moisture regime relative to the inter-canopy habitat, depending on the net result of all these interactions.

Transpiration. Transpiration by woody plants is a major component of the water balance in semi-arid savannas (Bate, Furniss & Pendle 1982). The immediate consequence of tree removal is therefore an increase in soil moisture, which stimulates an increase in grass production. In the longer term, transpiration by the increased grass biomass reduces the soil moisture content again except in the deepest soil levels where they have few roots. Soil moisture contents under an induced grassland may in the long term be lower than under the savanna from which it was derived (Strang 1969a). Deep drainage losses may increase where the grasses are shallow-rooted. Losses due to evaporation from the soil surface will decrease provided that a complete grass cover is maintained, but will increase if the soil is exposed.

1.3.2 PRIMARY PRODUCTION

Photosynthetic pathway. Woody plants have a C3 photosynthetic pathway and therefore under the warm, high light-intensity savanna conditions would be expected to have lower instantaneous photosynthetic rates than C4 grasses.

Transpiration pattern. Woody plants, due to their larger tissue water capacity, more sclerophyllous leaves and access to moisture in deep soil layers are likely to have a more conservative water use strategy than grasses do. In other words, their maximum transpiration rates are expected to be lower but sustained for longer into the drying cycle.

The differences in photosynthetic pathway and transpiration pattern will lead to differences in water use efficiency (WUE, $gH_2O.gCO_2^{-1}$) between trees and grasses. Which growth form will have the higher WUE depends on the specific environment in which they are grown; under savanna conditions C4 plants would be expected to have the advantage.

Total primary productivity could therefore decline or increase following tree removal, depending on environmental circumstances, species involved and clearing practices. Grass production increases unless the process of tree removal has also disturbed the herbaceous layer or altered its composition in favour of less productive (i.e. less efficient) species (Dye & Spear 1982).

Above-ground primary production in semi-arid savannas is in the region of 3000 $kg.ha^{-1}yr^{-1}$, with woody plants contributing about two-thirds of this (Rutherford 1978). Over half of the woody-plant production is leaf and current stem material, while the rest is woody tissue increment. These estimates are based on a very small data set, and the actual range is likely to be high. Considerably more data are available for the herbaceous layer alone, where annual aboveground production is in the range of 100-3000 $kg.ha^{-1}$. The range of primary production in savannas is largely a function of the available moisture and nutrients rather than mean annual rainfall *per se*, since the efficiency of conversion of rainfall into production is influenced by soil type (Rutherford 1980) as well as the seasonal distribution of rainfall. The proportion contributed by woody plants is a function of the savanna structure.

1.3.3 SECONDARY PRODUCTION

Forage availability and quality. Woody plant tissues differ in availability and quality from grass tissues, and are consumed by a different spectrum of herbivores. The crude protein content of tree leaves is higher than that of grass and is fairly constant throughout the season, but may be rendered unavailable by the presence of digestion-inhibiting compounds. The total fibre is lower but the proportion of indigestible fractions (lignin and cellulose) to digestible fractions (hemicellulose) is higher. Overall digestibility is consequently lower (Owen-Smith 1982).

Fodder availability is a function of its distribution in space and time. Browse is less available than grass since it is sparsely distributed over a range of height classes. The rate of energy acquisition by browsers may become critically low during the late dry season in deciduous savannas. Grazers are more likely to be faced with a protein scarcity during this period due to the decline in grass protein content with age (Barnes 1979). Even when woody plant biomass is high, the proportion of browsers to grazers in savannas tends to be low, and the proportion of browse to grass in the diet of mixed feeders is similarly low (Cooper 1984).

Food reserves. Despite the high intraseasonal fluctuations in browse availability, it is more stable interseasonally than grass, since tree leaf production is less directly linked to rainfall in the current season than is grass production (Knoop 1982; unpublished litterfall data from Nylsvley). The tree leaf flush frequently precedes the first rains of the season. During periods of stress browse provides a reserve food source for grazers. Fallen flowers, fruits and leaves form an important dietary component of many non-browsing species.

1.3.4 NUTRIENT CYCLING

Nutrient pools. Trees tend to have at least a few deep roots, and therefore have access to nutrients beyond the rooting range of grasses (Walter 1971). Complete tree removal would therefore reduce the nutrient pool available to the ecosystem, and nutrient losses would be increased because more leachate would pass below the rooting depth.

Nutrient concentrations. The horizontal root extent of trees is usually several times the crown radius (Rutherford 1982). Nutrients are gathered over a large area, but are recycled by leaching and leaf fall mainly in the vicinity of the crown. The resultant mosaic of nutrient depleted sites between canopies and nutrient enriched sites below canopies is

particularly pronounced on dystrophic soils. In combination with hydrological and microclimatic changes in the canopy vicinity it creates a distinct sub-canopy habitat, which typically supports a different suite of herbaceous species to those growing between canopies. In particular, the productive and preferred species *Panicum maximum* is almost exclusively found in this habitat, despite its ability to grow elsewhere (Bosch & van Wyk 1970, Kennard and Walker 1973).

The sub-canopy habitat is gradually lost after tree removal (Brock, Haas & Shaver 1978, Barnes 1979, Dye & Spear 1982), resulting in a loss of spatial heterogeneity (patchiness) in the sward. The sward nutritional quality declines as a consequence of the disappearance of the palatable sub-canopy species. This quality decline counteracts the increase in forage quantity, and may be responsible for the disappointing increases in secondary production despite large increases in primary production (Louw & van der Merwe 1973, Harrington 1973b, Teague 1973, Pratchett 1978).

Nutrient turnover. Leaf turnover in grasses occurs several times per season (Dankwerts *et al* 1984) but in savannas woody plants usually drop their leaves only once a year. Input into the litter layer by grasses is therefore fairly continuous but is concentrated into an annual peak for deciduous trees.

Grass leaves and roots are more rapidly decomposed than tree leaves, and much more rapidly than lignified tissues (Bezuidenhout 1980). This has largely unknown implications for the dynamics of soil micro-organisms and organic matter.

The nutrient pool bound in living and dead woody tissues may represent a significant portion of the total system nutrients on highly leached soils, and is protected from leaching itself. The combination of high turnover, low reserves and rapid decomposition makes nutrient cycling through grasses much faster than through trees, but also more labile (Frost 1985b). Clearing could result in an overall decline in system nutrient status if the woody tissues are harvested.

1.3.5 MICROCLIMATE

The microclimatic consequences of tree removal are an increase in radiant energy at the level of the herbaceous layer, an increase in wind run and a widening of temperature extremes. These have direct consequences on plant productivity and mammal thermoregulation (Gifford 1973, Pratchett 1978). Macroclimatic changes are unlikely provided the scale of clearing remains small.

