhabitat.

The results of regression analysis between the ETTE ha^{-1} and number of seeds distributed m^{-2} of the seeds collected from the subhabitat under the tree, in both directions, are presented in Figures 6.5a and 6.5b.

The correlation between ETTE ha^{-1} and seed distribution m^{-2} of the seeds collected from the subhabitat under the tree canopy were also non-significant (P = 0.98 for "a" and 0.67 for "b" respectively), with low correlation coefficients.
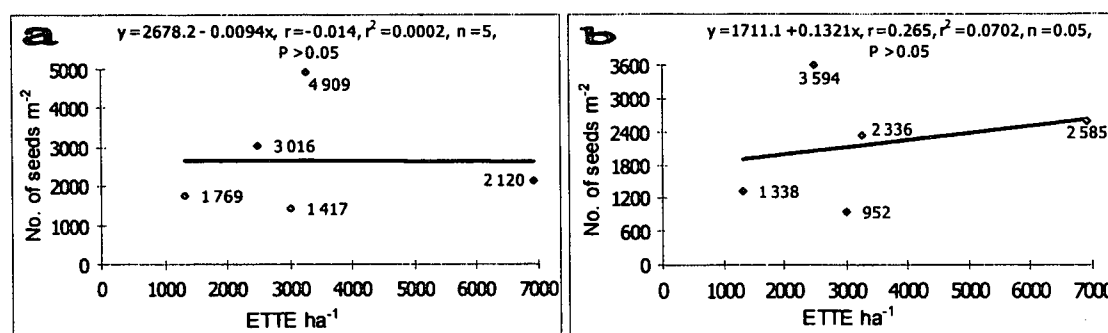
Figure 6.5 Regression analysis between ETTE ha^{-1} and seed distribution in the subhabitat under the tree canopies ("a" the direction with the wind and "b" the direction against the wind).

No marked differences in the number of seeds distributed between plots were observed in the subhabitat under the tree canopies. However, the number of the seeds distributed in this subhabitat was much higher than the number of seeds collected from the stem base area.

The results of regression analysis between the ETTE ha^{-1} and number of seeds distributed m^{-2} of the seeds collected from the open area (uncanopied subhabitat), in both directions, are presented in Figures 6.6a and 6.6b.
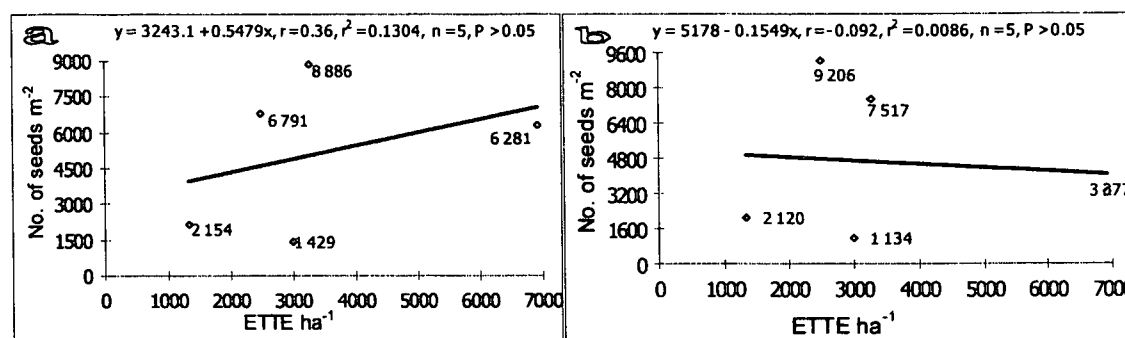
Figure 6.6 Regression analysis between ETTE ha^{-1} and seed distribution in open area (uncanopied subhabitat) ("a" the direction with the wind and "b" the direction against the wind).

The correlation between ETTE ha^{-1} and seed distribution m^{-2} of the seeds collected from the open area (uncanopied subhabitat) were also non-significant (P = 0.55 for "a" and 0.88 for "b" respectively), again with low correlation coefficients.

Unlike the previous two subhabitats, there was a marked difference in the number of seeds distributed m^{-2} between the tree density plots in both directions. The number of seeds collected from the higher tree density plots (30%, 50% and 100%), in both directions, was higher than those of the lower tree density plots (10% and 20%). In almost all the tree density plots, the distribution of seeds in the direction of the prevailing winds was higher than against wind direction, the exception being the 30% plot.

According to Donaldson (1969), the presence of relatively large numbers of plants of various age groups in the area around the mother plant is a typical characteristic of *A. mellifera*. Seeds of *A. mellifera*, while still attached to the papery pods were observed to be blow into this zone by the wind.

6.5 CONCLUSIONS

(i). It was concluded that there is no carry over of *A. mellifera* seeds from one season to another, and thus no persisting seed bank exists. The reasons for this being that the seed of *A. mellifera* are very susceptible to rotting due to exposure to moisture and other environmental factors.

(ii). It was observed that the percentage viable fresh *A. mellifera* seeds decreased with the increase of the time of exposure to high temperature and moisture fluctuations. After approximately three and half months all seeds were observed to be decomposed.

(iii). In all subhabitats along the tree density gradient, a larger number of seeds were blown toward the prevailing wind direction in comparison to the direction opposite the wind direction. The number of seeds accumulated in the open subhabitats in both wind directions was also higher in comparison to the canopied subhabitats. The pattern of this increase was clearly observed in the higher tree density plots (30%, 50% and 100%) possibly due to the reduced inter-tree distance and overlapping tree canopies at high tree densities.

(iv). A non-significant and very low correlation was observed between the potential tree competitiveness (ETTE) ha^{-1} and seed distribution along the tree density gradient of the three subhabitats.

(v). In general, the survival and perpetuation of the seeds of the remaining *A. mellifera* trees are more likely to depend on prevailing environmental factors rather than the tree thinning intensities.

CHAPTER 7

SEED GERMINATION AS INFLUENCED BY BRUCHID BEETLES AND TREE THINNING

7.1 INTRODUCTION

According to Bradbeer (1988), the eventual function of the surviving seed is its germination. Mayer & Poljakoff-Mayber (1975) defined germination as that consecutive number of steps which causes a quiescent seed, with a low water content, to show a rise in its general metabolic activity and to initiate the formation of a seedling from the embryo. Like any seed of angiosperm, the seed of *Acacia mellifera* develops from a fertilized ovule and consists of an embryo, endosperm and seed coat.

Germination may be impaired when seeds have been heavily parasitised and invertebrates may damage seedlings (Coe & Coe, 1987). According to Smit (1999a), infestation of seeds by bruchid beetles may affect species differently. He noted that the germination of *Acacia gerrardii* seeds was negatively influenced by bruchid beetle infestation, while infestation promoted early germination and establishment in *A. sieberiana*. According to Smit & Rethman (1998a) the seed germination potential of *Colophospermum mopane* was not affected by different tree densities, that is, they seem to have the same germination potential. The ability to germinate, however, did not necessarily mean that the seedling would survive (Smit, 1994), but the greatest germination was achieved from fresh seeds and they conclude that no dormancy exists in *C. mopane* seeds. However, Donaldson (1969) reported that, *A. mellifera* seeds were not attacked by insects as readily as those of other woody plants such as *A. erioloba* and *A. hebeclada* which have a much harder testa.

Miller (1996a) conducted a field study in Africa on the predation of *Acacia* species by bruchids. In his study *Acacia tortillis, A. nilotica* and *A. mellifera* seeds on the ground suffered greater bruchid infestation than seeds within canopy-held pods. Seeds of indehiscent and dehiscent *Acacia* species showed no difference in the rate of bruchid infestation. He also observed that more bruchid species attacked seeds of indehiscent (*A. nilotica, A. tortillis, A. hebeclada and A. robusta*) than dehiscent (*A. karroo, A. mellifera* and *A. caffra*) species. In his study bruchid infestation differed between *A. tortillis* trees, and for *A. tortillis* and *A. hebeclada* between years. There was no

difference in bruchid attack on *A. nilotica* between years. Stored *Acacia* seeds were infested more than fresh seeds (Miller, 1996a).

Since germination is the most important determinant of the survival and perpetuation of a plant community, the need for the study of the germination dynamics of *A. mellifera* in relation to tree density and seed predation by insects such as bruchid beetles is of great importance.

The objectives of this study were:

(i)   To determine if differences exist in the germination potential of *A. mellifera* seeds collected from trees along the tree density gradient.

(ii)   To determine if differences exist in the root growth and coleoptile development of *A. mellifera* seedlings from the seeds collected along the tree density gradient.

(iii)   To determine whether *A. mellifera* seeds are subject to dormancy.

(iv)   To understand the influence of bruchid beetles on the germination potential of *A. mellifera* seed.

(v)   To understand and evaluate the relationship between *A. mellifera* seed germination parameters and potential tree competitiveness.

7.2 PROCEDURE

Seeds were harvested from 50 randomly selected *A. mellifera* plants along the tree density gradient (10 plants/plot). The date of actual seed harvest was 20 November 2000 when ripening of *A. mellifera* seed was at its peak (Smit, 1999a). For the germination potential assessment, 50 seeds (5 seeds/sample tree) from each plot were randomly selected from the bulk seed harvest after all bruchid beetle infested seeds were removed.

For the assessment of the germination potential of bruchid beetle infested seeds, 20 infested *A. mellifera* seeds were randomly selected from each plot. The germination tests were conducted during February 2001 for about 30 days at the facilities of the Department of Agronomy of the University of the Free State.

The validity of seed germination tests is dependent on the provision of optimal conditions subject to the correct combination of moisture, temperature and light. While light and temperature requirements for optimum seed germination of most agricultural crops have been standardized by the International Seed Testing Association (ISTA) (Loubser & van de Venter, 1990), the specific requirements of *Acacia mellifera* seeds are unknown. However, Palma *et al.* (1995b) reported an optimum germination temperature of 25^0C for *A. senegal* seeds and Cox *et al.* (1993) found an optimum temperature range of 26 to 31^0C for germination of *A. constricta* and *Prosopis velutina* shrubs.

Seeds were subsequently placed horizontally at the top 10 cm line of a 30 cm long folded filter germinating paper used as germination substrate. Then, it was immersed in a 1 000 ml flask filled with 400 ml distilled H_2O and incubated in an incubator in the dark, standardized at a temperature of 25^0C. Germination counts was regularly performed every 24 hours. Root length and coleoptile length were measured for 10 days and 8 days, respectively after the germination of each seed using a calliper.

To identify the type of bruchid beetle species affecting *A. mellifera* seeds 100 bruchid beetle infested seeds were collected and kept in glass bottles for identification. Genus identification was done by of the Department of Zoology and Entomology of the University of the Free State.

7.3 DATA ANALYSIS

To assess the germination potential of *A. mellifera* seed collected from trees along the tree density gradient, the percentage frequency of seeds germinated after each successive day was plotted graphically over time (days) (Smit, 1994; Smit & Rethman, 1998a).

To determine the total germination percentage of the seeds from the various tree density plots, the total number of seeds from the sample trees that successfully germinated were counted and graphically presented as percentages. The mean root length and coleoptile length as well as the mean root and coleoptile growth rates of seedlings from the various tree density plots were also compared graphically (Microsoft Excel, 1997).

Regression and correlation analysis was used (Mstat-C, 1991) to determine the relations between ETTE ha^{-1} and the various parameters of seed germination, and the regression lines were presented graphically using Microsoft Excel graphics (Microsoft Excel, 1997).

7.4 RESULTS AND DISCUSSION

7.4.1 Germination potential of *Acacia mellifera* seeds

Results of the percentage germination of the fresh *A. mellifera* seeds harvested during the onset of the growing season (20/11/2000) are presented in Figure 7.1. No marked differences in the germination percentage were observed between the seeds collected from the different tree density plots. High germination (100%) were obtained from seeds harvested in the low tree density plots as compared to the control plot, although lower, was still high at 98% (Figure 7.1). Bein *et al* (1996) reported a germination percentage of 50 – 80% for *A. mellifera* seed.
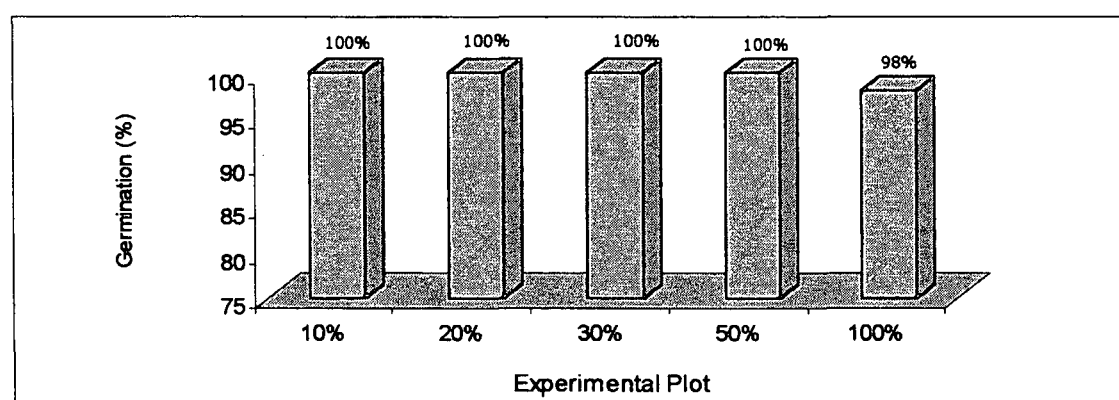
Figure 7.1 Percentage germination of fresh *A. mellifera* seeds collected along the tree density gradient.

While the seeds from the lower tree density plots (10%, 20%, 30% and 50%) were smaller and lighter than the control plot (100%) (see chapter 5) almost the same germination percentage was achieved for all plots. Smit (1994) and Smit & Rethman (1998a) reported similar results regarding the germination potential of the different sized *Colophospermum mopane* seeds harvested along a tree density gradient in the Northern Province.

Results of the seed germination potential are presented in Figure 7.2. The highest accumulated germination (> 60%) during the first two days of incubation of the fresh *A.*

mellifera seeds were obtained from seeds harvested in all tree density plots, except the control (100% plot), which achieved only 24%.
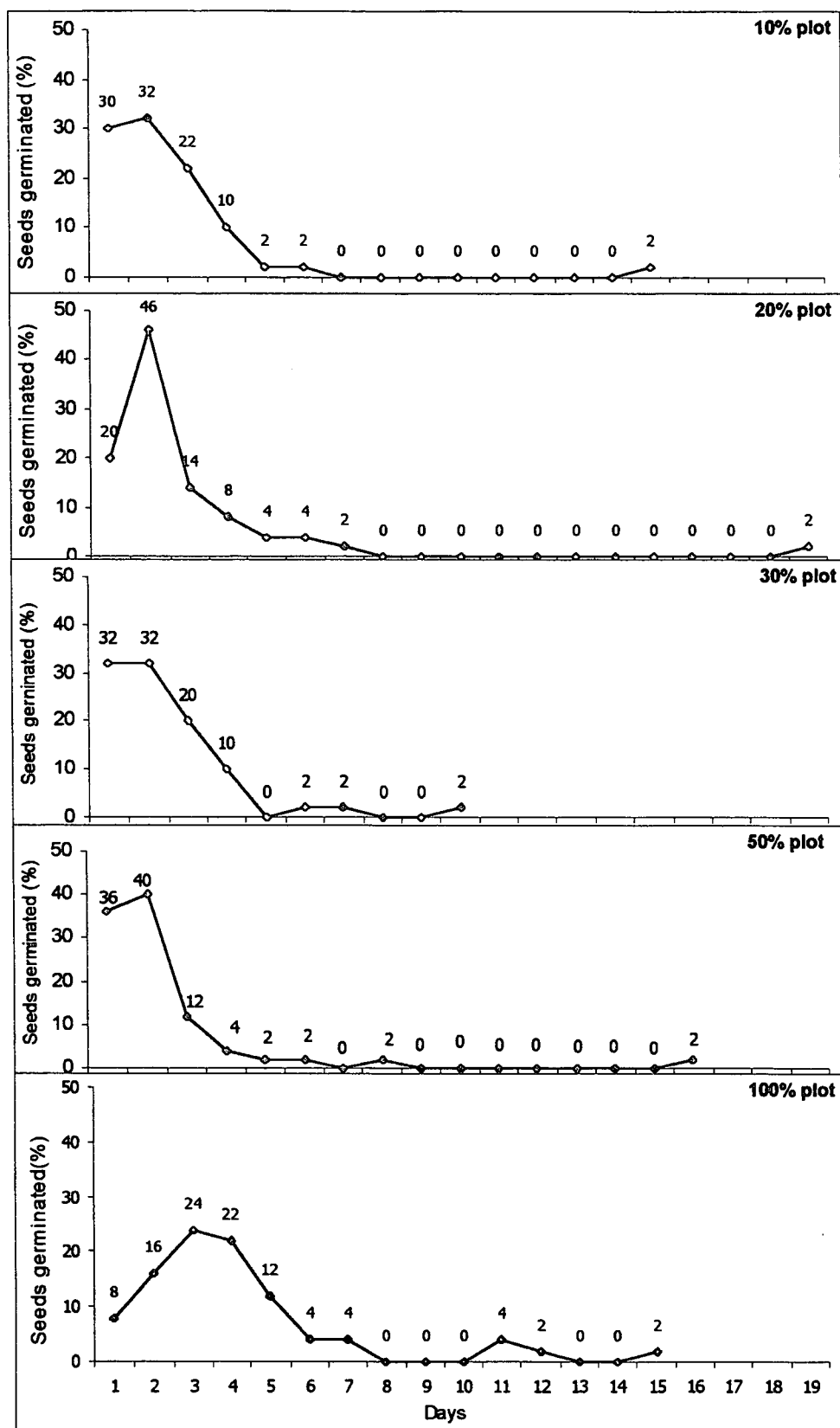
Figure 7.2 Seed germination potential of fresh *A. mellifera* seeds collected along the tree density gradient.

The total germination potential of all seeds germinated is presented in Figure 7.3. Most of the seeds germinated within two days (55.4%). The peak period of germination of the fresh *A. mellifera* seeds was after day two (33.2%). There were no marked differences in the germination period of seeds from the different experimental plots and no seed dormancy was observed. In general, no further germination was recorded after 19 days.

Similar to the results of this study were the results of Bein *et al.* (1996) who reported a period of 2 – 14 days in which seeds of *A. mellifera* germinated. In another study, Smit (1994) and Smit & Rethman (1998a) reported no marked difference in the germination period of seeds collected from different tree density plots. Of the seeds harvested at the end of the growing season, those from the 10%, 20%, 35% and 50% plots, achieved peak germination after 12 days, while the smaller seeds from the 75% and 100% plots achieved peak germination after only 8 days.
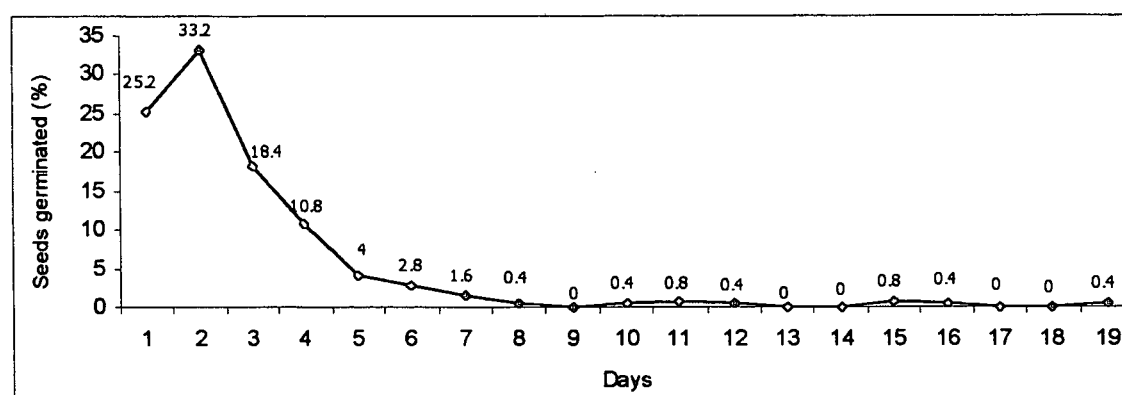
Figure 7.3 Total germination potential (rate) of the fresh *A. mellifera* seeds from all the tree density plots combined.

A very high total germination percentage of 99.6% was achieved. From this result it can be concluded that seeds of *A. mellifera* are not subject to any dormancy. According to Smit (1994), the ability to germinate, however, did not necessarily mean that the seedlings would survive.

7.4.2 The influence of bruchid beetles on the seed germination potential

The bruchid beetles that infested the *A. mellifera* seeds were identified as belonging to the genus *Bruchidius* of the family Bruchidae. According to Van Tonder (1981), the seeds and pods of *A. mellifera* are the main hosts for one or more *Bruchidius* species. Their occurrence can often be related to an altitudinal gradient. According to Abdullah & Abulfatih (1994), *Acacia* species, and their bruchid seed pests, occupy a specific range

along an altitudinal gradient. They investigated that, at low to intermediate altitudes, between sea level and 1 750 m, in hot to warm environments, *Acacia asak, A. ehrenbergiana, A. hamulosa, A. oerfota* and *A. seyal* were found to be the main host for *Bruchidius* species in south-western Saudi Arabia. The range of this altitudinal gradient and climate relates to the present study area.

