

**ASPECTS OF THE BIOLOGY OF CLIMBERS  
IN SOUTHERN AFRICA**

by

**DAVID ANDREW BALFOUR**

University of Cape Town

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

# **ASPECTS OF THE BIOLOGY OF CLIMBERS IN SOUTHERN AFRICA**

by

**DAVID ANDREW BALFOUR**

**A Thesis Submitted in Partial Fulfilment of the Degree**

**Master of Science in Botany**

**Botany Department**

**University of Cape Town**

**April 1991**

The University of Cape Town has been given the right to reproduce this thesis in whole or in part. Copyright is held by the author.

# Table of Contents

<b>Abstract</b> .....	ii
<b>Chapter One :</b> .....	1
<b>Chapter Two :</b> .....	6
Introduction .....	6
Methods .....	11
Results .....	13
Discussion .....	27
Conclusion .....	30
References .....	31
<b>Chapter Three :</b> .....	33
Introduction .....	33
Methods .....	35
Results .....	39
Discussion .....	45
Conclusion .....	47
References .....	48
<b>Chapter Four :</b> .....	51
Introduction .....	51
Methods .....	52
Results .....	55
Discussion .....	61
Conclusion .....	63
References .....	64
<b>Chapter Five :</b> .....	67
Introduction .....	67
Methods .....	71
Results .....	74
Discussion .....	83
Conclusion .....	87
References .....	88
<b>Chapter Six :</b> .....	92

## Abstract

This study examines factors that may limit the abundance and distribution of climbers and the influence that climbers may have on the regeneration of forests.

The abundance of climbing plants (climbers), was established over a soil nutrient gradient, under standardised light conditions. Abundance was found to be positively correlated with the potassium concentration and the soil S - value, but not with other nutrients. Thus, the association between climbers and soil nutrient levels is challenged. Instead the abundance of climbers was found to be positively correlated with tree canopy architecture and trellis availability. More climbers entered host trees with low canopies (< 15 m) than those with high canopies. Trees with low canopies had more climbers entering vertically into the canopy while trees with high canopies had more climbers entering the canopy horizontally. Evidence was found to suggest that climbers facilitate the entry of each other into tree canopies.

Tree and climber saplings were grown under three nutrient and two light treatments to compare the relative growth rates of their terminal shoots under the different conditions. While climbers were found to have greater shoot extension rates than trees, they did not grow relatively faster than trees under any of the combination of treatments. Thus light levels and soil nutrient availability may not influence the competitive ability of climbers compared to trees.

Three aspects of the carbon gain capacity (maximum photosynthetic rate, leaf nitrogen concentration and leaf water use efficiency) were compared between climbers and trees. While the climbers had a significantly higher leaf nitrogen concentration than trees, as well as higher leaf water use efficiency, the maximum carbon assimilation rates of climbers and trees did not differ. These differences between trees and climbers are slight and suggest that differences in growth rates between the two growth forms are largely due to differences in carbon allocation in trees (to support structures) and in climbers (shoot elongation), rather than carbon gain mechanisms.

Patterns of canopy tree regeneration in gaps and sub-canopy plots were determined for lowland and highland forests to determine whether climbers influenced the regeneration of canopy trees. More canopy trees regenerate in the sub-canopy of highland forests, while in lowland forests treefall gaps are the major sites of canopy tree regeneration. These patterns of regeneration were found not to be related to the density of the ground layer, the extent of the lateral infill of the

gap-forming trees or the abundance of woody climbers. Instead, a negative correlation was found between the percentage of regenerating canopy species and the density of the herbaceous and shrubby understory layer in both lowland and highland forests. Thus in both forests the understory layer has an important influence on the regeneration of canopy trees. The role of vertebrate herbivores may be important in providing the necessary release from suppressive effect of the dense understory layer and to enable the regeneration of canopy tree species in the lowland forests.

## Acknowledgements

I thank William Bond, my supervisor, for unfailing encouragement, useful suggestions, discussions and criticism during the project and for reading and commenting on earlier manuscripts of this thesis. Mostly I thank him for a new way of looking at biology.

I am grateful to Ruth Beukman, Maanda Ligavha and William Bond for assistance in the field, Mike Cramer for help with the IRGA equipment, Desmond Barnes for making up nutrient solutions as well as Craig Hilton-Taylor for help on the computer and John Lanham for help with the carbon isotope work. Rosena de Villiers of Forestek is thanked for help with nutrient analyses.

I thank Rod Saunders of the nursery at Kirstenbosch Botanical Gardens and the City Council staff at Orange Kloof for providing me with plants. I am grateful to the Cape Town City Council for allowing me to work in Orange Kloof, and the Natal Parks Board and Kwa Zulu Bureau of Natural Resources for giving me access to various forests in Natal.

I appreciate the efforts of Guy Midgely, Willy Stock, Eugene Moll and particularly Jean Harris who read and commented on portions of the earlier manuscript.

This work was funded by a grant from the Department of Environmental Affairs (Forestry) as well as a CSIR (FRD) MSc. Bursary.

Finally I thank my parents for their support when I made the change to biology from engineering, and Jean for all her support and encouragement in writing this thesis.

# Chapter One

## Introduction

### Context of the study

The abundance and diversity of climbing plants varies greatly in different forests (Grubb 1987). Although climbers are generally associated with tropical forests (Richards 1952; Givnish and Vermeij 1976) they are often common in temperate forests (Siccama *et al* 1976). Despite the fact that climbers are common growth forms in many forests, the study of their ecology has been much neglected (Putz 1984).

Climbers differ from trees in their absence of a rigid woody support (Darwin 1867). They are thus dependent on free-standing trees for vertical support, and have variously been termed structural dependents (Richards 1952) or structural parasites (Stevens 1987). The dependence of climbers on trees for support suggests that their ecology is closely linked to trees, and the role of climbers in forest ecology and the interrelations between trees and climbers has recently become the focus of a number of studies (Putz 1984; Putz and Chai 1987; Clark and Clark 1990).

Climbers are documented as causing damage to tree sapling growth (Fox 1968) and as impeding tree regeneration after logging in tropical forests (Kochummen 1966) and temperate forests (Phillips 1931). Climbers may arrest the growth of individuals in treefall gaps (Putz 1984; Whitmore 1989) as well as forming impenetrable mats in the forest margins (Huntley 1965). The impact of climbers on mature trees ranges from negative effects such as a reduction in the fecundity of the host tree (Stevens 1987), reduction in tree growth (Wigham 1984) and eventual death of the tree (Putz *et al.* 1987) to positive effects such as mutual support of trees by a cross linking of climbers in their canopies (Richards 1952; Smith 1973).

The abundance and distribution of climbers has been linked to a number of abiotic factors. Climbers have been associated with high levels of light intensity (Putz 1984), with dry soil types (Phillips 1931) and low rainfall (Longino 1986). Climbers have been repeatedly associated with nutrient rich soils (Richards 1952; Proctor *et al.* 1983; Putz 1985; Putz and Chai 1987; Grubb 1987). However this relationship remains to be substantiated and its causes are not well understood.

Climber presence has further been associated with biotic factors such as disturbed forest canopies (Lowe and Walker 1977; Putz 1985) and forest margins (Williams-Linera 1990). Other factors such as the availability of adequate trellises for climbers to attach themselves, in order to climb to the canopy of a forest, have been suggested as influencing the distribution of climbers within a forest (Putz 1984).

Some ecophysiological aspects of the carbon gain mechanisms of climbers have recently been investigated. In an attempt to explain the success of exotic climbers in northern America the photosynthesis of two exotic invasive weedy climbers was compared with that of indigenous climbers by Carter *et al.* (1989) but they found no differences. Carter and Teramura (1988a) found that differences in non-summer stomatal conductance between two exotic climbers might contribute to different invasive abilities while the climbing mechanics of climbers has been related to their photosynthetic rates (Carter and Teramura 1988b).

Little is known of the abundance and distribution of climbers in southern Africa and the factors influencing their distribution patterns. Climbers are generally more abundant in Guineo-Congolian forest (White 1978) than in Afromontane forest (White and Moll 1978). The ecology of climbers in southern Africa is poorly studied. Most ecological studies are restricted to comment on the presence or absence of climbers or their role in preventing tree regeneration (Laughton 1938), or on the damaging effects of climbers on mature trees (Phillips 1931; Venter 1976).

### **Key questions:**

#### **1. What limits the abundance of climbers and why?**

I initially approached this question by testing two hypotheses 1. That climber abundance is determined by soil nutrient levels, and 2. That trellis availability and host tree architecture determine climber abundance. This work was done by considering the abundance of climbers over a naturally occurring soil nutrient gradient. I followed this up by experimentally growing trees and climbers under different nutrient and light conditions to determine the relative influence, if any, of soil nutrients on climbers compared with trees. I further investigated whether aspects of the carbon gain physiology of trees and climbers differ and if this can explain the competitive abilities of climbers and their distribution patterns, associated with nutrient rich soils.

## **2. Do climbers influence the regeneration of forest trees?**

I considered the dynamic effects of climbers in forests by comparing the interactions between climbers (and other growth forms), and canopy tree regeneration. I tested the hypothesis that the regeneration dynamics differ between lowland and highland forests in southern Africa, and that these differences can be explained by interactions between different growth forms.

### **Structure of the thesis**

In Chapter Two I investigate the abundance of climbers in the Knysna forest over a soil nutrient gradient to test the idea that their abundance is correlated with soil nutrient levels. I also test an alternative hypothesis that tree canopy architecture and the availability of trellises influence the distribution and abundance of climbers.

In Chapter Three I address the hypothesis that climbers are dependent on high nutrient availability to sustain higher growth rates than trees. I describe an experiment in which the growth of trees and climbers was compared under different nutrient and light treatments. One aim was to determine under which conditions, if any, the climbers grew faster, and were thus more competitive, than the trees.

Aspects of the ecological physiology of climbers are considered in Chapter Four. I ask whether differences in growth rates between trees and climbers are due only to differences in carbon allocation to leaves and wood or whether they also differ in carbon uptake capacity. Photosynthetic rates as well as leaf nitrogen levels and the water use efficiency of the leaves (determined using carbon isotope ratios) are compared between trees and climbers.

In Chapter Five the role of climbers in forest dynamics is investigated. The influence and importance of climbers, as well as different vegetation layers, on forest regeneration, is examined in treefall gaps and below intact forest canopy. I consider the hypothesis that interactions between different growth forms influence the dynamics of highland and lowland forests differently and may influence the composition of the forests.

The final chapter, Chapter Six, draws together the conclusions of the thesis and suggests directions for further research.

## References

- Carter GA and Teramura AH. 1988a. Non-summer stomatal conductance for the invasive vines kudzu and Japanese honeysuckle. *Can. J. Bot.* 66:2392-2395.
- Carter GA and Teramura AH. 1988b. Vine photosynthesis and relationships to climbing mechanics in a forest understory. *Amer. J. Bot.* 75(7):1011-1018.
- Carter GA, Teramura AH and Forseth IN. 1989. Photosynthesis in an open field for exotic versus native vines of the southeastern United States. *Can. J. Bot.* 67:443-446.
- Clark DB and Clark DA. 1990. Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *J. Trop. Ecol.* 6:321-331.
- Darwin C. 1867. On the movements and habits of climbing plants. *J. Lin. Soc.(Bot.)* 9:1-118.
- Fox JED. 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *The Malayan Forester* 31(4):326-347.
- Givnish TJ and Vermeij GJ. 1976. Sizes and shapes of liana leaves. *Am. Nat.* 110:743-778.
- Grubb PJ. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. In: Gee JHR and Giller PS (Eds.) *Organization of communities - past and present*. Blackwell Scientific Publications. Oxford.
- Huntley BJ. 1965. A preliminary account of the Ngoye Forest Reserve, Zululand. *J. S. Afr. Bot.* 31:177-205.
- Kochummen KM. 1966. Natural plant succession after farming in Sg. Krog. *The Malayan Forester* 29:170-181.
- Laughton FS. 1938. The silviculture of the indigenous forests of the Union of South Africa with special reference to the forests of the Knysna region. *Science Bulletin* 157, Forestry series 7, Government Printer, Pretoria. 168 pp.
- Longino JT. 1986. A negative correlation between growth and rainfall in a tropical liana. *Biotropica* 18(3):195-200.
- Lowe RG and Walker P. 1977. Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. *J. Appl. Ecol.* 14:897-903.
- Phillips JF. 1931. Forest succession and ecology in the Knysna region. *Memoirs of the botanical survey of South Africa* No.14.
- Proctor J, Anderson JM, Chai P and Vallack HW. 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. *J. Ecol.* 71:237-260.
- Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6):1713-1724.

- Putz FE. 1985. Woody vines and forest management in Malaysia. *Commonw. For. Rev.* 64(4):359-365.
- Putz FE and Chai P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* 75:523-531.
- Putz FE, Lee HS and Goh R. 1987. Effects of post-felling silvicultural treatments on woody lianas in Sarawak. *Malaysian Forester* 47:
- Siccama TG, Weir G and Wallace K. 1976. Ice damage in a mixed hardwood forest in connecticut in relation to *Vitis* infestation. *Bull. Torr. Bot. Club.* 103:180-183.
- Smith AP. 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107:671-683.
- Stevens GC. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecol.* 68(1):77-81.
- Venter HJT. 1976. An ecological study of the dune forest at Mapelana, Cape St. Lucia, Zululand. *J. S. Afr. Bot.* 42:211-230.
- Whigham D. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Can. J. For. Res.* 14:37-39.
- White F. 1978. The afro-montane region. In: Wergner M.J.A. (Ed.), *Biogeography and ecology of southern Africa*. W.Junk, The Hague, pp 436 - 513.
- White F and Moll EJ. 1978. The Indian ocean coastal belt. In: Wergner M.J.A. (Ed.), *Biogeography and ecology of southern Africa*. W.Junk, The Hague, pp 563 - 598.
- Whitmore TC. 1989. Canopy gaps and two major groups of forest trees. *Ecol.* 70:536-538.
- Williams-Linera G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78:356-373.

## Chapter Two.

### **What Determines Climber Distribution and Abundance? A Gradient Study in the Knysna Forest; Southern Cape.**

#### **Introduction**

Climber distribution and abundance varies greatly with the geographic locality of forests. Woody climbers are commonly associated with tropical forests where they are present in high diversity (Richards 1952), and are found in greater abundance than in temperate forests (Givnish and Vermeij 1976; Putz 1984a, Grubb 1987). The question of what limits the abundance and distribution of climbers has not been answered. A number of studies provide descriptive (Phillips 1931; Richards 1952) and quantitative data (Proctor *et al.* 1983; Putz 1984a; Putz and Chai 1987) on climber abundance but little work has been done to establish the factors controlling the observed patterns of abundance and distribution.

Forest locality and type appear to influence the occupancy of forests by climbers (Grubb 1987). Davis and Richards (1934) and Putz (1983) suggest that tropical heath forests may have fewer lianas (woody climbers) than lowland rainforests, while White (1978) suggests that in Africa lianas are less common in the Afromontane forests than in the lowland Guineo-Congolian forests. In addition different topographical regions of forests have been noted as having varying abundances of lianas e.g. the valleys of the Lambir National Park, Malaysia have twice the abundance of lianas compared to the hilltops (Putz and Chai 1987).

Climbers are commonly thought to be associated with more fertile soils (Richards 1952; Putz 1985; Putz and Chai 1987) suggesting that nutrient availability may be an important limiting factor. A relationship between climber abundance and rainfall or soil nutrients has been suggested by a number of workers, but a clear pattern has not emerged. Phillips (1928) lists climbers as indicators of dry soils and Longino (1986) provides evidence that the growth of a tropical climber species is negatively correlated with rainfall. In contrast Proctor *et al.* (1983) show climber abundance in the Gunung National Park (Sarawak) to be higher in the frequently inundated alluvial forests where the soils have a high base saturation. Gentry (1982), however, found no significant correlation between the abundance of climbers and the annual rainfall of an area, and Fernandez (1987) suggests that water is less important in affecting climber distribution than is the longer growth period of climbers compared with their host trees.

Disturbance of the forest canopy often leads to an increase in the density of lianas (Richards 1952; Fox 1968; Lowe and Walker 1977; Putz, Lee and Goh 1987), as do natural tree fall gaps (Phillips 1931; Putz 1984a), and forest margins are frequently lined with dense tangles of lianas (Williams-Linera 1990). The close association between climbers and disturbed forest, treefall gaps and forest margins has led to the suggestion that they are a light demanding growth form (eg. Phillips 1931; Putz 1984a).

There is evidence that forest architecture is important in determining climber distribution. Climbers behave as structural parasites (Stevens 1987) relying on other plants for support. To be successful a young climber needs to be able to reach the forest canopy and a support structure is necessary. Putz (1984a) found the presence of trellises (young plants and small diameter branches) to be an important factor limiting liana access to the canopy on Barro Colorado Island, and suggests that trellis availability influences the distribution of lianas within the forest. Trellises are most commonly found where there has been a disturbance to the forest and there is regeneration of young vegetation. These areas are often also sites of high light intensity, and high nutrient levels and are ideal for liana growth (Whigham 1984).

There is little literature on the distribution, abundance or the ecology of climbers in southern Africa. Most reports are restricted to mention of the presence or absence of climbers with occasional subjective quantification of climber abundance (Phillips 1931; Huntley 1965; White and Moll 1978; White 1978). Ecological commentary is limited to a mention of the role of lianas in the prevention of regeneration of trees (Laughton 1938), as agents of damage to mature trees (Phillips 1931; Venter 1976) and as alien invaders in Natal woodlands (Gordon and Bartholomew 1989). Geldenhuys (1989a) is the only local study to consider the distribution and abundance of different growth forms in southern African forests, but it is a floristic study and little insight is gained about the ecological importance of the climbers.

In this study I test, firstly, the suggestion that soil nutrients are an important determinant of climber distribution. I quantify the abundance of climbers over a soil nutrient gradient and relate differences in abundance to changes in the soil nutrient environment. I include different topographical aspects in the gradient to test for their influence on climber abundance.

Secondly I test the hypothesis that community constraints, (eg. host tree crown characteristics) rather than abiotic factors such as light and soil nutrients, play an important role in determining the distribution and abundance of climbers. I suggest that the association between climber abundance and light or soil nutrients may not be directly causative and that trellis availability may be more directly correlated with climber distribution.

To test this idea I predicted firstly that in forest where the canopy is low, and by implication trellises more accessible, more climbers would enter the canopy of their host trees vertically while in forest where the canopy is high and access is limited, more climbers would enter the canopy of their host trees horizontally from a neighbouring canopy. Secondly that trees with lower canopy would be more prone to climber occupation than trees with higher canopies. Thirdly I consider whether the presence of one climber species in a tree facilitates the entry of other species by acting as a trellis.

### Study Area

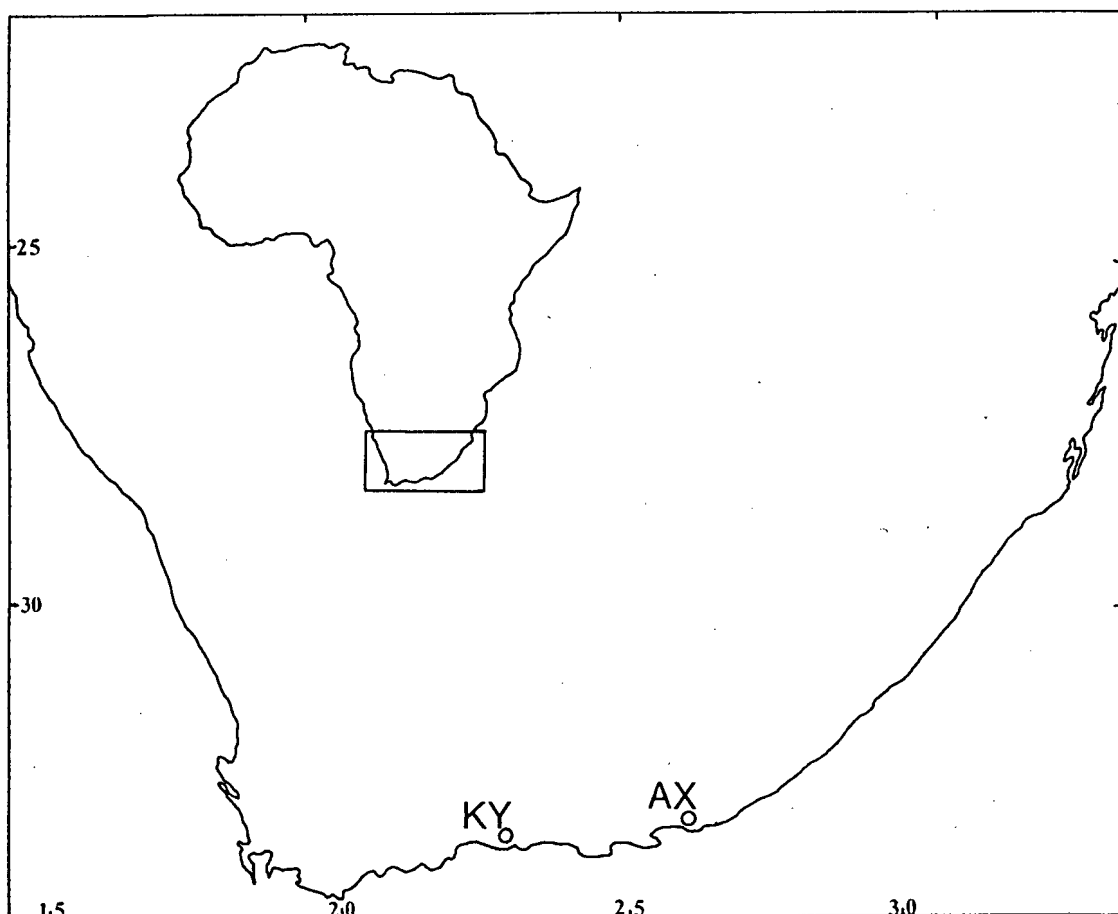
The study was conducted over a soil nutrient gradient in the Knysna forest (33°30'S; 22°40'E) in the southern Cape, South Africa (Fig. 1). I used a second study site, the Alexandria forest (33°15'S; 26°30'E) as an independent test of the results gained from the Knysna forest gradient. The Alexandria forest was chosen because of its geographical proximity yet ecological independence of the Knysna forest.

The Knysna forest is situated on the coastal scarp of the Outeniqua range of the Cape Folded Mountains. The mountains rise to 1600 m above mean sea level and are restricted to a narrow coastal strip less than 40 km wide. The topography of the area consists of high mountain slopes above and separate from a plateau which can be divided into a higher plateau and a lower plateau, which then falls away rapidly to a coastal plain (see Table 1). The lower plateau and portions of the higher plateau are fissured by river valleys running south into the Indian Ocean.

**Table 1.** The number of plots in each gradient group (n), the mean altitude of each group (mean  $\pm$  SE), the slope of each group (mean  $\pm$  SE), the mean width of the plots at each group (the figure in parenthesis shows the number of plots greater than 50 m wide, these have not been included in the average) the canopy height, and the mean number of trees per plot in each group ( $\pm$  SE). MT = mountain site, HP = high plateau, LP = low plateau, VS = valley slope, VF = valley floor, CP = coastal plain and AX = Alexandria forest.