1.3.6 HABITAT

Woody plants provide cover and breeding requirements for a wide range of animal species. The abundance of these species can be expected to decrease following bush clearing, while the abundance of species with a preference for open areas will increase. For example, many antelope species (including impala, kudu and giraffe) leave their newly-born offspring concealed under bushes for long periods during the day, while in others (such as wildebeest) the young are born sufficiently mobile to escape predation by flight. The former group would suffer increased calf mortality following bush clearing, but not the latter. Similarly tree-nesting and fruit-eating birds would be disadvantaged relative to ground-nesting seed-eating species.

1.4 COMPETITION AND COEXISTENCE IN SAVANNAS

1.4.1 THE DETERMINANTS OF COMMUNITY STRUCTURE

Coexistence is often implicitly regarded as the absence of competition, much as health is regarded as the absence of disease (Aarsen 1983). This is not necessarily true, since competitition is an instantaneous interaction between two organisms, while coexistence is the long-term resultant of a large number of interactions (including competition) operating with varying strengths on the different life stages of the great number of organisms comprising two populations. Much of the controversy regarding the role of competition in determining community structure has arisen due to a failure to differentiate between its long-term evolutionary consequences (measured by fitness at a population level) and its shorter-term ecological consequences (measured by the density, biomass and productivity of the competitors). Although the two are linked, they operate at different time scales. This study is concerned only with the ecological time scale, that is, of the same order as the lifespans of the organisms involved.

The role of competition in structuring communities has been the focus of intense debate for several decades, as is illustrated by the extensive literature on the subject. The evidence is reviewed by Schoener (1983) and Connell (1983). There are two opposed schools of thought and a spectrum of intermediate positions.

The **equilibrium school** has its origins in the succession and climax concepts developed early in the century, and the mathematical models of competition developed by Lotka (1925) and Volterra (1926). Community structure is considered to be determined by internal biotic interactions, primarily competition and predation. Since Gause (1934) showed that complete competitors could not coexist, coexistence in nature was explained in terms of a competitive balance. Many factors have been suggested as mediators of this balance, including an unstable environment,

predation, balanced competitive abilities, resource partitioning (niche differentiation) and a balance of intra- and interspecific competition. If the system is moved a small distance from its equilibrium state, it will tend back to that state. This view is exemplified for savannas by the hypothesis presented by Walter (1971).

His proposal (Figure 4 on page 25) was that trees required a relatively continuous water supply, which was obtainable only from deep soil layers. They also have roots in the topsoil, but are outcompeted there by grasses, whose roots are restricted to the topsoil. The competitive balance is therefore determined by the frequency with which water penetrates to the subsoil, thus explaining the greater woodiness under wetter climates and on sandy soils. The "Walter hypothesis" was the first explicit statement of the determinants of savanna structure and has formed the basis of most models of savanna dynamics (Walker *et al* 1981; McMurtrie & Wolf 1983). Walker & Noy-Meir (1982) point out that partial rooting depth separation and superior competitiveness by the grass are sufficient conditions for coexistence.

The opposing viewpoint, the **stochastic school**, holds that abiotic perturbations originating outside the system are more important than internal dynamics in structuring communities, which are therefore non-equilibrium, indeterministic assemblages (Grossman, Moyle & Whittaker 1982).

An example of an intermediate viewpoint is that of Wiens (1977) who considers competition to be an effective force, but only during sporadic periods of resource limitation.

Even if resources were constantly limited, the various phases in the life history of an organism would be differently affected by this limitation. Competition may be important during one phase, but ineffectual during another. The importance of the regenerative phases in particular in determining plant community structure has been pointed out by Grubb (1977).

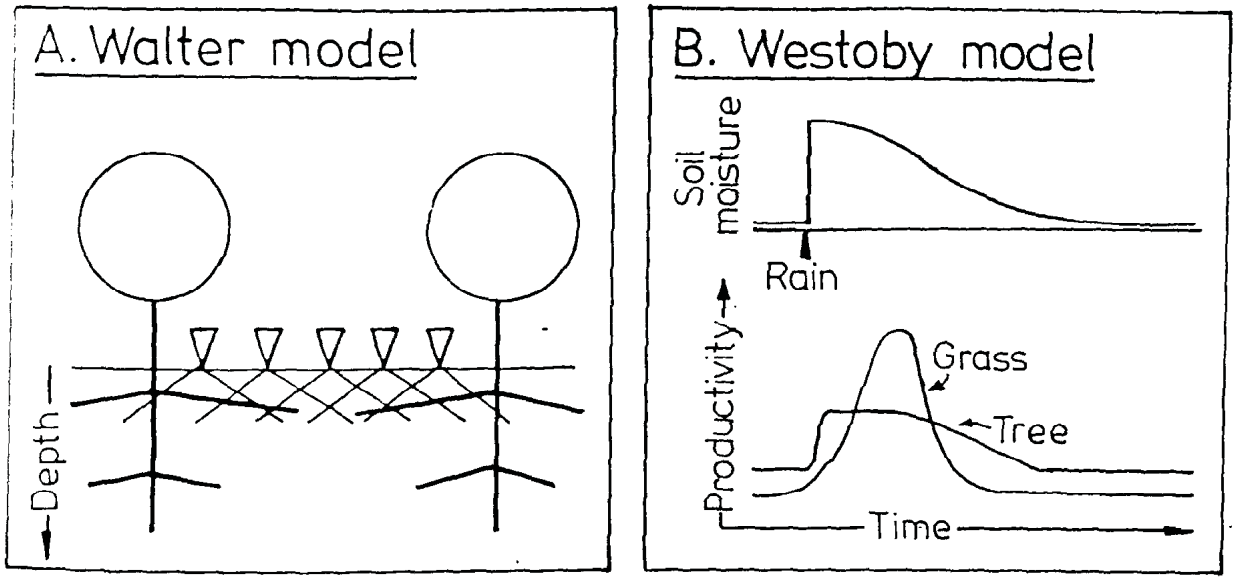

Figure 4. Two models of savanna structure and function: A. The Walter (1971) model is based on niche separation on a spatial axis (rooting depth). B. The Westoby (1980) model depends on separation in time between the different growth forms.

The attributes of the complete life cycle, viewed in the context of the environment in which it is conducted, are termed a strategy (Grime 1979). Westoby (1980) has built on this concept to develop a model of arid rangeland dynamics which depends on the interaction of plant strategies with an unpredictable environment. This approach includes elements of both the stochastic and equilibrium schools and is particularly relevant to semi-arid savannas. There are four main elements to his model:

1. Competition may be strongly asymmetrical, and favours established plants over regenerative phases;

2. The biotic and abiotic components of the system are interdependent;

3. Grazing operates differently on different life-forms;

4. Unpredictable rainfall offers a series of growth opportunities of variable lengths, which the different growth forms are variously equipped to exploit.