The number and percentage of fresh *A. mellifera* seeds infested by bruchid beetles as compared to the total seed production is presented in Figure 7.4.
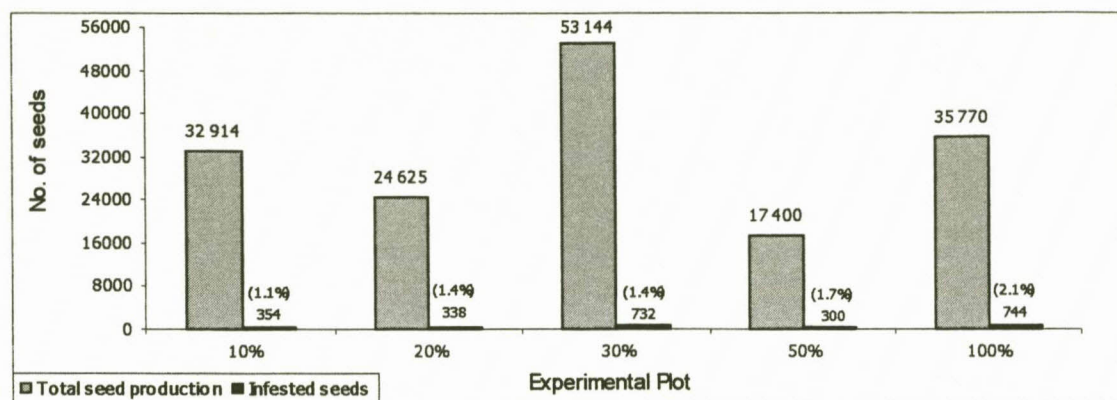
Figure 7.4 The number of bruchid beetle infested *A. mellifera* seeds compared to the total seed production of a number of *A. mellifera* trees from the various tree density plots.

According to the results in Figure 7.4 the percentage of seeds damaged by bruchid beetles, as compared to the total production, was very minimal. This observation supports the observations made by Donaldson (1969) that *A. mellifera* seeds are not attacked by insects as readily as those of other woody plants such as *A. erioloba* and *A. hebeclada*. A possible explanation for this phenomenon may lie in the fact that the cotyledons of *A. mellifera* seeds are much thinner and smaller than those of the other plants mentioned (Donaldson, 1969). In addition the seed of *A. mellifera* are dehiscent, unlike the indehiscent seed of *A. hebeclada* (Miller, 1996b).

The germination percentage of bruchid infested *A. mellifera* seeds are presented in Figure 7.5. A very low germination percentage was recorded compared to the uninfested seeds and no marked differences in the germination of seeds from the different experimental plots were observed. This is in accordance with Mucunguzi (1995a) who reported that bruchid beetles significantly reduced ($P < 0.05$) the germination and seedling establishment in *A. sieberiana*. The possible reason for the low germination potential of bruchid infested *A. mellifera* seed could be the damage of embryos (Figure

7.6). Hashim (1990) reported that seeds damaged by bruchid beetles failed to germinate if their embryos were eaten.
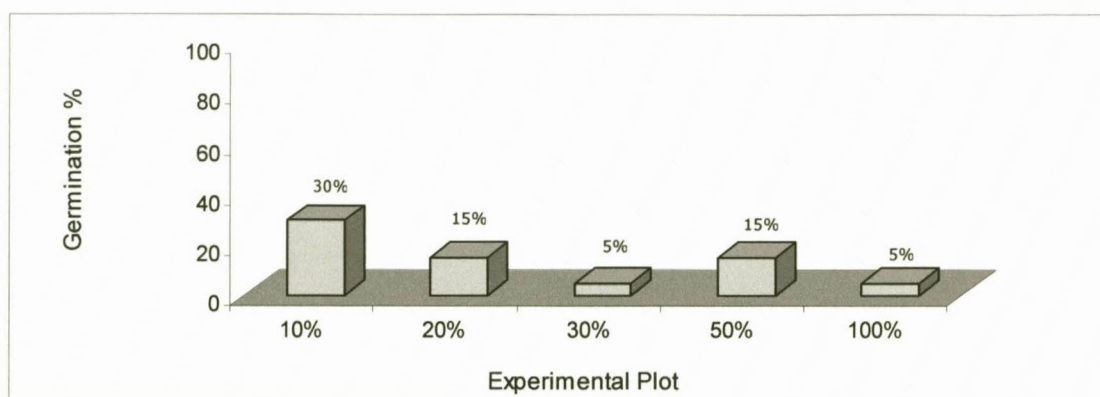
Figure 7.5 Percentage germination of bruchid beetle infested *A. mellifera* seeds.

Damaged seeds, however, promoted fast imbibition periods and quicker germination as compared to the undamaged seeds. All the germinated seeds emerged within 24 hours. Similar to this finding, Hashim (1990) reported that the germination of damaged seeds whose embryos were not eaten was sometimes some times even higher than those of undamaged seeds where the bores made by the bruchids in the seeds may have facilitated moisture imbibition.

Figure 7.6. Bruchid beetle infested *A. mellifera* seeds collected from the various tree density plots of the study area.

7.4.3 Root length and Coleoptile length of the germinated *A. mellifera* seeds

Results of the root length and coleoptile length of the germinated fresh *A. mellifera* seed are presented in Figures 7.7 and 7.8, respectively.
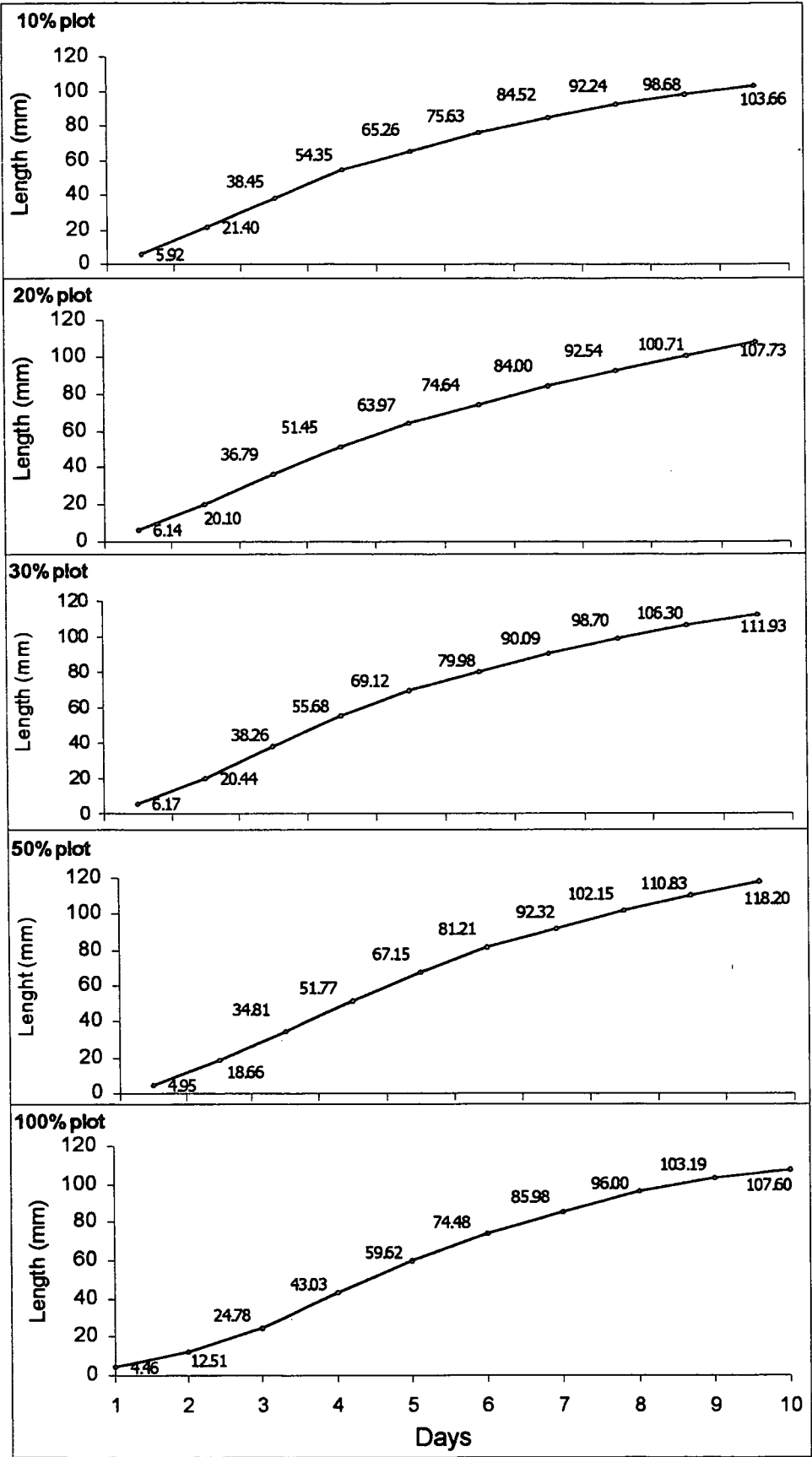
Figure 7.7 Mean root length of the germinated *A. mellifera* seeds (n = 50) collected from the various tree density plots.
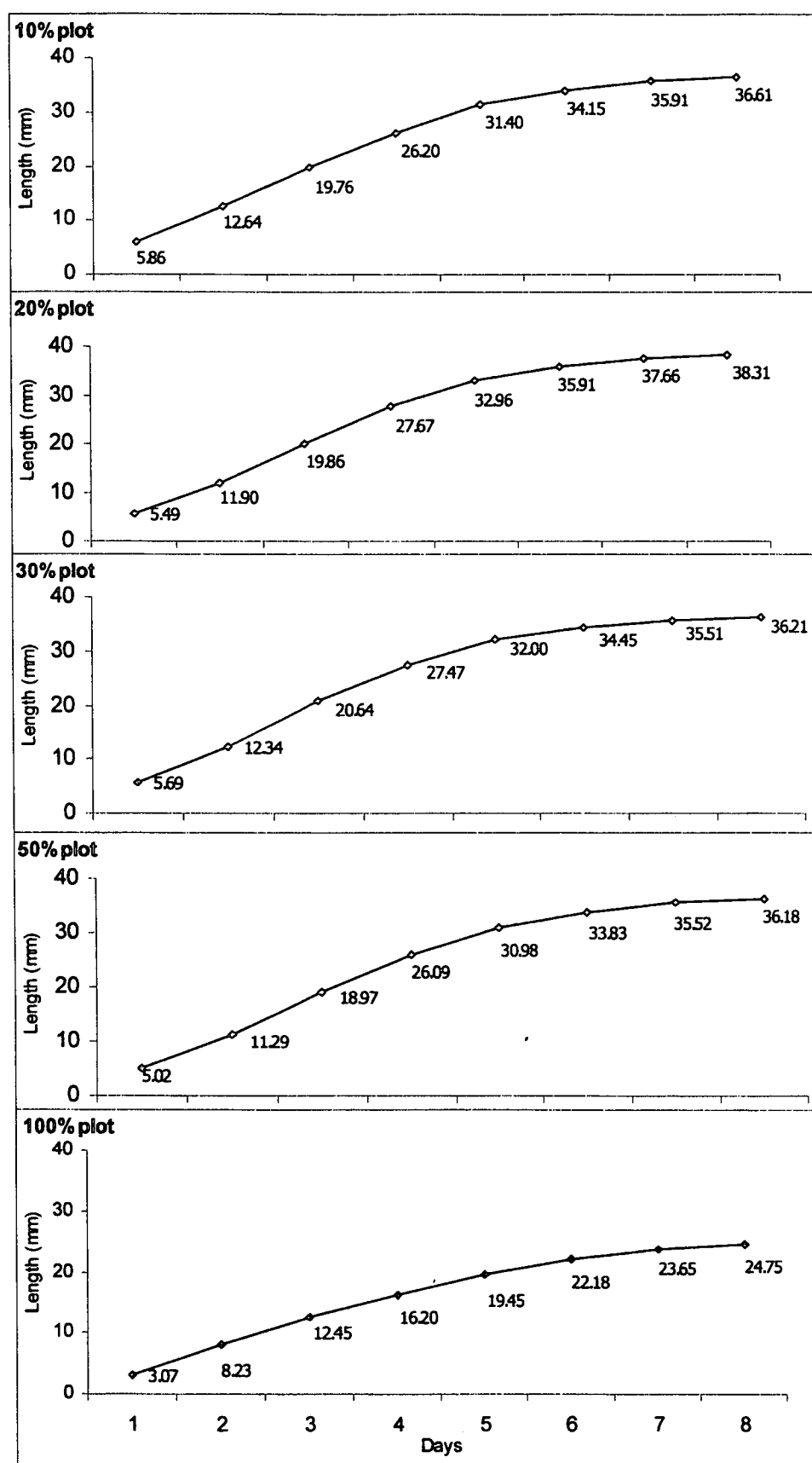
Figure 7.8 Mean coleoptile length of the germinated *A. mellifera* seeds (n = 50) collected from the various tree density plots.

Although seeds harvested from the lower tree density plots were smaller in size and lighter than the high tree density plot (control), no marked difference in root lengths were observed between seeds from the different tree density plots. However, a marked difference in coleoptile length was found. Seeds harvested from the lower tree density plots (10%, 20%, 30% and 50%) also exhibited a higher growth rate compared to the control plot. Therefore, the endospermal content of the smaller and lighter *A. mellifera* seeds may allow the same growth rate as large and heavier seeds for a limited period of time.

7.4.4 Root and Coleoptile growth rates of the germinated *A. mellifera* seeds

The results of the mean root growth rate are presented in Figure 7.9. There was no marked difference in the growth rate of the roots of germinated *A. mellifera* seeds harvested from the different tree density plots.

The pattern of the root growth followed an initial exponential growth rate in the seeds of all plots. Seeds harvested from the lower tree density plots (10%, 20% and 30%) achieved a peak root growth rate after three days of germination and thereafter the growth rate declined linearly. However, the root growth of the seeds harvested from the higher tree density plots (50% and 100%) achieved a peak growth rate after four days following their germination (Figure 7.9).

In contrast to the root growth rate, marked differences in the coleoptile growth rate were observed between the germinated seeds from the different tree density plots. The *A. mellifera* seeds harvested from the lower tree density plots showed a higher coleoptile growth rate than the control plot (Figure 7.10). The pattern of the coleoptile growth of the seeds from the lower tree density plots displayed an initial exponential growth rate, which peaked after three days following germination, thereafter the growth rate declined linearly. However, a linear growth pattern with a peak after two days following germination was observed for seeds from the control plot (100%).

In general, seeds harvested from the lower tree density plots were smaller and lighter than the seeds harvested from the high tree density plot (see chapter 5). However, they displayed a higher germination potential and growth rate compared to seeds from the high tree density plot. It could be the adaptive mechanism of this species to survive, distribute and perpetuate on areas that are already thinned/cleared and degraded.
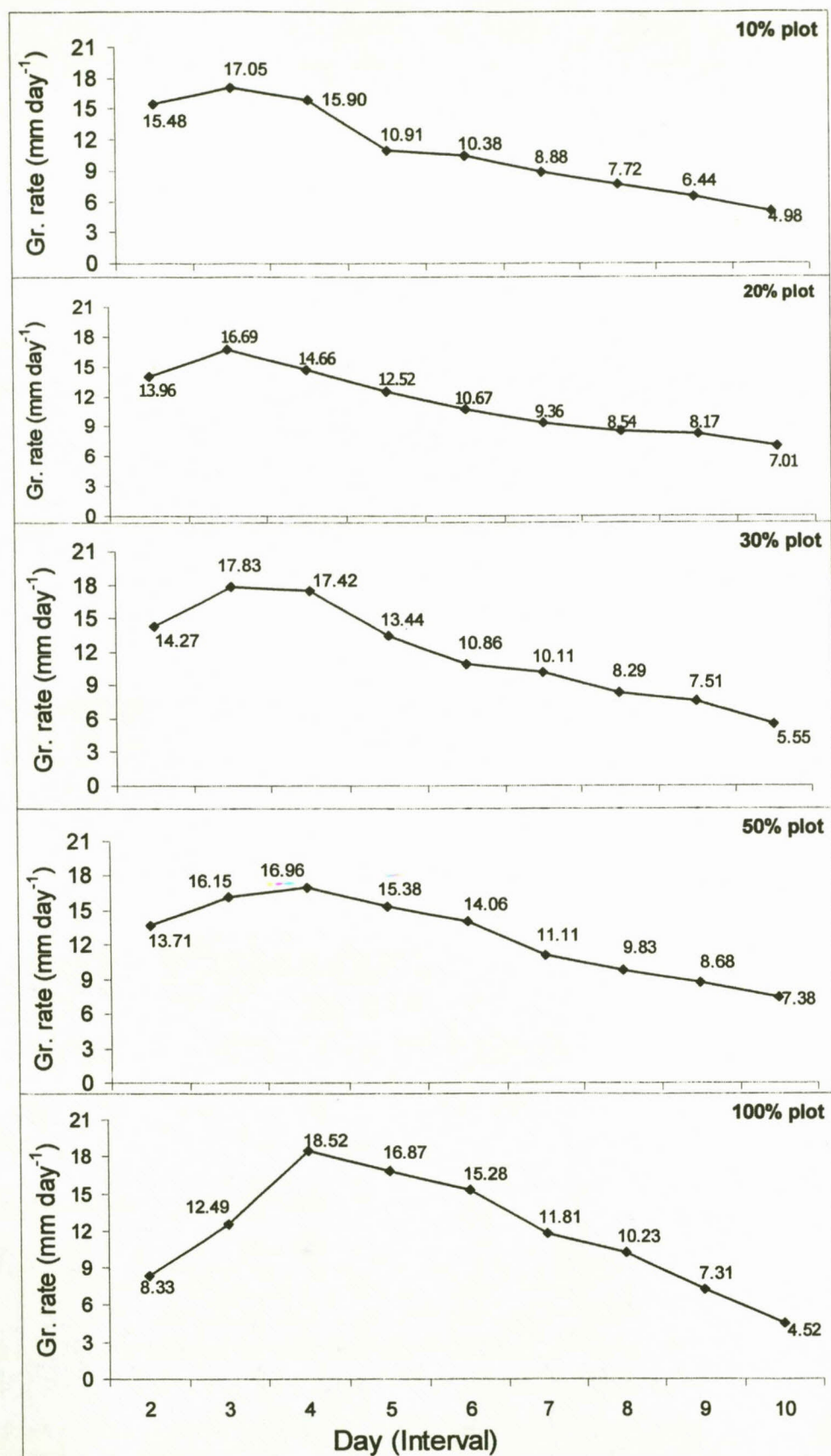
Figure 7.9 Mean root growth rate of germinated *A. mellifera* seeds (n = 50) harvested along the different tree density plots.

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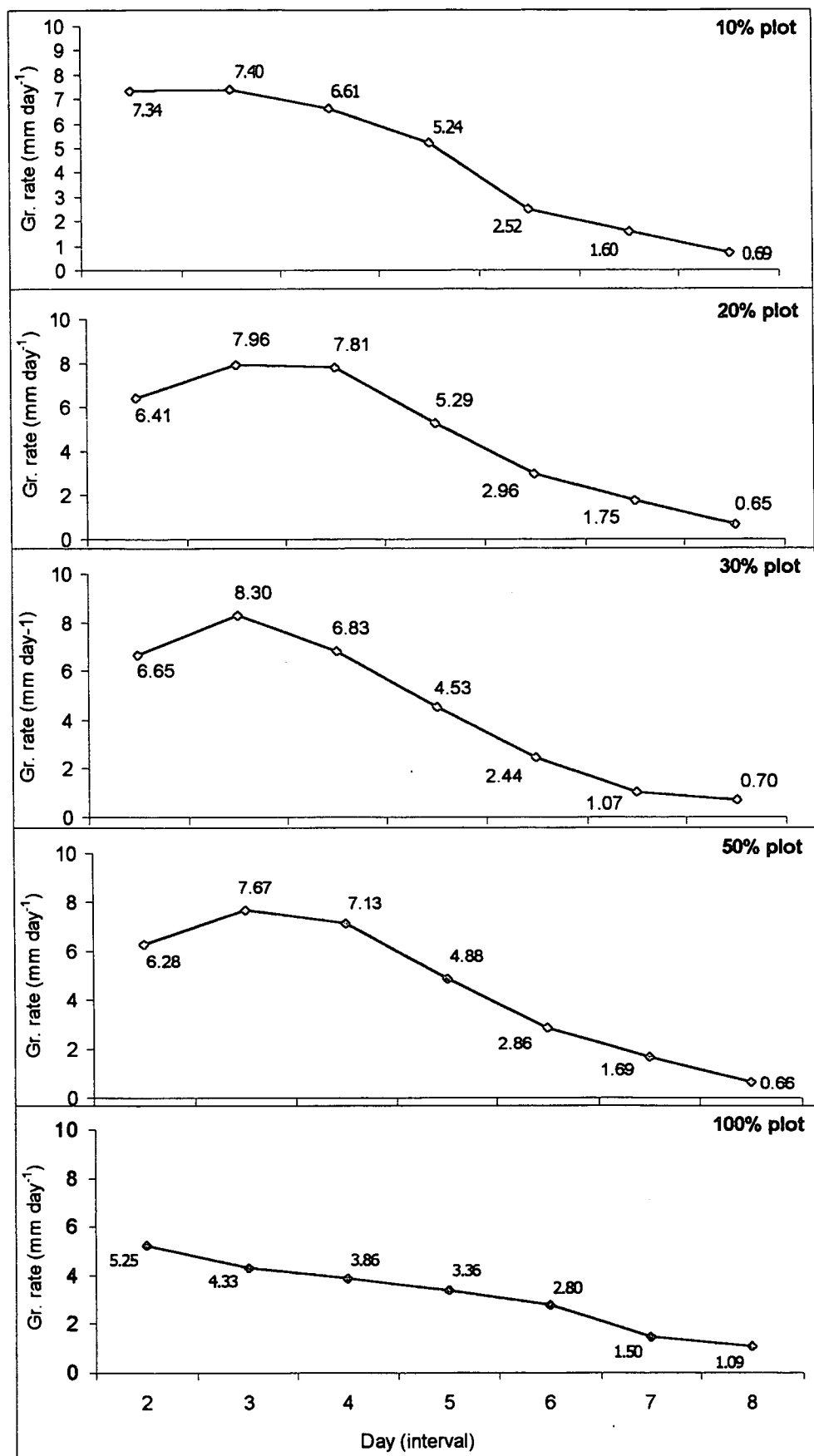
Figure 7.10 Mean coleoptile growth rate of germinated *A. mellifera* seeds (n = 50) harvested along the different tree density plots.