Group	n (#)	Altitude (m)	Slope (°)	Plot Width (m)
MT	4	635 $\pm$ 64	28 $\pm$ 12	11.5 (0)
HP	4	365 $\pm$ 41	10 $\pm$ 7	8.7 (0)
LP	4	230 $\pm$ 53	4 $\pm$ 4	12.8 (0)
VS	6	182 $\pm$ 43	26 $\pm$ 6	8.5 (0)
VF	4	235 $\pm$ 111	17 $\pm$ 7	9.0 (0)
CP	6	40 $\pm$ 21	20 $\pm$ 12	7.5 (2)
AX	4	220 $\pm$ 16	9 $\pm$ 3	7.3 (1)

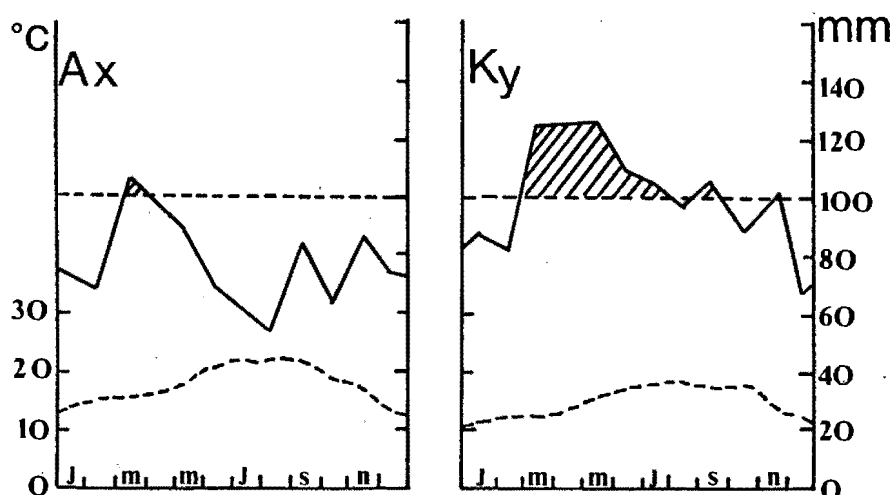
The parent rock of the Outeniqua mountain range is quartzitic sandstone of the Cape Super Group (Truswell 1977) and is found on the upper slopes of the plateau and in the river valleys. The coastal belt has a more varied substrate comprising broken areas of old leached dune sands, granite, shales and schists (1 : 250 000 Geological Survey map of the Oudtshoorn area 1979). The soils of the mountain areas are generally podsolised, acid sands, low in nutrients while the soils of the coastal regions tend to be richer in nutrients (Personal Communication G. Shafer, Saasveld Forestry Research Station).



**Figure 1.** Map of the study area showing the position of the Knysna forest (KY) and the Alexandria forest (AX).

The region has a mild climate and receives an all year rainfall, with a summer peak, ranging from 600 mm in the coastal region to 1200 mm in the high mountains (Fig. 2). The mean daily maximum and minimum temperatures range respectively from 23.8°C & 19.7°C (February) to 18.2°C & 8.9°C (August). Frosts rarely occur (Geldenhuys 1989b).

The Knysna forest, which represents veld type 4 of Acocks (1953), is described by Phillips (1931) and Von Breitenbach (1974). The wetter mountain patches carry high forest ( $\pm 25$  m) while the forest of the lower plateau is moist to dry ( $\pm 15$  m) and that of the coastal belt is generally dry forest ( $\pm 10$  m). The forests have not experienced large scale disturbances (Geldenhuys and Maliepaard 1983), and the major disturbance regime is the gaps formed by the uprooting or snapping of individual or a few trees.



**Figure 2.** Climate diagrams for the Alexandria forest (Langebos forest station) and the mountain site of the Knysna forest. Ax = Alexandria, Ky = Knysna. (Adapted from Marker and Russell 1984). The horizontal axis show months beginning with January. Solid line is rainfall, dotted line shows temperature.

The Alexandria forest (Fig. 1), has been described by Marker and Russell (1984) and phytogeographically placed by Phillipson and Russell (1988). Although there are floristic links between the Alexandria forest and the Knysna forests (White 1978), they are phytogeographically distinct. The soils of the area are deep well drained dune sand over lying a limestone base (Marker and Russell 1984). The altitude of the forest ranges from 100 m to 350 m. The area gets an all year rainfall that ranges from 700 - 900 mm for the forest (Rainfall isohyet map 1979). The mean monthly temperature seldom rises above 22 °C and seldom drops below 11 °C (Fig. 2). The

area is topographically diverse with forest height ranging from 15 m in the wetter valley floors to 5 m on the drier hill tops and toward the coast.

## Methods

I chose six sites along the gradient to cover a range of soil nutrients and to include two topographical aspects of the forest. The sites were a mountain site (MT), a high plateau site (HP), a low plateau site (LP), a valley slope site (VS), a valley floor site (VF), and a coastal plain site (CP). The valley slope and the valley floor sites provided a topographical comparison of plants on the forest's gradient. A seventh independent site in the Alexandria forest was chosen as a control against which the results gained from the gradient sites in the Knysna forest could be compared.

Within each site I randomly located four to six plots by marking a point on a road on a 1:50 000 topographical map falling within a site. To standardise light conditions as well as sample area of the plots over the gradient I defined a plot as being a 50 m stretch of road frontage. This "standardized gap" represents a gap in the forest canopy (the road cutting) that is standardized in respect of lighting conditions (i.e. it is cleared to ground level with no advanced regeneration in the "gap") and gap size, for all plots. Only trees having canopies abutting directly on the road margins were recorded in the survey.

At each plot I recorded the gap orientation, gap width, slope of the ground, orientation of the slope, and plot altitude. A soil sample was collected from each site from scrapings of the side of a pit dug 15 cm deep, and sited 10 m into the forest on the upslope side of the forest to avoid any influence of road construction materials. The soil was analyzed for total N, total P and total K as well as the S - value (sum of exchangeable Ca, Mg, Na and K, expressed as g/100g soil), the pH, organic matter content and percentage of clay in the soil. Although the total concentration of N and P are not the same as the plant available concentrations, plant available N and P are difficult to estimate and the total concentrations are used as approximations in this study.

Within each plot I recorded the species of each tree, taller than five meters. The size class (0 - 10cm; 11 - 20cm; 21 - 50cm; > 50cm) of the diameter at breast height (DBH) and the height class (< 2 m; 2 - 5 {<5} m ; 5 - 10 {<10} m and 10 - 15 {<15} m) of the lowest height of the canopy on each tree were noted. I refer to the height class of the canopies as canopy height.

For each tree I recorded the presence of each climber species occupying it. Due to the difficulty of differentiating between sexually produced individuals (genets) and vegetative offshoots (ramets)

I considered all climbing stems that were apparent between the heights of two and three meters to be separate individuals. To overcome the problems involved in counting every climber individually, estimates of abundance were made by grouping species into abundance classes of 0 - 10; 11 - 20; 21 - 50 and > 50. As even climbers of small sizes can support a large leaf area in the forest canopy (Putz 1983), the abundance of three size classes of climber (< 1 cm; 1 - 2 cm; > 2 cm) was recorded for each species. Climber diameter was measured at a height of between two and three meters above the ground.

To determine how climbers enter the canopy of their host trees, I recorded the direction of entry into the canopy i.e. vertically into the canopy or horizontally from a neighbouring tree. In addition the height of entry was recorded and I noted whether climbers entered the canopy via the main stem or directly into the canopy branches.

The nature of the data recorded for the abundance of climbers i.e. the number of times a climber species was present in each of the abundance and size classes, made it not possible to deal with absolute numbers of climbers in the results. Instead I discuss the data in three forms: 1) as the abundance of climbers - the average number of times that a different size and abundance class of climber occurs per 50 m plot) the weighted abundance of climbers 2) - the abundance of climbers in each size class multiplied by a weighting factor. The weighting factor used is the median of the abundance class. i.e. weightings of 5, 15, 35 are respectively used for the abundance classes 0 - 10, 11 - 20, and 21 - 50) the number of climbers and 3) - the weighted abundance of climbers but with all the size classes grouped.

I performed a  $\chi^2$  analysis to determine if the frequency of climbers entering the canopy vertically and horizontally conformed with a theoretical expected frequency. The expected frequency was generated by taking the occurrence of the vertical and the horizontal entries of the weighted abundances for all the gradient groups and Alexandria combined.

$\chi^2$  analysis was performed to determine if the frequency of climber species occupying a tree conformed to a Poisson distribution. Departure from Poisson might indicate competition or facilitation between climber species. Facilitation of one species entry into a tree by another would result in more trees having a higher number of climber species than expected while competition would be indicated by the reverse trend. I generated the expected frequency using the weighted abundance of climber species, ignoring size classes, for all the sites in the study.

I used standard correlative statistical techniques to relate climber abundance to soil nutrient data and standard one way ANOVA to determine statistical differences between groups. To gain some understanding of the relationship between the individual species of trees and climbers with the

average site altitude and edaphic conditions I used canonical correspondence analysis (Terbraak 1987). This is a multivariate direct gradient analysis technique which has been developed to relate community composition to known variation in the environment (Terbraak 1987), it is an extension of the reciprocal averaging technique. The output is a biplot diagram with species and sites being represented by plotted points and the environmental variables being represented by arrows. From this one can read the approximate distribution of a species along the environmental gradients that best explain community composition (Terbraak 1987). This method as opposed to other correspondence analyses techniques was used as it incorporates the environmental variables into the ordination analysis and does not attempt to superimpose them at a later stage using the help of previous knowledge.

## Results

### Nutrients

The nutrient status of the soils of the different gradient sites is given in Fig 3. There were no significant differences (ANOVA) between the sites in the Knysna forest for nitrogen ( $\mu\text{g/g}$ ) and potassium ( $\mu\text{g/g}$ ) concentrations or the S-values ( $\text{g}/100\text{g}$  soil), although there were clear trends indicated by the plotted means (Fig 3). The K concentration was highest at the coast ( $164 \pm 138 \mu\text{g/g}$ ) and lowest in the mountain ( $28 \pm 1.1 \mu\text{g/g}$ ) (Fig.3a), likewise for the S-value (Fig. 3b) where the highest value on the gradient ( $11.1 \pm 7.4 \mu\text{g/g}$ ) was recorded at the coast and the lowest value ( $1.69 \pm 0.85 \mu\text{g/g}$ ) in the mountains, which is a very low value indicating low soil fertility. There was a significant correlation between the concentration of K as well as the S - value and the weighted abundance of climbers in the small ( $< 1 \text{ cm}$ ) size class ( $p < 0.05$  in both cases), which suggests a link between these factors and climber abundance.

For N this trend is reversed with values of  $142 \pm 98 \mu\text{g/g}$  at the coast and  $321 \pm 312 \mu\text{g/g}$  in the mountain. The N concentration was positively correlated with the level of organic matter in the soil ( $r^2 = 0.67$ ;  $p < 0.01$ ), which was highest in the mountain and lowest in the coast (Table 2). For phosphorous there was a significant difference ( $p < 0.01$ ) between the site at the coastal plain ( $9,86 \pm 2,7 \mu\text{g/g}$ ) and the rest of the gradient sites. The pH value decreased from 6.5 to 3.5 as the sites go up the gradient from the coast to the mountain.

The site at Alexandria had a K value just less than that at the coastal plain ( $136 \pm 83.6 \mu\text{g/g}$ ) and a P value of  $66 \pm 85.8 \mu\text{g/g}$  which was higher than the highest value in the gradient sites. The S-value of  $12.4 \pm 2.0 \text{ g}/100\text{g}$  was higher than that of the coastal plain as was the N value of  $204 \pm 36 \mu\text{g/g}$  which compares with the low plateau on the gradient. Alexandria had the highest pH

value of 7.1 (Table 2). Thus the Alexandria site most resembled the coastal site in the Knysna gradient.

**Table 2.** The pH, organic matter content (g/g soil) and the clay fraction (%) of the soils for the different gradient sites. The values are averages for the site  $\pm$  SE.

	MT	HP	LP	VS	VF	CP	AX
pH	3.5	4.0	4.4	4.9	4.1	6.5	7.1
SE	$\pm 0.6$	$\pm 0.4$	$\pm 0.3$	$\pm 1.2$	$\pm 0.7$	$\pm 1.4$	$\pm 0.6$
Org	12.0	10.7	10.5	7.2	6.8	5.6	6.9
SE	$\pm 8.2$	$\pm 6.9$	$\pm 1.5$	$\pm 4.0$	$\pm 6.6$	$\pm 3.9$	$\pm 2.1$
Clay	1.0	4.0	4.4	4.9	4.1	6.5	7.1
SE	$\pm 1.0$	$\pm 2.1$	$\pm 3.2$	$\pm 9.9$	$\pm 7.5$	$\pm 9.0$	$\pm 0.8$

Trends that are apparent for the altitudinal gradient are not as clearly seen in the topographical gradient (Fig. 3). There were no significant differences between the soil nutrients of the valley slope and the valley floor although for all of the factors except N and P there were higher levels in the valley slope site than the valley floor site. The S - value was substantially different between the two groups (7.3 & 4.9 g/100g respectively).

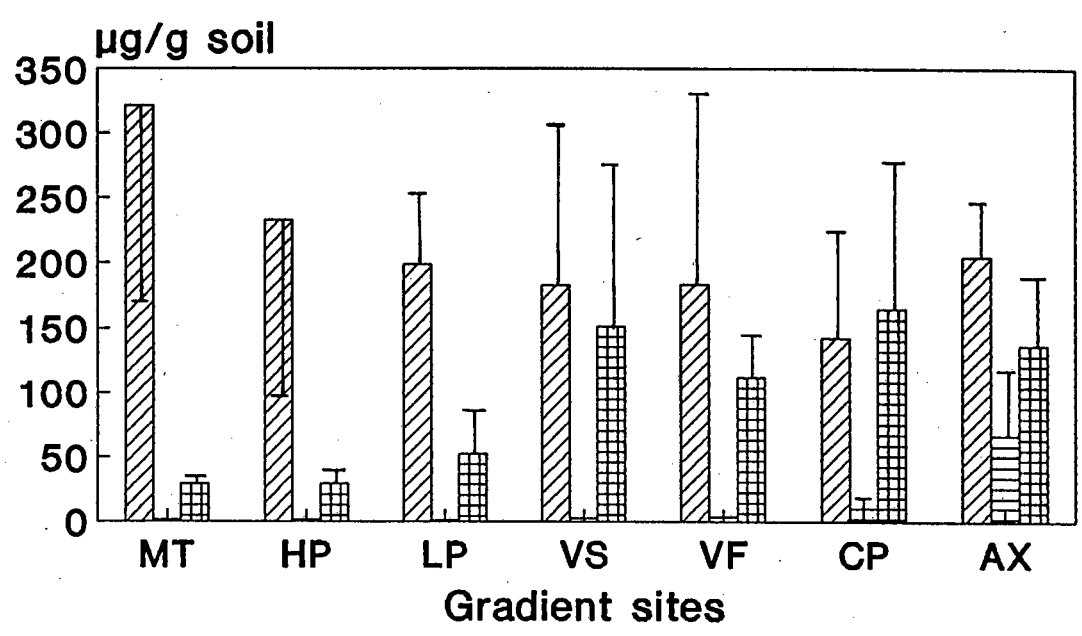
#### Species distribution

The separation of the sites surveyed based on their soil nutrient status is clear from Fig. 4. The mountain, coastal plain and Alexandria sites stand clearly apart with the high and low plateau and the two valley sites clustered together in between, reflecting the trends shown in Fig. 3 and Table 2.

There is a tendency for the climbers of all species, to lie to the left of the plot in the region of enhanced levels of P, K and a higher pH and S-value, while the trees species are more widely spread. The distribution of individual species of trees and climbers show patterns clearly linked with sites (Fig. 4).

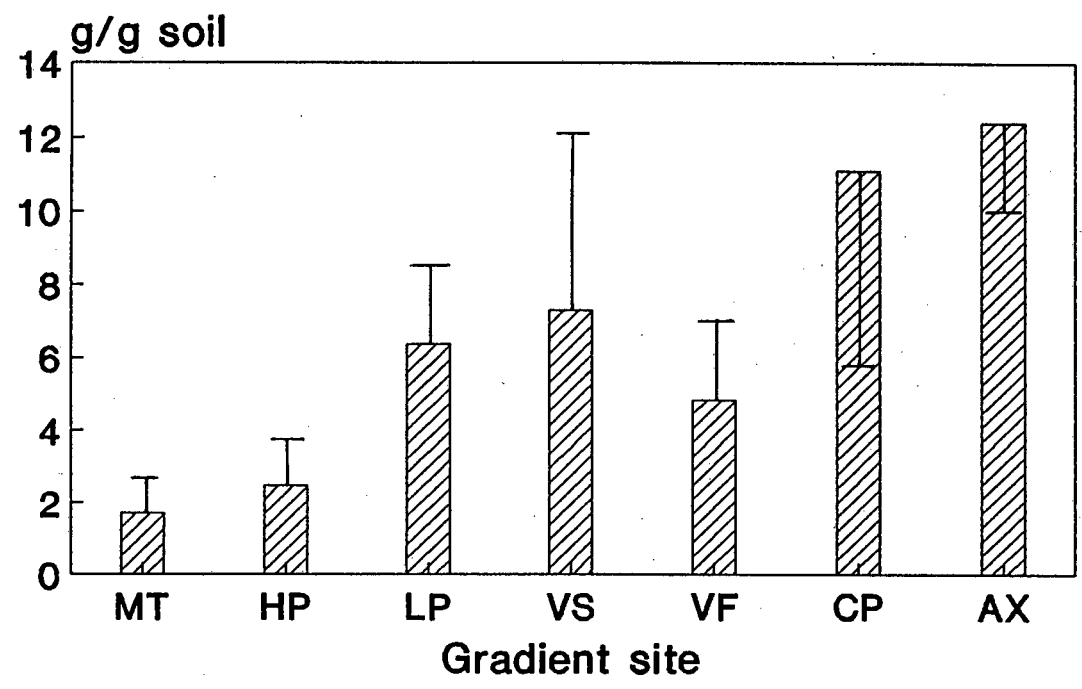
The trees *Cunonia capensis*, *Ocotea bullata* and *Rapanea melanophloes* are clearly linked to the Knysna mountain forests while *Cordia caffra* and *Erythrina caffra* are linked to the Alexandria forest. There is only one climber that appears to be site specific to the mountain region and that is the understory vine *Pyrenacantha scandens*. The climbers *Tylophora cordata* and *Kedostris nana* stand out as coastal plain specialists and *Solanum geniculatum* and *Jasminum angulare* as Alexandria specialists. *Rhoicissus tomentosa* is clearly more generalist climber and is found across the gradient. Although the distributions indicated in this biplot are not absolute (see Geldenhuys 1989a), they indicate that there is a response by individual species to the gradient.

A.



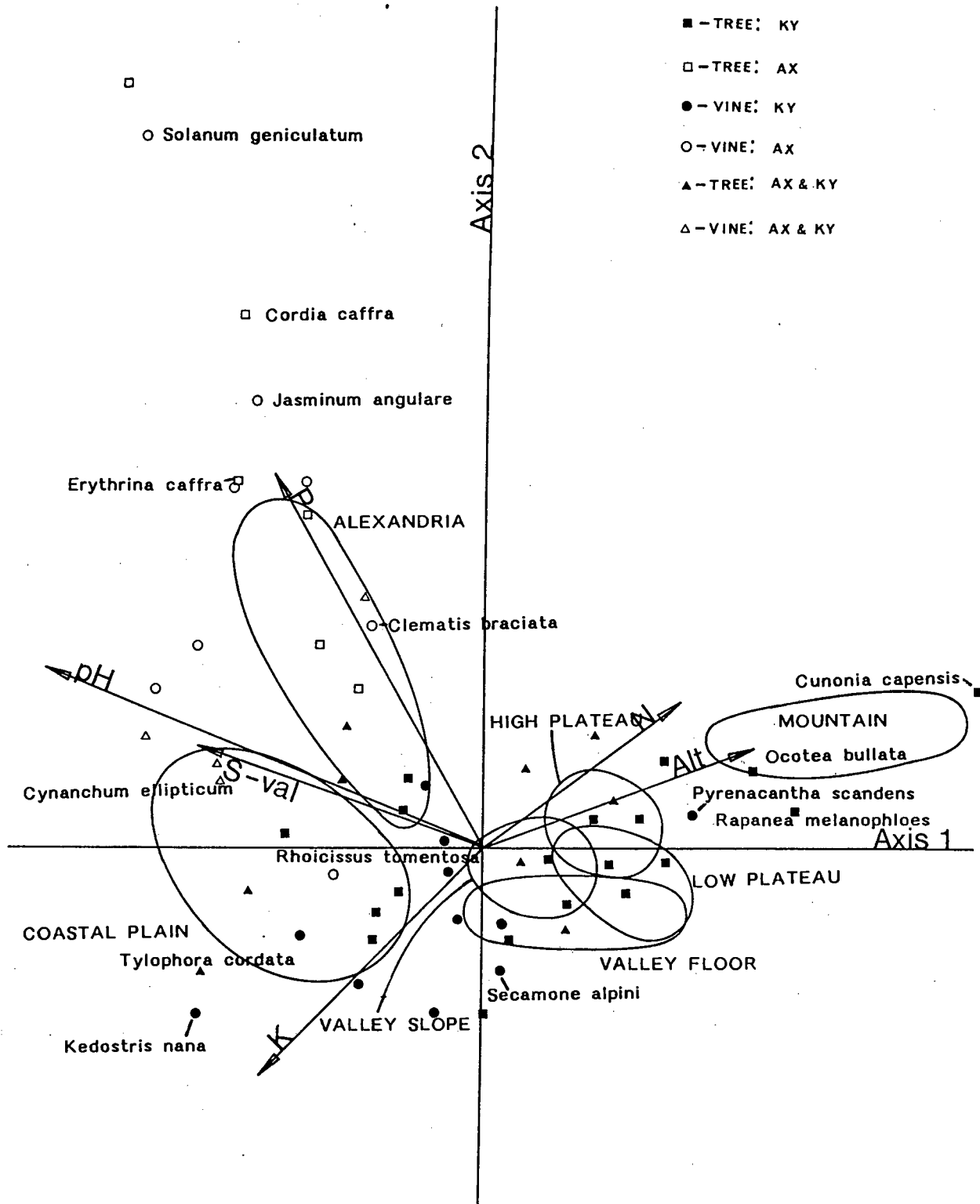
Nitrogen      Phosphorus  
 Potassium

B.



S - value

**Figure 3.** A. The average concentrations of N, P, K for the different sites (µg/g). B. The average S - value (g/100g soil) for the sites.



**Figure 4.** The biplot of the results of the canonical correspondence analysis. Not all species are indicated in the biplot for clarity. Key species are plotted and labelled, the environmental variables are indicated by the arrows and their relative importance is indicated by the length of the vector.

### Forest architecture

The forest was highest in the high plateau ( $22 \pm 3.4$  m) and lowest in the coastal plain ( $9.1 \pm 1.5$  m) (Table 3). There was a significant difference between the height of the forest in the coastal plain and the height of the forest in the mountain and high plateau sites ( $p < 0.05$ ). There was a significant difference ( $p < 0.05$ ) between the number of trees per plot (Table 3) in the coastal plain ( $11 \pm 2.8$ ) and the high and low plateau ( $20 \pm 2.6$  and  $19 \pm 3.3$  respectively). There were no significant correlations between the orientation or width of a plot and the abundance of climbers at the plot.

**Table 3.** The height of the canopy (mean  $\pm$  SE) and the number of trees per plot (mean  $\pm$  SE) for each of the sites.

Site	Canopy height (m)	Number of trees (#)
MT	$18 \pm 3.2$	$16 \pm$
HP	$22 \pm 3.4$	$20 \pm 5.4$
LP	$16 \pm 4.6$	$19 \pm 3.3$
VS	$14 \pm 5.5$	$17 \pm 3.0$
VF	$13. \pm 4.9$	$15 \pm 5.7$
CP	$9.1 \pm 1.5$	$11 \pm 2.8$
AX	$9.5 \pm 1.7$	$11 \pm 2.8$

### Climber abundance (per plot)

At each plot on the gradient group as well as in Alexandria there were more climbers with low abundances (1 - 10) than higher abundances (Table 4). There were also more small climbers ( $< 1$ cm) than larger climbers (1 - 2cm &  $> 2$ cm) for all the plots, except for the medium sized climbers (1 - 2cm) in the Alexandria plots which were more abundant in the 1 - 10 abundance class. There were no climbers at all recorded in the mountain plots (Table 4).