The Westoby model therefore relies on the interaction of a variety of plant strategies with an episodic and unpredictable water supply to explain the dynamics of the dominant growth forms found in arid regions. Interpreted in the context of semi-arid savannas (Figure 4 on page 25), this model suggests that trees have an advantage during the initial and final phases of a wetting cycle, at the price of slow growth rates, while grasses can achieve rapid growth, but only during the middle phase of the wet period. Established individuals of either group have an advantage over regenerative stages of the other group which means that changes following a disturbance such as a drought or heavy herbivory may persist after the disturbance has been removed. Irreversible changes can occur as a result of modifications to the soil. The model is as yet untested by field data. Since it is a probabilistic rather than deterministic model, it does not lend itself easily to simulation studies.

In the context of this study, competition is between two broad growth forms, woody plants and grasses, and not between genetically defined individuals. Thus this study is concerned with the coexistence and structure of a functional rather than taxonomic community. The higher genetic diversity within a group of species than within a single species should permit a greater plasticity in the response to competition and altered environments and thus permit coexistence more easily.

1.4.2 CONDITIONS FOR COEXISTENCE

The mechanism most commonly advanced for semi-arid savannas in Africa is niche separation along a rooting-depth axis (Walter 1971). Sarmiento, Goldstein & Meinzer (1985) emphasise a temporal separation of plant

production by phenological adaptations. These two options have also been advanced for explaining coexistence in grasslands (Parrish & Bazzaz 1976, Berendse 1979, Fowler & Antonovics 1981). Both fire and herbivory have been suggested as mediators of a competitive outcome in savannas, and can be viewed as differential predators (Cresswell 1978). Seasonality and fluctuations in resource levels are obvious in savannas and could potentially contribute to the avoidance of competitive exclusion (Ayala 1971).

1.4.3 DETECTION AND MEASUREMENT OF COMPETITION

Connell (1983) regards a change in abundance or resource use by a species following an opposite change in the abundance of a potential competitor to be sufficient field evidence for interspecific competition. The marked increase in grass production which has been universally observed following the removal of woody vegetation from savannas meets this requirement (see Table 1.3 for African experiments; Walker *et al* (1972) and Beale (1973) in Australia, Clary & Jameson (1981) and Herbel *et al* (1983) in North America). The reverse influence, that of grass removal on tree performance, was demonstrated by Knoop & Walker (1984) in one case but not in another.

Regularity of distribution of individuals in a population (Pielou 1977), as well as an inverse correlation between plant separation and some measure of individual performance (usually crown diameter or volume) has been regarded as evidence for competition in desert shrubs (Yeaton and Cody 1976), and has been demonstrated for some savanna trees (Smith and Walker, 1983).

1.4.3.1 Limiting factors

The classical theory of plant limitation predicts that plant production should be linearly related to the availability of the single necessary factor in shortest supply and should be insensitive to small changes in the levels of other factors. Biologists have long realised that this is a gross over-simplification, since the availability of one factor commonly influences the assimilation efficiency of other factors. Thus while annual herbaceous production in semi-arid savannas is linearly related to annual rainfall (see review in Rutherford 1980), the slope of the relationship varies according to soil nutrient status (Bell 1982). Fertilisation of savannas also leads to increases in herbaceous production. Nitrogen and phosphorus act synergistically to increase production more when applied together than when applied separately (Donaldson, Rootman & Grossman 1984).

Savannas receive very high levels of radiant energy relative to other biomes (Nix 1983), but the position of the tree layer between the herbaceous layer and the light source makes competition for light a potential factor in tree-grass interactions (McMurtrie & Wolf 1982). The canopy of most savannas (unlike woodlands or thickets) is however insufficiently dense to reduce light levels in the herbaceous layer below the light compensation point of C4 grasses. Harrison (in prep) indicates a reduction in irradiance of about 50% in the sub-canopy habitat. Most studies (Grossman 1978, Barnes 1979) show a slightly lower grass production beneath the canopy, but observation of semi-arid savannas, particularly in drought years, will frequently show the reverse. The exclusion of tree roots results in a large increase in grass production (Knoop & Walker 1984), suggesting that competition in savannas mostly occurs below-ground. It is possible that the grass canopy is sufficiently dense to deprive tree seedlings of light and thus prevent their establishment. Light levels and water use efficiency may also interact.

It is therefore difficult to isolate a single limiting factor in semi-arid savannas, despite the clear evidence of competition. In the view of de Wit (1960) it is seldom possible to isolate a single limiting factor, but this does not prevent the analysis of competitive effects. Since moisture is a

prerequisite of nutrient mineralisation, transport, uptake and assimilation, it seems logical to examine water availability as a first approximation to resource limitation in savannas.

1.4.3.2 Niche overlap

The degree of niche overlap has frequently been used as an index of interspecific competition, and as frequently criticised (Abrams 1980). The criticisms have three main bases.

1. Degree of niche overlap is only equivalent to the competition coefficient (*sensu* Levins 1968) if the resource is limited and if the efficiency with which a unit of the resource is converted to biomass by each of the competitors is taken into account.

2. Presence of an organism in a resource category is not necessarily related to the amount of resource taken. Availability of the resource in the category must also be considered.

3. Several different formulae are used to calculate niche overlap, some of which are not appropriate to all circumstances.

Properly applied, it is an index of the relative strengths of inter- and intraspecific competition, and not an absolute measure of the strength of competition *per se*. The degree of niche overlap between trees and grasses in savannas has never been measured except for casual observations regarding the relative depth of rooting and differences in phenology.

1.5 BUSH CLEARING AS A MANAGEMENT TOOL

Although frequently advocated as a technique of savanna management (Donaldson 1969, Ward & Cleghorn 1970, Barnes 1979, 1982), the high cost of extensive bush clearing has restricted its application in Africa. The problem of bush encroachment and the need to increase savanna productivity , coupled with the increasing value of the land and the decreasing relative cost of clearing are likely to make it a more attractive option in the future. Many semi-arid regions of Africa with a high rural population density are effectively undergoing bush clearing due to the huge demand for fuel wood.

1.5.1 REASONS FOR BUSH CLEARING

The motivations for bush clearing are conveniently treated under three headings, although they are not mutually exclusive.

1.5.1.1 Ecological

Bush encroachment. If it is assumed that a long-term equilibrium value for woody plant density is associated with every combination of climatic and soil conditions, and there is evidence that recent disturbance has increased the woody density above this level, then clearing could be used to return the system to equilibrium. Equilibrium theory predicts that the woody density should return to its "normal" value of its own accord if the disturbances causing the encroachment are removed; however, the process may have progressed to such a degree that the system is functionally altered, and will not return to the equilibrium mix (Walker & Noy-Meir 1982). In a less extreme case recovery may be possible under

fire and grazing management alone, but may proceed at an unacceptably slow rate due to the longevity of woody plants. Under these circumstances intervention by bush clearing may be justified.