7.4.5 Relations between tree density (ETTE ha⁻¹) and seed germination parameters

7.4.5.1 ETTE ha⁻¹ versus germination potential

The relation between potential tree competitiveness and the germination potential of the seeds is presented in Figure 7.11.
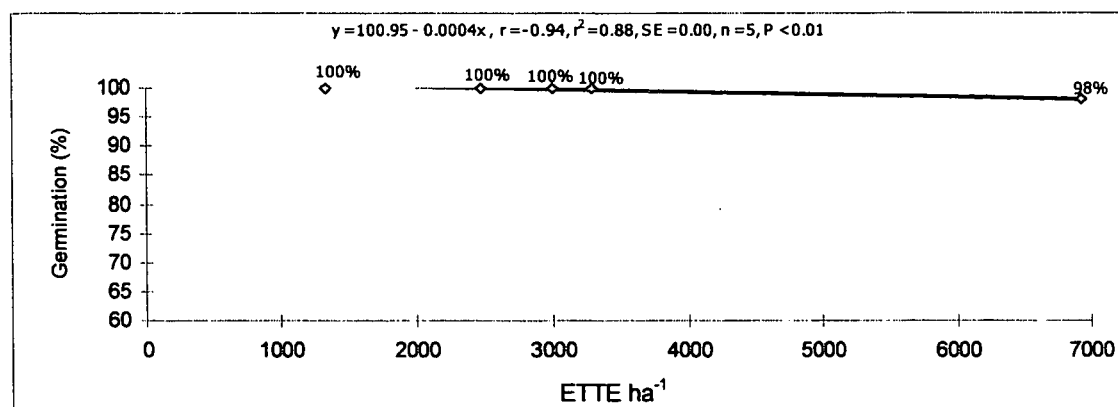
Figure 7.11 Regression analysis of the relation between ETTE ha⁻¹ and seed germination potential along the tree density gradient.

There was a significant (P = 0.01) negative correlation between the two parameters. With an increase in tree density a very slight linear decrease in seed germination potential was observed.

7.4.5.2 ETTE ha⁻¹ versus root length and coleoptile length
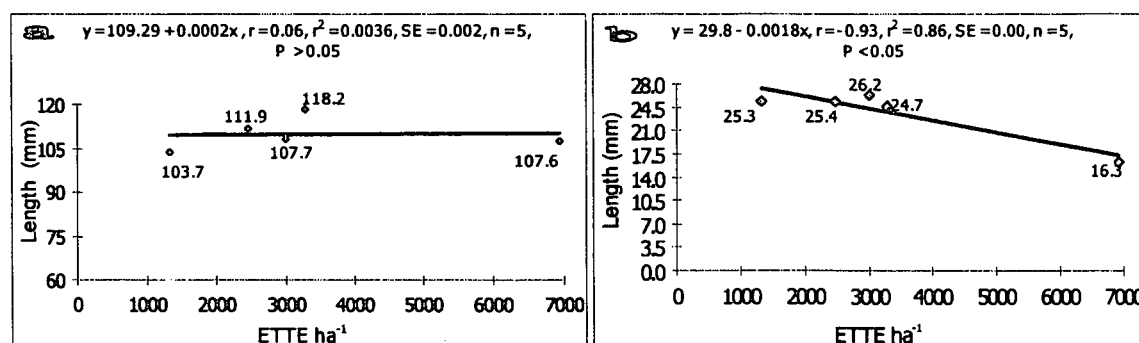
Figure 7.12 Regression analysis of the relations between ETTE ha⁻¹ versus (a) root length and (b) coleoptile length of the germinated seeds.

There was a non-significant relation (P = 0.92) between ETTE ha⁻¹ and root length of the germinated seeds (Figure 7.12a). However, there was a significant (P = 0.012) relation between ETTE ha⁻¹ and coleoptile length (Figure 7.12b). With the increase in tree

density a linear decline in coleoptile length was observed. It must be noted, however, that these relations originate within differences in the seeds produced in the various tree density plots and were independent of actual competition from the established trees.

7.4.5.3 ETTE ha^{-1} versus root and coleoptile growth rates

There was a very low, non-significant positive relation (P = 0.56) between the ETTE ha^{-1} and root growth rate of the seeds harvested from the different tree density gradients (Figure 7.13a).
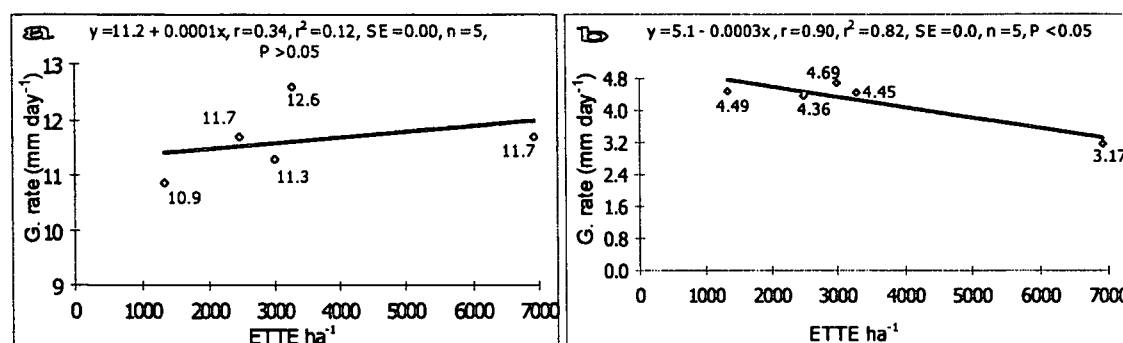
Figure 7.13 Regression analysis of the relations between ETTE ha^{-1} versus (a) root growth rate and (b) coleoptile growth rate of the germinated seeds.

A significant (P = 0.022) negative relation was observed between ETTE ha^{-1} and coleoptile length (Figure 7.13b). With the increase in tree density a linear decline in coleoptile growth rate was observed. Once again, this is an indirect relation independent of any direct competitions between the germinated seeds and the established trees.

7. 5 CONCLUSIONS

The following general conclusions can be drawn from this investigation:

(i). Thinning of *A. mellifera* trees had no effect on the germination potential of the seeds produced by trees from the various tree density plots.

(ii). An extremely high germination potential of the fresh *A. mellifera* seeds was found (> 99%) with no signs of any seasonal dormancy.

(iii). The bruchid beetles that specifically affect the seeds of *A. mellifera* are *Bruchidius* species that belongs to the family Bruchidae. Bruchid beetles infested seeds exhibited a

low, but fast germination rate possibly due to faster imbibition of moisture. In general, the damage due to bruchid beetle infestation was very minimal (< 2%).

(iv). No marked differences in root length and root growth rate were observed for the germinated seeds harvested from the different tree density plots. However, seeds harvested from the lower tree density plots attained a longer coleoptile length and a faster coleoptile growth rate than those from the control (100%) plot.

(v). The correlation between the potential tree competitiveness (ETTE ha^{-1}) versus root length and root growth rate were very low. Potential tree competitiveness was, however, correlated (indirectly) with the coleoptile length and coleoptile growth rate of the germinated seeds.

CHAPTER 8

SOIL NUTRIENTS WITHIN CANOPIED AND UNCANOPIED SUB-HABITATS IN RELATION TO THE TREE DENSITY GRADIENT

8.1 INTRODUCTION

Established trees create subhabitats that differ from the open habitat and which exert different influences on the herbaceous layer (Belsky *et al.,* 1989; Smit & Rethman, 1989; Smit, 1994; Smit & Swart, 1994). Most comparative studies, which have involved *Acacia* species, have shown that soil enrichment under their canopies were higher than under non-leguminous tree species (Smit, 1999a). The relatively high nutrient status of soil beneath, compared to between tree canopies (Smit & Swart, 1994), would be expected to lead to a relatively higher nutrient content of the grasses growing under the tree canopy.

In general, studies have shown that soil under tree canopies has higher concentrations of nitrogen, soil organic matter, phosphate and exchangeable cations like potassium, magnesium and calcium compared to soils from the open areas (Kellman, 1979; Belsky *et al.,* 1989; Smit & Swart, 1994, Asferachew *et al.,* 1998; Smit, 1999a). In addition, soil under tree canopies often exhibits a higher pH and electrical resistance than soil between tree canopies. The influence of the tree canopy on the pattern of soil enrichment is clearly demonstrated by the gradient of soil nutrients found away from the trunk. The highest concentrations are often found adjacent to the trunks, and decline away from the trunk (Smit, 1999a). In Mopane veld, Smit (1994) reported that subhabitat differentiation by Mopane trees did provide some qualitative benefits. Some good forage grass species, which typically have high crude protein and *in vitro* digestibility values, prefer the canopied subhabitat to the open subhabitat and would probably be lost with the removal of all the Mopane trees.

Taking into consideration the positive aspect of soil enrichment by trees, it is necessary to decide wisely on the intensity of tree thinning. For this reason, the need for the study of subhabitat differentiation on soil nutrient status, under and between *Acacia mellifera* shrubs, along the tree density gradient, was of crucial importance.

The objectives of this study were:

(i) To determine the extent of differences in soil nutrient status under *A. mellifera* canopies in comparison to the uncanopied (open area) subhabitats.

(ii)   To understand the influence of tree thinning on the pattern and status of soil nutrients along the tree density gradient.

8.2 PROCEDURE

8.2.1 Soil sampling

Six *Acacia mellifera* trees, three from the right edge and three from the left edge of the transects, were randomly selected from each plot and labelled accordingly. The random selection was done in such a way as to avoid the overlapping of selected trees especially in high tree density plots.

According to the procedures followed by Smit & Swart (1994), three subhabitats were distinguished per sample tree in the experimental plots: between trees (open/ uncanopied area) and two canopied subhabitats, that is, around the stem base area and under the canopy spread (see Figure 6.1). Due to the close proximity of the trees, especially in the high tree density plots and the extensive shallow lateral root system of *Acacia mellifera* (Rutherford, 1980; Smit, 1999a), the uncanopied open subhabitat fell within the root zone.

A quadrat of 0.25 m x 0.25 m was used to excavate a volume of 0.0125 m^3 (0.25 m x 0.25 m x 0.2 m) soil from each subhabitat of the sample trees along the tree density gradient. The soil was thoroughly mixed.

For soil chemical analysis, soil samples were only collected from three sample trees per plot. In this case the 45 soil samples were represented by soils from 3 randomly selected samples x 3 subhabitats x 5 experimental plots. For the determination of soil particle size (soil physical analysis) all soil sample were thoroughly mixed and one sub sample taken for analysis.

8.2.1 Soil physical analysis

Soil texture (particle size) analysis of the experimental site was determined by means of the standard Bouyoucos (hydrometer) method. Analysis conducted included % clay, % sand and % silt.

8.2.3 Soil chemical analysis

Soil chemical analysis was done in the soil chemistry laboratory of the Department of

Soil Science of the University of the Free State according to the standards of the Non-Affiliated Soil Analysis Work Committee (1990).

Analysis conducted included soil pH, total nitrogen in soil (Kjeldahl method), % organic matter (Walkley–Black method), phosphorus (Bray-2 method), and exchangeable cations, viz. sodium (Na), potassium (K), calcium (Ca) & magnesium (Mg). The exchangeable cations were extracted by leaching the sample soil with normal ammonium acetate extract and analyzed spectrophotometrically.

8.3 DATA ANALYSIS

The soil chemical analyses for the various subhabitats were done in replicate. The averages of all sample soils of the three soil subhabitats viz. (i) soil around the stem base area, (ii) soil under the canopy spread, and (iii) soil in open area was used for data analysis. For each subhabitat, the three randomly selected soil samples from each plot and the five tree density gradients were considered as replications of the subhabitats, that is, fifteen replications for each subhabitat (Smit & Swart, 1994). For the test of differences in the soils between the three soil subhabitats, a computerized model of one factor Randomized Complete Block Design (RCBD) was implemented (Mstat-C, 1991, Mead et al., 1993). Least significant differences (LSD's) test for means separation were also calculated from the appropriate standard errors (SE) (Mstat-C, 1991).

The mean results of the soil chemical analysis along the tree density gradient were presented graphically using Microsoft Excel graphics (Microsoft Excel, 1997).

8.4 RESULTS AND DISCUSSION

8.4.1 Soil particle size

The results of the soil particle size, as determined by the physical analysis of the soils of the experimental site, indicated that the soil of the study area is very sandy (93.116%) with a limited percentage of clay and silt (4.917% and 1.967% respectively). This corresponds with similar reports by Donaldson (1969) and Acocks (1988) which described the soil as Kalahari sand.

8.4.2 Soil chemical analysis

The mean results of the soil chemical analysis of the experimental site are presented in

Table 8.1. Donaldson (1969) reported that the sands of the Molopo area are extremely low in organic matter and mineral elements. Similar results were obtained from this investigation, indicating a very low nutrient and mineral content of the soil of the study area.

TABLE 8.1 Mean values of the soil chemical analysis of all the soil samples (n = 45) collected in the experimental plots.

pH (H$_2$O)	Phosphorus (mg kg^{-1})	Total N (mg kg^{-1})	Org. matter %	Exchangeable cations (mg kg^{-1})			
				Ca	Mg	K	Na
5.12	2.98	241.71	0.69	379.78	77.96	30.89	66.71

8.4.2.1 Soil pH in relation to soil subhabitat

The mean soil pH (all plots combined) in relation to the three soil subhabitats, viz. around the stem area, under the canopy spread and in the open area is presented in Figure 8.1. The pH differed non-significantly between the three subhabitats. However, the pH values were the lowest close to the stem and increased further away (Figure 8.1).
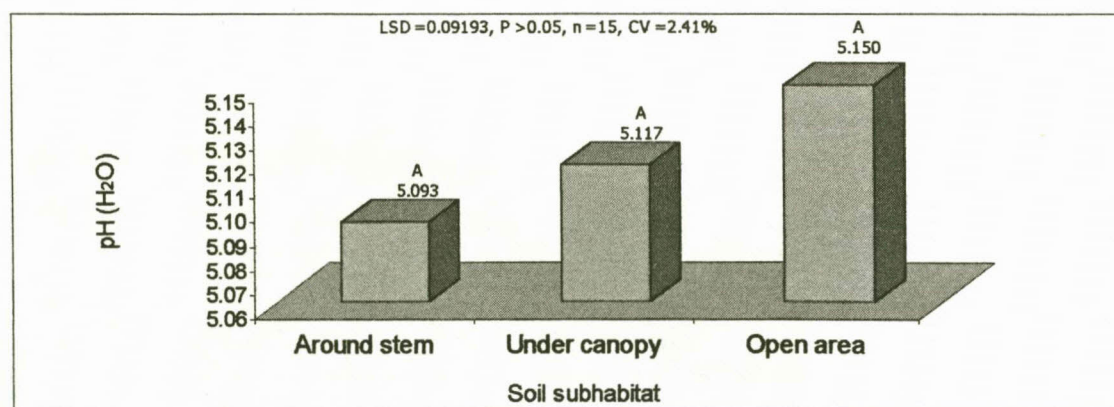
Figure 8.1 Mean soil pH of the three soil subhabitats.

In general, a higher pH was found in open areas (between canopies) than under canopies. This result corresponds with the findings of Belsky *et al.* (1989) who recorded a lower pH (5.4) at the base of *Acacia* trees than further from the trunk (6.3). In contrast to these results, Smit & Swart (1994) reported a higher pH under tree canopies (*Acacia erubescens* and *Combretum apiculatum*) than in the uncanopied subhabitat (open area).

Marked differences in soil pH were recorded between the soil from the low tree density plot (10%) and the other four tree density plots (Figures 8.2a and 8.2b). The very acidic nature of the 10% plot may be due the lower concentrations of exchangeable cations like Ca & Mg in this plot (Bornman et al., 1989).
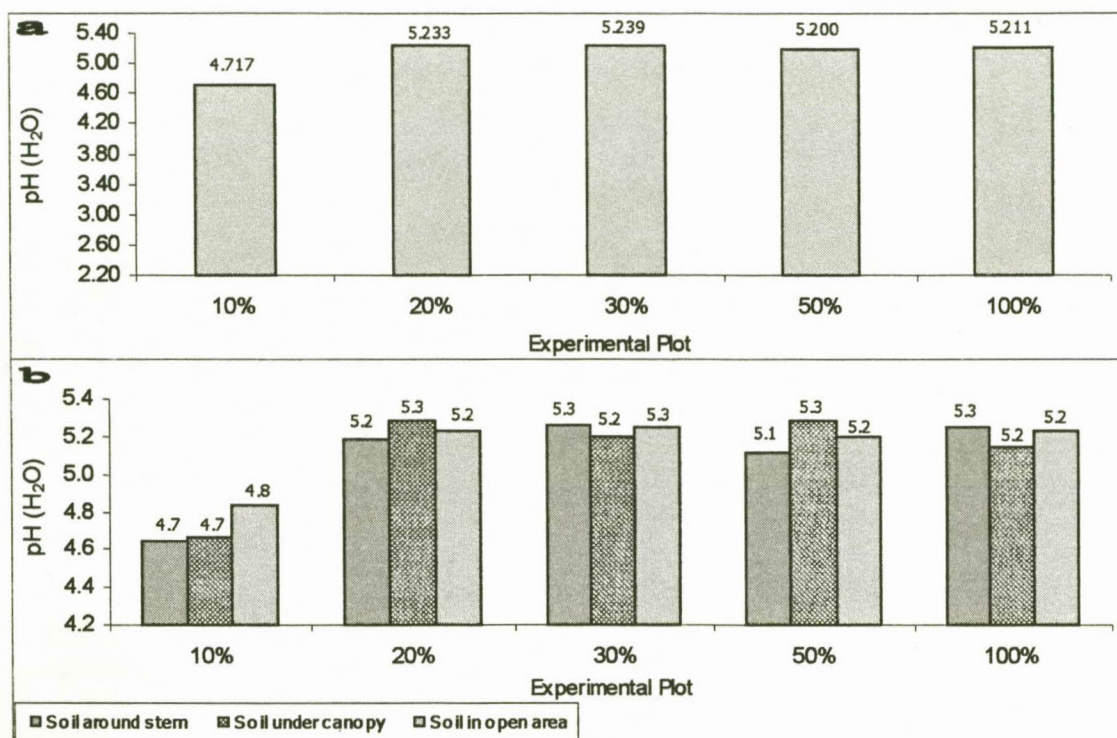
Figure 8.2 Mean soil pH of the experimental plots (a = all subhabitats combined (n = 9), and b= defined subhabitats (n =3)).

8.4.2.2 Soil Phosphorus content

The mean soil P (all plots combined), in relation to the three soil subhabitats is presented in Figure 8.3
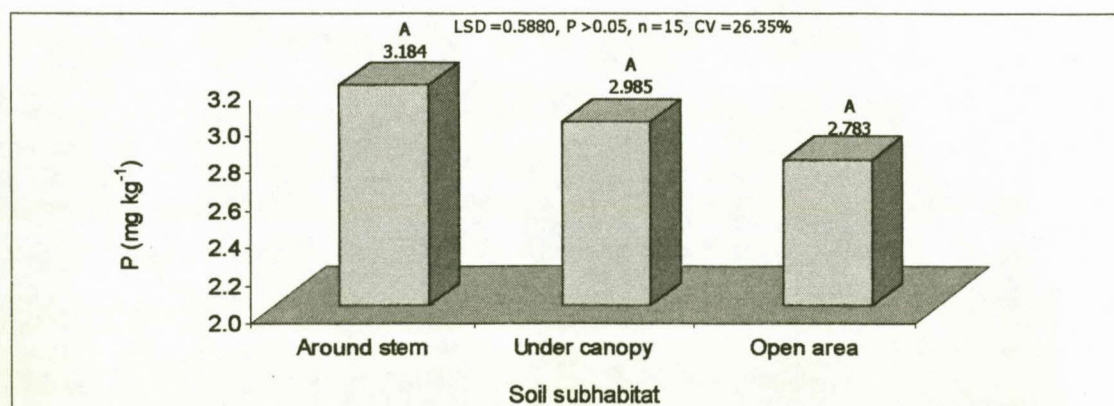
Figure 8.3 Mean soil P concentrations of the three soil subhabitats.

The mean P content of the three defined subhabitats did not differ significantly (P = 0.235). However, the mean P content was higher in soils around the stem base and declined linearly towards the open area (between trees) (Figure 8.3). Similar to this result, Smit & Swart (1994) reported a non-significant difference in P concentration between soils under trees and between trees, with the P concentration marginally higher in soils from between trees (13.96 mg kg^{-1}) than under tree canopies (13.40 mg kg^{-1}). In another study, this time involving *Colophospermum mopane*, a significantly higher P content was recorded under their canopies in comparison to that in the open (Smit, 1994). Several other studies also reported a higher P content under tree canopies than in the open (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Kellman, 1979; Belsky *et al.,* 1989; Smit & Swart, 1994).