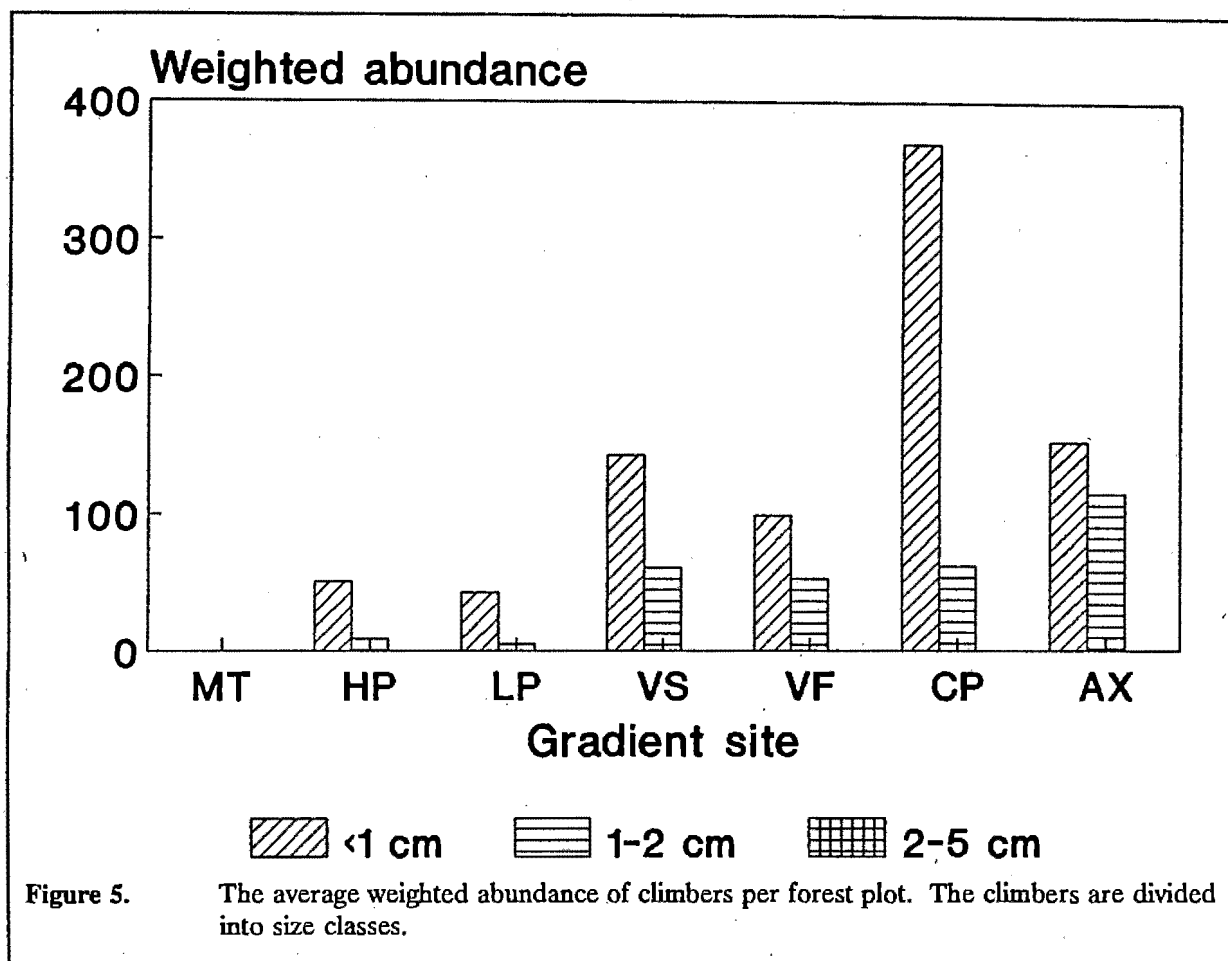
The highest abundance of climbers was found in the small size class in the coastal plain plots ( $16.0 \pm 2.9$ ) in the 1 - 10 abundance class. There were significantly more small climbers in the 11 - 20 ( $p < 0.005$ ) and the 21 - 50 ( $p < 0.01$ ) abundances classes in the coastal plain plots than in the plots of the other sites (Table 4). There were significantly more large ( $> 2$ cm) climbers in the 1 - 10 abundance class in the Alexandria plots ( $2.0 \pm 0.07$ ) than there were at any of the gradient sites ( $p < 0.01$ ). There were no significant differences between the climber abundances of the

valley slope and the valley floor plots (Table 3). The variability of climber abundance per plot (Table 4), was fairly high except for the abundance of the small climbers (< 1cm) in the 1 - 10 abundance class.

**Table 4.** The mean abundance of climbers ( $\pm$  SE) in the different size and abundance classes for each plot.

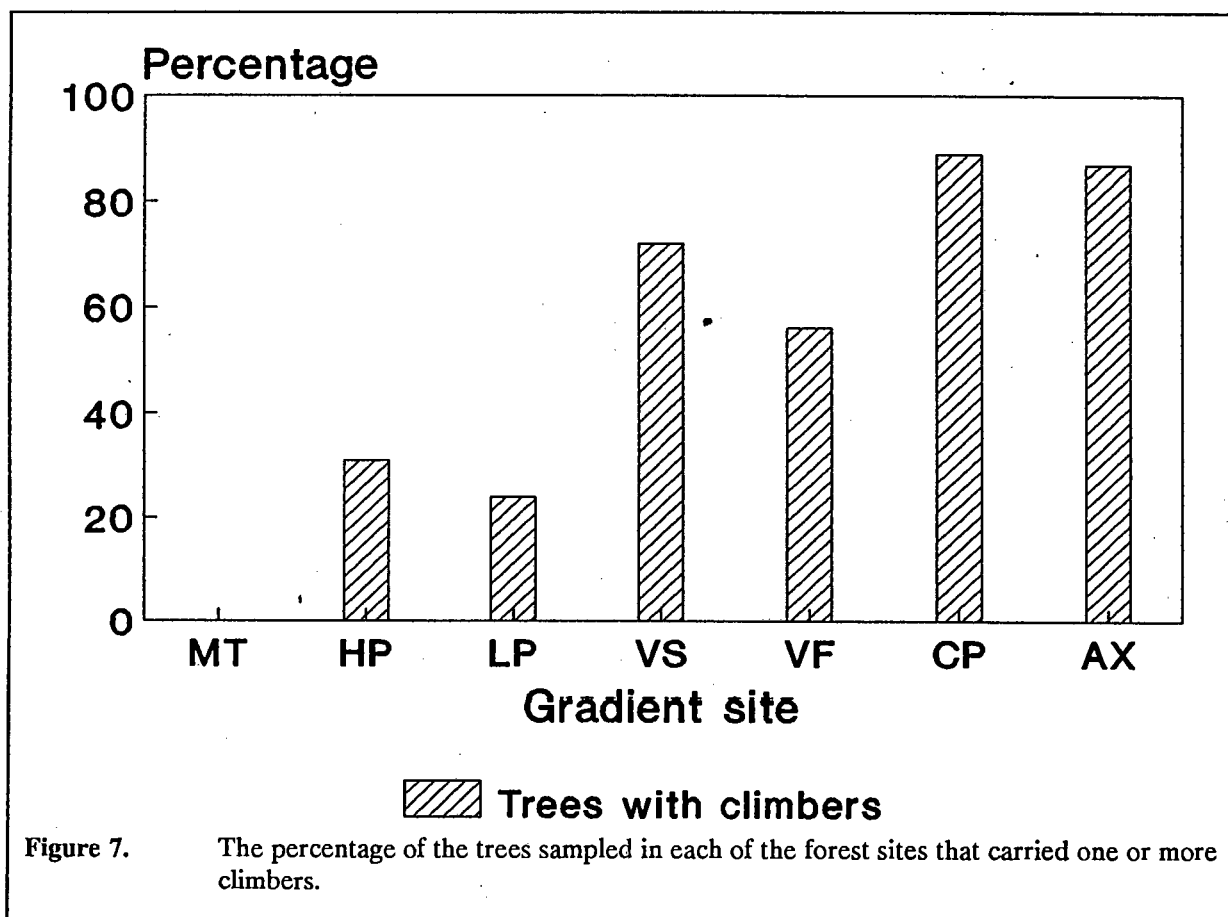
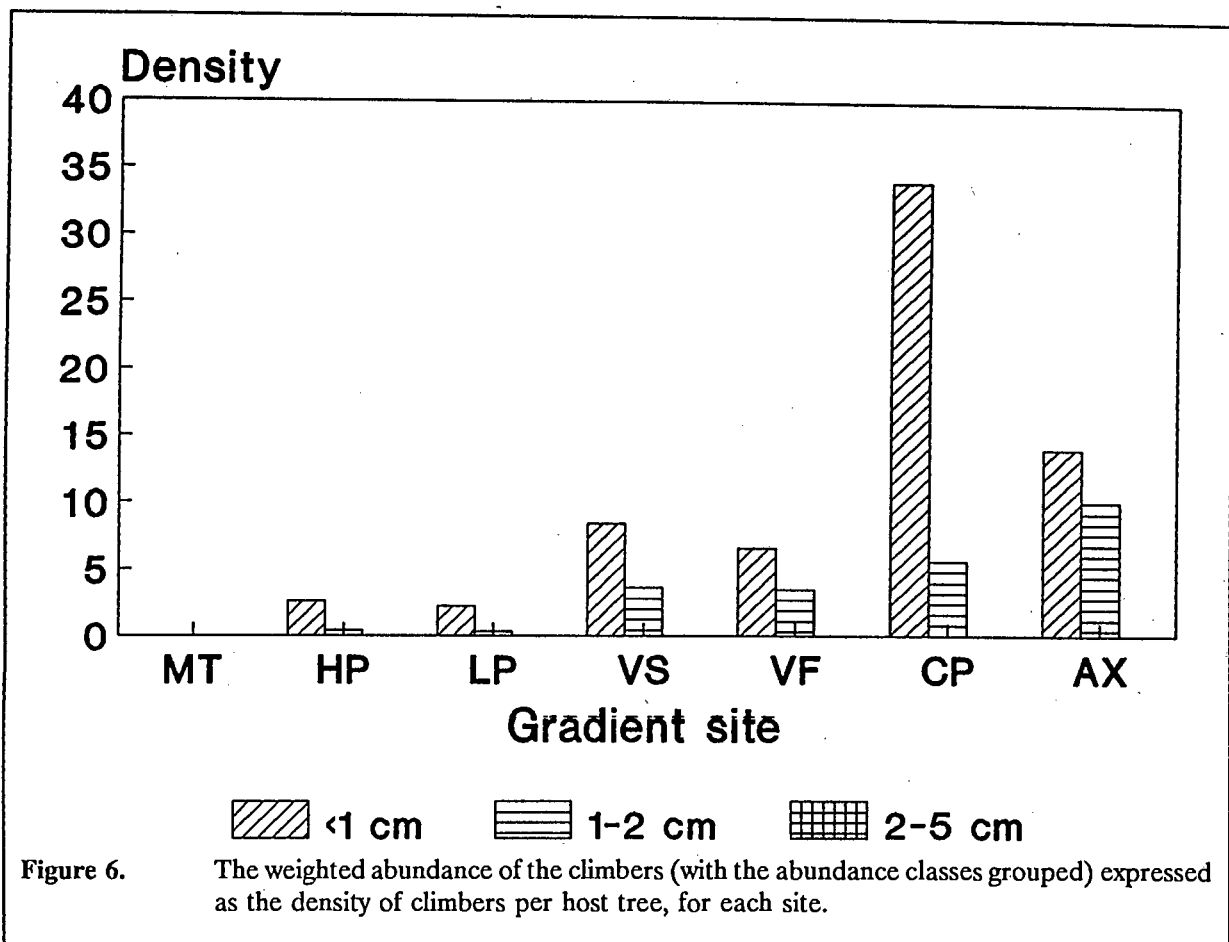
Gradient Group	Size Class	Abundance Class			
		1 - 10	11 - 20	21 - 50	>50
Mountain	< 1	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
	1 - 2	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
High Plateau	< 1	5 $\pm$ 1.2	0.5 $\pm$ 0.5	0.5 $\pm$ 0.5	0 $\pm$ 0
	1 - 2	1.8 $\pm$ 1.4	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Low plateau	< 1	6.3 $\pm$ 3.3	0.8 $\pm$ 0.8	0 $\pm$ 0	0 $\pm$ 0
	1 - 2	1.0 $\pm$ 0.7	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Valley Slope	<1	14 $\pm$ 2.9	4.0 $\pm$ 1.4	0.3 $\pm$ 0.3	0 $\pm$ 0
	1 - 2	8.2 $\pm$ 2.0	1.3 $\pm$ 0.8	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0.5 $\pm$ 0.2	0 $\pm$ 0	0 $\pm$ 0	0 $\pm$ 0
Valley Floor	< 1	10 $\pm$ 3.6	2.0 $\pm$ 2.0	0.5 $\pm$ 0.5	0 $\pm$ 0
	1 - 2	7.5 $\pm$ 2.7	1.0 $\pm$ 1.0	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0.5 $\pm$ 0.3	0.5 $\pm$ 0.5	0 $\pm$ 0	0 $\pm$ 0
Coast Plain	< 1	16 $\pm$ 2.9	11 $\pm$ 1.9	3.3 $\pm$ 1.1	1.5 $\pm$ 1.0
	1 - 2	6.3 $\pm$ 3.5	2.0 $\pm$ 1.2	0 $\pm$ 0	0 $\pm$ 0
	2 - 5	0.2 $\pm$ 0.2	0.7 $\pm$ 0.7	0 $\pm$ 0	0 $\pm$ 0
Alexandria	< 1	12 $\pm$ 2.4	3.0 $\pm$ 0.7	0.8 $\pm$ 0.5	0 $\pm$ 0
	1 - 2	16 $\pm$ 2.3	2.3 $\pm$ 1.1	0.5 $\pm$ 0.5	0.5 $\pm$ 0.5
	2 - 5	2.0 $\pm$ 0.7	1.3 $\pm$ 0.8	0.3 $\pm$ 0.3	0 $\pm$ 0

To approximate the number of climbers at each site I calculated the weighted abundance of climbers for each plot. A clear trend of increasing climber abundance with decreasing altitude was apparent (Fig. 5). The high and low plateaus had the lowest number of small ( $\pm$  50) and medium (< 10) climbers per plot while the coastal plain had over 350 small climbers and about 50 medium sized climbers. The valley slope, valley floor and coastal plain sites had very similar numbers of medium sized climbers per plot ( $\pm$  50) while the site at Alexandria had over 100 medium sized climbers per plot (Fig. 5).



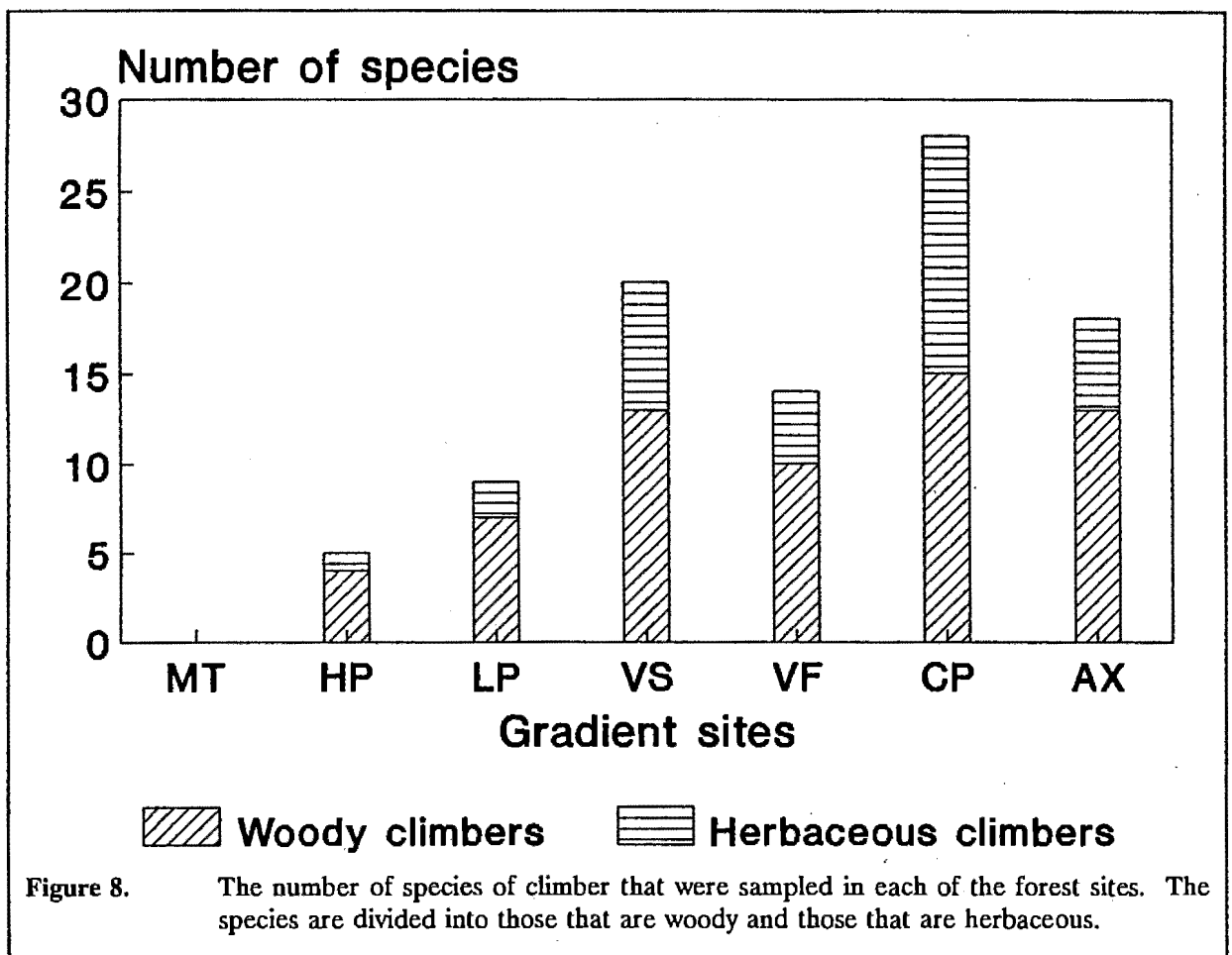
#### Climber abundance (per host tree)

Any impact that climbers have on trees will depend on their abundance per host tree. I calculated the weighted abundance of climbers per host tree for the sites as a measure of the density of climbers per tree (Fig. 6). The density of climbers per host tree increased with a decrease in altitude. The densities of the small climbers ranged from < 5 climbers per tree in the higher forests to > 30 climbers at the coastal plain and 15 climbers at Alexandria. There was less than one medium sized climber per host tree in the higher forests compared to more than five in the coastal plain and double this number ( $\pm 10$ ) at Alexandria. For the gradient sites the percentage of trees with no climbers on them was highest in the Mountain (100%) and lowest in the Coastal Plain (10,3%) (Fig. 7).



### Climber diversity

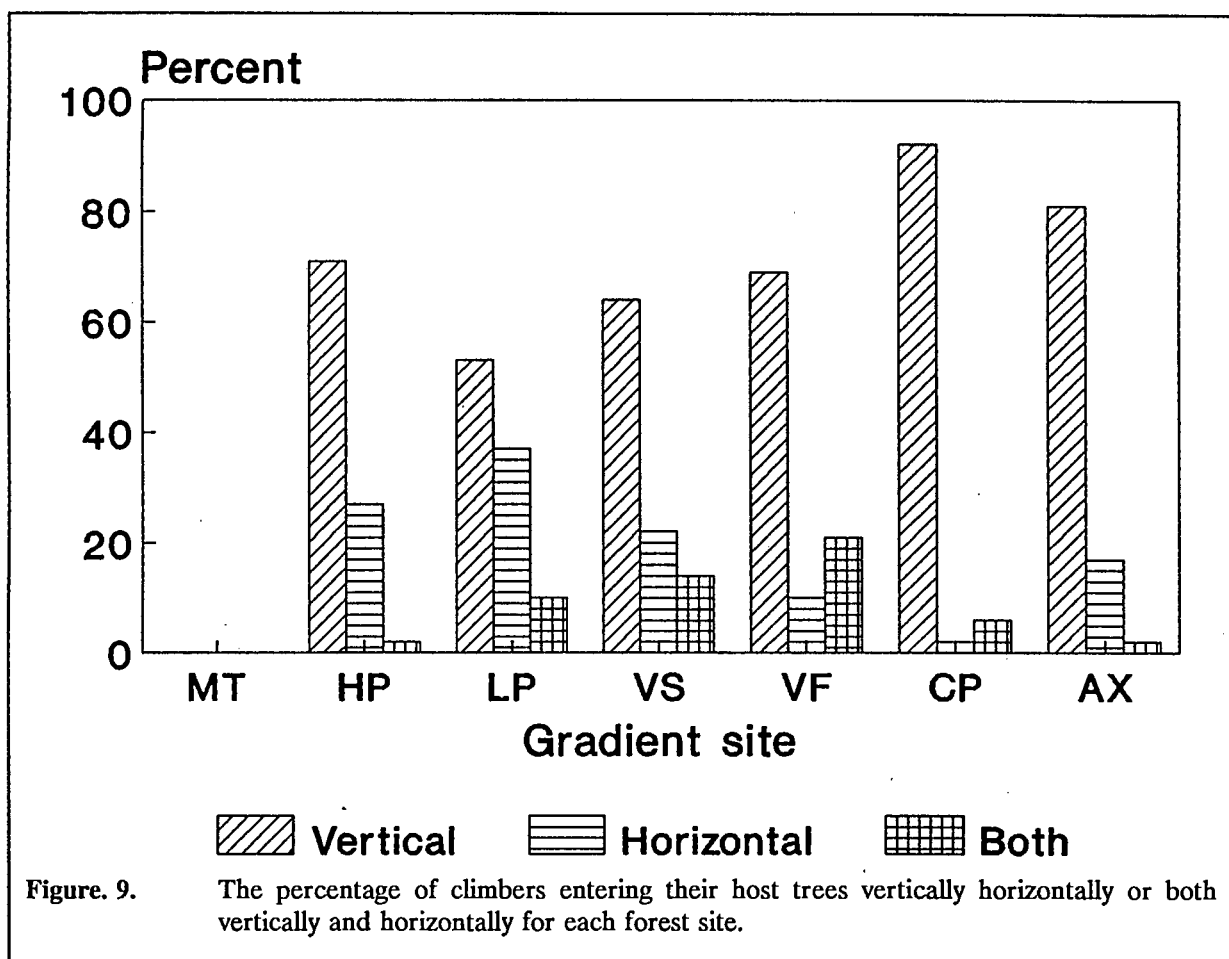
The number of species recorded at each site is shown in Fig. 8. Most species were recorded at the coastal plain sites (28) while only 5 were recorded in the high plateau. There was a significant correlation between the number of species present and the weighted abundance of small climbers at each site ( $r^2 = 0.85$ ;  $p < 0.01$ ), but not for the larger size climbers. This indicates an increasing diversity across the gradient. There was an increase in the percentage of the climber species that are herbaceous as the number of species recorded increases (Fig. 8). A comparison of the 36 species of climber recorded in this study (36% herbaceous and 67% woody) with the 57 species (79% herbaceous and 21% woody) listed by Geldenhuys (1989a) shows a preponderance of woody species in this study.