Habitat modification. Selective bush clearing in a homogeneously wooded area will result in a mosaic of cleared and uncleared areas. There are theoretical reasons to expect a diverse habitat to be more resilient in the presence of disturbance and stress than a homogeneous one (Walker *et al* 1981). For this theory to apply to bush clearing, the cleared area must be functionally (and not just visually) different to the uncleared area.

A more diverse landscape should be able to support a more diverse animal community. Certain animal species (eg wildebeest) have a preference for open rather than in densely bushy habitats. This may relate to their feeding requirements or to predator evasion. Since grassland areas are relatively rare in savanna regions, and the tendency is towards increasing woodiness, these "plains game" may present conservation problems. It may thus be justifiable to create habitats which will enhance their viability.

1.5.1.2 Economic

Cattle ranching. The principle economic activity in savanna regions is beef production. Cattle make very limited use of browse, so any treatment which increases the production of grass has an economic benefit, which must be balanced against the cost of the treatment. Large increases in herbage production following bush clearing have been reported in numerous studies (see Table 1.3). Those studies which have measured the consequent boost to beef production report a more modest increase (Louw & van der Merwe 1973, Harrington 1973, Teague 1973, Pratchett 1978). No detailed cost-benefit analyses of bush clearing have been made for African conditions. The cost analyses alone suggest at best a

marginal economic viability (Donaldson 1978, Scholes 1986) under current economic conditions. The wood yielded by bush clearing may have economic value in an increasingly fuel and timber starved rural economy.

Recreational use. Where the land use is tourism or hunting it is conceivable that profits may be positively linked to the numbers and visibility of animals, both of which can be increased by bush clearing. The extremely high value placed on recreational land may make bush clearing a more economical method of increasing wildlife numbers and diversity than the acquisition of additional land.

1.5.1.3 Aesthetic

A grassland with scattered trees is widely perceived to be aesthetically more desirable than denser, more shrubby vegetation types. Selective bush clearing can achieve such a park-like landscape.

1.5.2 METHODS OF BUSH CLEARING

This study is concerned with the general consequences of removing trees from savannas rather than with the specific disturbances caused by the application of a particular method of clearing. It therefore does not address the question of which methods should be used, except where the method has in itself major ecological consequences. Provided proper precautions are observed against the known hazards, the choice of clearing method is essentially determined by practical and economic rather than ecological factors. Table 1.2 lists a number of trials of bush clearing methods which have been undertaken within the area of reference of this study. Most clearing operations use a combination of methods drawn from the following broad groups.

Table 1.2 Some bush clearing methodological trials conducted in semi-arid savannas of Southern and East Africa.

Reference	Method	Species
Chemical methods		
Ivens (1958)	2,4,5-T	*Acacia* spp.
Philip (1962)	2,4,5-T	*Acacia* spp., *Lannea Commiphora*
Harrington (1968, 1973a)	Picloram	*A. hockii*
Lloyd, Bromwich & McNeill (1978)	Picloram/2-4D	*Brachystegia boehmii Colophospermum mopane*
Du Toit (1973)		*A. karoo*
Lamprechts (1974)	Various	Various
Sousa de Almeida (1974)	2,4-D/2,4,5-T	*Acacia* spp, *Dichrostachys*
Mechanical methods		
Glover (1959)	Chaining Buldozing	Various
Glascow & Duffy (1959)	Hand felling & burning	*Euclea divinorum Acacia pennata*
Evans Jones (1962)	Chaining	*A. mellifera*
Ward & Cleghorn (1964)	Ring-barking	*Brachystegia spiciformis*
Pratt (1966a,b)	Bush-breaker Mower Mattocking	*Disperma* sp. *Tarchonanthus camphoratus Acacia* spp.
Noel (1967)	Ring-barking	Various
Clatworthy (1969)	Slashing	*Brachystegia spiciformis*
Thomas (1970)	Mattocking	*Brachystegia spiciformis*
Rees (1974)	Mattocking	*Brachystegia spiciformis*
Denny (1968)	Ring-barking	Various
Natural methods		
Barnes (1965)	Fire & mattocking	*Brachystegia spiciformis*
Pratt & Knight (1971) Thomas & Pratt (1971)	Fire	*Tarchonanthus camphoratus* and *Acacia* spp.
Donaldson (1966,1967)	Fire	*Acacia mellifera*
Ward & Cleghorn (1970)	Grazing	*Brachystegia spiciformis*
Harrington (1974)	Chaining & fire	*Acacia hockii*
Trollope (1982b)	Fire & goats	*Acacia karroo*

The natural methods use browsers or fire to retard tree growth. Neither is consistently effective on its own against established woody plants (Barnes 1965, Ward & Cleghorn 1970, Aucamp 1980 and Trollope 1982b), but they can retard re-invasion of woody plants into a grassland created by other methods. In combination they may be considerably more effective in reducing the woody biomass (Trollope 1982b).

Burning can only be successfully used where sufficient fuel accumulates between burns to provide a hot fire. This is incompatible with heavy grazing in an area of low grass productivity. Apart from the loss of the standing crop once every three to four seasons, the major detrimental effect of burning is the alteration of species composition in favour of fire resistant plants (Trapnell 1959).

The mechanical methods physically sever the woody plants from their root stock, and include felling, root ploughing, chaining, bulldozing and ring-barking. The main ecological hazards relate to the soil disturbance by heavy machinery. Compaction and increased erosion may result (Buckhouse & Gifford 1976), especially if the debris is windrowed. A common drawback of these methods when applied in Africa is the widespread ability of woody plants to coppice from surviving root material. This growth form is especially common on sandy soils, where woody plants have a high root to shoot ratio. Mortality due to clearing is frequently low (Pratt, 1966a) and the coppice usually results in a denser vegetation than the original.

Chemical methods involve the application of arboricides as granules, foliar sprays, basal injections or cut-stump treatments. The compounds are generally toxic to both plants and animals, and rely on precision of application and dosage for specificity to woody plants. They result in standing dead material which may have to be removed to allow access by grazers.

..6 REVIEW OF RELATED STUDIES

1.6.1 COMPETITION EXPERIMENTS IN SEMI-ARID SAVANNAS

1.6.1.1 *Bush clearing trials*

Numerous bush clearing experiments have been carried out in Australia (Walker *et al* 1972, Beale 1973), North America (Scifres, Mutz & Durham 1976, Clary & Jameson 1981) and Africa. Reviews are provided by Teague (1976) for Zimbabwe and O'Connor (1985) for Southern Africa. A summary of the details and findings of those performed in Southern and East Africa is presented in Table 1.3 and a map of their locations is given in Figure 5 on page 37.