Marked differences in soil phosphorus concentration between the high tree density plot (100%) and the lower tree density plots (10% and 20%) were observed (Figure 8.4a). With the increase in tree density, the amount of phosphorus in the soil also increased linearly. Though statistically non-significant (P < 0.05), these results suggest that a high intensity of tree thinning may in time result in a reduced P content of this sandy soil.
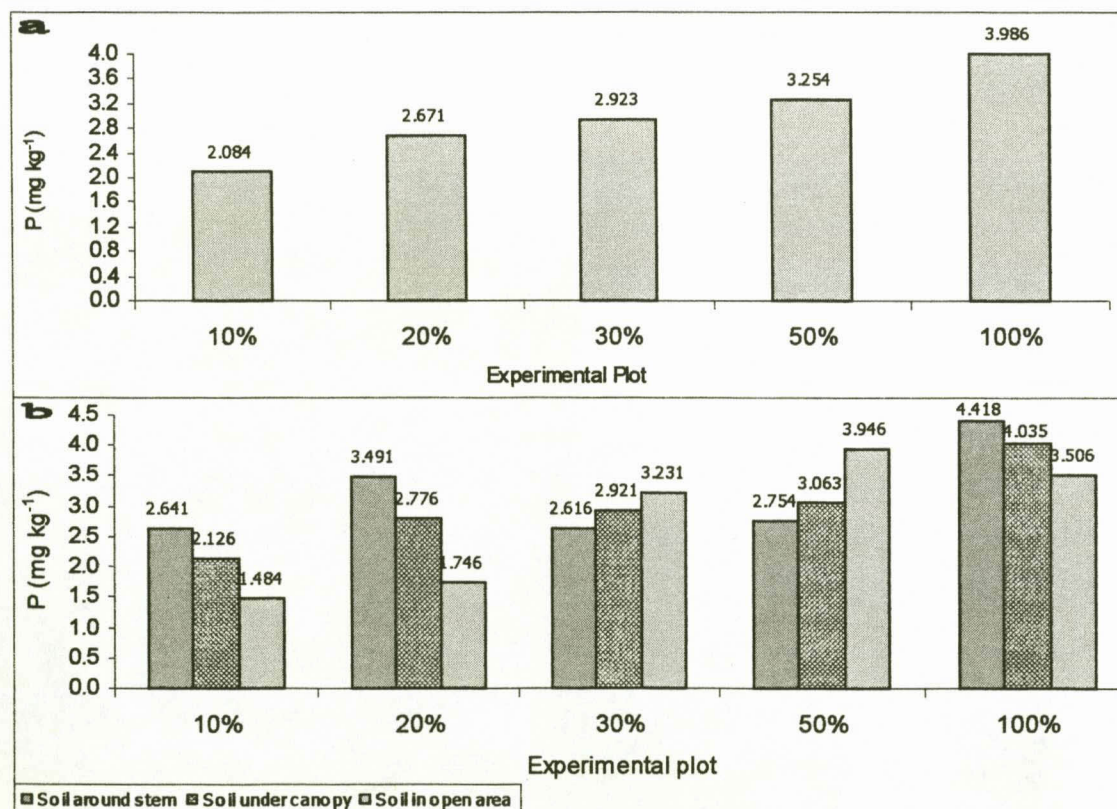
Figure 8.4 Mean soil phosphorus of the experimental plots (a = all subhabitats combined (n = 9), and b= defined subhabitats (n =3)).

From Figure 8.4b it is clear that a consistent pattern in the P content in the soil from the different subhabitats along the tree density gradient is lacking.

8.4.2.3 Total Nitrogen content

A highly significant difference (P = 0.000) was found between the mean total N content in the soils from the stem base area and the remaining two subhabitats, with the N content much higher under the tree canopies (Figure 8.5).
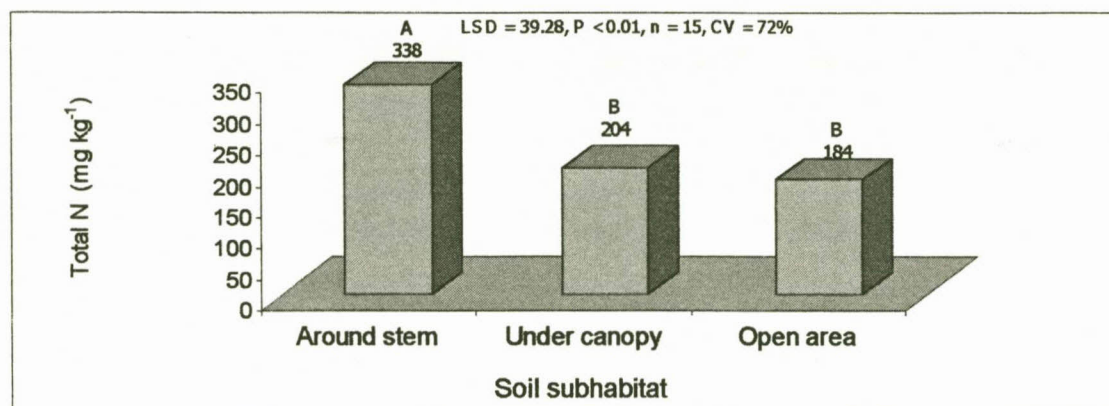
Figure 8.5 Mean total N concentrations of the three soil subhabitats.
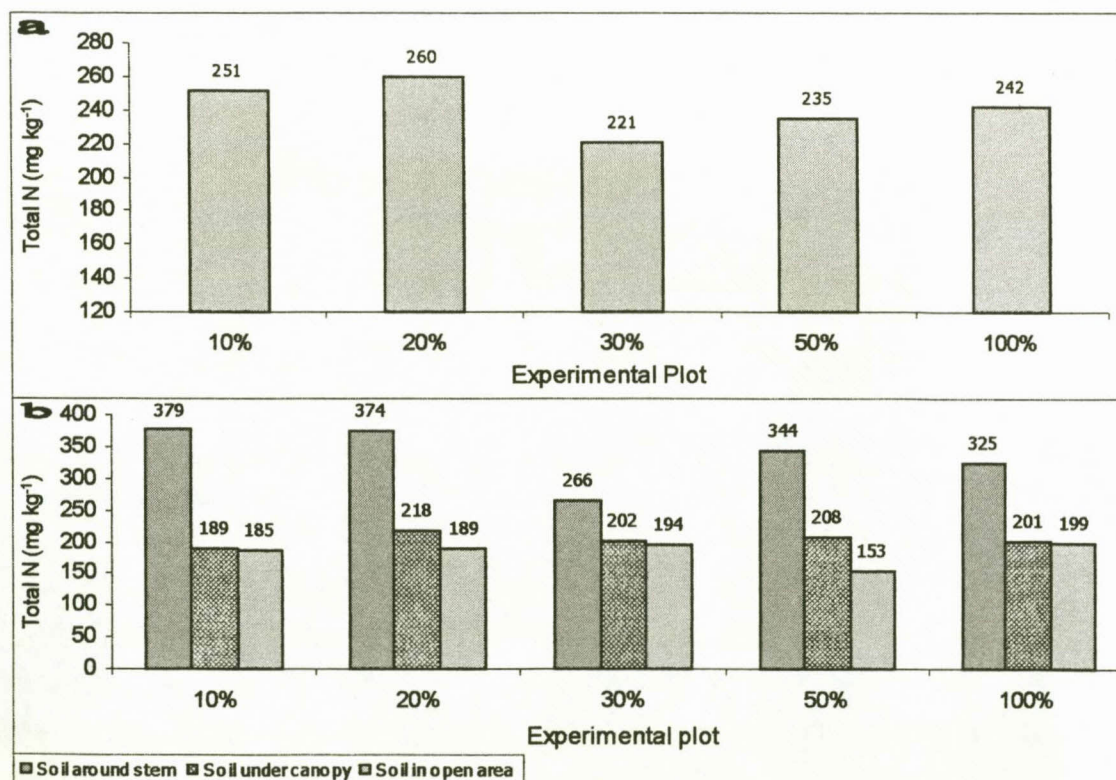
Figure 8.6 Mean total N of the experimental plots (a = all subhabitats combined (n = 9), and b= defined subhabitats (n =3)).

This corresponds with several other studies, which also reported a higher N content under canopies than in the open (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Tiedemann & Klemmedson, 1973; Smit & Swart, 1994).

No marked differences in total N content of the soils along the tree density gradient were observed. According to Teague & Smit (1992), a temporary increase in soil nutrient content after clearing may result from the nutrient release from decaying roots of felled trees. This could account for the slightly higher N status in the soil of the 10% and 20% plots. However, with thinning that commenced more than 10 years ago, this is an unlikely explanation. The relatively high concentration of total N in the low tree density plots could also be attributed to the fact that *Acacia mellifera* trees have extended root system and microbial synthesis of N always occurs by nitrogen fixing bacteria located in the root nodules.

In all plots along the tree density gradient the total N content was substantially higher within the two canopied subhabitats than the uncanopied (open) area. This confirmed previous reports of a high N content in soil from under tree canopies (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Tiedemann & Klemmedson, 1973; Smit & Swart, 1994) and emphasize the importance of *A. mellifera* in maintaining soil fertility on this sandy soil.

8.4.2.4 Organic matter of the soil

A highly significant difference (P = 0.0002) was found between the mean organic material content in the soils from the stem base area and the remaining two subhabitats, with the organic material much higher under the canopies (Figure 8.7).
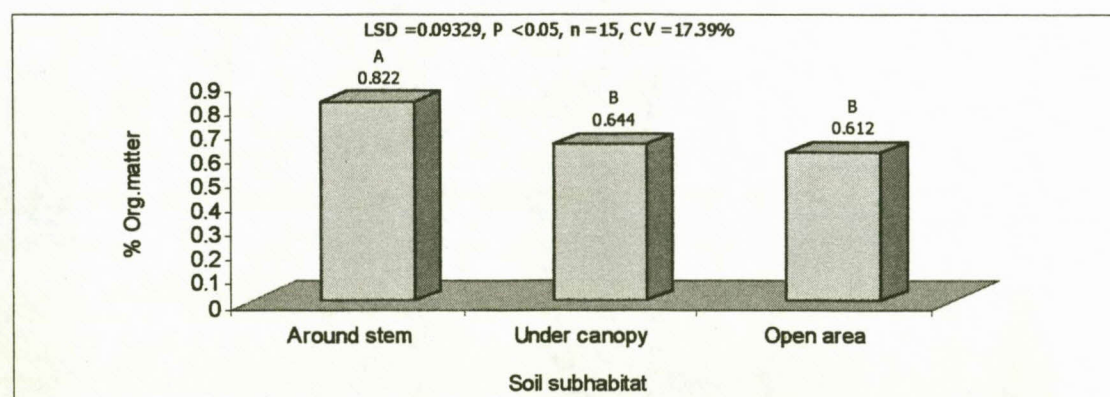
Figure 8.7 Mean percentage organic matter of the three soil subhabitats.

There are several other studies that also reported a higher organic matter content under tree canopies than in the open (Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Kellman, 1979; Belsky *et al.,* 1989; Smit & Swart, 1994).

The percent organic matter of the soils along the tree density gradient is presented in Figure 8.8a. There was no marked difference in organic matter content of the soils between plots. However, the magnitude of organic matter content increased marginally from low tree density to the high tree density plots. All this result implies is that the soil under and adjacent to individual trees did not differ between the tree density plots. However, based on a higher tree canopy cover with an increase in tree density, the total organic matter content should be higher in the high tree density plots in comparison to the low tree density plots.

In all plots along the tree density gradient, the organic matter content was substantially higher within the two canopied subhabitats in comparison to the uncanopied subhabitat (Figure 8.8b). Similar to the results of the total N, these results once again emphasize the importance of *A. mellifera* in maintaining soil fertility.
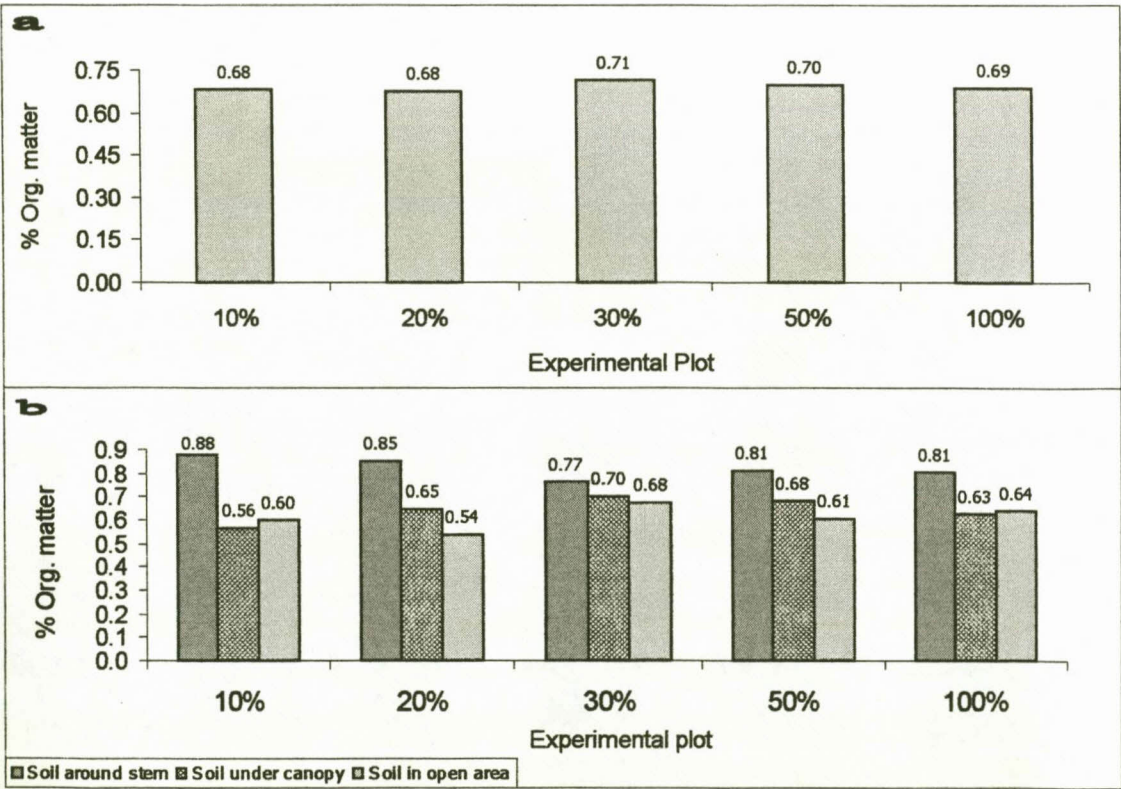
Figure 8.8 Mean organic matter of the experimental plots (a = all subhabitats combined (n = 9), and b= defined subhabitats (n =3)).

8.4 2. 5 Exchangeable cations

The results of the exchangeable cation variables of the soils excavated from the three soil subhabitats of the experimental site are presented in Figure 8.9.
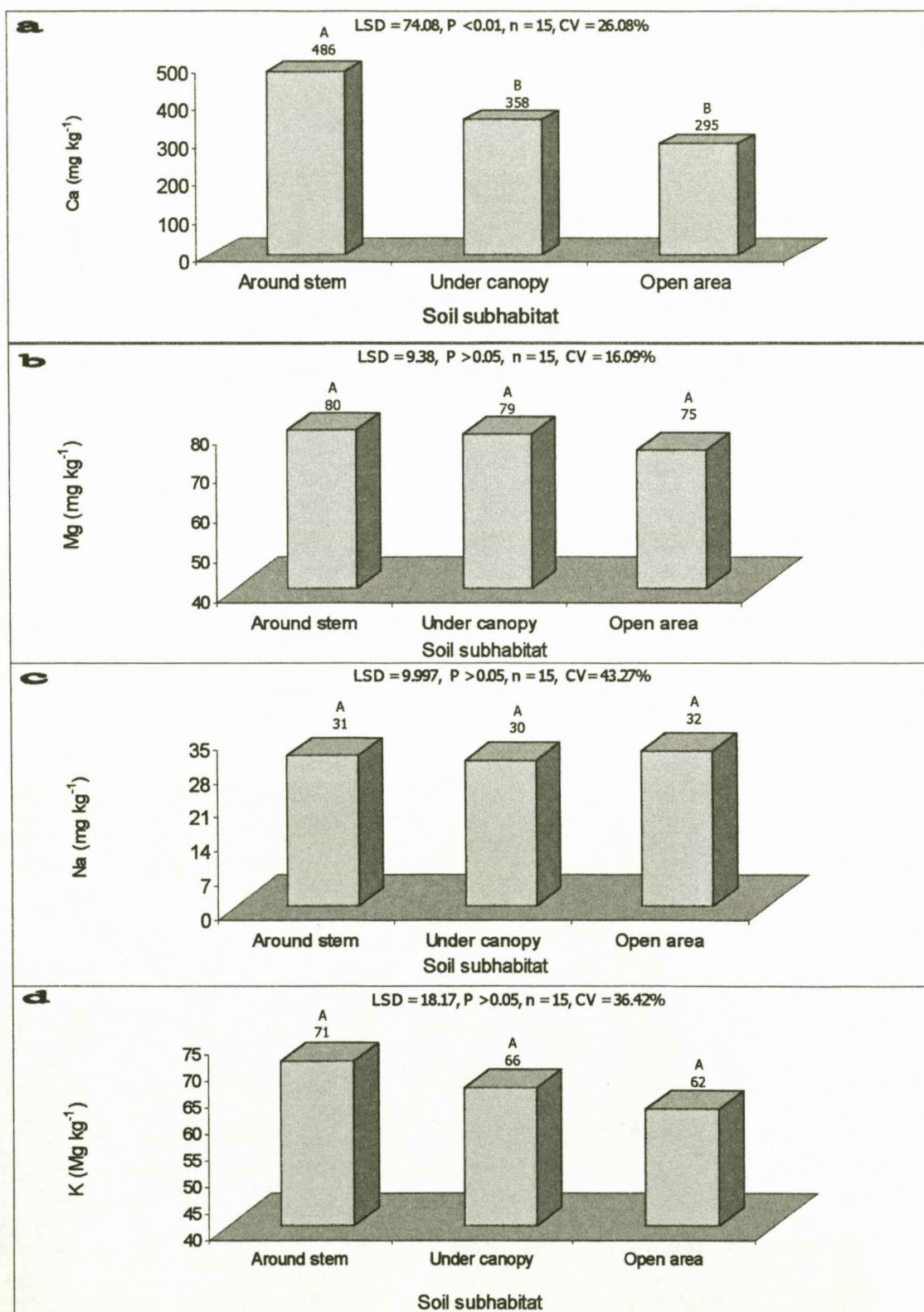
Figure 8.9 Results of the mean exchangeable cation contents (Ca, Mg, Na & K respectively) of the three soil subhabitats.

Similar to the results of Bosch & Van Wyk, 1970; Kennard & Walker, 1973; Kellman, 1979; Belsky et al., 1989; Smit & Swart, 1994), there was highly significant differences (P = 0.0000) between the mean Ca content between the canopied and uncanopied subhabitats (Figure 8. 9a). The highest Ca content was recorded close to the stem and the Ca content declined towards the uncanopied area.
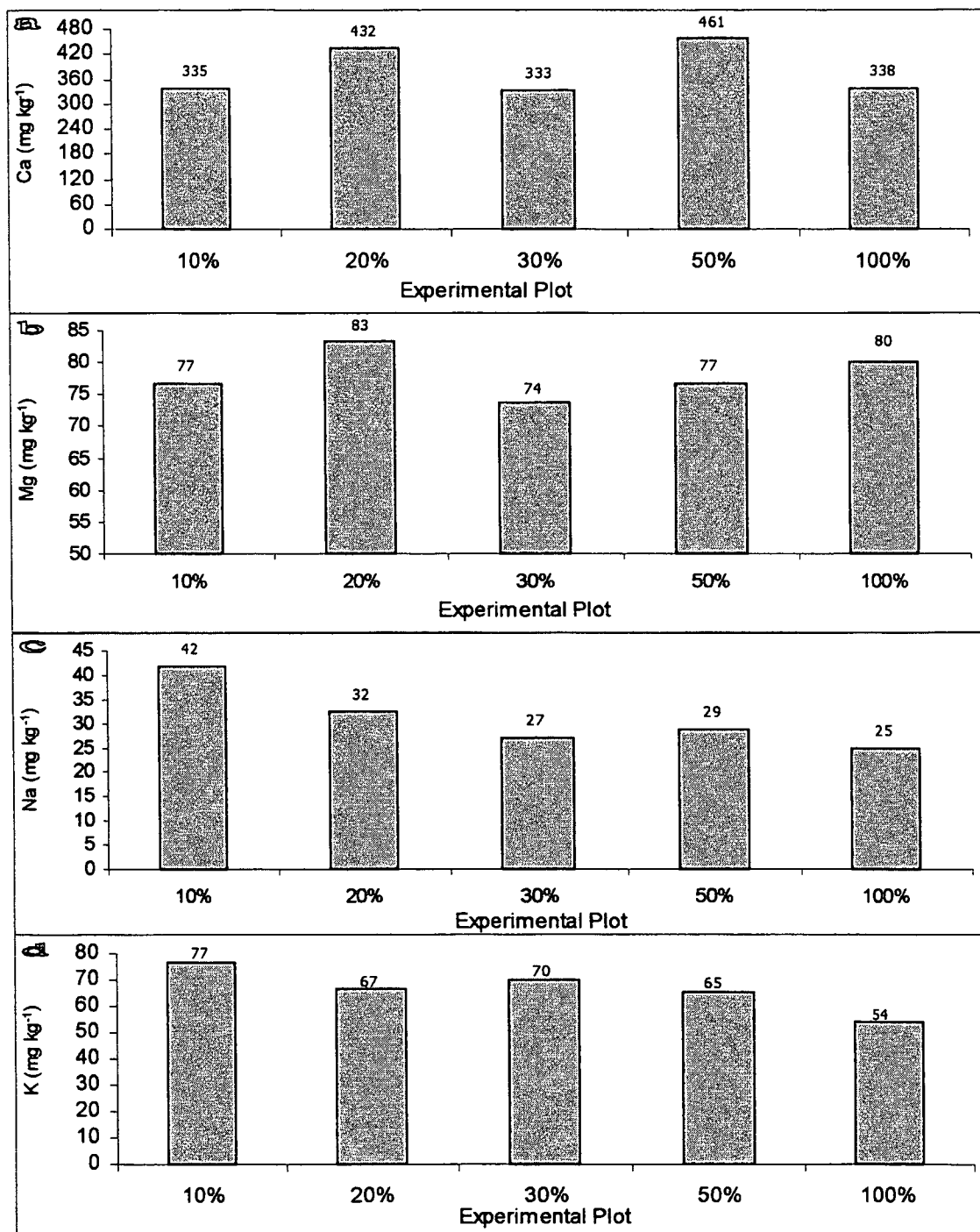
Figure 8.10 Mean results of the exchangeable cation variables along the tree density gradient.

No marked differences in the exchangeable cations Mg, Na and K between the canopied and uncanopied subhabitats were observed (Figures 8.9b, 8.9c & 8.9d respectively). Similar to this result, Smit & Swart (1994) reported a non-significant difference in Na content between the canopied and uncanopied subhabitats of *A. erubescens* and *Combretum apiculatum*. However, in contrast to this finding, significant difference for Mg and K variables between the subhabitats was reported in the same study by Smit & Swart (1994).