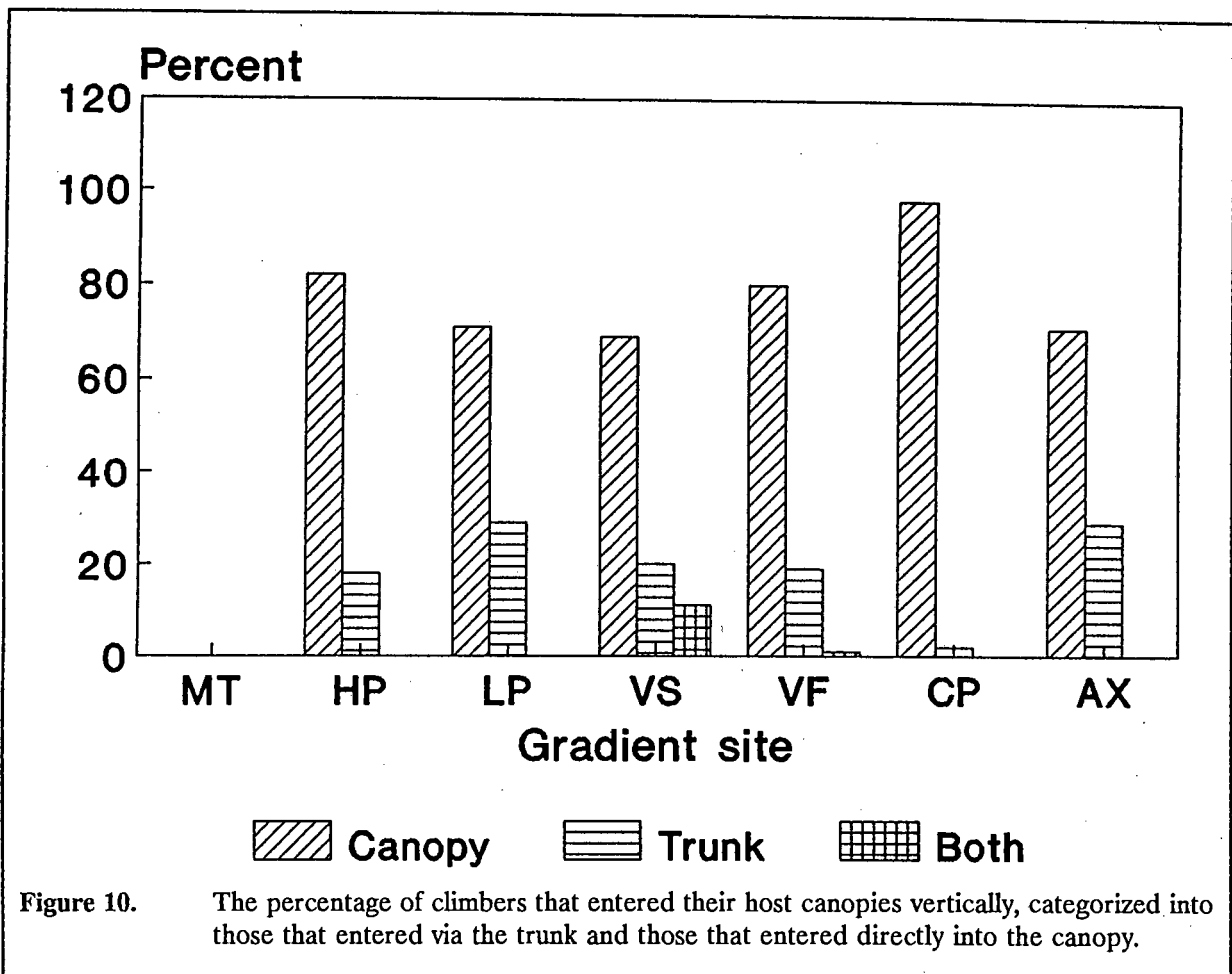


### Mode of entry

The percentage of climbers (weighted abundance) entering host trees vertically, horizontally or both vertically and horizontally for each of the sites gives an indication of the access routes available to climbers (Figure 9). The number of climbers entering the canopy of the individual trees horizontally from a neighbouring tree was significantly higher than expected in the high

plateau, low plateau and the valley slope sites ( $\chi^2 = 58, 125, 144$  respectively;  $df = 5; p < 0.01$ ) (Fig. 10). The presence of trellises can be important for climbers to gain access to the canopy of host trees (Putz 1984a). As the branches of a tree's canopy are smaller in diameter than the main trunk I predicted that in forest where the canopy is high and there are few trellises more climbers would enter the canopy of their host trees horizontally from neighbouring trees than in forest where the tree canopies are low and more trellises are available. The number of climbers entering the canopy of individual trees vertically in the Coastal plain was significantly higher than expected ( $\chi^2 = 48; df = 5; p < 0.01$ ), while for the same group the number of climbers entering their host tree canopy horizontally was significantly lower than expected ( $\chi^2 = 239; df = 5; p < 0.001$ ), (Table 5).





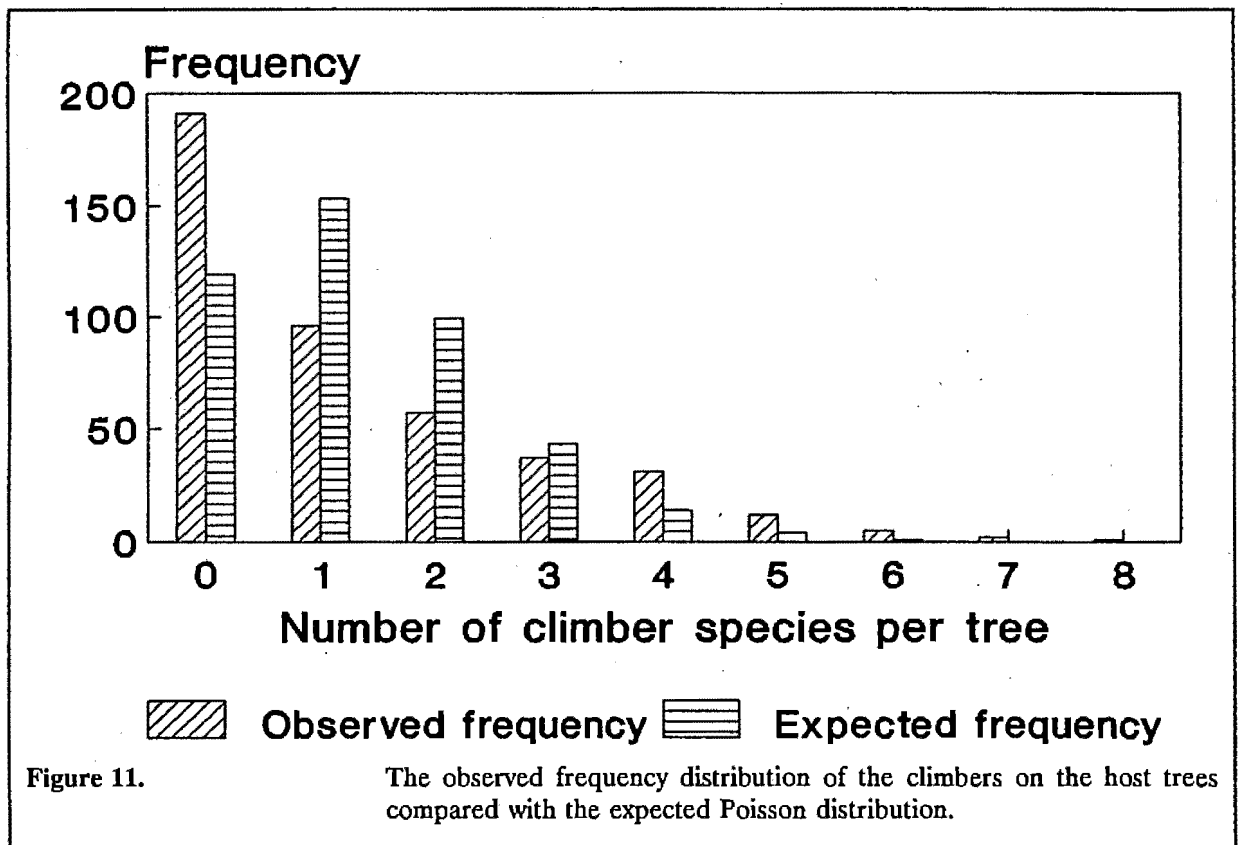
**Table 5.** The mode of entry of climbers into the canopy of individual trees. Low = indicates that the observed frequency is below the expected frequency, High = indicates that the observed frequency is higher than the expected frequency. \*\* indicates a  $\chi^2$  significance level of  $p > 0.01$ , NS indicates no significant difference.

Site	Vertical	Horizontal	Both
MT	No Climbers		
HP	Low NS	High **	Low NS
LP	Low **	High **	High NS
VS	Low **	High **	High **
VF	Low NS	Low NS	High **
CP	High **	Low **	Low **
AX	No Difference	High **	Low **

Of the climbers entering their host tree vertically, the highest percentage of climbers entering via the trunk was 32% in the Alexandria forest and the lowest 2% in the coastal plain (Fig. 10). The results suggest that the trunk of a tree is relatively unimportant as an access route to the canopy for climbers.

### Mutual facilitation

I tested the hypothesis that the presence of one climber species in the canopy of a tree will facilitate access to the canopy by other climber species. The null hypothesis was that the number of climber species in the canopy of host trees would follow a Poisson distribution. The alternative is that there were either fewer incidences of species co-occurring than predicted by the Poisson distribution suggesting that there is competition between species or that there were more species co-occurring than predicted which suggests facilitation between species for access to the host tree.



The distribution frequency of climbers was significantly different from a Poisson distribution ( $\chi^2 = 13.2$ ;  $df = 5$ ;  $p < 0.01$ ) with more species co-occurring than expected. This suggests that there is facilitation between the climbers for access to the canopy (Fig. 11), and that the presence of one climber species in a tree canopy may enhance the ability of other climbers in attaining the canopy by providing access trellises (Putz 1984a).

### Climber load

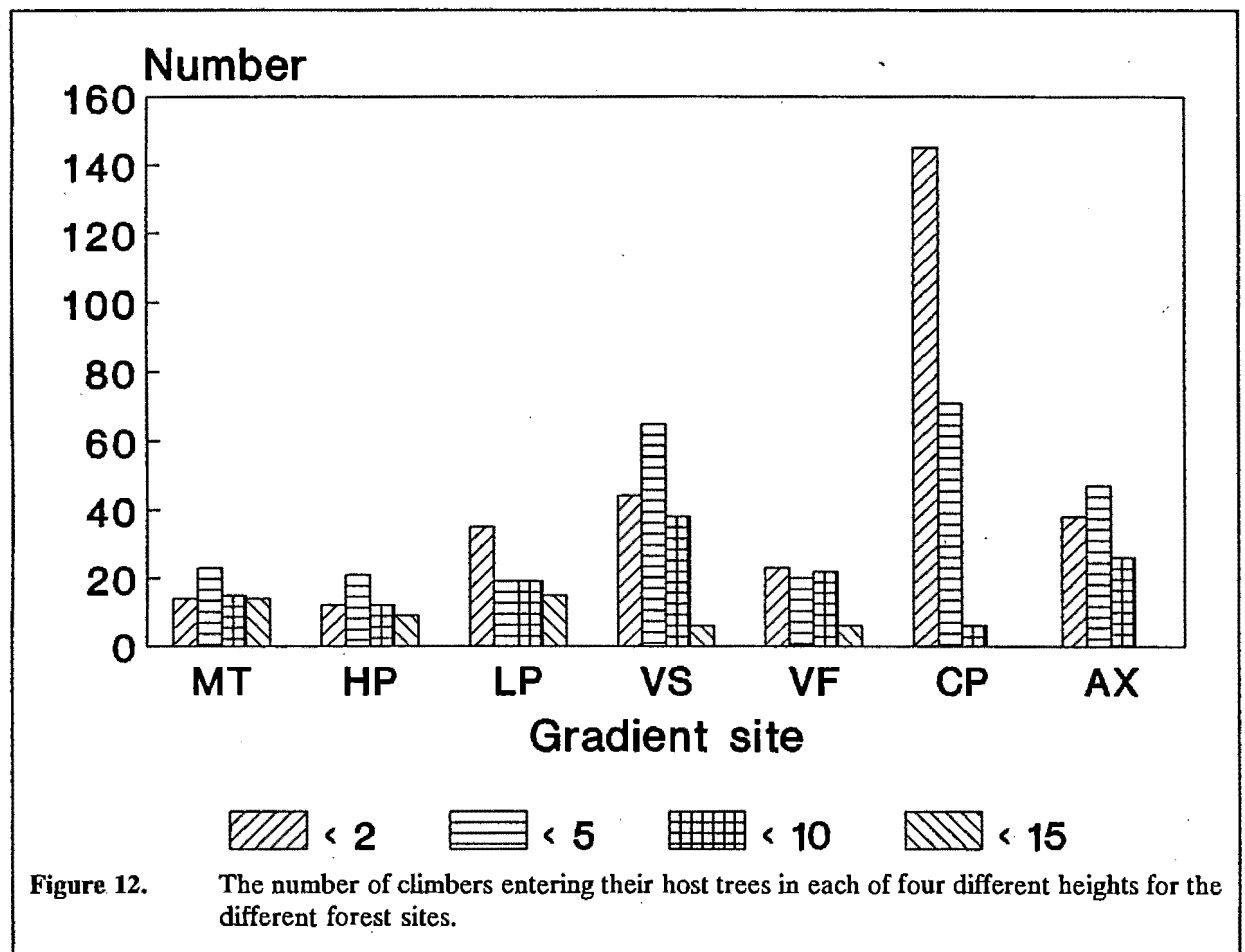
I was interested to know whether some of the host trees were more vulnerable to climber occupation or, on the other hand, if some trees were able to avoid climber occupation. Of the tree species sampled, and considering only those species of which there were more than ten individuals so as to minimise the effect of small sample size, only one species, *Cordia caffra*, carried one or more species of climber on every individual tree. *Cunonia capensis* was the only tree species to carry no climbers at all. Six tree species carried climbers on more than 65 % of the individuals sampled, while four tree species carried climbers on less than 20 % of the individuals sampled (Table 6). Of the six tree species that carried climbers on more than 65% of the individuals sampled, four (*Celtis africana*, *Cordia caffra*, *Nuxia floribunda*, and *Sideroxylon inerme*) have the same climber on more than 50% of their individual trees (Table 6).

**Table 6.** Tree species of the Knysna and the Alexandria forests with high climber loads (> 65 % of trees with 1 or more climbers) and low climber loads (< 20 % of trees climbers). Where more than half of the trees of one species host the same climber species this is shown in the column labelled 'Climber Species' and the host trees species is indicated in the first column.

Tree species	% Bearing Climbers >65%	Climber Species > 50 %	
<i>Buddleja saligna</i>	70 %		
<i>Celtis africana</i>	89 %	<i>Cynanchum elipticum</i>	56%
		<i>Scutia myrtina</i>	56%
<i>Cordia caffra</i>	100 %	<i>Cynanchum elipticum</i>	86%
<i>Nuxia floribunda</i>	65 %	<i>Rhoicissus tomentosa</i>	50%
<i>Rhus chirindensis</i>	85 %		
<i>Sideroxylon inerme</i>	100 %	<i>Capparis sepiaria</i>	52%
		<i>Rhoicissus tomentosa</i>	50%
	< 20%		
<i>Cunonia capensis</i>	0 %		
<i>Curtisia dentata</i>	19 %		
<i>Ocotea bullata</i>	15 %		
<i>Platylophus trifoliatus</i>	19 %		

It is not possible however to separate this data from the effect of the site and an element of circularity is introduced into the argument. To circumvent this circularity I asked if there were

any architectural features of a tree that made it more vulnerable to climber occupation. As most of the climbers entered the host tree canopy vertically from the ground (Fig. 9), I tested the hypothesis that trees with lower canopies would be more vulnerable to climber occupation and would carry a higher climber load than trees with a higher canopy. The alternative would be that there is no difference in the climber load of trees with different canopy heights. To avoid the influence of the extreme forest types I considered only the high plateau, low plateau, valley slope and valley floor sites. To generate the expected frequency the four sites were grouped together, and the trees were categorized into those with canopies in four height classes ie. < 2m; < 5m; < 10m & < 15m (Fig. 12). The proportion of trees in each height class were multiplied by the total



number of climbers at a site. This gave the expected frequency of climbers entering into trees in each canopy height class. The observed frequency was the total number of climbers entering trees in each canopy class. There was a significant difference between the expected frequency of climbers entering the trees in each canopy height class and the observed frequency ( $p < 0,001$ ) (Table 7). This suggests that the height of the tree canopy is important in determining the vulnerability of a tree to climber invasion.

**Table 7.** The observed number of climbers entering trees in each canopy height class and the expected poisson frequency - see text for details.

Low Point Class	Observed Frequency	Expected Frequency	Chi Squared
< 2m	670	808.5	23.7
< 5m	1272	870.7	185.0
< 10m	614	639.7	1.0
< 15m	65	302.1	186.1

## Discussion

### Abiotic factors

The concentration of the soil nutrients measured follow the altitudinal gradient with the potassium and phosphorus concentration, the pH and the S - value increasing and the nitrogen concentration decreasing as the altitude decreases demonstrating higher levels of soil bases in the lower gradient sites. The concentration of potassium as well as the S - value are both significantly correlated with the weighted abundance of climbers. This suggests that there is a relationship between the abundance of climbers and the soil base levels. The relationship between climbers and soil base levels is further supported by the distribution of climber species (Fig. 4) being linked to the S - value, and potassium and phosphorus levels in the soil.

The results from the gradient study are supported by those from the Alexandria (Fig. 3) forest (Proctor *et al.* 1983) who found higher liana abundances in forest types where there are high concentrations of total exchangeable bases in the Gunung Mulu National Park, Sarawak.

In general, increased levels of soil nutrients enhance the growth rates of plants. If the link between the abundance of climbers and soil nutrients in this study and suggested by Putz (1985) and Putz and Chai (1987) is a result of the competitive needs of the climbers, (ie. to be successful a climber needs to be able to out grow its host tree), a positive correlation would have to be shown between climber abundance and all limiting nutrients as any limiting nutrient will tend to restrict climber abundance. However in both this study and Proctor *et al.* (1983) the link is restricted to the soil cations (bases). Climber abundance is negatively linked to the total nitrogen concentration which does not support the argument that climbers are nutrient limited. This is

surprising, especially in the southern Cape, where nitrogen as well as phosphorus is a limiting nutrient (Donald *et al.* 1987; Van Daalen 1984).

Comparison of the topographical aspects of the low plateau (top of the valley), valley slope and the valley floor show there to be greater climber density in the valley floor, a result that agrees with studies of Putz (1984), Putz and Chai (1987) and Proctor *et al.* (1983). The soil potassium and S - values are lower in the valley floor than on the valley slope which also does not support the idea that soil nutrients are responsible for the increased climber abundance. The high climber abundance in the valley floor may be due to an increase in the disturbance level at this site. Although the disturbance rates have not been measured for the Knysna forest, Putz and Chai (1987) suggest high disturbance levels in the valley floor as being a factor causing higher liana abundances in the Gunung Mulu National Park forest in Sarawak.

The altitude of the gradient groups does not directly affect the vegetation (or climber abundance) but it can serve as an index of other factors such as soil nutrient status and moisture availability to the plant or it can merely be incidental to edaphic conditions (see Proctor *et al.* 1983). Further the S - value of the soil, a similar measure to the concentration of total exchangeable bases, of the soil is usually negatively correlated with macroclimatic conditions such as rainfall (Russell 1973), which increases up the gradient. I thus suggest that the relationship between climber abundance and soil nutrients may be correlative rather than causative.

The sampling method, ie. the use of a standardised light environment in each plot and the inclusion of herbaceous climbers in this study prevents comparisons of climber abundance being made with the results of other workers (eg. Proctor *et al.* 1983; Putz 1984; Putz and Chai 1987). What is clear though is that despite the standardised lighting conditions there is variation in the abundance of climbers over the gradient and that light is not the only factor limiting climber abundance. I suggest that the presence of trellises may play an important role in determining the abundance of climbers.

#### Interactions between trees and climbers

The significance of trellises is emphasized by the data in (Fig. 10) showing that most climbers enter their host trees directly into the canopy and not via the stem. This suggests that small diameter trellises and not the main tree trunk are the major route that climbers use to get to the forest canopy. These trellises are temporary vehicles which once used are shed (Richards 1952; Putz

1984), either by the trellis branch being broken off under the climber load, climber strangulation or by self thinning of the trellis plant.

To test the idea that trellis availability is an important factor in limiting climber abundance I considered the mode of entry of climbers into the host tree canopy. Evidence from this study supports the prediction that where the canopy is high and there are few trellises more climbers enter their host tree canopies horizontally from a neighbouring tree than vertically. The reverse should also be true i.e. that where the forest canopy is low and there are more trellises there would be more climbers entering their host tree canopies vertically from the ground. Most climbers in the taller parts of the Knysna forest (i.e. high plateau, low plateau and the valley slope sites) enter their host trees horizontally from a neighbouring tree (Table 5), while in the shorter forests (the coastal forest and that of Alexandria) most of the climbers enter the canopy of their host trees vertically.

A further prediction of the trellis hypothesis is that trees with lower canopies would have higher climber occupation than trees with higher canopies. There is a clear trend showing more climbers than expected occupying trees with short trunks and low canopies and fewer climbers in tall trees and high (< 15 m) canopies (Table 7). There is also greater climber abundance in the coastal plain and Alexandria forests, forests with lower canopy height (Table 1), than in the higher forests. As this data covers a number of different gradient sites (but excluding the extremes of the gradient), they lend support to the generality of the idea that climber abundance is limited by trellis availability rather than nutrients.

How this situation compares with the tropical forests is uncertain. Putz (1984a) suggests that the presence of young trellises in tropical forest, even in the shaded understory, would enable the lianas to get to the canopy. Physiognomically the taller Knysna forests more closely resemble the tropical forests in most other studies (eg. Kochummen 1966; Fox 1968; Lowe and Walker 1977; Appanah and Putz 1987), and the relative scarcity of trellises may explain the low climber abundance.

Do trees have mechanisms to help them avoid climber occupation? Putz (1984b) suggests that flexibility of the bole as well as long leaves may aid trees to shed or avoid lianas. This study provides support for the hypothesis that by growing tall and having the lowest branches placed high, trees may be able to escape climbers. I suggest that this may be an important refinement

on the suggestion of Putz (1984a) that there is no correlation between crown depth and liana occupation. It may not be the absolute crown depth but the height of the lowest extremities of the host tree canopy that determines the ability of the tree to avoid climbers.

### Interactions between climbers

Climber species co-occurrence patterns in trees further support the trellis argument. This study finds evidence that facilitation of access of climber species to host tree canopies may occur. This is suggested by the demonstration that the presence of one climber species in a tree canopy is associated with the presence of other species more than expected. This supports the suggestion of Putz (1984) that climbers can provide trellises to other climbers although Putz and Chai (1987) note that although a high percentage of trees carry lianas, few carry a particularly heavy load. The presence of such a process provides further support for the role of trellises in climber success.

### **Conclusion**

There are differences in climber abundance over the soil nutrient gradient in the Knysna forest. The results of the survey of the Alexandria forest, which has soil nutrient levels similar to the coastal plain of the Knysna forest, as well as similar climber abundances, validate the results of the gradient survey and extend the generality of the results. Under standardised light conditions, there are positive correlations between some of the soil nutrient levels (S - value and potassium concentration) and the abundance of climbers. However these correlations may merely reflect the altitudinal gradient and not be the cause of variation in climber abundances. I suggest that the presence of trellises may be the most important factor limiting the distribution and abundance of climbers. This hypothesis is supported by evidence showing that climbers predominantly enter a canopy vertically except where the canopy is high and the only access route is horizontally via a neighbouring canopy. Secondly differences in climber loads among trees can be related to the height of the canopy. Further the presence of one climber in a tree appears to facilitate access by another climber by providing a trellis. Climber distribution thus appears to be controlled by the biotic, rather than the physical environment.