The following general conclusions can be drawn from the studies reviewed.

1. Grass production increases on the cleared site.

2. Herbaceous species composition changes, usually in the direction of lower quality. This change can involve the loss of sub-canopy species (eg. *Panicum maximum*), the gain of more mesic species (eg. *Urochloa mossambicensis*) or the proliferation of pioneer species (eg. *Aristida* spp) (Dye & Spear 1982).

3. Herbaceous production and composition on both cleared and uncleared sites is strongly influenced by rainfall. The effects of the treatment may be less than the effects of climatic variation (O'Connor 1985).

4. Trees regrow in the grassland unless they are prevented from doing so.

Table 1.3 Bush clearing experiments conducted in Southern and East Africa.

Region	Site	Woody species	Soil Texture	Rain (mm)	Duration (yr)	Summary of results	Reference
1.Tanzania	Mpwapwa	Acacia, Albizzia,Grewia Commiphora.	SaLo	c.600	7	Grazing days inc. from 64 to 300 /ha. Many forbs. Less erosion on clearing.	Staples (1945a,b)
2.Kenya	Kisokon	A. senegal, Terchonanthus	SaLo	c.600	7	Tested grazing, fire, mowing & browsing. Trees regrew unless burned and mowed.	Bogdan (1954)
3.Zimbabwe	Makaholi	Brachystegia/Julbernardia	Sa	660	4	Hay yield inc. from 225 to 1350 kg/ha/yr Goats could not control regrowth.	Ward & Cleghorn (1964)
4.Zimbabwe	(11 sites)	Various		c.600	1	Mean hay yield inc. from 505 to 699 kg/ha/yr. (Range: wooded 88-1600; cleared 330-1940)	Ivy (1969)
5.Namibia	Damaraland	Acacia mellifera	Lo	430	5	Grass basal area inc., especially in desireable perennial species.	Joubert (1966)
6.E Cape	Cathcart	Acacia karroo		435	2	Hay yield inc. from 159 to 514 and from 623 to 973 kg/ha/yr. No species change.	Du Toit (1968)
7.N Cape (Molopo)	Bathburst	A. mellifera	Sa	345	8	Hay yield inc. from 149 to 258 kg/ha/yr	Donaldson & Kelk (1970, 1974a,1974b,1974c)
	De Kust		Sa	300	6	from 520 to 1100	
	Arizona		Sa	300	7	from 250 to 750	
	Buttermere		Sa	305	6	Animal carrying capacity inc. 14%	
8.N Transvaal	Towoomba	Acacia spp., Dichrostachys cinerea, Grewia spp.	Cl	588	20	Animal mass gain inc. from 7 to 14 kg/steer/yr Selective clearing ineffective.	Louw & vd Merwe (1973)
9.SE Zimbabwe	Nuanetsi	Combretum apiculatum/ Sclerocarya birrea	LoSa	600	4	Selective clearing trial. Hay yield inc. from 1554 to 2609 kg/ha/yr.	Kelly *et al* (1978)
10.Namibia	Tsumeb (2 sites: 1.Thornveld 2.Karst	1.Acacia mellifera/ Commiphora angolensis 2.Terminalia prunioides/ Combretum apiculatum	? Dolomite	c.600	2	1.Hay yield inc. from 1309 to 2822 kg/ha/yr 2.Hay yield inc. from 350 to 847 kg/ha/yr	van Niekerk & Kotze (19
11.N Transvaal	Mara	Combretum apiculatum & A. tortilis	SaLo SaLo	416 c.450	3 2	Grazing days inc. from 200 to 300 /ha/yr Hay yield inc. from 1600 to 2500 kg/ha/yr	Donaldson (1978) Pieterse & Grunow (1985)
12.Botswana	Morale	A. nigrescens/Sclerocarya	SaLo	c.450	12	Stocking rate inc. 33% No significant herb. species shift.	McKay (1968)
13.Botswana	(5 sites)	1.Central Kalahari bush 2.Arid sweet bushveld 3.Southern Kalahari bush 4.A.nigrescens/C.apiculatum 5.Semi-sweet mixed veld		c.450	4	Mean hay yield inc. from 1950 to 2246 kg/ha/yr Grass species composition improved, especially under partial clearing. Light level inc. from 60 to 190 $MJ/m^2/s \times 10^3$ Duration of plant-available water increased.	Pratchett (1978)
14.W Transvaal		Acacia erubescens	SaLo	473	10	0, 33, 66 & 100 % clearing. 33% had best grass species composith. P.maximum & D.eriantha inc.	Morris (1980)
15.SW Zimbabwe	Matopos	"Thornveld"	SaClLo	615	19	Hay yield inc. by 850 kg/ha/yr	Dye & Spear (1982)
	Matopos	"Sandveld"	Sa	615	19	525	
	Nyamandlovu	"Sandveld"	Sa	569	15	780	
	Tuli	"Sandveld"	Sa	450	15	100-1500	
						Species shift. Lost P.maximum & D.eriantha	
16.E Cape	Adelaide	Acacia karroo	Lo	290		Optimum grass prodn. with 100 trees/ha	Aucamp *et al* (1983)