The mean results of the exchangeable cation variables (Ca, Mg, Na & K) along the tree density gradient are presented in Figure 8.10.

Except for Na, no marked differences in exchangeable cations (Ca, Mg & K) were observed between plots (Figures 8.10a, 8.10b, 8.10c and 8.10d respectively). As mentioned, however, there was a visual marked difference in Na content between soils of the low tree density plots and the high tree density plots. The concentration of Na was higher in the low tree density plots (10% and 20%) as compared to the control plot (100%).

The mean results of the exchangeable cation variables of the three soil subhabitats along the tree density gradient are presented in Figure 8.11.

From the mean values of all the soil samples combined (Figure 8.9) it is evident that soil from the canopied subhabitats has a higher content of Ca (Figure 8.9a) and K (Figure 8.9d). The influence of subhabitat differentiation had a less distinct influence on Mg (Figure 8.9b) and Na (Figure 8.9c). The former distribution pattern of Ca along the subhabitat gradients was fairly consistent along the tree density gradient (Figure 8.11a), but some variation was recorded in the case of Mg, Na and K (Figure 11b, c and d).

As in the case of N and organic matter the results presented in Figure 8.10 merely show the mean difference in soil under and adjacent to individual trees. If the higher tree canopy cover of the high tree density plots is taken into consideration, it is evident that some cations, especially Ca and K, should be higher in the high tree density plots.
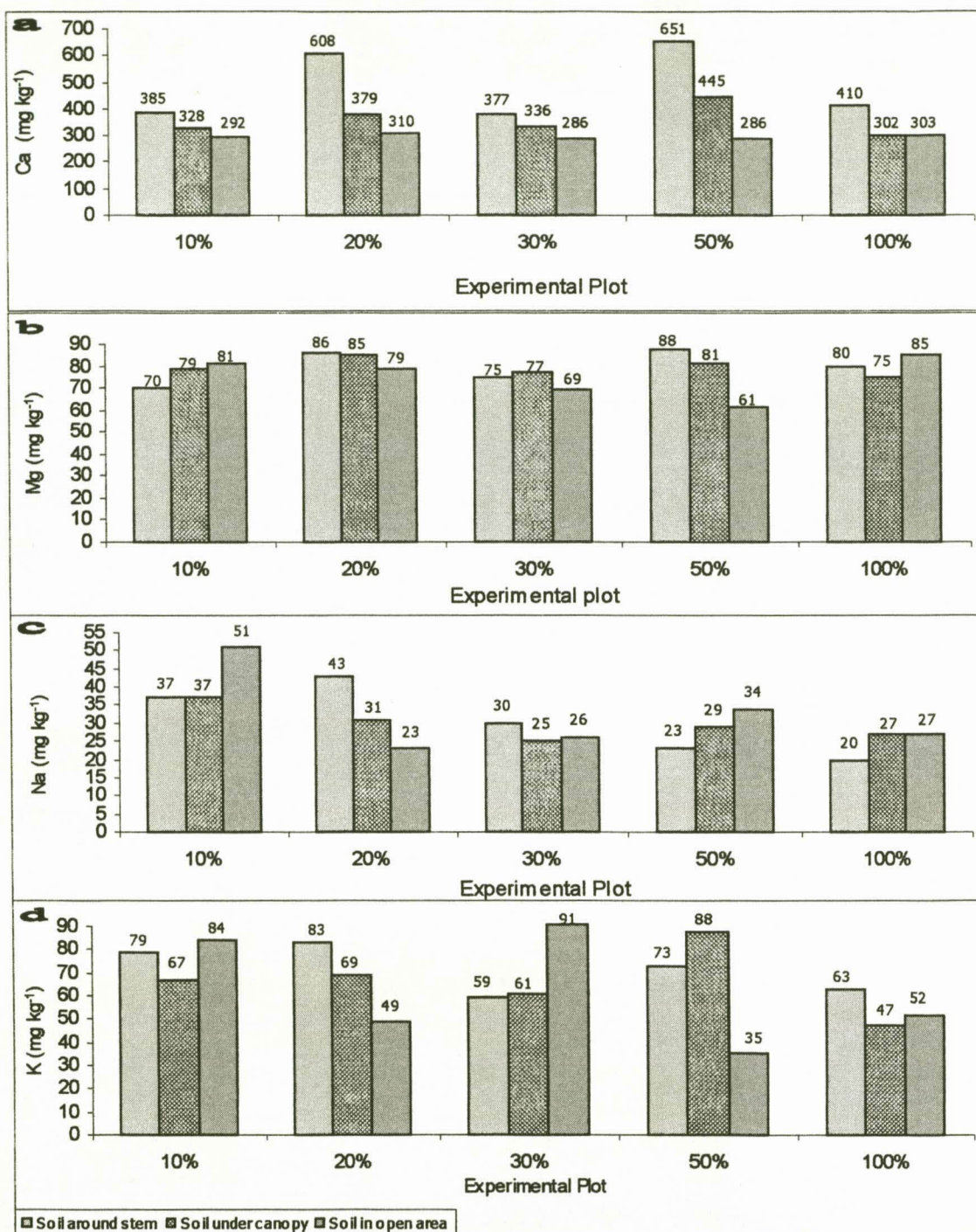
Figure 8.11 Mean results of the exchangeable cation variables of the three soil subhabitats along the tree density gradient.

8.5 CONCLUSIONS

The following general conclusions can be drawn from this investigation:

(i). The soils excavated from the canopied subhabitats were more acidic than the uncanopied subhabitat. At a low tree density, the soils were also more acidic than at

higher tree densities. This lower soil pH could be due to the relatively low Ca and Mg content and low availability of P in the low tree density plot (10%), possibly as a result of tree thinning.

(ii). The soils from the canopied subhabitats displayed higher concentration of P than the uncanopied (open) subhabitat. Marked difference in P content was also observed in all plots. The amount of P was much higher in the control plot (100%) than the lower tree density plots. This result clearly indicates the effect of three thinning in the depletion of soil P content.

(iii). A higher total N content was recorded at the stem base area than in the remaining two subhabitats. The results of the organic matter are remarkably similar to that of the total N. This confirms other reports of a high N and organic matter content in soil from under tree canopies and emphasizes the importance of A. mellifera in maintaining soil fertility on this sandy soil possibly up to a certain threshold value (density).

(iv). In general, no marked differences in exchangeable cations were demonstrated between the canopied and uncanopied soil subhabitats, except for Ca. The canopied subhabitats had a higher Ca concentration than the uncanopied (open) area. The trend of exchangeable cation concentration was relatively higher in the canopied subhabitats. Similarly, no marked difference in exchangeable cations was observed between plots except for Na. The concentration of Na and K in the low tree density plot was higher than the control plot. The very acidic nature of the low tree density plot could be due to the availability of a higher concentration of Na in it as opposed to the control plot (100%).

CHAPTER 9

SEEDLING ESTABLISHMENT WITHIN DIFFERENT SOIL SUB-HABITATS ALONG THE TREE DENSITY GRADIENT

9.1 INTRODUCTION

According to Dye & Spear (1982), differences in the response to clearing may be ascribed to differences in soil type and soil fertility, both of which are important determinants of the magnitude of the response to tree thinning. Plant analysis indicated greater nutrient contents (N, P, K, Ca and Mg) in the leguminous than the non-leguminous species (Pakrashi, 1991) and he suggested that the addition of leguminous leaves might increase the soil nutrient content, which will benefit seedling establishment. Dunham (1991) compared soil nutrient concentrations under *Acacia albida* and *Kigelia africana* trees growing in Zambezi riverine woodland with soils in the open area. Concentrations of N, C, P, and K were greater under canopies, but the content of Ca and Mg were not different to those from soils in the open.

However some tree species, including *Acacia* species, may have allelopathic effects that inhibit growth of other species, such as grasses, below them. To investigate allelopathic effects of *Artemisia scoparia,* as donor plant, and their biological activities, seed germination and seedling growth of receptor plants were examined at different concentrations of essential oil of the donor plant (Hyeon *et al.,* 2001). The treatment of the volatile essential oils of the *A. scoparia* caused significant inhibition in the germination, shoot and radicle growth of the receptor plants. The radicle growth of receptor plants was inhibited more severely than that of shoot growth. The results of this experiment on seed germination, seedling growth, anti- microbial test and tissue and culture indicated that naturally occurring chemical substances of essential oil from *A. scoparia* would be responsible for the allelopathic effects.

This specific chapter deals with the seedling establishment of *Acacia mellifera* trees in soils from defined subhabitats (see Figure 6.1) collected along the tree density gradient.

The objectives of this study were:

(i)   To determine differences in seedling establishment and survival of *A. mellifera* in soils from under canopies and between the canopies along the tree density gradient.

(ii)   To determine the differences in stem and root lengths of *A. mellifera* seedlings grown in soils from under canopies and between canopies along the tree density gradient.

(iii)   To determine differences in dry matter production between seedlings grown in soils from different subhabitats along the tree density gradient.

(iv)   To understand the relations between seedling root length, stem length and dry mass and the tree density (ETTE ha^{-1}).

9.2 PROCEDURES

9.2.1 Soil sampling

The procedures followed for soil sampling was similar to that described in Chapter 8 (see section 8.2.1), except that all soils sampled from the selected *A. mellifera* trees were used. In this case, the 90 soil samples are represented by soils from 6 randomly selected samples x 3 subhabitats x 5 experimental plots. Medium sized plastic pots were filled with these soils to represent 6 sample trees x 3 subhabitats for each plot (Figure 9.1).

9.2.2 Seedling establishment

A seedling establishment trial was undertaken that commenced on 17 March 2001 in a controlled environment at the green house of the Department of Grassland Science of the University of the Free State. Temperature was regulated at 27°C by means of a thermostat and the relative humidity was maintained above 65%.

In order to establish *Acacia mellifera* seedlings successfully in all the pots, 300 *A. mellifera* seeds (6 seeds/sample tree) were randomly selected and thoroughly mixed. To ensure seed imbibition to facilitate germination in pots, the seeds were immersed in cold water for about 24 hours. A total of 270 already imbibed seeds were selected and three seeds per pot were sowed. After emergence only one randomly selected seedling per pot was kept and the rest removed.

Seedlings were watered regularly every forth day and plant height was measured every five days from 10 days of emergence for about two months.
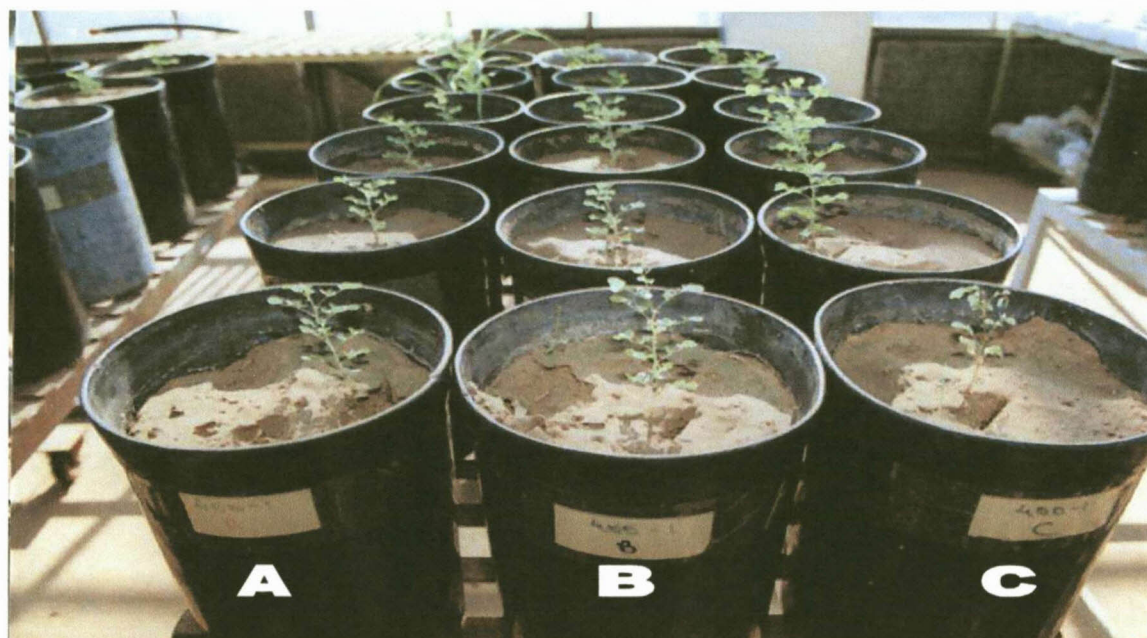
Figure 9. 1. An illustration of the soil collected from the three subhabitats of the six sample trees of each tree density plot (a = soil around stem, b = soil under canopy spread, c = soil in open area).

9.2.3 Harvesting of seedlings

All the *Acacia mellifera* seedlings were harvested on 30 May 2001. Roots were separated from the soil by washing the soils in the mentioned pots with medium pressurized water. This procedure reduces the damage of roots and root hairs and also helps to wash the soils from the root system and the seedling in general.

Leaves and leaflets of each seedling were counted, stem thickness was measured using a caliper and root length was measured using a normal tape by stretching the coiled root stalks.

9.2.4 Seedling dry mass

The leaves, stems and roots of the *Acacia mellifera* seedlings were separated and put in small paper bags. The material was dried to a constant mass at 70°C for 72 hours. Leaf dry mass, stem dry mass and root dry mass was weighed separately using a digital balance at four decimals of a gram.

9.3 DATA ANALYSIS

The average measurements of all *Acacia mellifera* seedlings grown in the sample soils

of the three soil subhabitats, *vs* (i) soil around the stem base area, (ii) soil under the canopy spread and (iii) soil from the open area (uncanopied subhabitat) were used for data analysis. For each subhabitat, the six randomly selected sample soils from each plot and the five tree density gradients were considered as replications of the subhabitats, that is, thirty replications for each subhabitat (Smit & Swart, 1994). For the test of differences between the various seedling establishment measurements, grown in the three different soil subhabitats, a one factor Randomized Complete Block Design (RCBD) was implemented (Mstat-C, 1991). Least significant differences (LSD) were calculated from the appropriate standard errors to estimate the significance of the differences between means (Mstat-C, 1991).

To test the correlation between potential tree competitiveness (ETTE ha^{-1}) and the mean results of the various plant growth parameters of the already established seedlings of the five tree density gradients, regression and correlation analysis was used (Mstat-C, 1991). Microsoft Excel graphics (Microsoft Excel, 1997) was used to present all the results graphically.

9.4 RESULTS AND DISCUSSION

9.4.1 Seedling measurements

9.4.1.1 Plant height

The results of the plant height measurements are presented in Figures 9.2, 9.3 and 9.4.
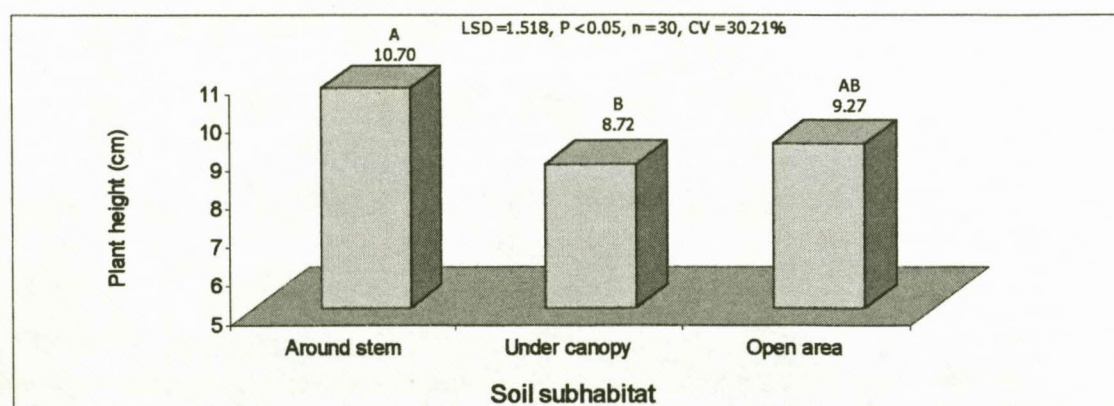
Figure 9.2 Mean plant height of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).

A significant difference (P = 0.033) in plant height between the seedlings grown in soil collected around the stem base area in comparison to the other two subhabitats was

observed (Figure 9.2). The mean plant height of the seedlings that was grown in the soil around the stem area was higher than the seedlings from the other two subhabitats. The higher soil nutrient status of the soil from around the stem base area (N, P, Organic matter and exchangeable cations like Ca, Mg, Na and K) could be the reason for the increase in plant height (see chapter 8). This finding also indicates that no allelopathic substance that inhibits seedling growth is present in soil from under the *A. mellifera* canopies.

The mean plant height of seedlings grown in soil from the low tree density plot (10%) was relatively higher when compared to those grown in soil from the high tree density plot (100%). In general, the seedling height decrease with the increase in tree density, except for seedlings grown in soil from the 50% plot (Figure 9.4a). These results verify that the effect of soil subhabitat differentiation was more important than differences in soil between tree density plots.

The mean results of the plant height of tree seedlings grown in the three soil subhabitats of the five tree density plots are presented in Figure 9.4b. In all plots the seedling heights of those grown in the soil collected from around the stem base area were higher than the other two subhabitats. These results confirm the former conclusion relating to the importance of the enhanced soil nutrient status of the soil from around the stem base on seedling growth.

Figure 9. 3. Selected 70 day old *A. mellifera* seedlings representing the mean height of seedlings grown in soil from the three subhabitats (a = soil around stem, b = soil under canopy spread, c = soil in open area).
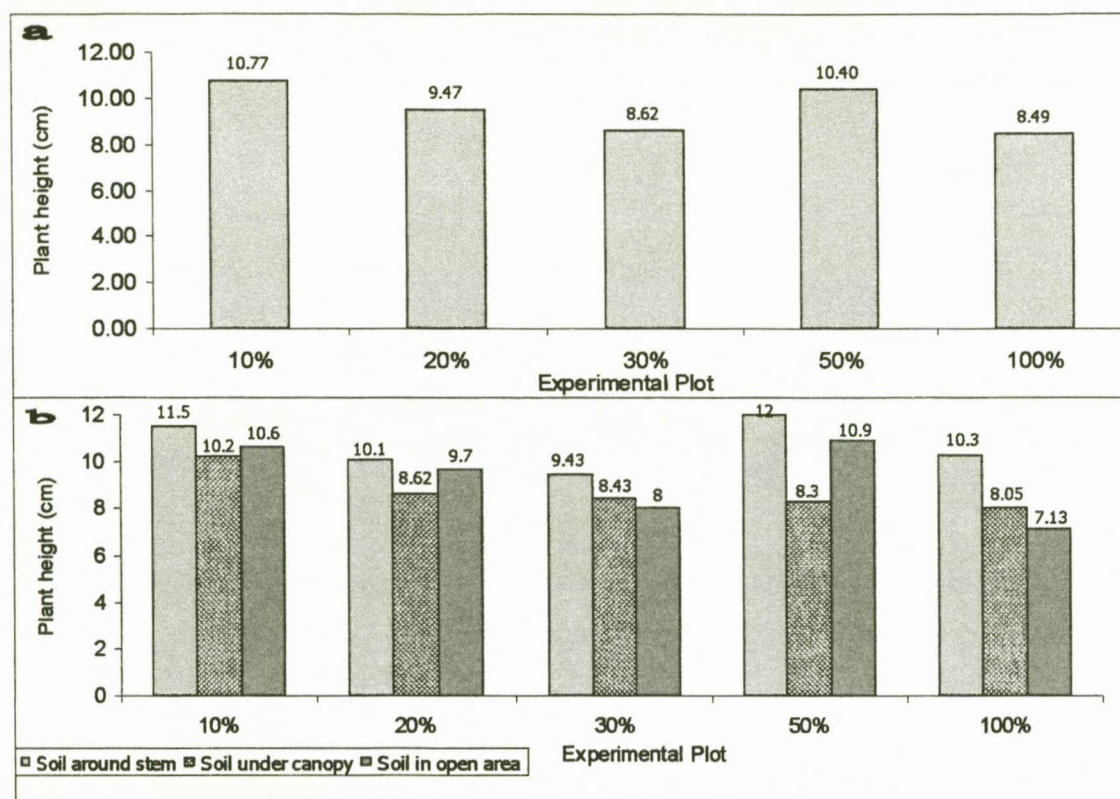
Figure 9.4 Mean plant height of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