## References

- Acocks JPH. 1953. The veld types of Southern Africa. Memoirs of the botanical survey of South Africa. No. 40.
- Appanah S and Putz FE. 1987. Climber abundance in virgin dipterocarp forest and the effect of pre-felling climber cutting on logging damage. *Malaysian Forester* 47:335-342.
- Davis TAW and Richards PW. 1934. The vegetation of Moraballi Creek, British Guiana: An ecological study of a limited area of a tropical rain forest. Part 2. *J. Ecol.* 22:106-155.
- Donald DGM, Lange PW, Schultz CJ and Morris AR. 1987. The application of fertilisers to pines in southern Africa. *S. Afr. For. J.* 141:53-62.
- Fernandez SR. 1987. Auswirkungen der Kletterstrategie der lianen auf deren Verbreitung. *Tuexenia* 7:447-458.
- Fox JED. 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *The Malayan Forester* 31(4):326-347.
- Lowe RG and Walker P. 1977. Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. *J. Appl. Ecol.* 14:897-903.
- Marker ME and Russell S. 1984. The application of biogeographical techniques to forest site-factor analysis. *South African Geographical Journal* 66(1):65-78.
- Phillips JFV. 1928. The principle forest types in the Knysna region - an outline. *S. Afr. J. Sci.* 25:188-201.
- Phillips JF. 1931. Forest succession and ecology in the Knysna region. Memoirs of the botanical survey of South Africa No.14.
- Phillipson PB and Russell S. 1988. Phytogeography of the Alexandria forest (southeastern Cape province). *Monogr. Syst. Bot. Missouri Bot. Gard.* 25:661-670.
- Proctor J, Anderson JM, Chai P and Vallack HW. 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. *J. Ecol.* 71:237-260.
- Putz FE. 1983. Liana biomass and leaf area of a "tierra firma" forest in the Rio Negro basin, Venezuela. *Biotropica* 15(3):185-189.
- Putz FE. 1984a. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6):1713-1724.
- Putz FE. 1984b. How trees avoid and shed lianas. *Biotropica* 16(1):19-23.
- Putz FE. 1985. Woody vines and forest management in Malaysia. *Commonw. For. Rev.* 64(4):359-365.

- Putz FE and Chai P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* 75:523-531.
- Putz FE, Lee HS and Goh R. 1987. Effects of post-felling silvicultural treatments on woody lianas in Sarawak. *Malaysian Forester* 47:
- Rainfall Isohyet Map of the Alexandria area. Government Printer, Pretoria, South Africa.
- Richards PW. 1952. The tropical rain forest. Cambridge University Press, Cambridge.
- Russell EW. 1973. Soil conditions and plant growth. Longman. London.
- Stevens GC. 1987. Lianas as structural parasites: the *Bursera simaruba* example. *Ecol.* 68(1):77-81.
- Terbraak CJF. 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 69:69-77.
- Truswell JF. 1977. The geological evolution of South Africa. Purnell, Cape Town, South Africa.
- Van Daalen JC. 1984. Distinguishing features of forest species on nutrient-poor soils in the southern Cape. *Bothalia* 15:229-239.
- Venter HJT. 1976. An ecological study of the dune forest at Mapelana, Cape St. Lucia, Zululand. *J. S. Afr. Bot.* 42:211-230.
- Von Breitenbach F. 1974. Southern Cape forests and trees. Government printer, Pretoria. 328 pp.
- Whigham D. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Can. J. For. Res.* 14:37-39.
- White F. 1978. The afro-montane region. In: Wergner M.J.A. (Ed.), *Biogeography and ecology of southern Africa*. W. Junk, The Hague, pp 436 - 513.
- White F and Moll EJ. 1978. The Indian ocean coastal belt. In: Wergner M.J.A. (Ed.), *Biogeography and ecology of southern Africa*. W. Junk, The Hague, pp 563 - 598.
- Williams-Linera G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78:356-373.

## Chapter Three

### **The response of trees and climbers to nutrients and light:**

#### **A field experiment.**

##### **Introduction**

The distribution and abundance of climbers has been associated with nutrient rich soils (Richards 1952; Putz 1985; Putz and Chai 1987; Grubb 1987). Proctor *et al.* (1983) show climber abundance to be higher in forests on alluvial soils where there are high levels of base saturation, while White (1978) found climbers to be less common in the Afromontane forests with nutrient poor soils than in the nutrient rich lowland Guineo-Congolian forests of southern Africa.

Within a forest, climbers are commonly associated with forest margins (Williams-Linera 1990) and disturbances such as clear felling (Fox 1968; Lowe and Walker 1977) and natural tree fall gaps (Phillips 1931; Putz 1984). This association has been interpreted as an indication that the climbers are a light demanding growth form (Phillips 1931; Putz 1984), although they can be found in deep shade (Forseth and Teramura 1987; Carter and Teramura 1988a).

To be successful a climber needs to be able to grow faster than its host tree (Putz 1984). High growth rates, or in the case of climbers high shoot extension rates, are dependent on high nutrient availability (Grime 1977) and adequate CO<sub>2</sub> uptake which is related to light conditions (Schulze 1982). Is the success of a climber dependent on high light and nutrient levels or are there other factors that are more important, with light and nutrient levels merely being coincidental? Although studies have been made of the photosynthetic rates of climbers in relation to their ecology (Forseth and Teramura 1987; Carter and Teramura 1988a; Kupperts 1985), they have not considered the relative growth rates of trees and climbers under different light conditions. To date there have been no studies that have looked specifically at the growth rate of climbers under different nutrient conditions.

In this study I investigated the growth rates of trees and climbers grown under different light and nutrient conditions. The aim is to determine whether climbers respond differently to the different

conditions and under which conditions, if any, the shoot extension rates of climbers are greater than trees, thus conferring a competitive advantage to the climbers.

### Study area

The study site was situated in the Orange Kloof valley at the southern end of Table Mountain ( $18^{\circ} 25' W$ ,  $34^{\circ} 05' S$ ) (Fig. 1). The area lies in the winter rainfall region of the south western Cape and experiences a mediterranean climate of hot dry summers and cool wet winters with an average annual rainfall of 1230 mm. There are no evapotranspiration figures for the area but a nearby area on Table Mountain has an overall annual water surplus of 792 mm with a deficit occurring in January, February and March (McKenzie *et. al.* 1977). Temperature ranges from  $33^{\circ} C$  in summer to  $5^{\circ} C$  in winter. Frosts are rare. Although the valley is generally well sheltered it is subjected to strong south easterly winds channelling through the valley in summer and north westerly winds in winter.

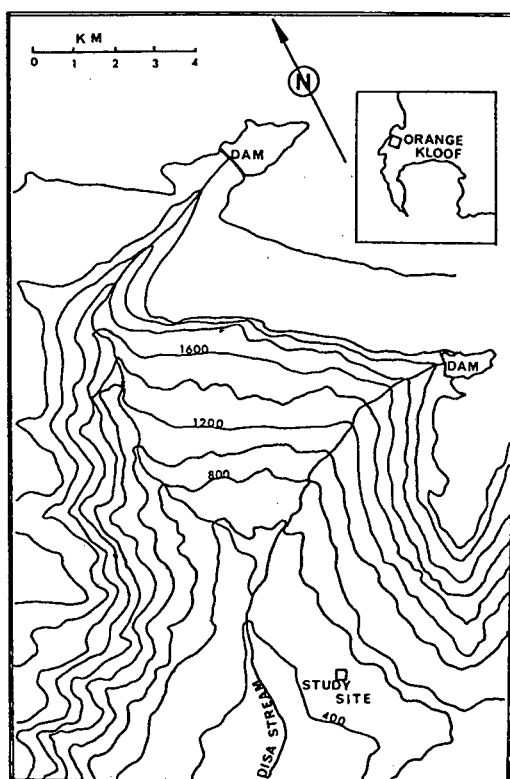


Figure 1. Map of the orange Kloof valley and the position of the study site.

The altitude of the valley as a whole ranges from 140 m to 600 m above mean sea level, with the study site being at approximately 250 m. The geology of the valley consists of an upper layer of Table Mountain Series sandstone at altitudes above 350 m, and granite partially covered by colluvial sandstone at lower altitudes (Geological survey map, Government Printers, Pretoria). Much of the vegetation of the valley is mountain fynbos (McKenzie *et al.* 1977), but there is well established indigenous forest following the major water courses and in the bowl of the valley. In parts of the lower regions of the valley Pine (*Pinus sp.*) plantations have been established for the last 50 years (McKenzie *et al.* 1977).

## Methods

### Study plot and species

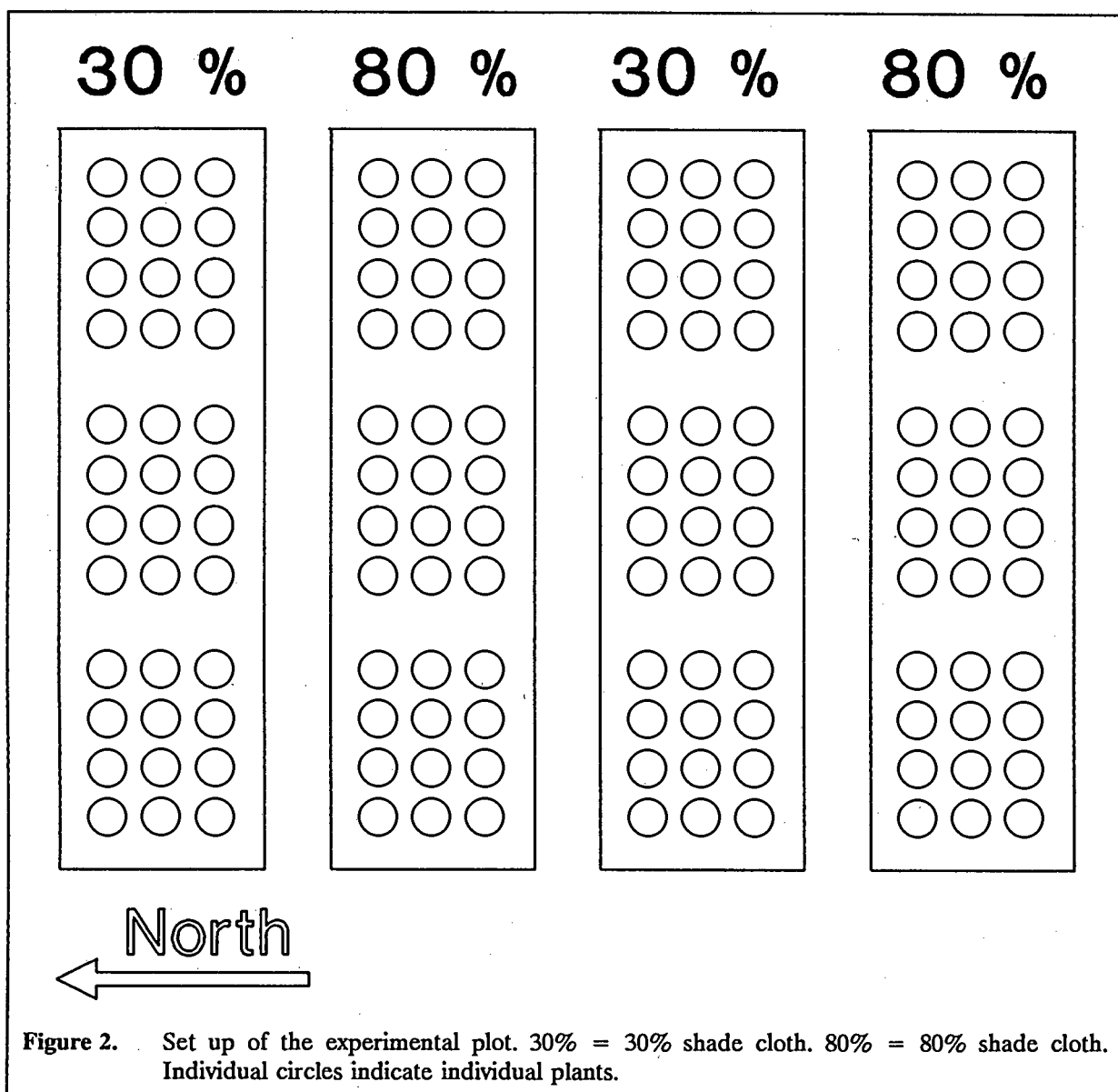
The position of the study plots (Fig. 1) is in an old felled plantation neighbouring on existing indigenous forest. Although there is debate about the original extent of the forested portion of the valley and the extent to which anthropogenically induced fire and other influences have reduced the forest (McKenzie *et al.* 1977), the area is sufficiently close to the indigenous forest to have at some stage been under indigenous trees. As there was no suitable site within the forest in which to conduct the study this was the best option available for simulating forest conditions.

Three of the four species used in this experiment are indigenous to the south western Cape. The trees, *Kiggelaria africana* L. and *Cassine peragua* L. and the woody climber *Rhoicissus digitata* (L.f.) Gilg & Brandt are commonly found in the forests of the south-western Cape (Bond and Goldblatt 1984). The fourth species, a herbaceous climber *Senecio thamnoides*, is a commonly grown garden plant in the southern Cape which is also found in the forests and is well suited to growing in the area. Each plant used was between two and four years old and had been established in nutrient rich, well watered soils under nursery conditions in the Cape Peninsula. No plant had been subject to stress prior to the experiment. The experiment was run for one year (August 1989 - August 1990).

### Experimental setup

I erected four shade cloth shelters with two replicate shelters each of a 30% and an 80% shade cloth. The shelters were 2.5 m high 5.5 m long and 2 m wide. All sides of the shelter had shade cloth extending to the ground except the south facing side which had shade cloth extending down

0.5 m. Shelters were separated by 4 m to avoid mutual shading. At all times all plants were shaded from direct sunlight. The 80 % shade cloth was designed to simulate the growth environment within a forest and the 30 % shade cloth the growth environment in a treefall gap or forest margin where the light levels are higher but shading still occurs. Within each shelter I established three replicate plots 1.5 by 1.0 m (Fig. 2). Each plot contained twelve plants, i.e. three individuals of each of the four study species investigated. Each individual plant of each species within a plot received a different nutrient treatment. There were thus, in all, six replicates of each treatment.



### Nutrient treatments

Within each plot one individual of each species was subjected to a high (H), one to a medium (M) and the third to a low (L) nutrient addition treatment. The position of the individuals as well as the nutrient treatments were randomised within each plot. I calculated the high nutrient addition on the basis of increasing the mean base level of the natural soil in Orange Kloof (ca. 2400  $\mu\text{g/g}$  nitrogen and 151  $\mu\text{g/g}$  phosphorus) to levels reflecting the higher recorded levels in the southern Cape forests (ca. 4500  $\mu\text{g/g}$  N and 450  $\mu\text{g/g}$  P) (Van Daalen 1984; Donald *et al.* 1987; Unpublished data G. Shafer, Saasveld Forestry Research Station). The medium nutrient addition was one half the high addition, and the low nutrient treatment received no nutrient addition. The calculation of the amount of nitrogen to add was based on the assumption that three percent of the total nitrogen determined to be in the soil is available to the plant (Mitchell *et al.* 1987) and the assumption that all the nitrogen added would be available.

To ensure that the nutrients were confined to the individual plants to which they were applied I grew each plant in a six litre plastic pot (26 cm top diameter) with the bottom cut out. This provided isolation of the plants from one another, while still allowing the plants access to the ground water, thus minimising the need for additional watering.

I added nutrients every two months to avoid any form of nutrient toxicity and to reduce leaching losses (Groves and Keraitis 1976). This method of application also avoided a nutrient induced growth burst followed by a return to the nutrient poor conditions. High nutrient nitrogen additions, in the form of urea formaldehyde ( $\text{H}_2\text{NCONH}_2 \cdot \text{HCHO}$ ) a slow release granule, were 66  $\mu\text{gN/g}$  soil (0.52 g/pot) and medium nutrient additions 33  $\mu\text{gN/g}$  (0.26 g/pot) (Table 1). Phosphorus, the next most limiting nutrient in the southern Cape, was added to create a N : P ratio of ten to one (Mitchell *et al.* 1987). I added phosphorus as part of a Long Ashton nutrient solution (Smith *et al.* 1983) from which the nitrogen had been excluded. This allowed a balanced nutrient addition for the rest of the macro and micro nutrients to be achieved (Table 1). The nutrients in the Long Ashton solution were added with two litres of water after the urea to moisten the urea granules and initiate the release of nitrogen. Two litres of deionised water were added to the plants receiving the low nutrient treatment at the time of each nutrient application. In the hot dry summer months it was necessary to water the plants as the ground water proved inadequate at the depth of the pots. Equal treatments of deionised water were added to all individuals.

**Table 1.** The nutrients and the quantities used for the medium and high nutrient additions to the potted trees and climbers every two months. The ratio of the components of the solution follows the Long Ashton nutrient solution; see text for explanation.

Nutrient source	Quantity (ml/pot)	
	High Treatment	Medium Treatment
UREA $\text{H}_2\text{NCONH}_2 \cdot \text{HCHO}$ (g/pot)	0.52	0.26
$\text{MgSO}_4$	2.5	1.25
$\text{K}_2\text{SO}_4$	2.5	1.25
$\text{CaCl}_2$	2.5	1.25
$\text{NaH}_2\text{PO}_4$	1.25	0.625
$\text{Na}_2\text{HPO}_4$	1.25	0.625
EDTA	0.25	0.125
Balanced $\mu$ .nutrients	0.25	0.125

## Growth analysis

### Shoot extension

I established grow rates by measuring the extension of the main shoots of both trees and climbers. The initial lengths of the main shoot of each plant were recorded and, subsequently these shoot were remeasured every two months at each nutrient application. Measurements were made from a set mark on the pot in which the plant was growing to the terminal bud of the main shoot. For trees I made no attempt to straighten the stem but climber stems were loosely unravelled and laid out for measurements to be made. I express the growth as the plotted ratio of the length of the stem at a time  $x$  ( $L_x$ ) to the initial length ( $L_0$ ). This enables the comparison to be made between the different species. Because August is the first month of the experiment, the plot at August has a ratio one. The slope of the plotted curve is a measure of the growth rate of the plant. To test if any of the variance in the growth rates of the plants was attributable to them being grown under either of the replicate shade cloths I performed a two-way anova on log transformed data from the two replicates with the nutrient treatments used as a second factor.

### Total biomass

To enable comparison of the influence of the light and nutrient treatments on the overall above ground carbon gain of the individuals, I recorded initial biomass readings of the leaves and stems

of 5 random plants of each species, from the same nursery cohort as the experimental plants. After one year I made final biomass measurements of the leaves and stems of three replicate individuals of each species grown under each of the light and nutrient treatments.

#### Leaf specific weights

At the beginning and the end of the experiment I made measurements of the leaf specific weights (dry mass/leaf area in g/cm<sup>2</sup>) of ten fully expanded leaves of each species grown under each of the light and nutrient treatments.

#### Leaf nitrogen content

At the end of the experiment I obtained total leaf nitrogen content of three replicate fully expanded leaves of each species, grown under each of the light and nutrient treatments.

### **Results**

#### Initial nutrient levels

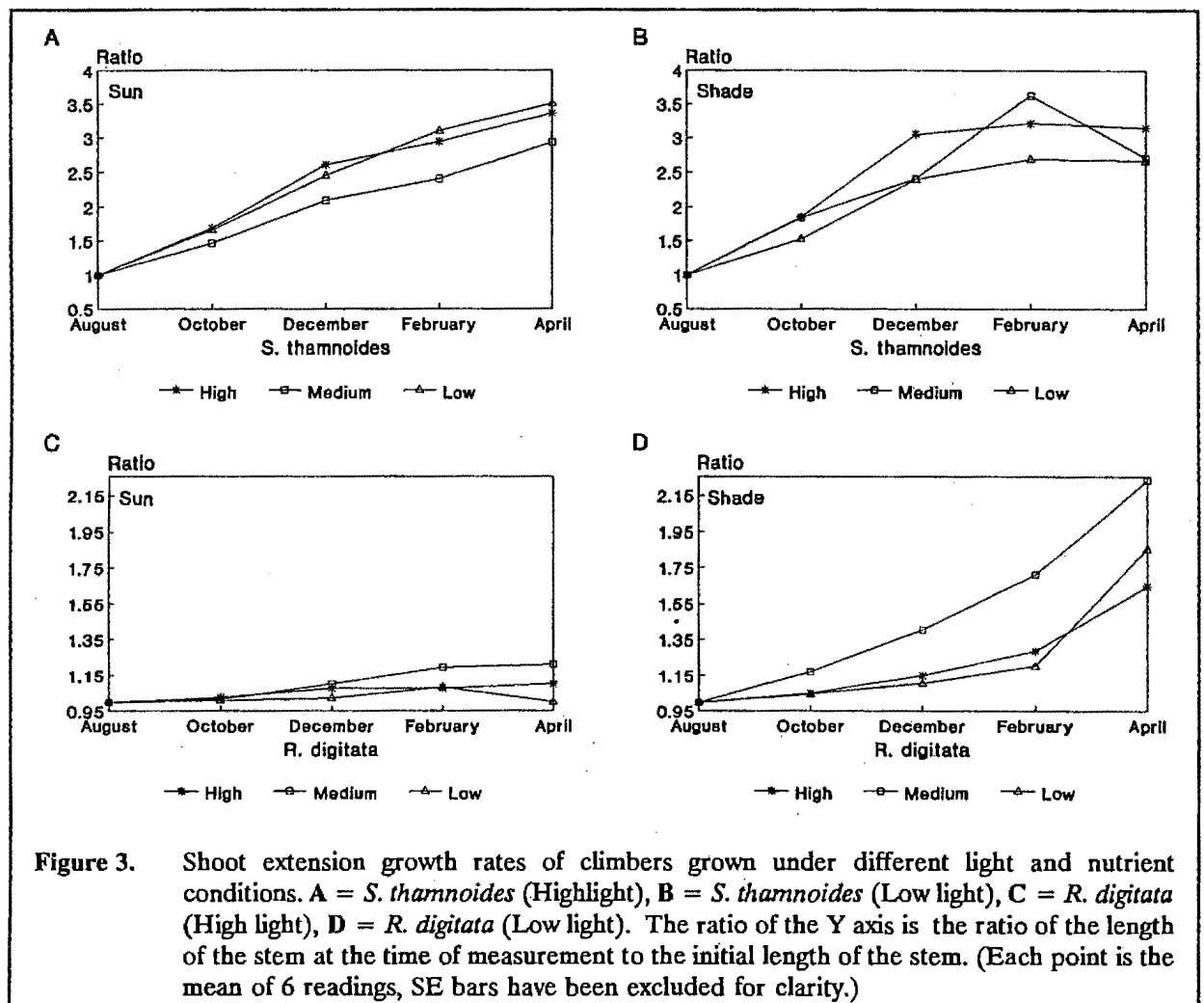
The initial nutrient levels in the pots were  $2.4 \pm 0.41$  mg/g nitrogen and  $151.7 \pm 3.46$  µg/g phosphorus which are in the lower range of nutrient levels reported for southern Cape forests (Masson and Moll 1987)