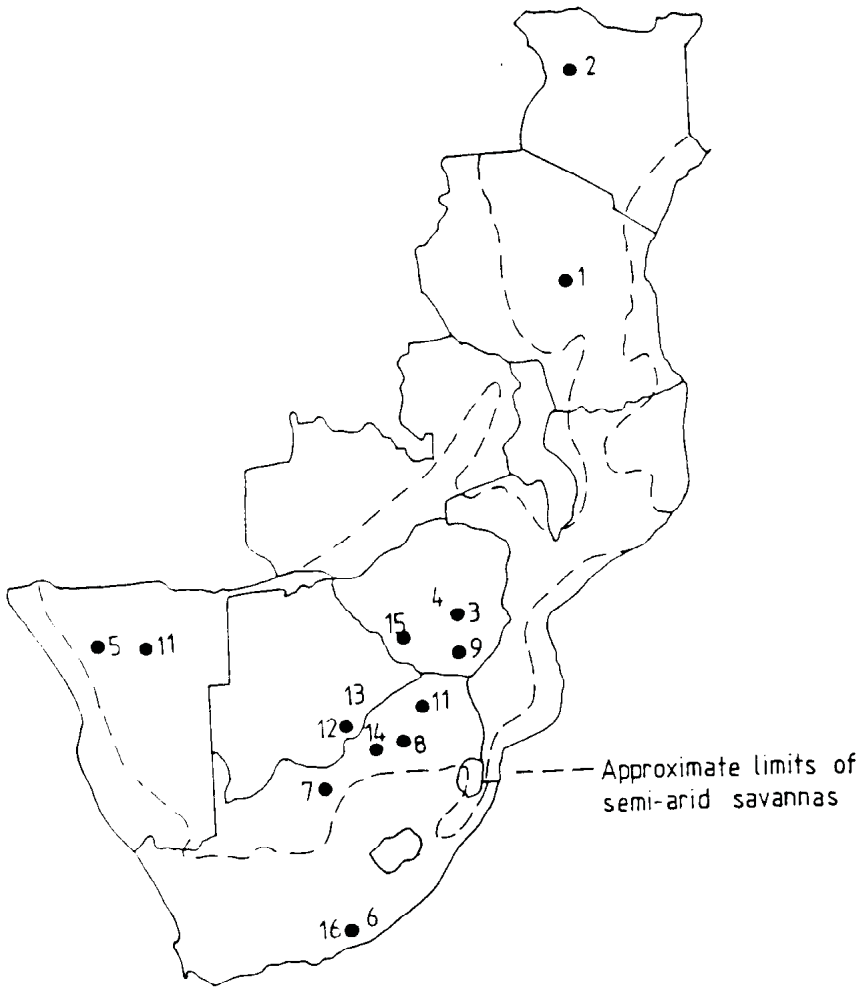

Figure 5. The location of bush clearing studies listed in Table 1.3

These studies can be criticised on one or more of the following grounds.

1. The mechanism by which grass production is increased is at best only inferred. Most studies attribute the increase to a reduction in competition, but few monitor changes in the resource levels.

2. The initial standing crop and productivity of woody plants is seldom measured. Where quoted, it is usually given in terms of tree density or basal area, which bear a site-specific relationship to woody plant biomass.

3. The above factors prevent the development of a general model of the bush clearing response and render the individual studies non-comparable and site-specific.

4. Usually only annual grass production and species composition are monitored. Other parameters, such as changes in runoff and erosion, are not measured.

The study reported by Dye and Spear (1982) is outstanding because it ran over a fifteen year period and was replicated on four different soil types. Their results are presented in Figure 6 on page 39. They came to the following conclusions.

1. Water use by trees was fairly constant between years on the same site. Thus over a wide range of annual rainfalls, absolute increases in grass production of 600-1000 $kg.ha^{-1}$ could be expected. The exception was the site at Tuli, where water use by trees appeared to increase with increasing rainfall. The authors offer no explanation for this result, which is possibly due to a greater degree of niche overlap on this arid site with shallow soil, or possibly to a water-nutrient interaction. On this site the grass production on the cleared treatment appeared to become nutrient rather than water limited at annual rainfalls above 600mm.

2. The slopes of the regressions between grass production and annual rainfall are higher on clayey than sandy soils but have a lower intercept. This means that grass production on clayey soils is lower at low rainfalls but higher at high rainfalls, and is therefore more variable overall.

3. The correlation coefficient for the regressions is higher on clays, implying a stronger water limitation and less carry-over of moisture between seasons. Similarly, the correlation coefficients were higher on uncleared sites relative to cleared sites.

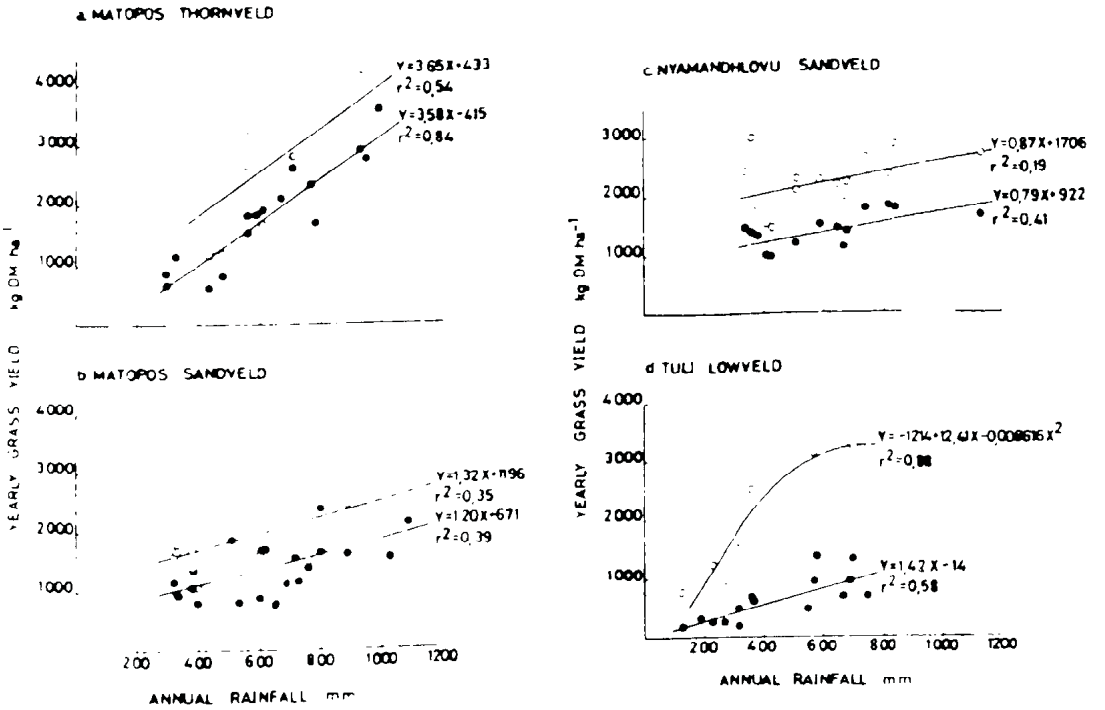

Figure 6. The relation between annual rainfall and grass production: cleared (O) and uncleared (●) plots in four veld types. (Dye & Spear 1982).