9.4.1.2 Stem thickness

The results of the stem thickness measurements are presented in Figures 9.5 and 9.6.
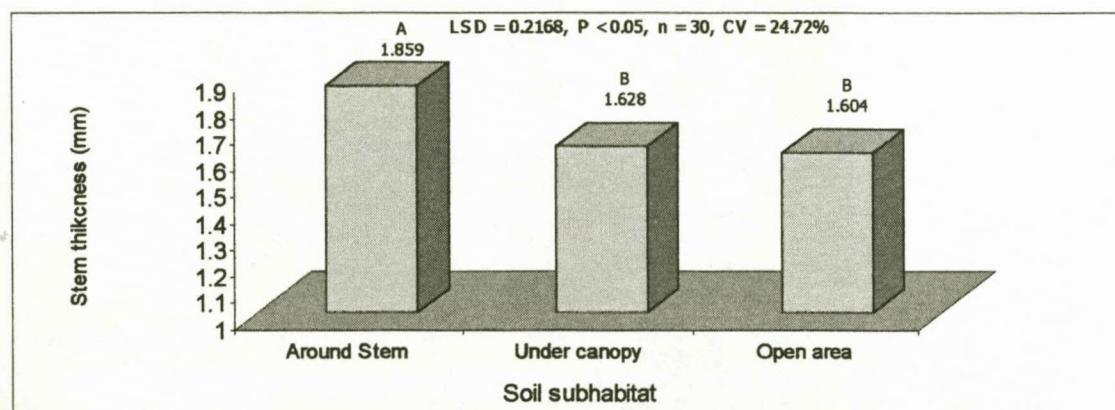
Figure 9.5 Mean stem thickness of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).
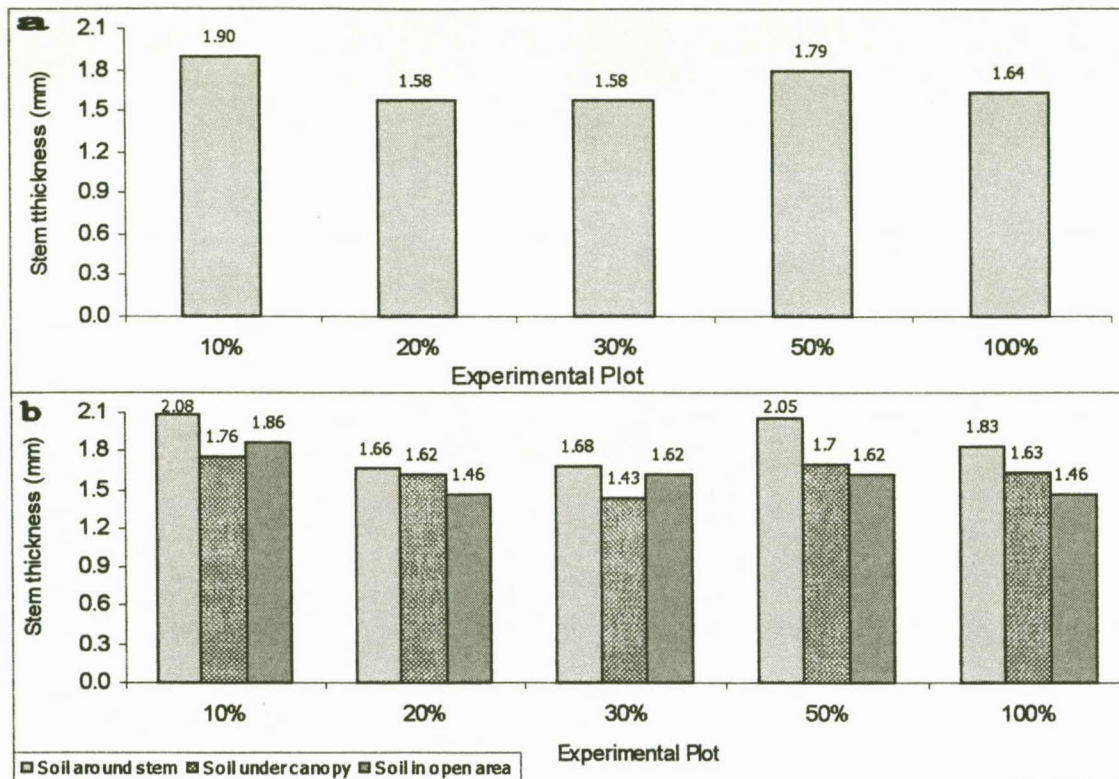
Figure 9.6 Mean stem thickness of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

A significant difference (P = 0.038) in stem thickness between the seedlings grown in soils collected from around the stem base area, and those grown in soils from the subhabitats under the canopy spread and the open area (uncanopied) was observed. The mean stem thickness of the seedlings that were grown in the soil from around the stem area subhabitat was higher than those grown in the soil from the other two subhabitats (Figure 9.5). As in the case of plant height the higher soil nutrient status of the soil from the stem base area is the most likely explanation for this result (see chapter 8).

The mean stem thickness of the seedlings established in soil from the low tree density plot (10%) was relatively higher when compared to those grown in soil from the high tree density plot (100%). In general, no marked differences in stem thickness were observed between plots (Figure 9.6a).

The mean results of the stem thickness of the seedlings grown in the three soil subhabitats of the five tree density plots are presented in Figure 9.6b. In all plots the seedling stem thickness of those grown in soil from around the stem base area were higher than those of the other two subhabitats.

These results, once again, confirmed that the effect of soil subhabitat differentiation was more notable than soil differences between the tree density plots for seedling growth.
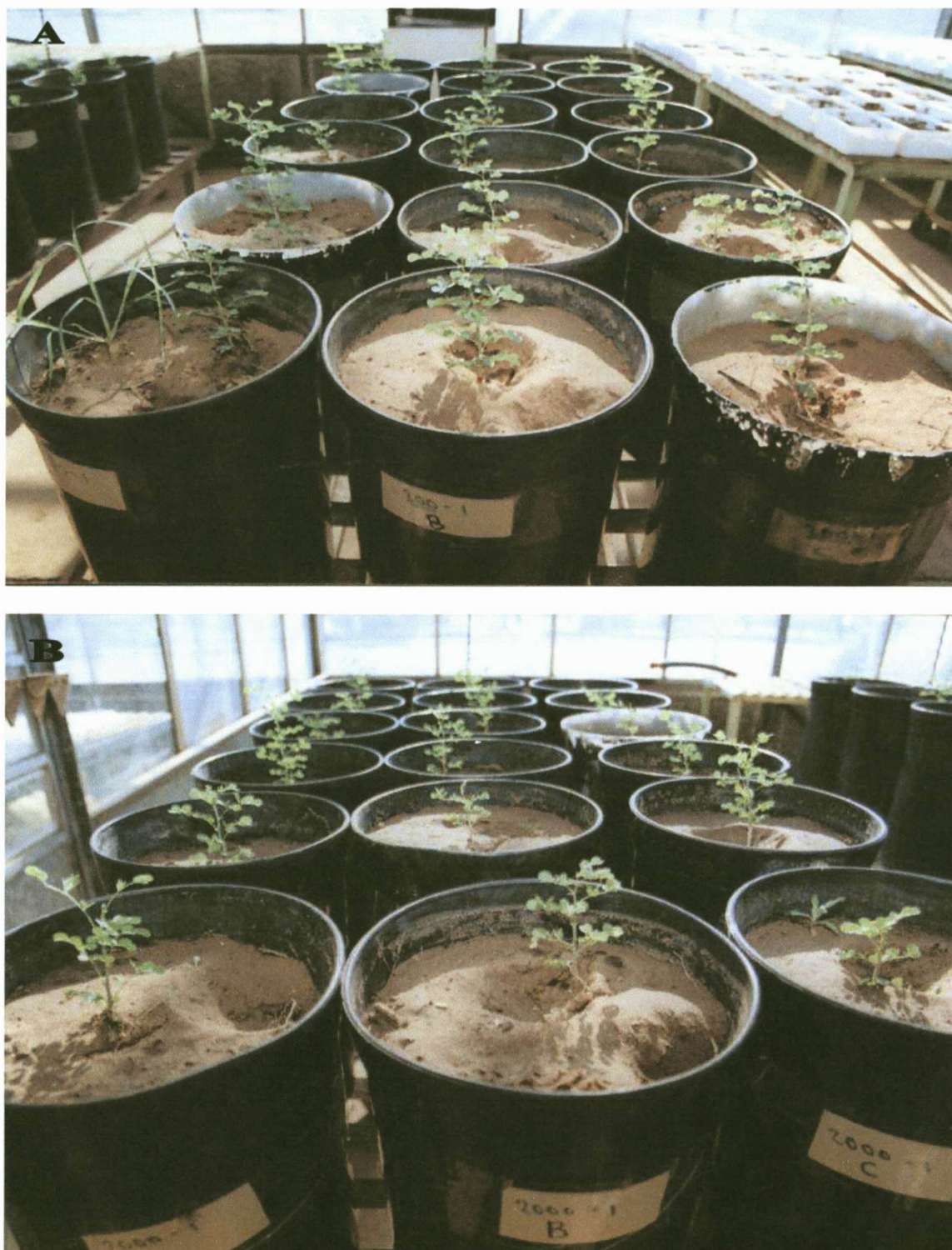
Figure 9. 7. Seventy day old *A. mellifera* seedlings grown in a controlled green house environment (a= soil from the 10% plot, b = soil from the 100% plot).

9.4.1.3 Number of Leaves

The results of the leaf number counts of the *A. mellifera* seedlings are presented in Figures 9.8 and 9.9.

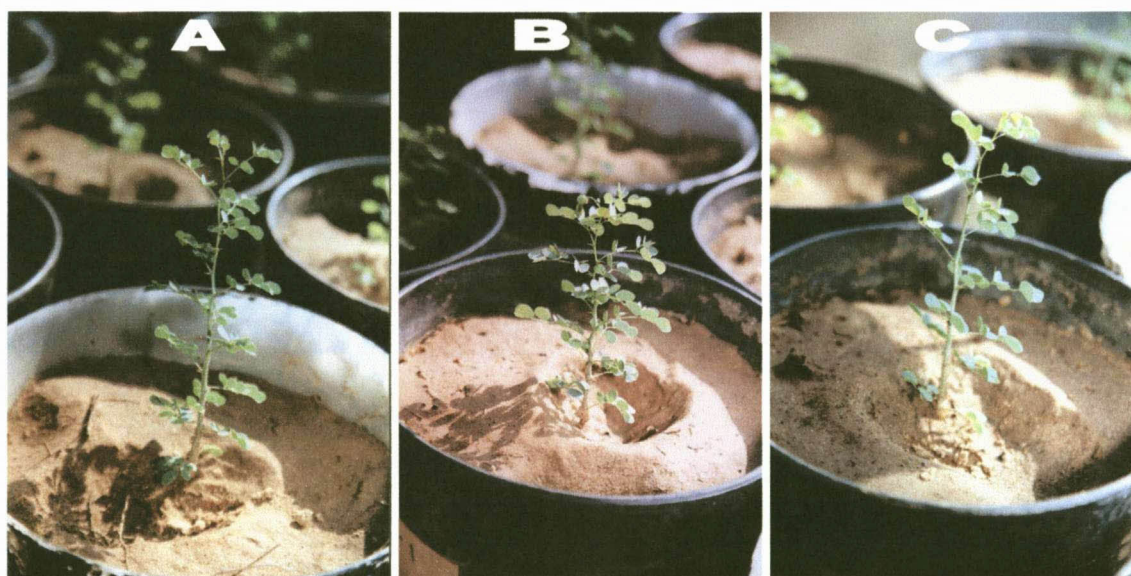

Figure 9.8 Mean leaf number of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).
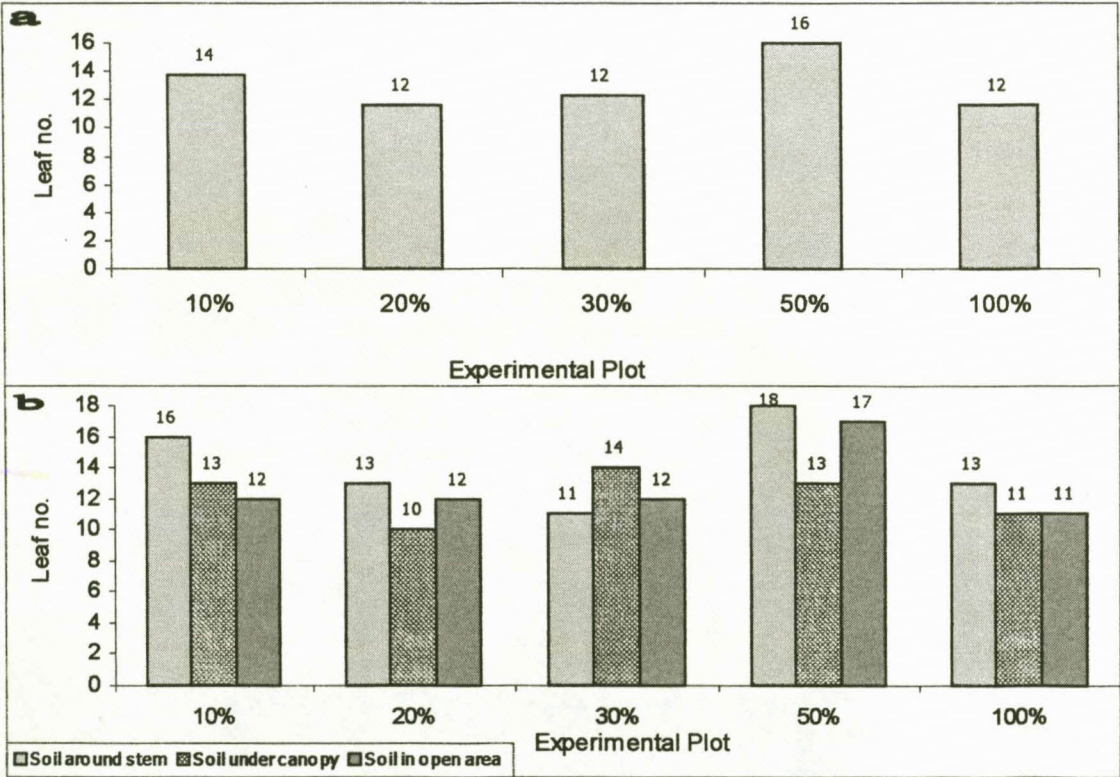
Figure 9.9 Mean leaf number of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

The mean number of leaves (n = 90) of all the seedlings after 70 days was 13 with 110 leaflets. There was a non-significant difference (P = 0.241) in leaf numbers of seedlings grown in the soil from the three soil subhabitats (Figure 9.8). However, the mean number of leaves (14) and leaflets (130) produced in soils around the stem base area were more than the leaf number (12 and 13) and leaflet number (91 and 108) produced by seedlings in soil from under the canopy spread and the open area subhabitats, respectively. These results are, also, probably the results of the higher soil nutrient status under the tree canopies (see chapter 8).

No marked difference in the mean leaf count were observed between the tree density plots, except for the 50% plot where the seedlings, on average, had more leaves than those from the other plots (Figure 9.9a). In all subhabitats along the tree density gradient, the number of leaves produced around the stem base area was relatively higher than the other two subhabitats (canopy spread and open area), except for the 30% plot (Figure 9.9b).

9.4.1.4 Root stalk length

The results of the root stalk length measurements are presented in Figures 9.10 and 9.11. Root stalk length refers to the main root length without the root hairs.
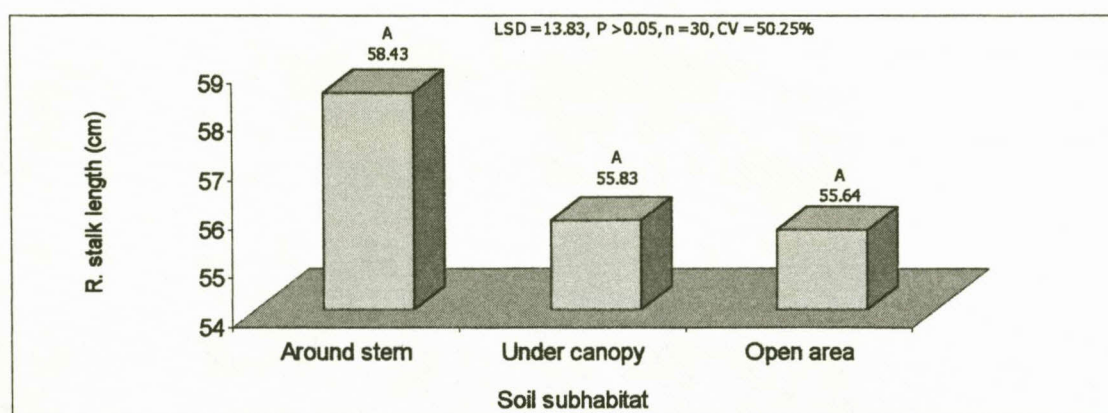
Figure 9.10 Mean root stalk length of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).

The mean (n = 90) root stalk length of the harvested *A. mellifera* seedlings was 55.5 cm (range = 9 cm – 120 cm), which is about six times longer than the mean plant height. Longer roots were observed coiled throughout the base of the plastic pot. This result corresponds to the findings of Rutherford (1980) that the lateral roots of *A. mellifera* commonly extend linearly up to seven times the area covered by the canopy.
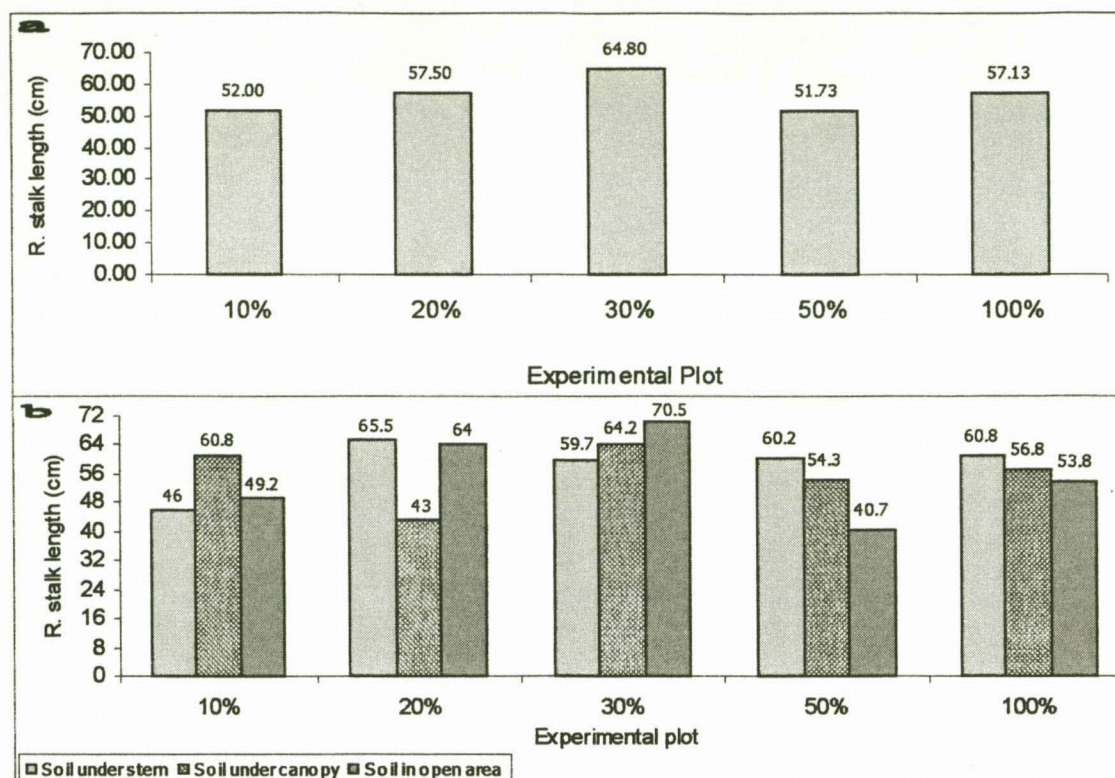
Figure 9.11 Mean root stalk length of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

No statistically significant difference (P = 0.102) in root stalk length was observed between the three soil subhabitats. However, *A. mellifera* seedlings grown in soils from around the stem base area developed a longer root stalk compared to those seedlings grown in soil from the other two subhabitats (Figure 9.10).

The mean root stalk lengths of the seedlings of all tree density plots are presented in Figure 8.11a. No marked differences in root stalk length were observed along the tree density plots. These results also indicated that root stalk growth is more likely to be influenced by soil differences due to subhabitat differentiation rather than soil differences due to differing tree densities. The pattern of the mean root stalk growth of the seedlings in the three soil subhabitats along the tree density gradient was not similar in all plots (Figure 9.11b). However, in general the seedlings grown in soils from around the stem base area generally developed a longer root stalk than those from the other two soil subhabitats, the exceptions being the 10% and 30% plots.

9.4.1.5 Total root length

The results of the total root length of the *A. mellifera* seedlings harvested after 70 days

are presented in Figure 9.12 and 9.13. Total root length refers to the complete root system length including the extensions of the root hairs.

The mean root length of all seedlings (n = 90) after 70 days was 5.97 meters (range = 0.33 m – 19.10 m). These results indicated that newly established seedlings of *A. mellifera* are able to develop an extensive root system in a relatively short time period. Knoop & Walker (1985), Smit & Rethman (1998b) reported that a large portion of roots of some savanna trees are concentrated at a shallow depth where they would actively compete with the shallow rooted herbaceous plants. Smit (1994) also reported that the roots of *Colophospermum mopane* trees could extend horizontally to a distance of approximately 7.6 times their height and 12.5 times the extent of their canopies. While the restrictions of the plots on the spatial distributions of the roots made it difficult to determine the pattern of root distribution, it is known that mature *A. mellifera* trees have a very shallow root system with an extensive horizontal spread (C. G. F. Richter, pers. Comm[1]).