#### Shoot extension

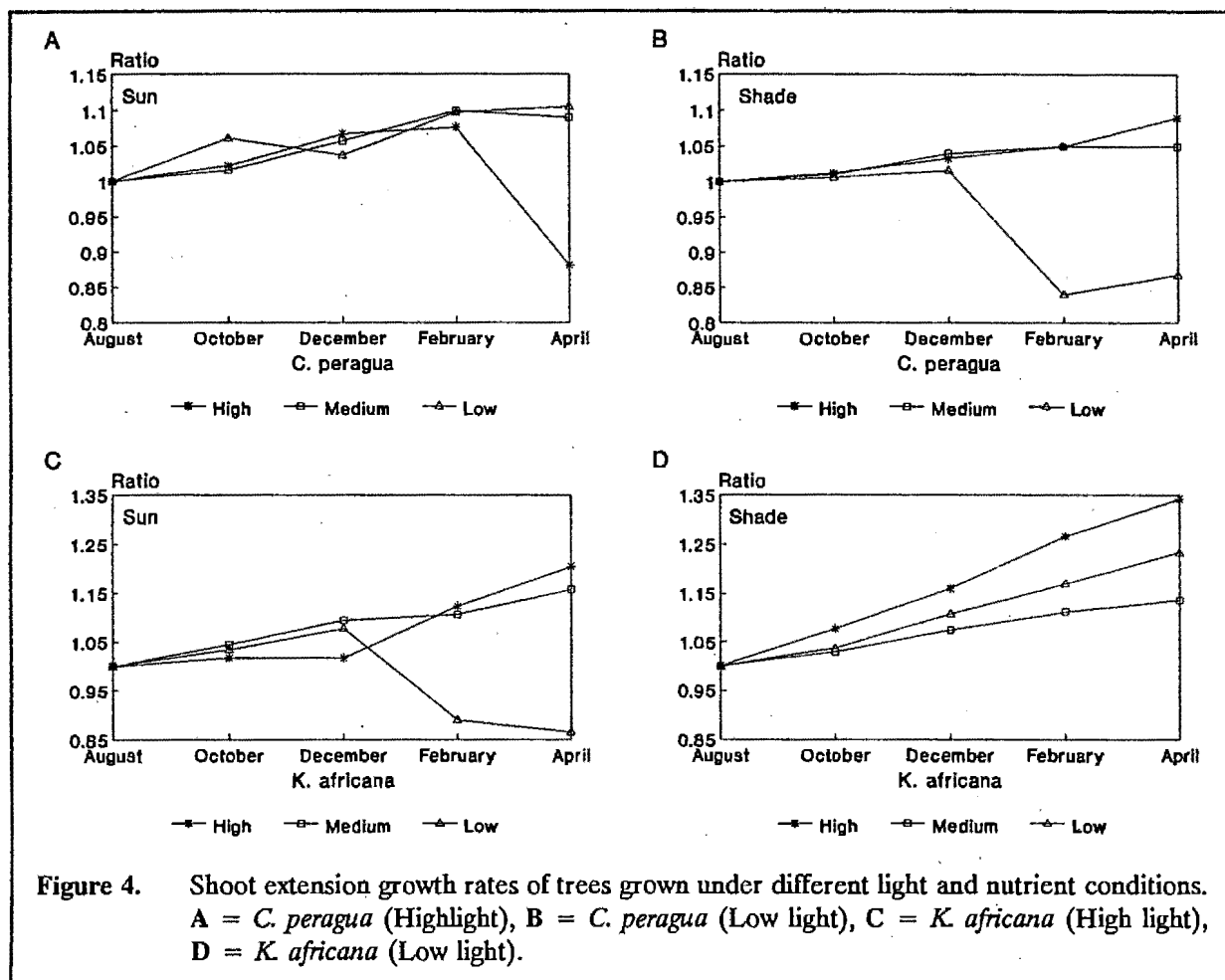
The initial heights of the individuals of the four species ranged from  $52 \pm 12$  cm for *S. thamnoides* to  $101 \pm 14.5$  cm for *C. peragua*, (*R. digitata* =  $96 \pm 28.3$ cm and *K. africana* =  $75 \pm 8.5$  cm). All species experienced a measure of die-back of the terminal shoot region from December. *K. africana* leaves were selectively fed upon by the caterpillar *Acraea horta* between October and January, and the die-back of this species appears to be related to a heavy caterpillar infestation. For this reason only the results until April (8 - months) are shown as the effects of the die back become too dominant later in the year. The die-back was not restricted to either of the nutrient or the light treatments although there was a tendency for more die-back to occur in the plants grown under high light conditions.

There were no significant differences between the growth rates of the plants grown in the replicate 30 % or the replicate 80 % shade cloths (Two way Anova, log transformed data). The maximum shoot extension of the climbers *S. thamnoides* and *R. digitata* (3.6 and 2.2 times original length respectively) (Fig. 3b,d) was greater than the maximum shoot extension of the trees *C. peragua* and *K. africana* (1.1 and 1.35 times original length respectively) (Fig. 4a,d), indicating that the climbers had higher growth rates.

Different nutrient conditions did not result in significant differences (Anova) in shoot extension of plants in any of the species of climber (Fig. 3) or tree (Fig. 4) investigated. There was also no clear pattern of response of the climbers or trees, grown under equal light conditions, to different nutrient treatments. For each species, there were no significant differences (Anova) in shoot extension of individuals grown under different light conditions, but equal nutrient treatments.



There was also no consistent trend in the response of any of the species to different light conditions. This suggests that at the levels investigated, nutrients and light have little effect on shoot extension rates of the climber and tree species studied.



### Biomass

For each species the greatest increase in stem and leaf biomass was for the individuals grown with a high nutrient application and under high light conditions (Table 2). The largest percentage increase in stem and leaf biomass was for *K. africana* (217% and 185%) respectively. The lowest percentage increase in stem biomass was for *R. digitata* (156%) and in leaf biomass was for *C. peragua* (132%) (Table 2). In terms of absolute stem biomass the mean increase for *C. peragua* ( $46.9 \pm 3.2\text{g}$ ) and *K. africana* ( $39.4 \pm 3.7\text{g}$ ) are significantly greater ( $P < 0.01$ ) (Anova) than the increase for *R. digitata* ( $11.9 \pm 2.2\text{g}$ ), while for the leaves there was no significant difference between the mean absolute biomass increase (Anova) between any of the species indicating that trees accumulate more stem biomass than the climber but that the leaf biomass increment is equivalent for the trees and climber.

**Table 2.** The average initial biomass of the plants used in the experiment and the final biomass of the plants after the different nutrient treatments, (n = 5).

Treatment		Climbers		Trees	
		S. thamnoides	R. digitata	C. peragua	K. africana
Light	Nutrient	Stem biomass (g)			
Initial		14.8 ± 2.3	21.2 ± 6.6	49.3 ± 7.8	26.0 ± 0.4
High	High	no data	33.1 ± 2.2	96.2 ± 6.2	56.4 ± 1.8
	Low	no data	28.1 ± 2.3	87.9 ± 5.3	55.8 ± 1.7
Low	High	no data	28.6 ± 1.9	86.4 ± 6.6	53.5 ± 1.7
	Low	no data	26.8 ± 2.6	79.9 ± 4.3	53.3 ± 2.0
Light	Nutrient	Leaf biomass (g)			
Initial		2.22 ± 0.4	16.5 ± 1.3	25.8 ± 0.9	13.7 ± 0.2
High	High	no data	25.3 ± 1.0	34.0 ± 2.1	25.0 ± 1.0
	Low	no data	28.0 ± 1.9	30.2 ± 1.4	23.2 ± 0.9
Low	High	no data	27.4 ± 1.8	28.0 ± 1.2	20.6 ± 1.1
	Low	no data	34.7 ± 2.0	33.9 ± 2.3	21.3 ± 0.7

The final stem biomass of both climber and trees grown under low nutrient conditions were not significantly different (Anova) from those grown under high nutrient conditions (Table 2). For each species there was also no significant difference in the leaf biomass of plants grown under the high and low nutrient conditions for each light treatment, with the exception of *C. peragua* ( $28.0 \pm 1.2$  and  $33.9 \pm 2.3$  respectively,  $P < 0.05$ ) and *R. digitata* ( $27.4 \pm 1.8$  and  $34.7 \pm 2.0$  respectively,  $P < 0.05$ ) where leaf biomass of plants grown under low nutrient conditions was greater than under high nutrient conditions. This suggests that nutrient levels do not effect leaf biomass under all except low light conditions.

Light levels did not effect the final stem biomass of plants grown under low nutrient conditions (Anova). Under high nutrient conditions the final stem biomass of the two tree species was similar, while the climber *R. digitata* displayed a larger increase under high ( $33.1 \pm 2.2$ ) than low ( $26.8 \pm 1.9$ ) light conditions ( $P < 0.05$ ). However, for the trees *C. peragua* and *K. africana* grown under high nutrient conditions the increase in leaf biomass was significantly greater for plants grown under high compared to low light conditions ( $34.0 \pm 2.1$  &  $28.0 \pm 1.2$ , ( $P < 0.05$ ) and  $25.0 \pm 1.0$  &  $20.6 \pm 1.1$ ,  $P < 0.05$ ) respectively) (Table 2). Under low nutrient conditions the increase in leaf biomass of trees was similar for plants grown under both light levels. In contrast the

increase in leaf biomass of the climber *R. digitata* grown under low nutrient conditions was greater in high than in low light conditions ( $34.7 \pm 2.0$  and  $28.0 \pm 1.9$ , ( $P < 0.05$ ))(Table 2). Under high nutrient conditions, light levels did not effect the growth of leaves of the climber. Thus the growth of leaves of the climber appears to be influenced directly by the soil nutrient availability.

In both the initial and the final condition for the plants grown under high light and high nutrients the climber *R. digitata* had a greater leaf biomass per unit stem biomass (78 %) than *C. peragua* (52 %) and *K. africana* (53 %).

### Leaf specific weight

I measured leaf specific weights (LSW) to determine whether differences between individual plants reflected the different light and nutrient treatments. For each species, grown under each light condition there were no significant differences in the LSW of plants grown in high and low nutrient treatments (Anova) (Table 3). There were also no significant differences for plants grown in high and low light conditions (Anova) (Table 3). There was, however, a trend with the LSW of plants grown in high light conditions being more than those of the plants grown under low light conditions (Table 3).

**Table 3.** The initial and final leaf specific weights ( $\text{g}/\text{cm}^2$ ) of the four species under the four treatments. 30 = 30% shade and 80 = 80% shade. H = high nutrient application and L = low nutrient application. There are no measurements of LSW for individuals of *S. thamnoides*,  $n = 10$ .

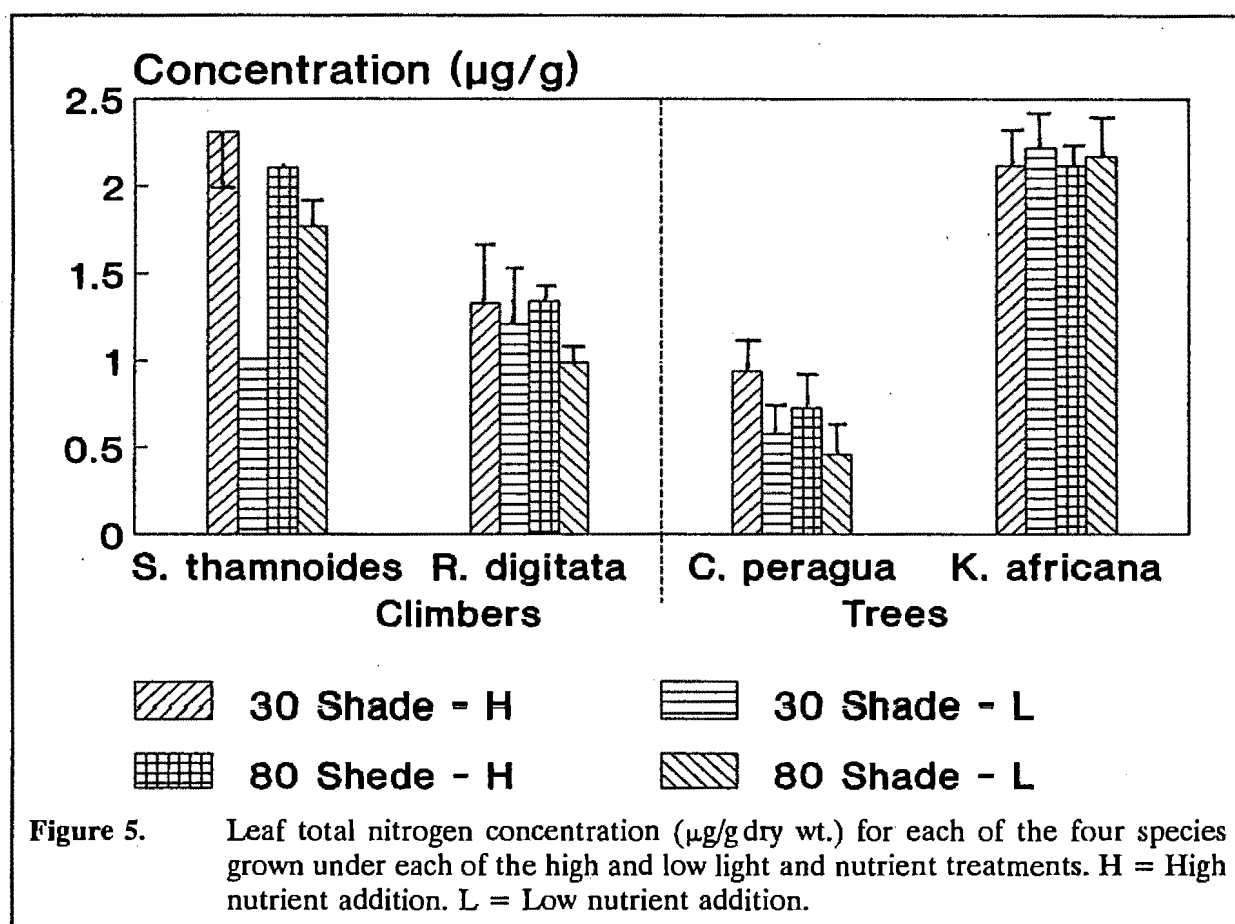
Treatment	Climbers		Trees	
	<i>S. thamnoides</i> *	<i>R. digitata</i>	<i>C. peragua</i>	<i>K. africana</i>
Initial	$29,8 \pm 3.2$	$22,9 \pm 1.8$	$30,8 \pm 1.1$	$24,7 \pm 1.6$
30 - H	$28,5 \pm 2.6$	$19,6 \pm 3.5$	$27,5 \pm 1.2$	$11,8 \pm 1.2$
30 - L	no data	$21,2 \pm 1.4$	$28,3 \pm 1.5$	$10,6 \pm 1.7$
80 - H	no data	$18,9 \pm 1.8$	$24,7 \pm 3.2$	$8,0 \pm 1.3$
80 - L	no data	$19,1 \pm 1.1$	$26,8 \pm 2.2$	$9,7 \pm 1.4$

\* the measurement is for a nursery grown plant

This suggests a positive response by leaves of both growth forms to increased light levels. There was no difference in the pattern of trees and climbers. The mean LSW of the climber *R. digitata* was significantly different from those of both tree species *C. peragua* and *K. africana*. There is however no clear difference between the different growth forms as the value of the LSW of the climber falls between that of the two tree species.

### Leaf nitrogen concentration

For the plants grown under high light and high nutrient conditions the herbaceous climber *S. thamnoides* and the pioneer tree *K. africana* had the highest nitrogen concentrations ( $2.31\mu\text{g/g}$  dry wt. and  $2.12\mu\text{g/g}$  dry wt.), while the woody climber *R. digitata* and the non-pioneer tree *C. peragua* had much lower nitrogen concentrations ( $1.33\mu\text{g/g}$  and  $0.94\mu\text{g/g}$ ) (Fig. 5). For each species under each light condition there was only a significant differences between the leaf nitrogen concentration of the plants of *S. thamnoides* grown in the high and low nutrient treatments ( $2.3\mu\text{g/g}$  and  $1.0\mu\text{g/g}$  respectively ( $P < 0.01$ )) (Anova) (Fig. 5). There was however a trend with all species from the high nutrient treatments having higher leaf nitrogen concentrations than those from the low nutrient treatment under the same light condition. For each species under each nutrient treatment there was no significant difference between the leaf nitrogen concentration of the plants grown under the different light conditions (Anova) (Fig. 5). The results suggest little response of leaf nitrogen concentration of the trees to the different light and nutrient treatments, while the climbers may respond to increased nutrient levels. There appear to be no responses to the different light conditions.



## Discussion

Die-back appears to have affected all species, and to be due to wind burn from the strong wind that can channel through the Orange Kloof valley. However, although the effective experimental period was thus shortened the growth season was sufficiently long (late winter to early summer) to realistically interpret the results.

Species with rapid growth rates require high nutrient availability to support the growth (Grime 1977). The presence of high nutrient levels however, does not ensure rapid growth rates (biomass accumulation) which are dependent on multiple environmental factors (Whitaker 1975; Field and Mooney 1986). The lack of significant differences in the rates of stem elongation of the climbers under the different light and nutrient conditions suggests that neither of these factors conferred a competitive advantage on the climbers. These results differ from those of Putz (1984) who found increased stem elongation of the climber *Dioclea reflexa* in the well lit canopy gaps compared to the forest sub-canopy. The absence of a difference in the growth rates of climbers grown under higher soil nutrient levels challenges the association between climber abundance and high nutrient levels (Richards 1952; Putz 1985; Grubb 1987; see also Chapter Two in this thesis).

There is a great range of stem extension growth rates, for the species considered in this study. The variability appears to be due to the response of the plants to the nutrients and not between the replicate light treatments. In general the climbers grew faster than the trees with the slower climber growth rates for *R. digitata* remaining higher than the faster tree *K. africana* while the faster growing climber *S. thamnoides* rapidly out grew both tree species (Fig. 3 & 4).

There are however some inconsistencies in the results which are difficult to explain. For example both *R. digitata* and *K. africana* displayed greater shoot extension rates under low light conditions. This is surprising for *K. africana*, a pioneer forest species, which is fairly shade intolerant in natural conditions. For *R. digitata* which displayed an initial slow growth response followed by a rapid increase in stem length, shoot extension growth may be dependent on the building up of sufficient reserves in root tubers which are then directed into stem growth. This suggests that whole plant growth phenology may be important in competitive interactions between trees and climbers.

Although *R. digitata* experienced a significant increase in stem biomass for the plants grown under high light and high nutrient conditions and the two tree species did not, the mean absolute

increase for the two trees is significantly greater than for the climber (Table 2). These differences in biomass accumulation patterns of the two growth forms suggest an inherently higher capacity of the trees to accumulate above ground biomass compared to the climber. The greater shoot extension of the climber (Fig. 3) does not compensate for the biomass that does not go into structural support, nor does the increased biomass that is placed into leaves (Table 2). It is possible that the extra biomass is allocated to basal stem support in a climber of this age as it may need to gain initial height to access other support structures (Putz 1984). There are no comparable studies to date with which to compare these results.

The greater ratio of leaf biomass to stem biomass of the climber in this study (Table 2) is supported by (Putz 1983) who found that woody climbers contributed 4.5 % of the above ground biomass in an evergreen tropical rain forest and 19 % of the leaf area index. The enhanced leaf area to stem biomass suggests that climbers have a greater capacity to gain carbon per unit stem biomass than trees (Putz 1983), although the above results do not support this.

The significant increase in the leaf biomass of *C. peragua* and *R. digitata* (Table 2) in response to increased nutrient levels and of all three species in response to increased light conditions suggests that there are no fundamental differences between the growth response in terms of leaf biomass increase of the two growth forms to the nutrients and light treatments. A pattern that is reflected by the response of stem biomass to increased nutrient conditions.

The absence of a leaf specific weight response to the light treatments differs from the general trend (Langeheim *et al.* 1984; Thompson *et al.* 1988). This result is possibly due to the low number of replicate leaves sampled as there is a trend for leaves of all species grown in high light conditions to have a higher LSW than those grown in low light conditions (Table 3). The average value of the LSW of the climber *R. digitata* falls between that of the pioneer tree *K. africana* and a climax tree *C. peragua* suggesting that there are no patterns of differences in LSW between the growth forms.

Plants that received high nutrient applications tended to have higher leaf nitrogen levels than those with the low nutrient application (Fig. 5) although this is only significant for *S. thamnoides*. This result agrees with the observation by Vitousek and Sanford (1986) that, within a species, the levels of nitrogen in a leaf are likely to reflect the nitrogen levels available in the soil. The light levels under which the experimental plants were grown appear to have had little effect on the

nitrogen concentration in the leaves (Fig. 5). This is contrary to the general trend of leaves growing under high light conditions having higher nitrogen concentrations than leaves growing under low light conditions (Kuppers 1984; Thompson *et al.* 1988). The reason for this is uncertain. As with leaf specific weight however there appears to be no pattern between the tree and the climber growth forms. There is limited data on the nutrient concentration of climber foliage but Greenland and Kowal (1960) report no difference between the nitrogen concentration of leaves in trees and climbers thus supporting this study.

## **Conclusion**

The study supports the general observation that climbers have greater shoot extension growth rates than trees. The application of nutrients and higher light levels resulted in increased shoot extension of both trees and climbers but does not particularly favour the climber. Thus higher shoot extension rates of climbers appears not to be a result of higher nutrient availability nor higher light conditions, but is possibly due to differences in allocation of carbon, growth phenology or leaf area index between the two growth forms. These results need to be treated as preliminary and further studies need to extend the experimental period as well as to include an investigation into the phenology of the experimental plants and carbon allocation to below ground structures, as well as cover a greater range of both tree and climber species.

## References

- Bond P and Goldblatt P. 1984. Plants of the Cape flora: a descriptive catalogue. J. S. Afr. Bot. Supplementary Vol. 13. pp455.
- Carter GA and Teramura AH. 1988a. Vine photosynthesis and relationships to climbing mechanics in a forest understory. Amer. J. Bot. 75(7):1011-1018.
- Carter GA and Teramura AH. 1988b. Nonsummer stomatal conductance for the invasive vines kudzu and Japanese honeysuckle. Can. J. Bot. 66:2392-2395.
- Donald DGM, Lange PW, Schultz CJ and Morris AR. 1987. The application of fertilizers to pines in southern Africa. S. Afr. For. J. 141:53-62.
- Fernandez SR. 1987. Auswirkungen der Kletterstrategie der lianen auf deren Verbreitung. Tuexenia 7:447-458.
- Field C and Mooney HA. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givnish T (Ed.) On the economy of form and function. Cambridge University Press. Cambridge. pp 25-55.
- Forseth IN and Teramura AH. 1987. Field photosynthesis, microclimate and water relations of an exotic temperate liana, *Pueraria lobata*, kudzu. Oecologia 71:262-267.
- Fox JED. 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. The Malayan Forester 31(4):326-347.
- Greenland DJ and Kowal JML. 1960. Nutrient content of the moist tropical forest of Ghana. Plant Soil 12:154-173.
- Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111:1169-1194.
- Groves RH and Keraitis K. 1976. Survival and growth of seedlings of three sclerophyll species at high levels of phosphorus and nitrogen. Aust. J. Bot. 24:681-690.
- Grubb PJ. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. In: Gee JHR and Giller PS (Eds.) Organization of communities - past and present. Blackwell Scientific Publications. Oxford.
- Kuppers M. 1984. Carbon relations and competition between woody species in a central European hedgerow. 1. Photosynthetic characteristics. Oecologia 64:332-243.
- Kuppers M. 1985. Carbon relations and competition between woody species in a central european hedgerow. IV. Growth form and partitioning. Oecologia 66:343-352.
- Langeheim JH, Osmond CB, Brooks A and Ferrar PJ. 1984. Photosynthetic responses to light in seedlings of selected Amazonian and Australian rain forest tree species. Oecologia 63:215-224.