1.6.1.2 Partial clearing experiments

Donaldson and Kelk (1970) cleared *Acacia mellifera* to varying degrees in the Molopo district of the Western Transvaal. Walker *et al* (1972) and Beale (1973) conducted similar trials in Australia, in *Eucalyptus populnea* and *Acacia aneura* woodlands respectively. These authors showed an inversely concave dependency of grass production on tree standing crop, as illustrated in Figure 7 on page 40, and quoted ten other studies reporting a comparable relationship. Aucamp *et al* (1980), on the other hand, found an inversely convex relationship when they measured herbaceous production after increasing degrees of *Acacia karoo* removal

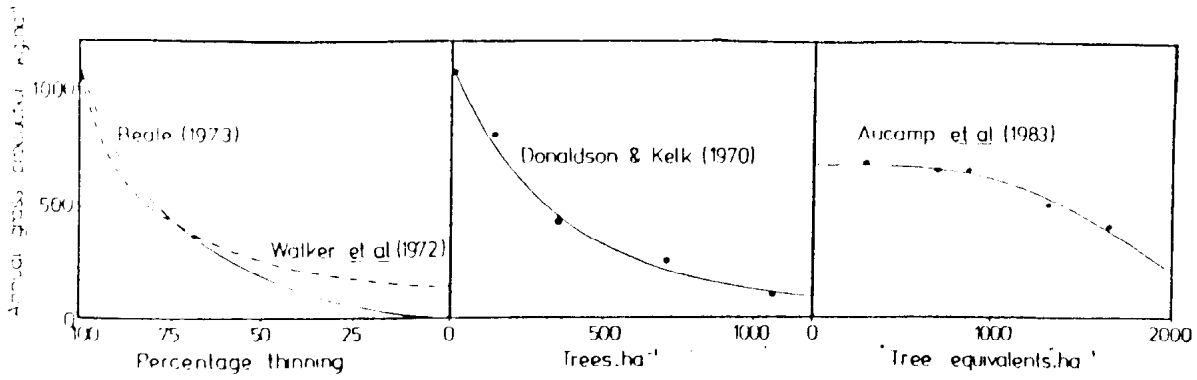

Figure 7. Form of the relationship beween tree biomass and grass yield

in the Eastern Cape, with a maximum grass production recorded at 300 "tree equivalents".ha^{-1}. The evaluation of these conflicting findings is difficult, since the degree of woodiness is quoted in non-comparable units. It is possible that the Aucamp *et al* curve represents the lower threshold of the other curves, but seems unlikely. The implications for bush clearing policy are large, since the concave curve predicts maximum cost-efficiency with total clearing, while the convex curve implies a non-zero optimum woody density.

Kelly, Schwim & Barnes (1978) investigated the removal of shrubs independently of trees. The results from the first two years following clearing show a large increase in grass production when the large trees were removed and when all woody plants were cleared but a small increase when only the small trees were removed. No data are provided as to the relative biomass of the large and small tree categories.

Knoop (1982) found no qualitative difference between the effect of trees and shrubs on grass production or soil moisture status.

1.6.1.3 Clearing with soil moisture monitoring

Strang (1969a) found an increase in soil moisture duration under grassland derived from *Brachystegia spiciformis / Julbernardia globiflora* woodland in Rhodesia, but that the grassland could dry the soil more completely than the woodland. Increases in soil moisture immediately following bush clearing have also been reported by Pratchett (1978) in Botswana, Knoop & Walker (1984) in the Northern Transvaal, Pieterse & Grunow (1985) in the Northern Transvaal and Gifford & Shaw (1973) in Arizona.

1.6.1.4 Reciprocal manipulation experiments

Knoop & Walker (1984) measured the effect of the removal of grass on the growth of woody plants, and *vice versa*. In a community dominated by *Burkea africana* on sandy, dystrophic soils, the removal of grasses did not significantly increase terminal twig elongation of the woody plants. In an adjacent community on slightly heavier-textured soils with a higher nutrient status, grass removal increased terminal twig growth of *Acacia tortilis*. The exclusion of woody-plant roots significantly increased grass growth on both sites. The conclusions drawn from this study are that competition between trees and grasses is asymmetrical in the favour of trees, and varies in strength between sites and/or species. They further attempted to test the hypothesis that competition between trees and grass was mediated by a separation in the depth of rooting activity, and found that trees did have a larger proportion of their roots at greater depths in the soil, but that grasses nevertheless had access to deep soil layers.

1.6.1.5 Regrowth of woody plants

Despite the general observation that coppice regrowth is a common consequence of bush clearing in Africa, very little work is published on the rate at which the woody biomass recovers. Strang (1969b) found that the dominant process of re-invasion in *Brachystegia spiciformis / Julbernardia globiflora* woodland was vegetative suckering rather than the establishment of new seedlings. He also measured the regrowth on clearings of known age (Strang 1974) and found that in the absence of fire full recovery required about fifty years. Recovery was rapid during the first twenty years, after which it slowed down. The number of stems per hectare reached a peak at twenty years, after which it declined. This may be in accordance with the "3/2 thinning law" (Yoda *et al* 1963, White & Harper 1970). Frequent burning did not affect the number of stems, but did reduce the basal area and height of the regrowth. Where the plots had been cleared and cultivated, and therefore regrowth was entirely from seed, the recovery was much slower. Taush & Teuller (1977) simulated the recovery of Pinyon-Juniper woodlands in Eastern Nevada on the basis of a study of tree growth rings from clearings of different ages. They predicted an almost complete recovery after fifteen years.

1.6.2 HYDROLOGY OF SEMI-ARID SAVANNAS

The basic procedure for studying the hydrology of semi-arid regions was established by Slatyer (1961). Portions of the hydrological cycle have been well studied, such as rainfall interception and partitioning (Pressland 1973, De Villiers & de Jager 1981), transpiration (Pendle 1982) and runoff (Dye 1984). However, few integrated water-balance studies have been published for semi-arid savannas. A catchment-scale study was initiated in Uganda but was abandoned before any meaningful results were obtained (Edwards & Blackie 1979). The estimates presented by Bate, Furniss and Pendle (1982) for the Nylsvley study site are estimates

derived from the sub-continental water budget proposed by Whitmore (1971).

Complete water budgets for sites with and without woody vegetation have been calculated for a Pinyon-Juniper vegetation in Arizona by Gifford (1975). Runoff was higher on cleared sites, but the other components of the cycle were little changed.

1.6.3 MODELS OF SAVANNA DYNAMICS

The dynamics of the "Walter hypothesis" model of savanna function (Walter 1971) were quantitatively explored by Walker *et al* 1981, who found three stable equilibria: a grassland, a woodland and a savanna. An increase in grazing pressure could move the system out of the savanna domain of attraction and into that of the woodland. This was offered as an explanation for the tendency of savannas to become thickets under heavy grazing. Walker & Noy-Meir (1982) showed that exclusive access to subsoil water was not a necessary condition for the stability of the tree-grass mixture, but that given superior water uptake rates by grasses, preferential access to subsoil water was necessary to prevent the competitive exclusion of trees.

McMurtrie & Wolf (1983) included competition for light, water and nutrients in their model, and come to similar conclusions. The model of Mankin & Risser (1983) also has rooting depth separation between trees and grass as the basis of coexistence. None of these models has been tested with parmeters derived from a real savanna.

1.7 STUDY OBJECTIVES

The overall aim of this study was to develop process-based models of the tree/grass interaction in semi-arid savannas. Such models can then be used to predict the effect of tree removal on grass production at any site for which the model parameters are known. The success of the models in predicting observed patterns of production acts as a test of current hypotheses regarding structure and function in semi-arid savannas. The detailed objectives were as follows.