The difference in the root length of the *A. mellifera* seedlings grown in the three soil subhabitats was not-significant (P = 0.126). However, the root length of the seedlings grown in soils from under the canopied subhabitats was higher than those of the seedlings grown in soils from the open (uncanopied) subhabitat (Figure 9.12).
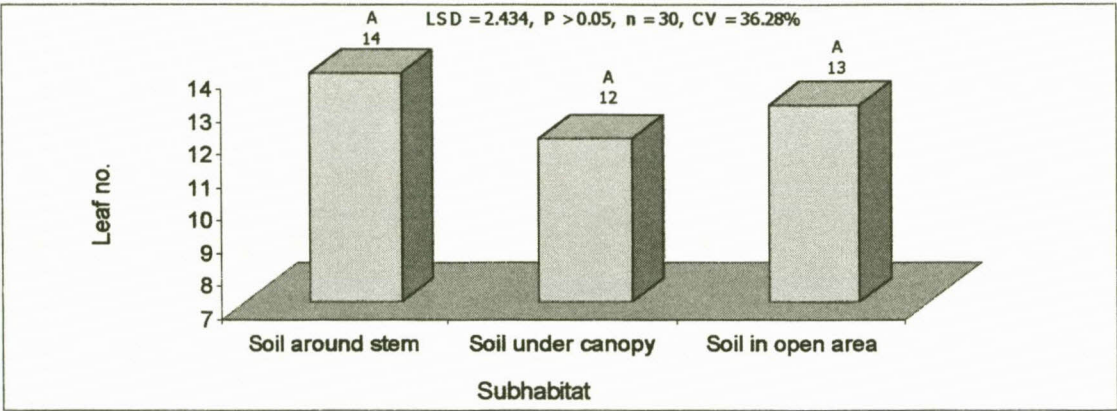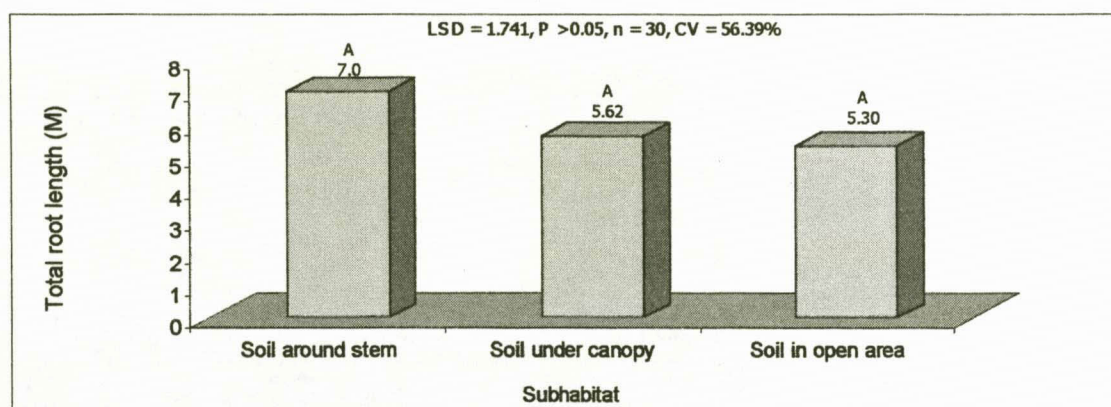

Figure 9.12 Mean total root length of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).

The mean total root lengths of the seedlings of each tree density plot are presented in Figure 9.13a. A marked difference in seedling root lengths between the lower tree density plots (10%, 20% and 30%) and high tree density plot (100%) was observed.

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[1] Mr. C. G. F. Richter, Free State Department of Agriculture, Private Bag X01, Glen 9360.
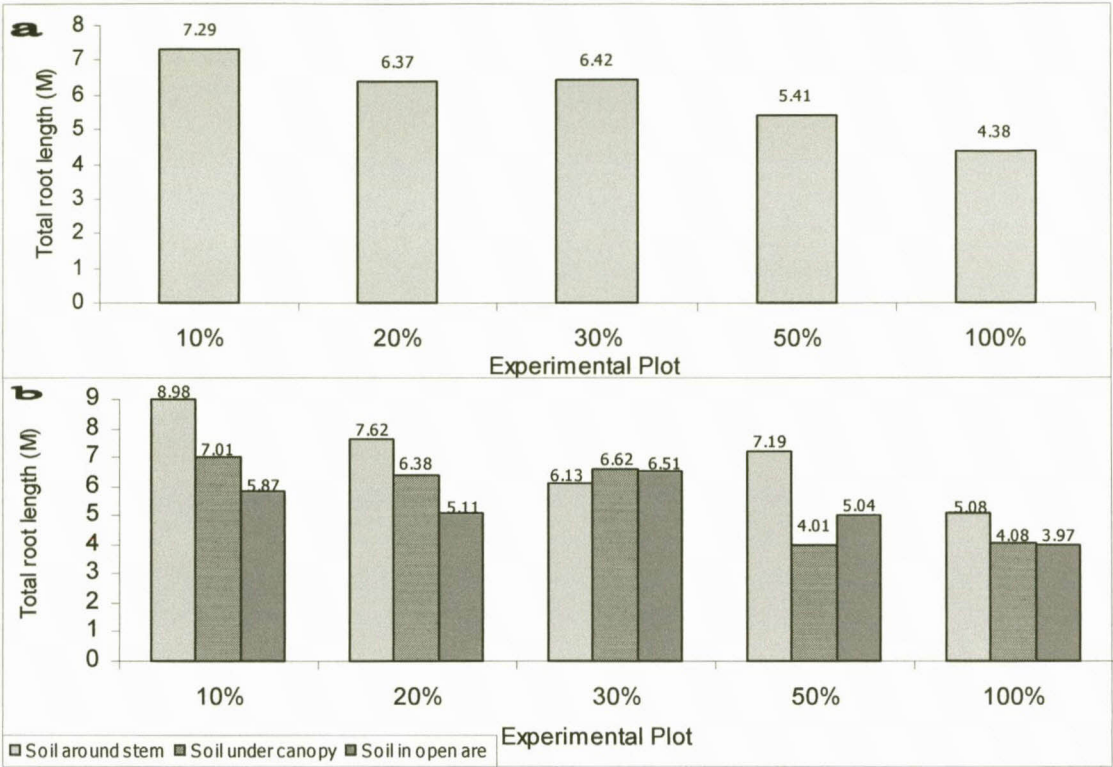
Figure 9.13 Mean total root lengths of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

Figure 9. 14 Illustrations of the typical root systems of seedlings that were grown in soil from the three soil subhabitats (1a = soil around stem, 1b = soil under canopy spread, 1c = soil in open area and 2 = dense root system of s seedling grown in the soil from the low tree density plot).

In general the root length of the A. mellifera seedlings declined with an increase in tree density. The reason for this high root length of the seedlings grown in the soil from the low tree density plots compared to the seedlings grown in soil from the control (100%) plot could be the adaptive mechanism of the roots of most savanna trees to utilize soil nutrients from the already thinned or cleared areas (Figure 9.14 1c and 2).

The mean root lengths of the seedlings grown in soil from the three soil subhabitats along the tree density gradient are presented in Figure 9.13b. Seedlings grown in soils from around the stem base area developed the longest root length in soil from all the tree density plots, with the exception of the 30% plot.

9.4.2 Stem growth rate

The results of the mean stem growth rates, obtained from the differences of consecutive measurements of stem lengths at intervals of five days, are presented in Figures 9.15 and 9.16.
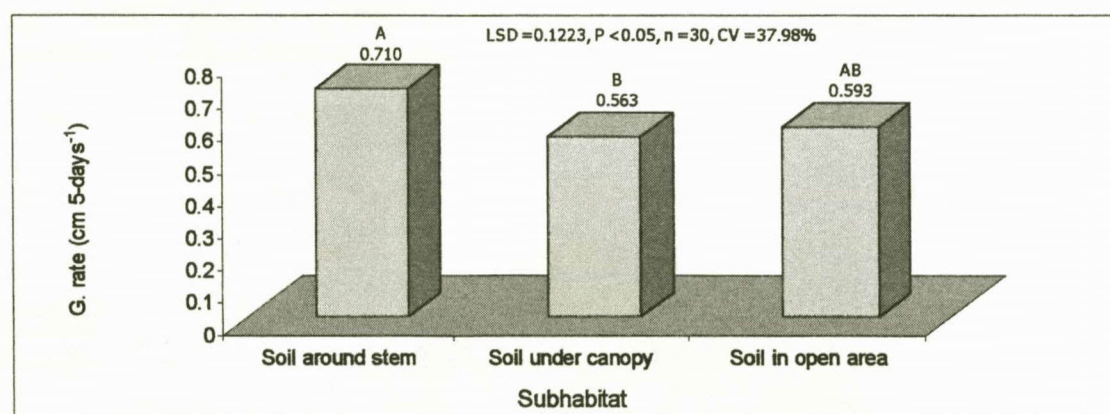
Figure 9.15 Mean stem growth rates of the seedlings grown in soils collected from the three different soil subhabitats measured at an interval of five days (all plots combined).

The mean stem growth rate (n = 90) of all the seedlings (plots combined) was calculated to be 0.62 cm for the five day period. There was a significant difference (P = 0.046) in stem growth rate of the seedlings grown in soils from around the stem base area and seedlings grown in soils under the canopy spread and the open area (Figure 9.15).

The mean stem growth rates of the A. mellifera seedlings grown in soils from the different tree density plots are presented in Figure 9.16a. In general, the rate of growth of those seedlings established in soil from the low tree density plots was higher than the control (100%) plot.

The mean stem growth rate (n = 6) of the seedlings grown in soils from the three subhabitats along the tree density gradient is presented in Figure 9.16b. In all plots, the rate of growth of seedlings grown in the soil from around the stem base area were higher than from the other two subhabitats. The relatively high soil nutrient levels that were recorded around the stem base area could be the reason for the increased rate of growth in this subhabitat (see chapter 8).
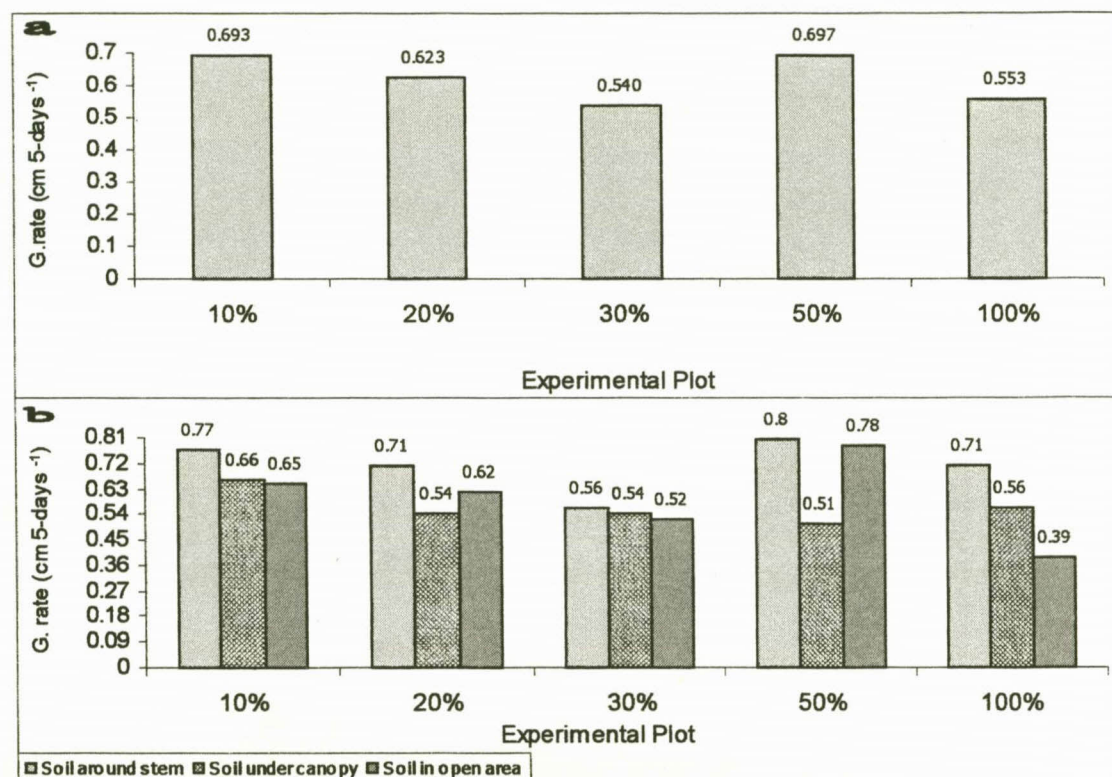
Figure 9.16 Mean stem growth rates of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

9.4.3 Seedling dry mass

9.4.3.1 Leaf dry mass

The mean leaf dry mass (n = 90) of all seedlings (plots combined) after 70 days was calculated to be 0.125 g. Statistically, there was non-significant difference (P = 0.06) in leaf dry mass of the seedlings grown in the soils of the three subhabitats (Figure 9.17). However, a higher leaf dry mass for seedlings grown in the soils around the stem base area was obtained compared to the leaf dry mass of seedlings grown in the soils under the canopy spread and open subhabitats. The higher leaf dry mass can be related to the larger number of leaves and leaflets of these seedlings (see section 9.4.1.3).

The mean leaf dry mass (n = 6) of the seedlings grown in soil from the different tree density plots are presented in Figure 9.18a. In general, a higher leaf dry mass was obtained for the seedlings grown in the soil from the lower tree density plots compared to the high tree density plot (100%). The leaf dry mass of the seedlings declined in the soil from the higher tree density plots, with the exception of the 50% plot.
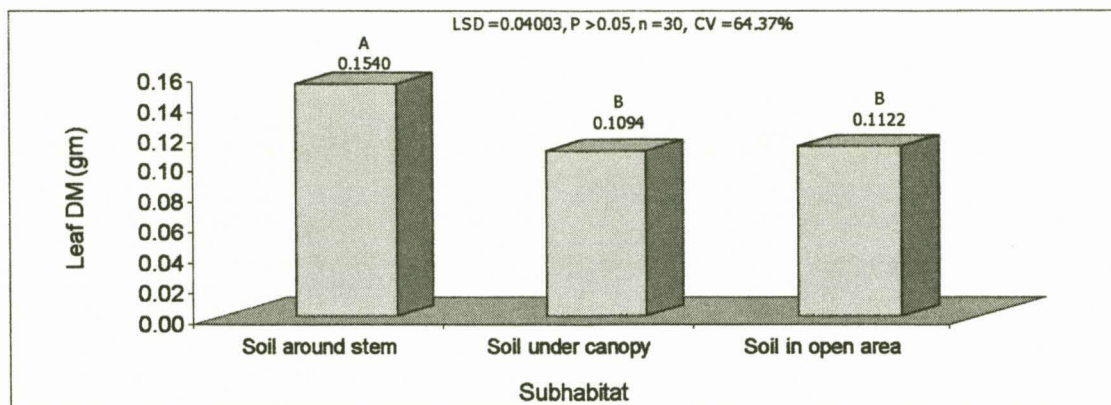
Figure 9.17 Mean leaf dry mass of the *Acacia mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).
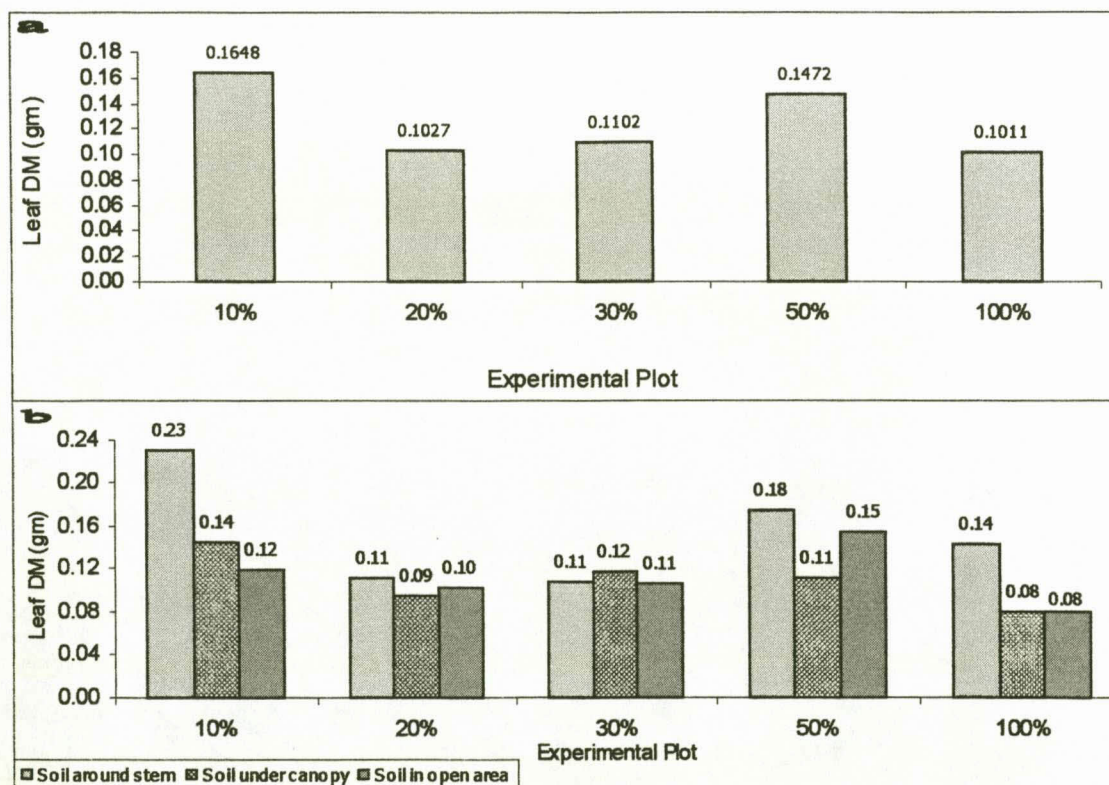
Figure 9.18 Mean leaf dry mass of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

The mean leaf dry mass of the seedlings grown in the soils from the three subhabitats along the tree density gradient is presented in Figure 9.18b. In almost all plots, the leaf dry mass of the seedlings grown in soils around the stem base area was higher than those of the other two subhabitats. This result, also, relates to the differences in the number of leaves and leaflets (see section 9.4.1.3).

9.4.3.2 Stem dry mass

The mean (n = 90) stem dry mass of all seedlings (plots combined) was 0.105 g. There was non-significant differences (P > 0.05) in the stem dry mass of the seedlings grown in soils from the three subhabitats (Figure 9.19). However, a relatively higher stem dry mass was recorded in the case of seedlings grown in soil from under the stem base area compared to those of the other two subhabitats (Figure 9. 19).
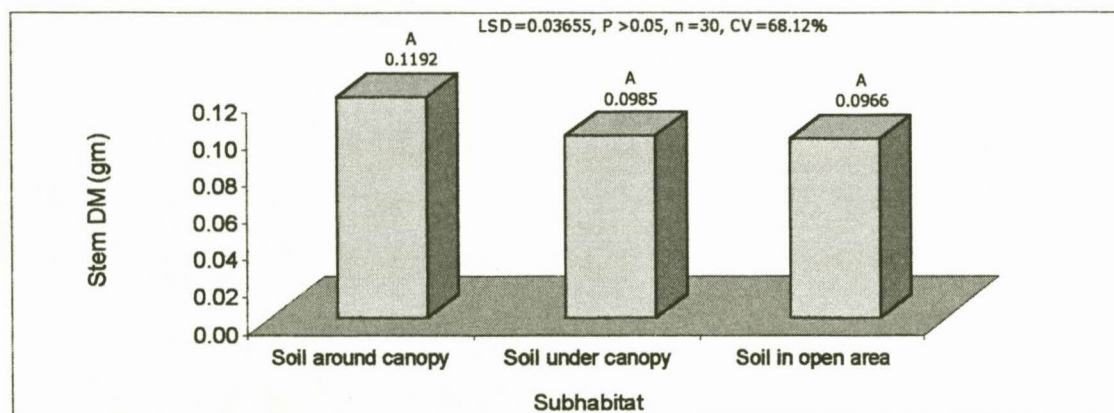

Figure 9.19 Mean stem dry mass of the A. mellifera seedlings grown in soil collected from the three different soil subhabitats (all plots combined).

The mean stem dry mass (n = 18) of the seedlings grown in soil from the different tree density plots is presented in Figure 9.20a. In general, a higher stem dry mass was recorded for seedlings grown in the soil from the low tree density plot compared to the seedlings grown in the soil from the high tree density (100%) plot. The stem dry mass also declined in the soil from the higher tree density plots, with the exception of the 50% plot.

The mean stem dry mass (n = 6) of the seedlings grown in soil from the three subhabitats and the different tree density plots is presented in Figure 9.20b. Except for the 20% plot, the stem dry mass of the seedlings grown in soil from around the stem base area was higher than those of the other two subhabitats.

Figure 9.20 Mean stem dry mass of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

9.4.3.3 Root dry mass

The mean (n = 90) root dry mass of all seedlings (plots combined) was 0.135 g. There was non-significant difference (P = 0.143) in root dry mass of the seedlings grown in soils from the three subhabitats (Figure 9.21). However, a relatively higher root dry mass was recorded for seedlings grown in soil from under the stem base area compared to those of the other two subhabitats. The root mass also declined from the stem base area to the open subhabitat.