- Lowe RG and Walker P. 1977. Classification of canopy, stem, crown status and climber infestation in natural tropical forest in Nigeria. *J. Appl. Ecol.* 14:897-903.
- Masson PH and Moll EJ. 1987. Factors affecting forest colonisation of fynbos in the absence of recurrent fire at Orange Kloof, Cape Province, South Africa. *S. Afr. For. J.* 143:5-10.
- McKenzie B, Moll EJ and Campbell BM. 1977. A phytosociological study of Orange Kloof, Table Mountain, South Africa. *Vegetatio* 34:41-53.
- Mitchell DT, Stock WD and Jongens-Roberts SM. 1987. Nitrogen and phosphorus cycling in the fynbos biome. A report of the terrestrial ecosystems section of the ecosystem programmes, Number 18.
- Peace WJH and MacDonald FD. 1981. An investigation of the leaf anatomy, foliar mineral levels and water relations of trees of a Sarawak forest. *Biotropica* 13:100-109.
- Philips JF 1931 Forest succession and ecology in the Knysna region. *Memoirs of the botanical survey of South Africa* No.14.
- Proctor J, Anderson JM, Chai P and Vallack HW. 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. *J. Ecol.* 71:237-260.
- Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6):1713-1724.
- Putz FE. 1985. Woody vines and forest management in Malaysia. *Commonw. For. Rev.* 64(4):359-365.
- Putz FE and Chai P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* 75:523-531.
- Richards PW. 1952. *The tropical rain forest.* Cambridge University Press. Cambridge.
- Schulze E-D. 1982. Plant life forms and their carbon, water and nutrient relations. *Encyclopedia of plant physiology, NS Vol 12B.* Springer Verlag, Berlin.
- Smith GS, Johnston CM and Conforth IS. 1983. Comparison of nutrient solutions for growth of plants in sand culture. *New phytol.* 94:537-548.
- Thompson WA, Stocker GC and Kreidemann PE. 1988. Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rain forest with broad tolerance to sun and shade. *Aust. J. Plant Physiol.* 15:299-315.
- Van Daalen JC. 1984. Distinguishing features of forest species on nutrient-poor soils in the southern Cape. *Bothalia* 15(1&2):229-239.
- Vitousek PM and Sanford RL. 1986. Nutrient cycling in moist tropical forest. *Ann. Rev. Ecol. Syst.* 17:137-167.
- White F. 1978. The afro-montane region. In: Wergner MJA. (Ed.) *Biogeography and ecology of southern Africa.* W. Junk, The Hague. pp 436-513.

Whittaker R.H. 1975. *Communities and Ecosystems*. Macmillan, New York.

Williams-Linera G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78:356-365.

## Chapter 4

### **Climber photosynthetic attributes:**

### **Or how do climbers grow faster than trees?**

#### **Introduction**

Climbers differ from trees in their absence of a rigid woody support (Darwin 1867; Givnish and Vermeij 1976; Halle *et al.* 1978). Many climbers are characterised by rapid stem extension rates while stem diameter growth is slow (Putz and Windsor 1987). Climbers also have higher leaf areas to stem biomass ratios than trees (Putz 1983). To be competitively successful a climber needs to be able to grow faster than its host in order to gain access to the canopy (Putz 1984). The competitive abilities of a plant can be expressed at different levels (Kuppers 1984). They can be expressed at the level of the whole plant, through patterns of carbon allocation to support structures or through differing branching patterns (Kuppers 1985; Givnish 1986). Alternatively they can be expressed at leaf level where high CO<sub>2</sub> assimilation rates, and thus carbohydrate supply to the plant, may contribute to the competitive ability of a plant (Chapin 1980).

Climbers are thought to be associated with well lit forests and high nutrient levels (Phillips 1931; Richards 1952, Proctor *et al.* 1983; Putz 1984; Grubb 1987). A number of studies have compared photosynthetic attributes of native and exotic climbers in an attempt to explain the invasive abilities of the exotics (Carter *et al.* 1989; Forseth and Teramura 1987) as well as to explain the ecology of vines with different climbing mechanisms (Carter and Teramura 1988). Kuppers (1984) investigated competitive interactions between different growth forms by measuring CO<sub>2</sub> uptake capacity of the leaves of shrubs and a climber. However with the exception of these studies the ecological physiology of climbers remains poorly understood.

In this study I investigate whether the differences in growth rates, defined as shoot extension, between trees and climbers is a function of different rates of carbon assimilation. I consider aspects of the carbon gain mechanisms of trees and climbers at the level of the leaf in an attempt

to determine if differences in the carbon assimilation patterns of the two growth forms can explain their relative successes. I do this in three ways:

Firstly, I measured the maximum photosynthetic rates and light response curves of two forest tree and two climber species. Measurements were made on plants that had been grown under different light and nutrient conditions, to test the idea that the differing environmental factors affect the relative photosynthetic rates, and potentially, the growth rates of trees and climbers.

Secondly, as the maximum photosynthetic capacity of leaves is related to the nitrogen content of those leaves (Field and Mooney 1986), I measured the nitrogen concentration of leaves from trees and climbers covering a broad geographical range to determine whether there were any general patterns of higher nitrogen content in climbers than in trees.

Thirdly, I investigated the water use efficiency of climbers, and by implication their productivity (Farquhar and Richards 1984), relative to trees by comparing the  $\delta^{13}\text{C}$  isotope ratio in leaves of trees and climbers from a broad range of forests.

## Methods

### Leaf collection and preparation

To enable generalization of the results over a broad geographical range, I collected leaf material from five each of the common tree and climber species at each of five southern African forests (only two from Alexandria) (Fig. 1). To reduce intra-forest variation in leaf  $\delta^{13}\text{C}$  values due to differences in light environment (Körner *et al.* 1986; Ehleringer *et al.* 1987) I standardised the collection process by taking leaf material only from the outer edge of the canopy where leaves were in full sunlight. Leaves were oven dried at 70 °C for four days and ground through a 0.4 mm mesh.

### Photosynthetic attributes

I used plants from the experiment described in Chapter Three. These comprised individuals of the canopy tree species *Cassine peragua*, the forest margin tree *Kiggelaria africana*, a woody climber *Rhoicissus digitata* and a herbaceous climber *Senecio thamnoides*, all  $\text{C}_3$  species. Each individual, except those of *S. thamnoides*, had been grown for 16 months under two shade cloth treatments,

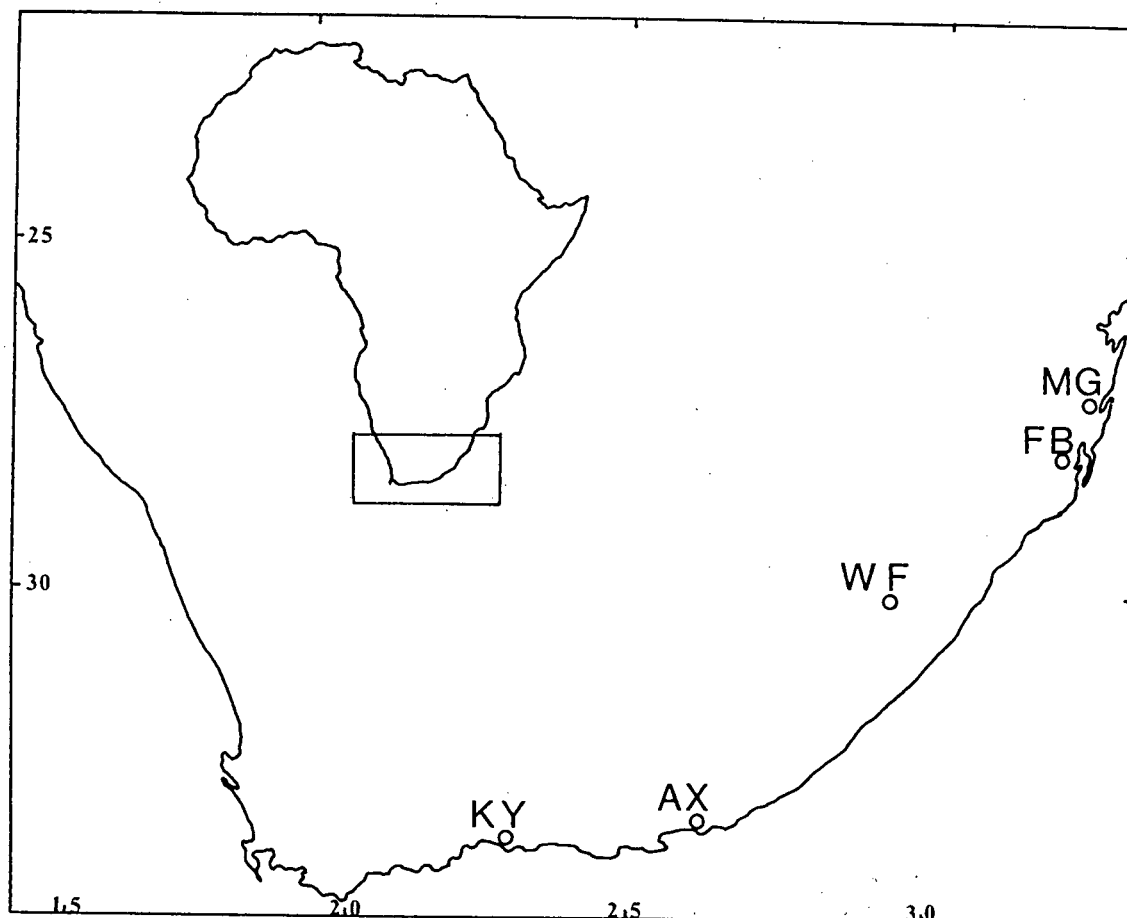
i.e. 30 % shade cloth (sun plants) and 80 % shade cloth (shade plants), and two nutrient conditions, i.e. a low condition with no nutrient additions to a nutrient poor soil and a high condition with nutrients added to simulate the high levels of some of the southern Cape forests (van Daalen 1984) (see Chapter three for details of the study site and the experimental design). The high nutrient additions were 66  $\mu\text{g/gN}$ , 6.6  $\mu\text{g/gP}$  and other nutrients in a Long Ashton ratio to the P levels (see Smith *et al.* 1983). All individuals of *S. thamnoides* grown in the experiment of chapter three had suffered a complete dieback, and nursery grown plants therefore were used. These plants had been grown under high light and high nutrient conditions.

I kept all plants used for photosynthetic measurements under their original shading conditions and watered twice a week until immediately prior to measurements, when they were transferred in their pots, to a phytotron. The light in the phytotron was produced by a bank of sodium and metal halide lamps to achieve a balanced light spectrum.

For each species, I made measurements on one leaf each of three replicate plants for each of the four treatments (only one treatment for *S. thamnoides*). To ensure that comparisons between the photosynthetic readings of leaves were not compounded by the effects of differing leaf phenology common in evergreen plants (Mooney and Gulmon 1982), the leaves selected were judged, by their appearance and position on the plant, to be even aged. To measure the gas exchange response to different light conditions as well as the maximum photosynthetic response ( $A_{\text{max}}$ ), I made initial measurements at a high photosynthetic photon flux density (PPFD) of 1600  $\mu\text{mol/m}^2/\text{s}$  to which the plants were allowed to acclimate for 15 to 20 minutes before readings were taken. Measurements were made on 5.5  $\text{cm}^2$  of fully expanded undamaged leaf placed in the cuvette of an ADC LCA2 (Hoddesdon, England) portable infra red gas analyzer (IRGA). After each set of readings the light intensity was reduced by the erection of shade cloth and a 15 - 20 minute acclimation period was allowed before taking the next set of readings. The light was reduced in steps from 1600, 1200, 600, 200, 100 and 50  $\mu\text{mol/m}^2/\text{s}$ .

### Leaf nitrogen

I used 5 g of dried and ground leaf material to determine the nitrogen concentrations of tree and climber leaves over the collection range. The analyses were done using phenate Colorimetry (Nicholson 1984). For statistical purposes I transformed the data using the arcsine of the square root of the percentage N in the leaves and analysed using two way ANOVA to identify any differences in the N concentration between trees and climbers as well as between forests.



**Figure 1.** Map of the southern Africa showing the position of the forests sampled. MG = Mangusi forest, FB = False Bay forest, WF = Wesa forest, AX = Alexandria forest and KY = Knysna forest.

### Water use efficiency

The yield of a plant, a measure of its productivity, is negatively correlated with its water use efficiency (WUE) (Farquhar and Richards 1984; White *et al.* 1990). Thus if the WUE, defined as the ratio of dry matter produced to water lost from a leaf, is low, the plant will generally have a high productivity. Farquhar *et al.* (1982) developed the theory which predicts that for  $C_3$  plants, the isotopic ratio of  $^{13}C$  and  $^{12}C$  ( $\delta^{13}C$ ) in the leaves of the plants resulting from discrimination against the  $^{13}C$  stable isotope during photosynthesis (Craig 1954), will be lowest in the most water

use efficient plants. Recently this theory has been empirically verified (Hubick *et al.* 1986; Farquhar and Richards 1984).

I combusted ground leaf material (5 - 8 mg) of each tree and climber at 800 °C for six hours. The combustion was done in an evacuated quartz tube with one gram copper oxide, a few coils of copper shavings and a sliver of silver to catalyze the complete conversion of carbon into CO<sub>2</sub> (Sofer 1980). The carbon dioxide resulting from the combustion was separated from the nitrogen and water vapour by cryogenic distillation techniques (Sofer 1980). This entails initially releasing the gasses into a stainless steel line evacuated to 10<sup>-2</sup> Torr. The carbon dioxide and water vapour were then frozen into a glass trap with liquid nitrogen while the remaining nitrogen is pumped off. The trap is then immersed in a slurry of dry ice and ethanol which causes the carbon dioxide to boil off and the water vapour to remain frozen. Finally the carbon dioxide is trapped in a collecting tube with liquid nitrogen and is sealed off with a flame.

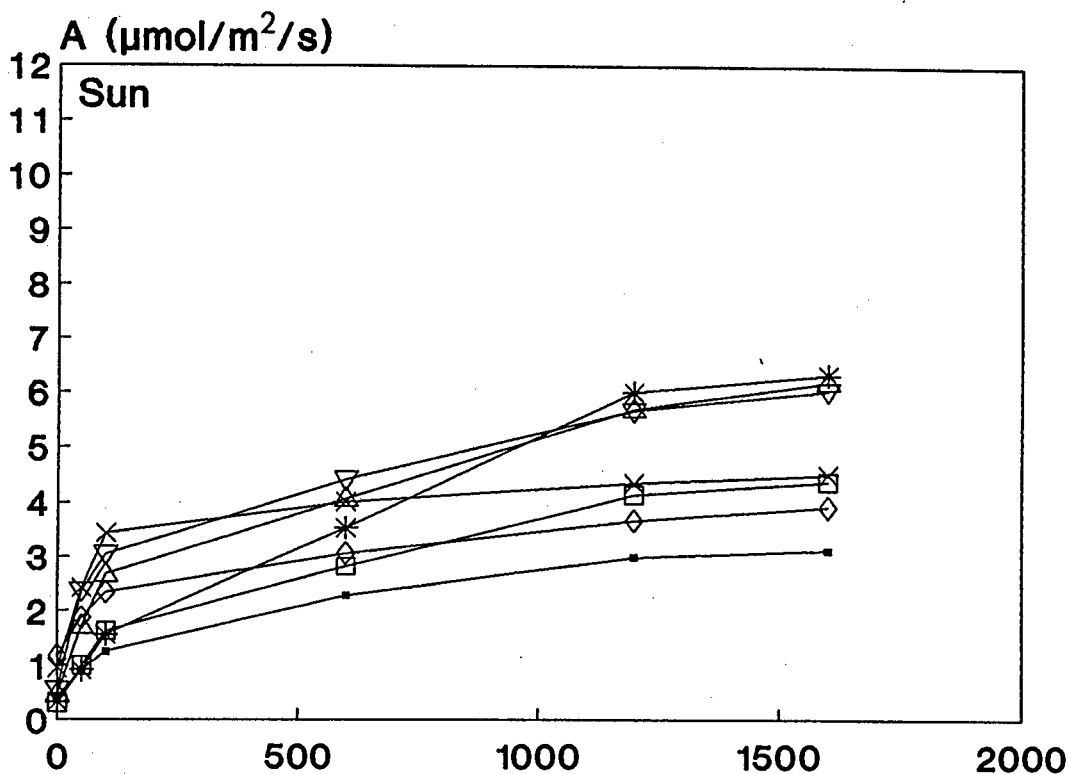
I analysed the carbon dioxide on a mass spectrometer (Micromass VG 602E) to determine the ratio of <sup>13</sup>C to <sup>12</sup>C and thus the δ<sup>13</sup>C value as described by Tieszen *et al.* (1987). The final δ<sup>13</sup>C values for the samples are expressed relative to the isotopic composition of the belemnite carbonate standard from Peedee (PDB), south Carolina (Craig 1957). As three replicate analyses of the δ<sup>13</sup>C ratio from one test leaf sample showed an error of less than 0.5 percent, I did not replicate subsequent sample measurements. I analysed the results statistically using two way Anova on log transformed data.

## Results

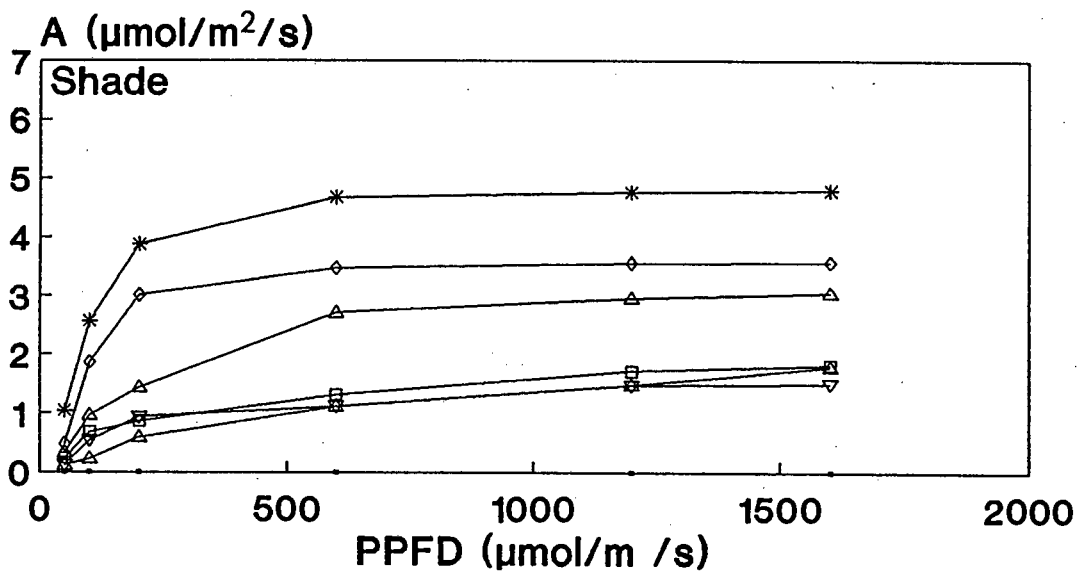
### Photosynthetic responses

Photosynthetic responses to PPFD differed for the trees and climbers grown in the shade and those grown in the sun (Fig. 2). For all sun grown plants photosynthesis was saturated at 1200 - 1600 μmol/m<sup>2</sup>/s (Fig. 2a) while shade grown plants were saturated at light intensities of 600 - 1200 μmol/m<sup>2</sup>/s (Fig. 2b).

A.



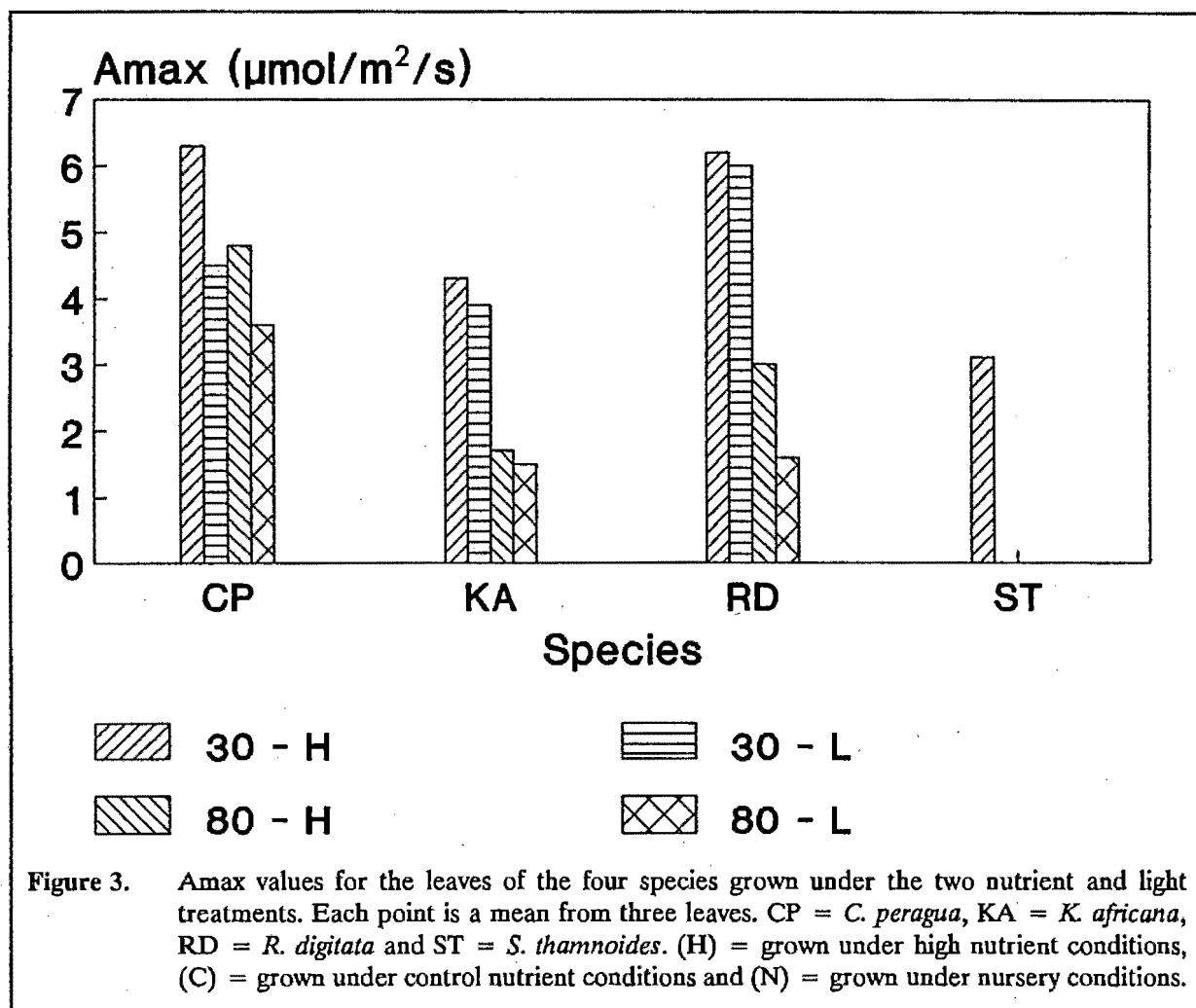
B.



\* CP (H)    □ KA (H)    ▲ RD (H)    ● ST (N)  
 ◇ CP (C)    ▽ KA (C)    △ RD (C)

**Figure 2.** Response curves of net photosynthetic carbon uptake (A) measured on leaves of the four species grown under the two nutrient treatments. A. Sun grown plants; B. Shade grown plants. Each point is a mean from three leaves. CP = *C. peragua*, KA = *K. africana*, RD = *R. digitata* and ST = *S. thamnoides*. (H) = grown under high nutrient conditions, (C) = grown under control nutrient conditions and (N) = grown under nursery conditions.

The maximum CO<sub>2</sub> assimilation rates (*A*<sub>max</sub>) for all the sun grown plants ranged between 3.1 and 6.3 μmol/m<sup>2</sup>/s (Fig. 3) while those of the shade grown plants ranged between 1.5 and 4.8 μmol/m<sup>2</sup>/s (Fig. 3). For all species, individuals grown in the high nutrient conditions had a higher *A*<sub>max</sub> than individuals grown under control nutrient conditions.