Conduct an experiment on three different soil types, monitoring selected ecological parameters on two treatments: a semi-arid savanna and the grassland derived from it by removal of all the woody plants. The soils were chosen to represent a range of fertility and hydrological properties, and the selected parameters were runoff, soil moisture availability, transpiration rates by the dominant woody plants and grasses, evaporation from the soil surface, herbaceous production and species composition.

2. Develop a simulation model for semi-arid savannas linking primary production to plant water use, calibrate it with data from the above experiment and test it against independently collected data.

3. Use the model to generate long term (40 year) simulations of the hydrology and primary production of plant communities on different soil types under increasing degrees of woody plant removal.

4. Use the model and independently collected data to test the following hypotheses.

   a. H1: Grass production in semi-arid savannas is water-limited.
      Ho: Variations in water supply have no effect on grass production.
      Test: Failure of a water-use based model of primary production in a savanna to account for qualitative and quantitative trends in harvest data will lead to rejection of the hypothesis.

b. H2: There are at least two axes (temporal and spatial) to the water-use niches of trees and grasses in semi-arid savannas, and both contribute to niche separation.
Ho: Water-use niche separation occurs on one or no axes.
Test: Determine the rooting-depth of trees and grasses in the field. Measure their transpiration and photosynthetic rates through a drying cycle in the field. Substitute both into the water balance model and validate it against field soil-water data. Run the model using historical rainfall records as input data, and test for niche separation using standard indices.

c. H3: In a two-species model of primary production in which the competition is asymmetric, the production of the species with the lower competition coefficient ("grass") will be an inversely concave function of the biomass of the other species ("trees").
Ho: The function has a linear or inverse convex form.
Test: Simulate grass production under a range of soil and rainfall conditions at several levels of tree biomass. Test the dependence of grass production on tree biomass for positive or negative curvature.

5. Estimate, from measurements of coppice regrowth, the rate at which woody plant biomass recovers following clearing.

6. Predict the combinations of annual grass production, woody biomass and herbivore stocking rate which permit the curtailment of woody plant recruitment by repeated burning.

2.0 THE STUDY AREA

2.1 GENERAL ECOLOGY OF THE KLASERIE PRIVATE NATURE RESERVE

2.1.1 LOCATION

The study area is a semi-arid savanna in the Klaserie Private Nature Reserve, adjacent to the western boundary of the Kruger National Park, 20 km south of the town of Phalaborwa, centered on 24° 15'S 31° 10'E. The reserve is a collectively-owned area of 650 km² managed for recreational game viewing and limited hunting. It is surrounded by properties under similar conservation-orientated management. Although most of the boundaries are fenced, a significant amount of game movement occurs between the Klaserie and adjacent areas. It would therefore be inaccurate to consider the Klaserie as an isolated ecosystem. It is part of a larger functional system which includes all portions of the Eastern Transvaal Lowveld that support wild ungulates as the dominant herbivores.

Prior to proclamation as a nature reserve in 1972, the main form of land use was hunting combined with some cattle ranching and crop farming. After 1972 factors such as fencing, water provision, reduction in hunting and control of poaching led to large increases in herbivore numbers. They reached levels unsupportable by plant production during the dry seasons of 1981/2 and 1982/3, when about 50% of the game population died (Schneebeli 1983, Scholes 1985). During the first two years of the study (July 1981-October 1983) the area was subjected to a severe drought and heavy grazing pressure. The last two years of the study (November 1983-June 1985) were characterised by good rains and light grazing.

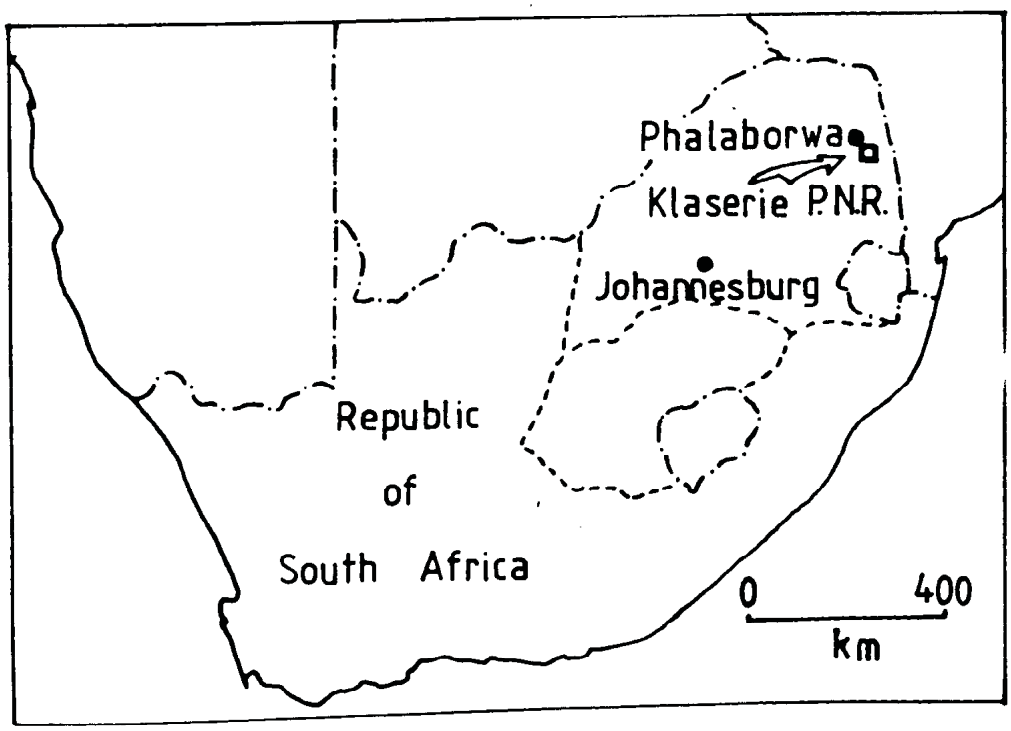

Figure 8. Location of Klaserie Private Nature Reserve

2.1.2 CLIMATE

A Walter climate diagram for Phalaborwa (Figure 9 on page 48) illustrates the characteristic features of a savanna climate: rainfall concentrated into a summer wet season of five to seven months, with a period of water stress for the remainder of the year and relatively high temperatures throughout the year with a virtual absence of frost. The mean annual class A pan evaporation at Phalaborwa is 2090 mm, which considerably exceeds the mean annual precipitation of 480mm. The classification under the Koppen (1931) system is BShw (Hot Savanna with summer rainfall). Under the system of bioclimatic units (Phillips 1983), the study site is transitional between sub-arid wooded savanna and arid wooded savanna.