The mean root dry mass (n = 18) of the seedlings grown in soil from the different tree density plots is presented in Figure 9.22a. A higher root dry mass was recorded for the seedlings grown in the soil from the lower tree density plots compared to the seedlings grown in the high tree density plot (100%). The root dry mass also declined in the soil with an increase in tree density. The higher root dry mass of the seedlings in the soil from the lower tree density plots is most likely a further consequence of the longer root length of these seedlings (see section 9.4.1.5).
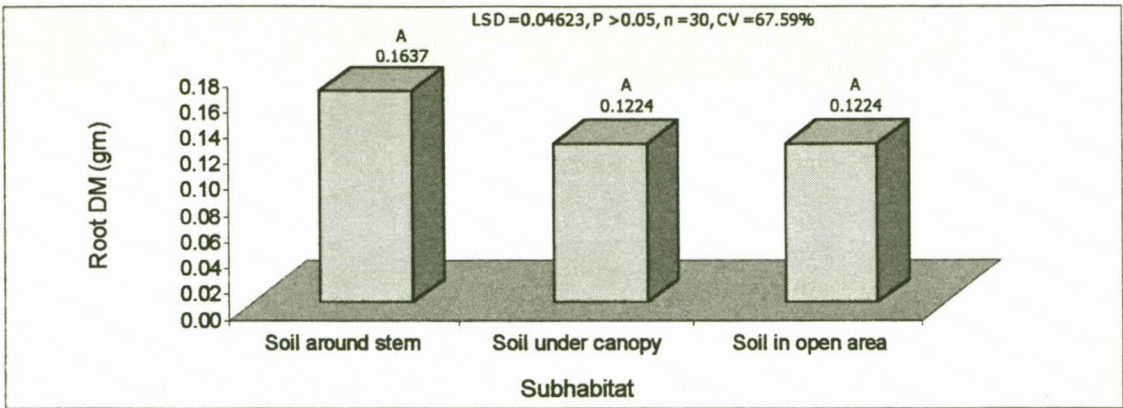
Figure 9.21 Mean root dry mass of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).
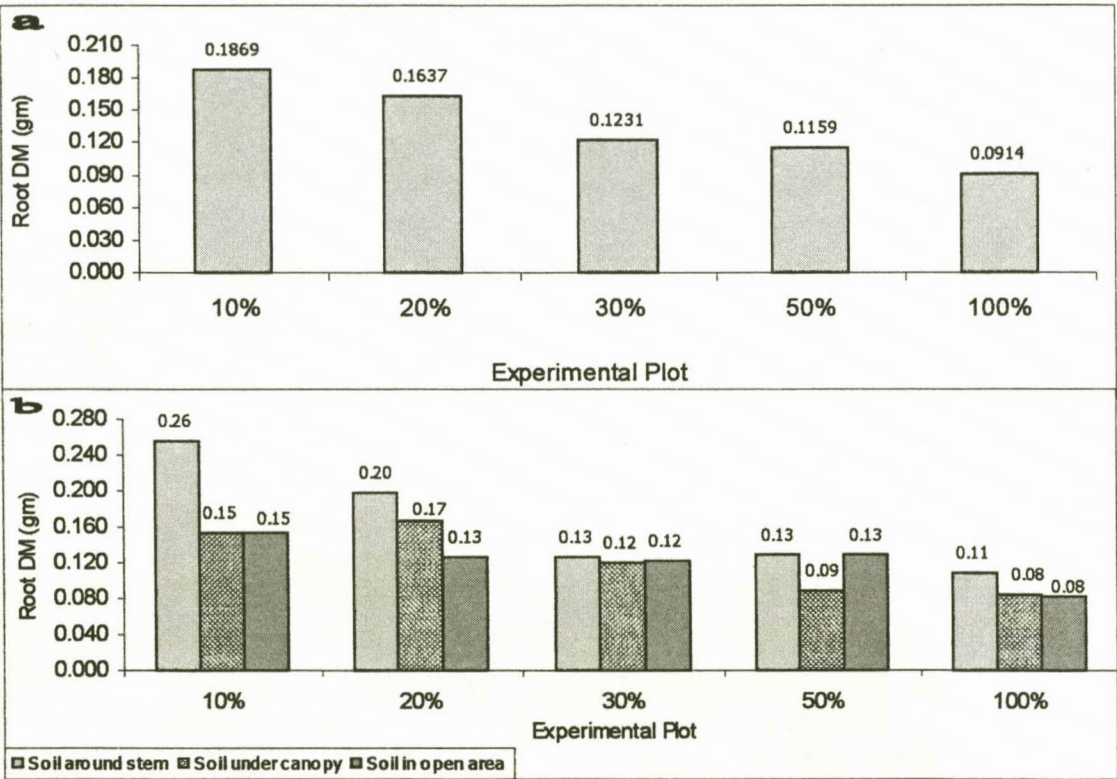
Figure 9.22 Mean root dry mass of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

The mean root dry mass (n = 6) of the seedlings grown in soil of the three subhabitats and the different tree density plots is presented in Figure 9.22b. In all plots, the root dry mass of the seedlings grown in soil from around the stem base area was higher than those of the other two subhabitats.

9.4.3.4 Total dry mass

The results of the total dry mass of the all the *A. mellifera* seedlings (plots combined) are

presented in Figures 9.23 and 9.24. The mean total dry mass (n = 90) of all the *A. mellifera* seedlings harvested at about 70 days was 0.365 g. There was non-significant difference (P = 0.119) in the total dry mass of the seedlings grown in soils from the three subhabitats (Figure 9.23).
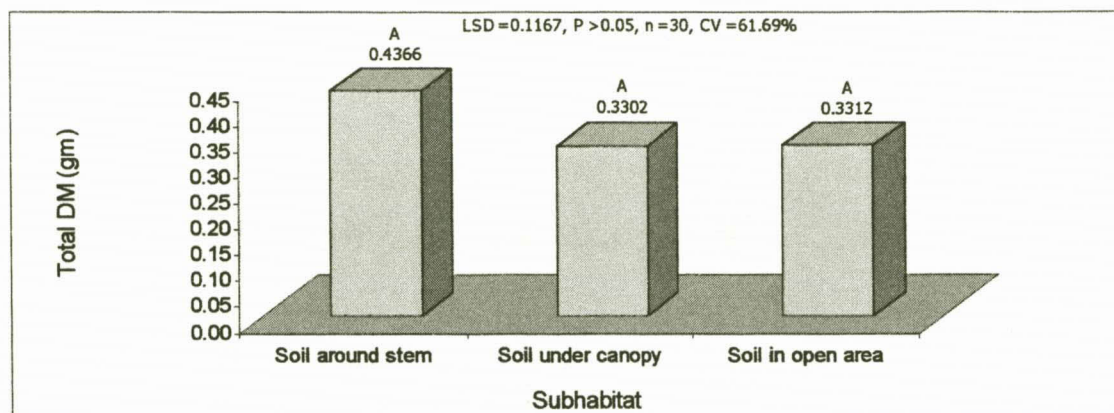
Figure 9.23 Mean of the total dry mass of the *A. mellifera* seedlings grown in soil collected from the three different soil subhabitats (all plots combined).
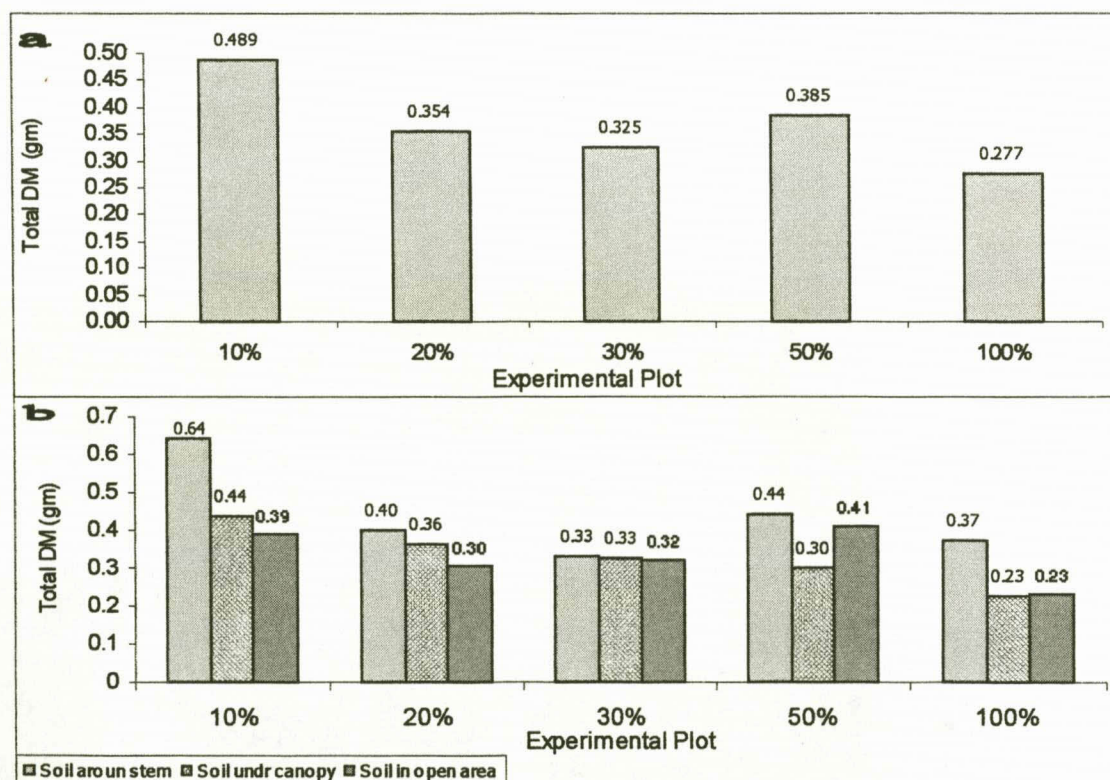
Figure 9.24 Mean of the total dry mass of the *A. mellifera* seedlings (n = 18(a) & n = 6 (b)) along the tree density gradient.

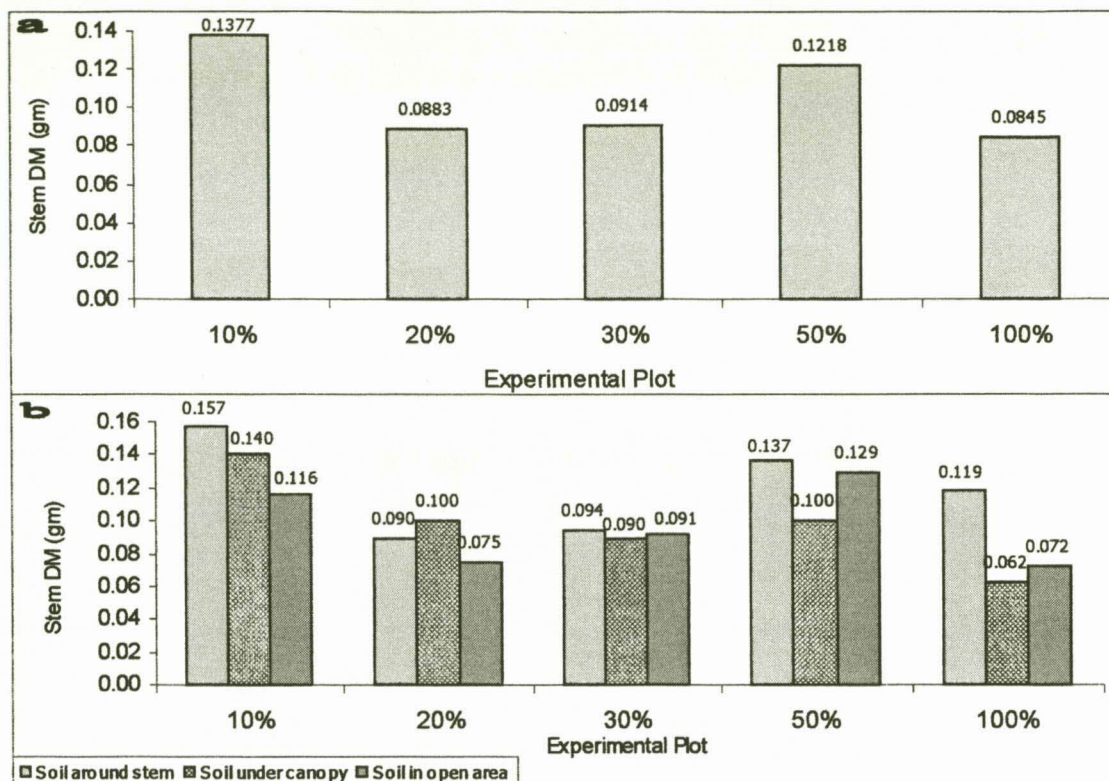As with most of the other measured parameters the total dry mass of the seedlings grown in soil from under the stem base area was higher compared to those of the other two subhabitats. The total dry mass also tend to decline from the stem base area to the open subhabitats. The relatively high soil nutrient status of soils around the stem base area could be the reason for these differences (see chapter 8).

The mean total dry mass (n = 18) of the seedlings grown in soil from the different tree density plots is presented in Figure 9.24a. A higher total dry mass was obtained for the seedlings grown in the soil from the lower tree density plots compared to the seedlings grown in the high tree density (100%) plot. The stem dry mass also tended to decline in the soil collected in the higher tree density plot, with the exception of the 50% plot.

The mean total dry mass (n = 6) of the seedlings grown in soil of the three subhabitats and the different tree density plots is presented in Figure 9.24b. In all plots, the root dry mass of the seedlings grown in soil from around the stem base area was higher than the other two subhabitats.

9.4.4 Relations between ETTE ha⁻¹ and different plant growth parameters.

The regression analyses between the potential tree competitiveness (ETTE ha⁻¹) and the means of the various plant growth parameters of the seedlings established in the soils of the five different tree density plots are presented in Table 9.1.

TABLE 9.1 Regression analysis between ETTE ha⁻¹ and various plant growth parameters of the seedlings established in the soil collected from the various tree density plots.

Parameters	n	Regression equation	r	r^2	SE	P-value
Plant height (cm)	5	y = 10.61 – 0.00031x	-0.633	0.401	0.000	0.229
Stem thickness (mm)	5	y = 1.78 – 0.000026x	- 0.388	0.150	0.000	0.500
Root stalk length (cm)	5	y = 53.78 + 0.00052x	+0.189	0.036	0.002	0.755
Leaf number	5	y = 13.22 – 0.00012x	-0.134	0.018	0.001	0.826
Stem growth rate (cm)	5	y = 0.684 – 0.000018x	-0.517	0.268	0.000	0.354
Leaf dry mass (g)	5	y = 0.154 – 0.0000083x	-0.603	0.364	0.000	0.260
Stem dry mass (g)	5	y = 0.128 – 0.0000068x	-0.605	0.366	0.022	0.259
Root dry mass (g)	5	y = 0.182 – 0.0000138x	-0.803	0.646	0.000	0.080
Total dry mass (g)	5	y = 0.468 – 0.0000298x	-0.790	0.624	0.000	0.089

The relations between the ETTE ha⁻¹ and the following growth parameters were not-significant ($P > 0.05$): plant height, stem thickness, root stalk length, leaf number, stem growth rate, leaf dry mass, stem dry mass, root dry mass and total dry mass. The correlation coefficients obtained were relatively low and negative except for root stalk length. The calculated coefficient of determination was also very low (Table 9.1).

The relation between the ETTE ha⁻¹ and the total root system length (m) of the established seedlings along the tree density gradient was highly significant ($P < 0.01$). There was a negative correlation with a high coefficient of determination (Figure 9.25). With the increase in tree density a linear decline in the length of the total root system was observed.
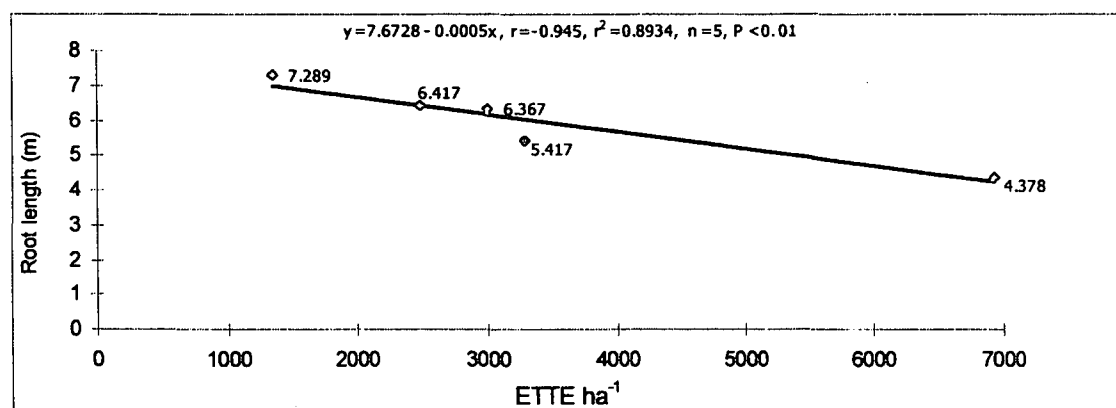
Figure 9.25 Regression analysis of the relations between ETTE ha⁻¹ and the complete root system length of *A. mellifera* seedlings.

It must be noted, however, that these relations are not a direct consequence of the competition interaction between tree seedlings and the established trees, but merely an indirect interaction as a result of the influence of tree density on the soil as described in Chapter 8.

These results were also obtained under conditions of no water stress as the seedlings were watered regularly. The actual effect of tree density on seedling establishment and growth will have to be studied in the field.

9.5 CONCLUSIONS

The following general conclusions can be drawn from this investigation:

(i). No allelopathic effect that inhibits the growth of seedlings is present in soil collected from under the *A. mellifera* seedlings.

(ii). Marked differences in plant height, stem thickness, stem growth rate, leaf number, root stalk length, total root system length, leaf dry mass, stem dry mass, root dry mass and total dry mass of the seedlings grown in the soil from around the stem base area in comparison to the other two subhabitats (canopy spread and open area) were observed. In all cases, the growth of *A. mellifera* seedlings grown in the soil from the subhabitat around the stem base area were more prolific and achieved higher lengths, thicker stem diameters, with more leaves and higher total dry masses. The relatively higher soil nutrient status observed in soil from this subhabitat is considered to be responsible for this increased growth.

(iii). No marked difference in the above mentioned growth parameters were observed in the case of seedlings grown in the soil from under the canopy spread area and the open subhabitats. Smaller differences in the soil nutrient status of the soil from these two subhabitats could account for this lack of differences in seedling growth.

(iv). In general, the *Acacia mellifera* seedlings grown in the soil from the lower tree density plots exhibited a higher plant height, stem thickness, stem growth rate, leaf number and total root length than the seedlings grown in the soil from the control (100%) plot.

(v). A denser root system, as reflected by higher total root lengths and root dry mass, was observed in seedlings grown in soil from the low tree density plot. These parameters and declined linearly in soil collected over the tree density gradient, reflecting a decline in root density with an increase in tree density.

(vi). In general the subhabitat differentiation had a more pronounced effect on seedling growth than differences associated with the tree density gradient.

SUMMARY

The study was conducted in an area described as "Kalahari Thornveld" in the vicinity of the towns of Bray and Pomfret in the North-West Province, where Acacia mellifera subsp. detinens is the dominant woody species. The soils of the area are deep sand to loamy soils described as Kalahari sand with an extremely low organic matter and mineral element content.

The study area consisted six 0.5 ha plots (50 m x 100 m), where the trees were thinned during November 1989 to different densities, ranging from a totally cleared plot (0%) to plots thinned to the equivalent of 10%, 20%, 30%, and 50% of the tree density of a control plot (100%) of about 2 000 tree equivalents (TE) ha^{-1}. The plots were located adjacently on a homogeneous area of 3.0 ha. Treatments were allocated randomly to the plots and not in numerical order. A permanent transect of 20 m x 100 m was established in the center of each plot for phenological observations and harvesting of seeds. The remainders of the experimental plots were used for soil sample collection and to determine seed distribution within the defined subhabitats. The spatial canopies of all rooted live A. mellifera trees encountered in the fixed transects (5 m x 100 m), located in the middle of each of the experimental plots, were measured and the number of Evapotranspiration Tree Equivalents (ETTE) ha^{-1} calculated, using the BECVOL-model. Estimates of the browsing capacities were also made from the leaf dry matter estimates.

For the study of the phenology, seed harvesting and leaf biomass estimates of individual trees, fifty (50) A. mellifera trees (10 sample trees/plot) were randomly selected. Only one phenological observation was done at the onset of flowering (August 2000) and all the pods and seed from the marked trees were harvested during late November 2000. Tree thinning brought about early flowering of A. mellifera in the lower tree density plots, possibly as a result of reduced inter-tree competition. However, the mean seed production over the tree density gradient did not follow a specific trend, and differences were observed between the seed production of individual trees. Significant correlations between ETTE ha^{-1} and leaf dry mass (kg ha^{-1}) and total seed production ha^{-1} were established. Although the correlation coefficients were low, there are indications that seed production of individual trees increase with an increase in ETTE tree^{-1} and leaf dry mass tree^{-1}.

For the determination of seed mass and seed dimensions ripe *A. mellifera* seeds were randomly selected from each sample tree (n = 10 and 50, respectively) after which they were weighed and measured. Seeds harvested from the high tree density plot were longer, wider and thicker than those from the lower tree density plots. The average seed dry mass production tree^{-1} showed no distinct pattern and was not correlated with the tree density, but the total seed dry mass ha^{-1} increased in relation to an increase in tree density. Leaf biomass of the *A. mellifera* trees per unit area, expressed as ETTE ha^{-1} and leaf dry mass ha^{-1}, was highly correlated with the seed dry mass ha^{-1}.

There is no carry over of *A. mellifera* seed from one season to another and thus no persisting seed bank exists. The percentage of viable fresh *A. mellifera* seeds was observed to decrease with the increase of the time and exposure to high temperature and moisture fluctuations.

For the study of seed distribution within defined subhabitats (stem base area, under canopy spread and open area), six *A. mellifera* trees in each tree density plot were randomly selected. Small rectangular plastic containers were inserted in the three subhabitats of all marked trees (in two opposing directions). In all subhabitats a larger number of seeds were blown toward the prevailing wind direction. The number of seeds accumulated in the open subhabitats in both wind directions was also higher in comparison to the canopied subhabitats. A very low, non-significant correlation was observed between ETTE ha^{-1} and seed distribution along the tree density gradient of the three subhabitats.

For the assessment of germination potential, 50 normal and 20 bruchid beetle infested seeds were randomly selected from each plot. Germination tests were conducted at the facilities of the Department of Agronomy, UFS, and root and coleoptile lengths and growth rates were also measured. Thinning of *A. mellifera* trees had no effect on the germination potential of the seeds from the various tree density plots and an extremely high germination potential of the fresh *A. mellifera* seeds were found. Though some damage was caused, bruchid beetle infested seeds exhibited a low but fast germination rate, possibly due to faster imbibition of moisture. No marked difference in root length and root growth rates were observed between seeds of the various plots. However, seeds harvested from the lower tree density plots developed a higher coleoptile length with a faster coleoptile growth rate than the control (100%) plot.

Soil from the canopied and uncanopied subhabitats were analyzed for soil nutrient status in order to evaluate seedling growth. Soils excavated from the canopied subhabitats were more acidic and displayed higher concentrations of P, total N and organic matter than the uncanopied (open) subhabitat. However, no marked differences in exchangeable cations were demonstrated between the subhabitats, except Ca that displayed higher concentrations in the canopied subhabitat.

No allelopathic effect that inhibits the growth of seedlings was found to be present in soil from the canopied subhabitats of *A. mellifera*. Marked differences in growth parameters of the seedlings grown in the soils from around the stem base area in comparison to the other two subhabitats were observed. The relatively higher soil nutrient status observed in soils of this subhabitat is considered responsible for this increased growth. In general, *A. mellifera* seedlings grown in the soil from the lower tree density plots exhibited higher growth rates than those from the control (100%) plot. A denser root system, as reflected by higher total root lengths and root dry mass, was observed in seedlings grown in soil from the low tree density plot and declined linearly in soils collected along the tree density gradient. In general, the subhabitat differentiation had a more pronounced effect on seedling growth than soil differences associated with the tree density gradient.

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