For the sun grown plants the canopy tree, *C. peragua* grown in the high nutrient treatment and the climber *R. digitata* grown in both the high and the control nutrient treatments, showed very similar maximum CO<sub>2</sub> assimilation rates of ± 6 μmol/m<sup>2</sup>/s. *S. thamnoides* had the lowest *A*<sub>max</sub> of 3 μmol/m<sup>2</sup>/s (Fig. 3). The percentage increase in *A*<sub>max</sub> between the low and the high nutrient treatments was greater for both *C. peragua* and *K. africana* than for *R. digitata* (Fig. 3).

For the shade grown plants, *C. peragua* grown under high nutrient conditions had the highest  $A_{max}$  rate ( $4.8 \mu\text{mol}/\text{m}^2/\text{s}$ ) while the climber *R. digitata* grown in the high nutrient treatment had an intermediate  $A_{max}$  rate ( $2.8 \mu\text{mol}/\text{m}^2/\text{s}$ ), similar to the  $A_{max}$  of *C. peragua* grown in control nutrient conditions (Fig. 3). *R. digitata* had low  $A_{max}$  rates for plants grown in the control treatment ( $1.6 \mu\text{mol}/\text{m}^2/\text{s}$ ), similar to those of *K. africana* of  $1.4 \mu\text{mol}/\text{m}^2/\text{s}$  for the control nutrient treatment and  $1.7 \mu\text{mol}/\text{m}^2/\text{s}$  for the high nutrient treatment (Fig. 3). The increase in  $A_{max}$  between the low and the high nutrient treatments was very similar for *C. peragua* and *R. digitata* and lower for *K. africana* (Fig. 3).

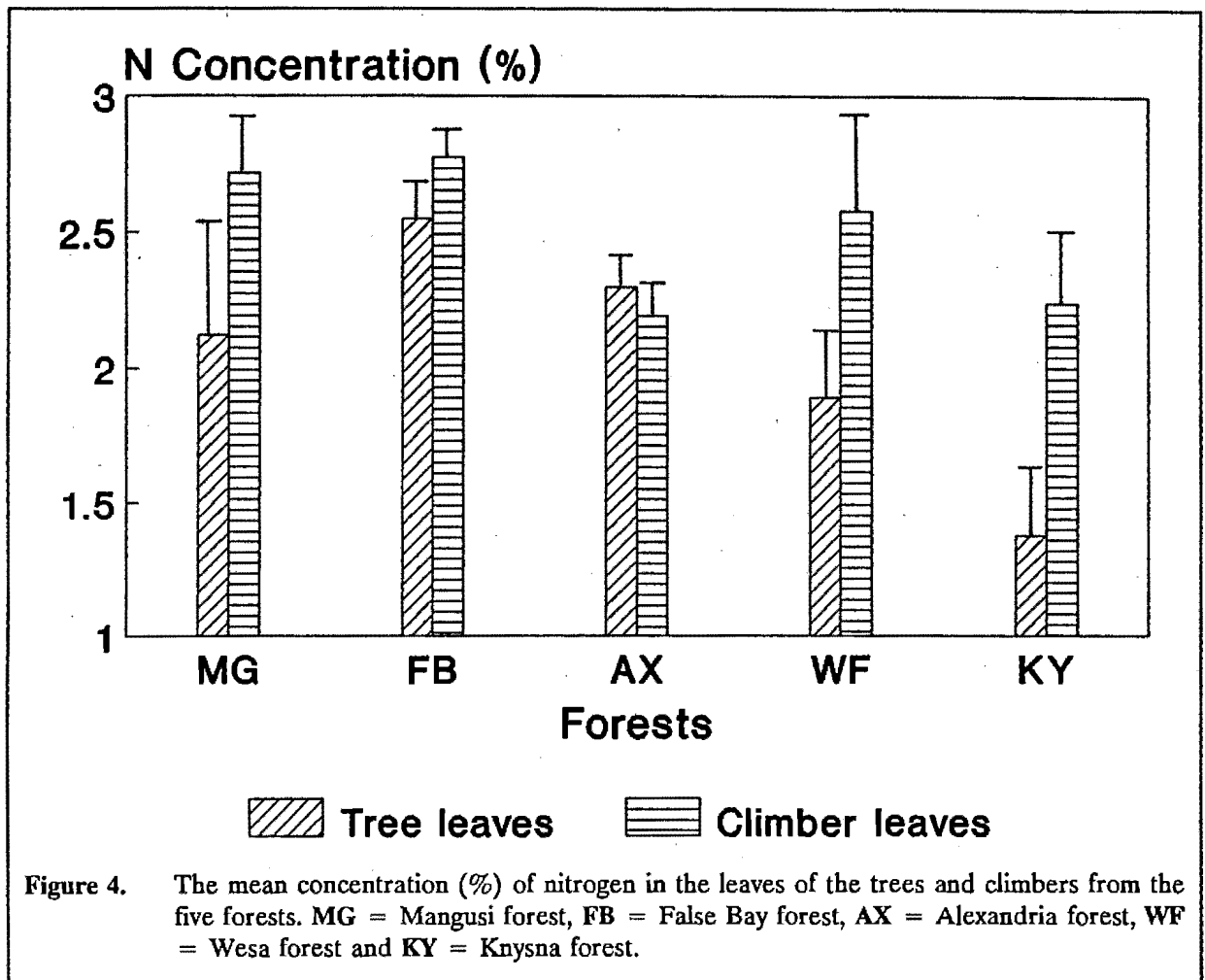
In both the sun and the shade conditions the mature forest tree *C. peragua* had a higher  $A_{max}$  than the climber *R. digitata* for both the high and the control nutrient treatments, while *R. digitata* had higher  $A_{max}$  readings than the pioneer tree *K. africana*. These results show no clear pattern of photosynthetic response between trees and climbers to the different light and nutrient conditions.

#### Leaf nitrogen

There was no significant difference between the nitrogen concentration in leaves of trees and climbers in each forest (Fig. 4). There was however a significant difference ( $p < 0.05$ ) (two way Anova on arcsine transformed data) (Table 1) between the mean leaf N concentration for climber and tree species grouped from all the forests ( $2.55 \pm 0.15 \%$  and  $2.02 \pm 0.14 \%$  respectively). There were no significant differences between forests and no interaction between forests and growth form. These results suggest that there may indeed be a difference in the photosynthetic capacity of trees and climbers.

Table 1. Anova table for two way analysis of arcsine transformed leaf nitrogen concentrations.

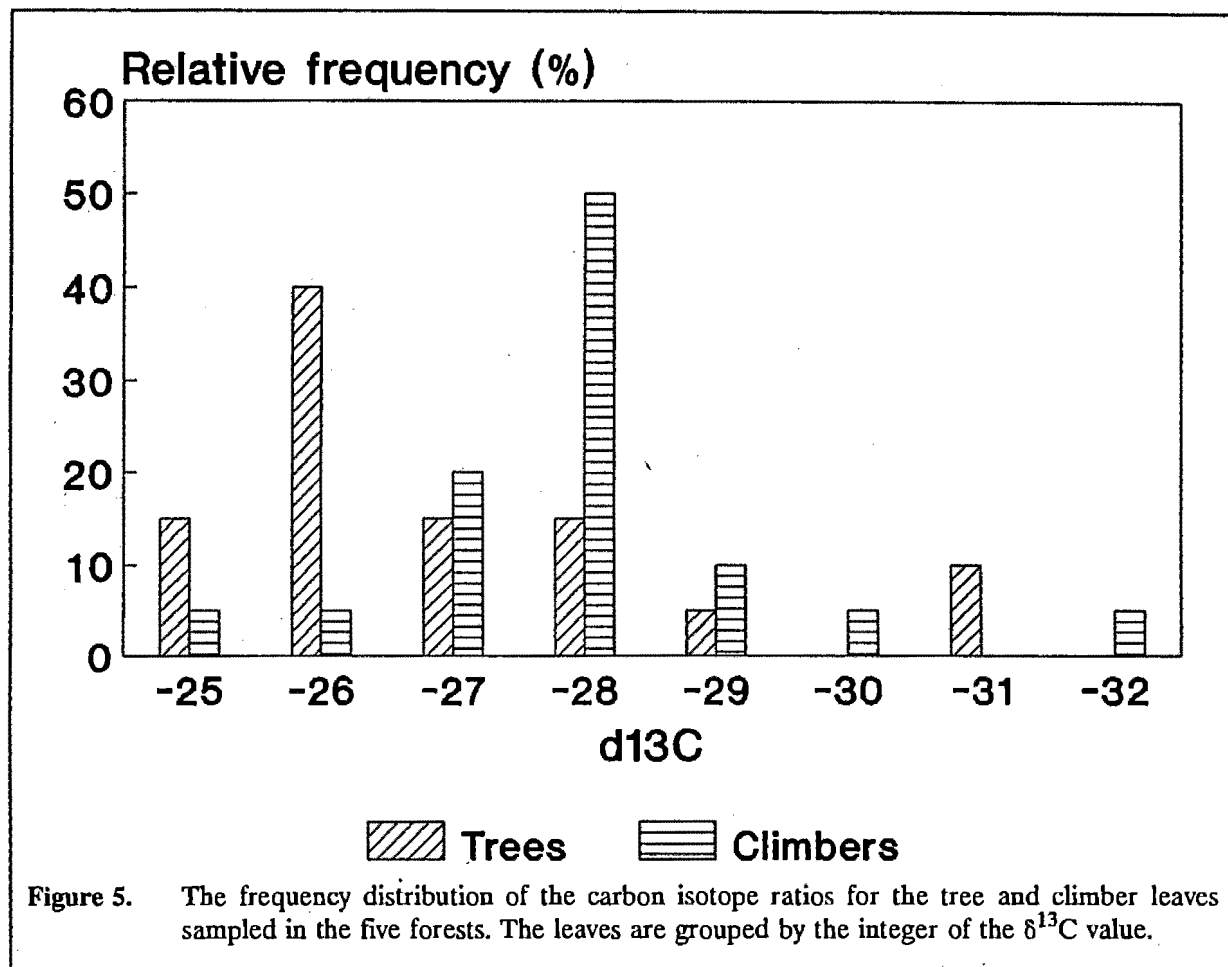
Source of variation	SS	d.f.	MS	F-ratio	p
Forests	0.00396	4	0.00099	2.072	0.1093
Growth form	0.00307	1	0.00307	6.428	0.0167
Interaction	0.00102	4	0.00025	0.535	0.7112



### Isotopic measurements

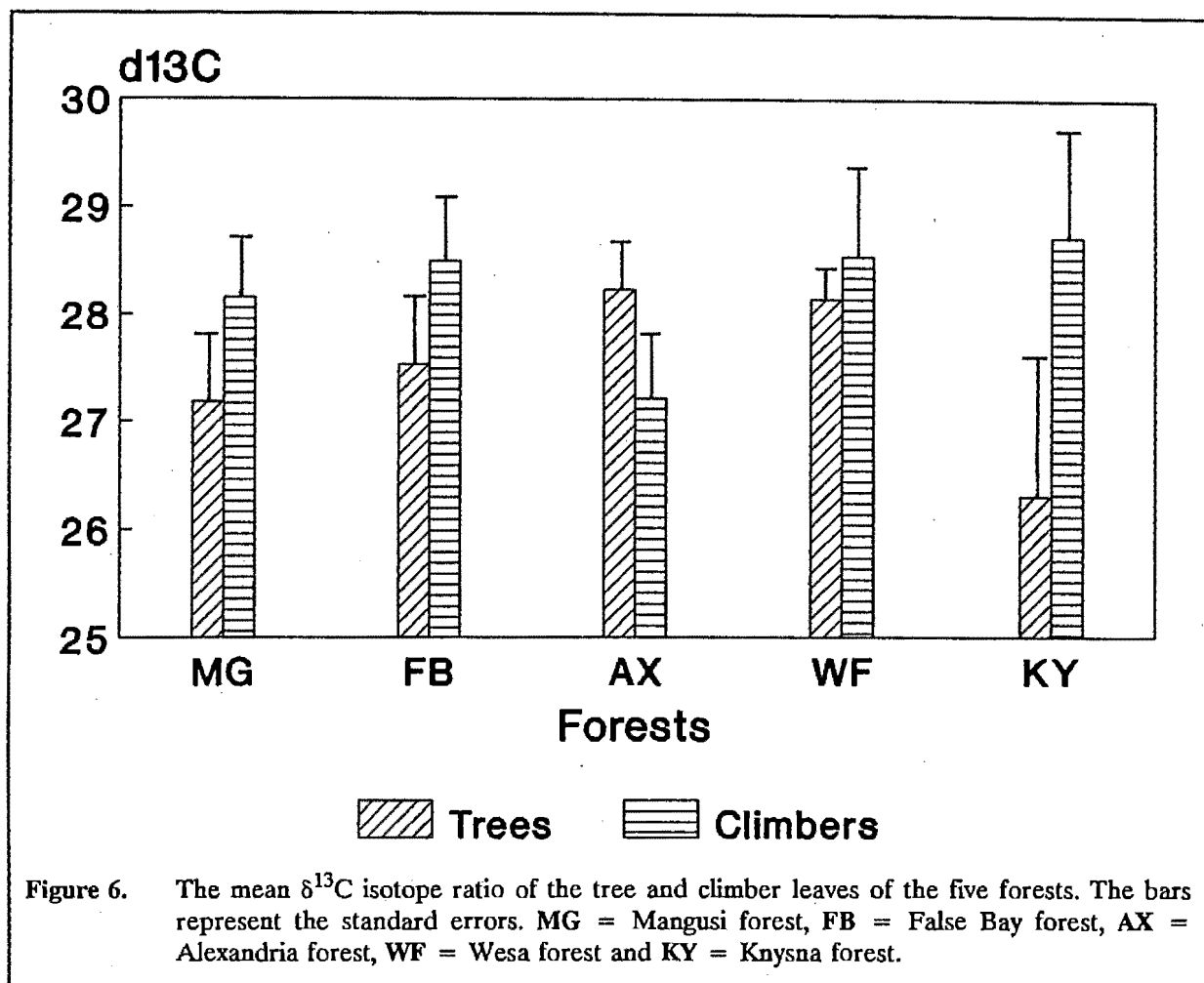
The measured leaf  $\delta^{13}\text{C}$  of trees covered a similar range (-25.47 to -31.23) to climbers (-25.28 to -32.24) (Fig. 5), although the two trees with  $\delta^{13}\text{C}$  values of -31 were both from Wesa forest and appear to be outliers. Within these ranges the mode of tree  $\delta^{13}\text{C}$  values at -26 indicates a tendency toward less discrimination against the  $^{13}\text{C}$  isotope than for climbers with a mode of -28 (Fig. 5).

There was no significant difference among the mean  $\delta^{13}\text{C}$  values for each forest (Anova)(Fig. 6). There was no significant difference between the mean  $\delta^{13}\text{C}$  value of tree ( $-27.49 \pm 0.37$ ) and climber ( $-28.32 \pm 0.33$ ) leaves from all the forests grouped (two way Anova,  $p < 0.1$ )(Table 2) although there was a trend with the climbers generally having more negative  $\delta^{13}\text{C}$  values than the trees, suggesting that the climbers are less water use efficient than the trees.



**Table 2.** Anova table for two way analysis of log transformed leaf  $\delta^{13}\text{C}$  values.

Source of variation	SS	d.f.	MS	F-ratio	p
Forest	0.00121	4	0.00030	0.502	0.734
Growth form	0.00180	1	0.00180	2.980	0.095
Interaction	0.00229	4	0.00006	0.946	0.451



## Discussion

Climbers generally have higher shoot extension rates than self supporting trees and shrubs (Putz 1984; see Chapter 3). I was interested to know if differences in the photosynthetic capacities between the two growth forms provide a physiological basis to explain growth differences or are they simply a function of differences in allocation. The results of this study show that, within a nutrient treatment, while the  $A_{max}$  of one of the climbers *R. digitata* was consistently greater than that of the pioneer tree *K. africana* it was also consistently lower than the later successional tree *C. peragua*. Further the climber *S. thamnoides* had the lowest  $A_{max}$  of all species. This lack of a clear pattern in the  $A_{max}$  values of the trees and climber suggests that the capacity to photosynthesize faster does not explain the differences in shoot extension growth rates between the two growth forms. This conclusion is supported by the results of Kriedemann and Smart (1971)

who found that the photosynthetic rates of the field vine *Vitis vinifera* L. were not inherently higher than those of other deciduous perennial shrubs.

Increased photosynthetic rates of plants grown under higher nutrient conditions have been documented (e.g. Thompson *et al.* 1988), while climbers have been associated with soils of higher nutrient status (Phillips 1931; Putz and Chai 1987; Grubb 1987). Implicit in the association is the idea that higher nutrient levels permit enhanced climber growth rates and confer a competitive edge to climbers over their host trees. However a causal relationship between climber abundance and soil nutrient status remains to be demonstrated (see Chapter Two). These results show that while the Amax of the climber *R. digitata* increased with increased nutrient availability the rate was still lower than that of the tree *C.peragua*. Further the percentage increase in the Amax of *R. digitata* in response to increased nutrients under high light conditions is less than that of *C.peragua*. This suggests that differences in maximum photosynthetic responses to increased nutrient levels are insufficient to explain the greater shoot extension rates recorded for this climber in Chapter Three.

The patterns of Amax readings of the two tree species are surprising considering the generally accepted idea that early successional plants have higher photosynthetic rates than later successional plants (Bazzaz and Pickett 1980; Medina 1986). The reasons for this are not clear but are possibly due to the plants having experienced sufficient stress to cause die back of the terminal shoots earlier in the year (see Chapter Three), and thus not accurately reflecting the nature of the growth forms under optimal conditions. The low levels of Amax recorded in the study are comparable with those of other sclerophyll leaves from southern Africa (Mooney *et al.* 1983).

The significant difference between the leaf nitrogen level of climber and tree species sampled from a number of forests (Fig. 4) suggests that climbers have the capacity to photosynthesise at a higher rate than trees. However the difference is small in magnitude and appears insufficient to be an important factor in explaining the faster shoot extension rates of climbers compared with trees. These results differs from those gained by the IRGA analysis of instantaneous photosynthesis, but because it reflects a more integrated measure as well as a number of species over a wide distribution this result probably carries more weight than those of the Amax readings. While the Amax readings represent an instantaneous measurement of the photosynthetic capacity of the trees and climbers under light saturated conditions the leaf nitrogen concentration provides a more integrated measure (see Field and Mooney 1986). The relationship between the leaf nitrogen

concentration and the  $A_{max}$  of  $C_3$  leaves is relatively insensitive to differences among species, their growth conditions and growth forms (Field and Mooney 1986, but see Evans 1989).

Finally the study shows climbers to have more negative  $\delta^{13}C$  values than trees, although the difference is not quite significant at the five percent level. Potential confounding effects due to sampling from different parts of the canopy (Ehleringer *et al.* 1987) have been minimised and the altitudinal effects are probably minimal (Körner *et al.* 1986), so that the differences between trees and climbers reflect real differences in water use efficiency. In a study covering many growth forms Ehleringer *et al.* (1987) found woody climbers to have a mean  $\delta^{13}C$  value of -31.22, which differs from trees with a value of -31.08. A lower water use efficiency for climbers would imply that they are inherently more productive than trees (Farquhar and Richards 1984), a result that supports the higher leaf nitrogen levels found in climbers compared with trees.

## Conclusions

Both the leaf nitrogen concentrations and the leaf  $\delta^{13}C$  ratios suggest that there are differences in the photosynthetic capacities of trees versus climbers. However the  $A_{max}$  readings recorded for trees and climbers grown under different light and nutrient conditions do not support this finding. This can possibly be explained by the photosynthetic rates recorded in this study being a result of the past history of the plants rather than reflecting the inherent properties of the growth forms.

The differences between the growth forms in foliar nitrogen concentration and  $\delta^{13}C$  are small, and there are probably other factors involved in the rapid shoot extension rates of climbers compared to trees. The most important of these must include differences in the allocation of carbon to shoot extension growth rather than to support structures as seen in Chapter Three, but could also include more complex factors such as branching patterns (Kuppers 1985) and factors such as seasonal variation in photosynthetic response to light as well as the length of the growing season (Kuppers 1984; Carter *et al.* 1989) and the ability to control leaf orientation (Forseth and Teramura 1987). More detailed studies of these factors will contribute greatly to our understanding of the ecology of climbers.

## References

- Bazzaz FA and Pickett STA. 1980. Physiological ecology of tropical succession: a comparative review. *Ann. Rev. Ecol. Syst.* 11:287-310.
- Carter GA and Teramura AH. 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understory. *Amer. J. Bot.* 75(7):1011-1018.
- Carter GA, Teramura AH and Forseth IN. 1989. Photosynthesis in an open field for exotic versus native vines of the southeastern United States. *Can. J. Bot.* 67:443-446.
- Chapin FS. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11:233-260.
- Craig H. 1954. Carbon-13 in plants and the relationships between carbon-13 and carbon-14 variations in nature. *J. Geol.* 62:115-149.
- Craig H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Acta* 12:133-149.
- Darwin C. 1867. On the movements and habits of climbing plants. *Journal of the Linnaean Society (Botany)* 9:1-118.
- Ehleringer JR, Lin ZF, Field CB, Sun GC and CY Kuo. 1987. Leaf carbon isotope ratios of plants from a subtropical monsoon forest. *Oecologia* 72:109-114.
- Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* 78:9-19.
- Farquhar GD, O'Leary MH and Berry JA. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Aust. J. Plant Physiol.* 9:121-137.
- Farquhar GD and Richards RA. 1984. Isotopic composition of plant carbon correlates with water use efficiency of wheat genotypes. *Aust. J. Plant Physiol.* 11:539-552.
- Field C and Mooney HA. 1986. The photosynthesis-nitrogen relationship in wild plants. In: *On the economy of plant form and function*. Ed. T Givnish. Cambridge University Press Cambridge.
- Forseth IN and Teramura AH. 1987. Field photosynthesis, microclimate and water relations of an exotic temperate liana, *Pueraria lobata*, kudzu. *Oecologia* 71:262-267.
- Givnish TJ and Vermeij GJ. 1976. Sizes and shapes of liana leaves. *Am. Nat.* 110:743-778.
- Givnish TJ. 1986. Economics of support. In: Givnish TJ (Ed) 'On the economy of plant form and function'. Cambridge University Press, Cambridge. pp 413-420.
- Grubb PJ. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. In: Gee JHR and Giller PS (Eds.) *Organization of Communities - past and present*. Blackwell Scientific Publications, Oxford.

- Halle F, Oldeman RAA and Tomlinson PB. 1978. Tropical trees and forests: An architectural analysis. Springer-Verlag, Hiedelberg, Germany.
- Hubick KT, Farquhar GD and Shorter R. 1986. Correlations between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. *Aust. J. Plant Physiol.* 13:803-816.
- Korner Ch, Bannister P and Mark AF. 1986. Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia* 69:577-588.
- Kriedemann PE, Smart RE. 1971. Effects of irradiance, temperature, and leaf water potential on photosynthesis of vine leaves. *Photosynthetica* 5(1):6-15.
- Kuppers M. 1984. Carbon relations and competition between woody species in a central European hedgerow. 1. Photosynthetic characteristics. *Oecologia* 64:332-243.
- Kuppers M. 1985. Carbon relations and competition between woody species in a central european hedgerow. IV. Growth form and partitioning. *Oecologia* 66:343-352.
- Medina E. 1986. Forests, savannas and montane tropical environments. In: *Photosynthesis in contrasting environments*. Eds. Baker NR and Long SP. Elsevier Science Publishers.
- Mooney HA and Gulmon SL. 1982. Constraints on leaf structure and function in reference to herbivory. *Bioscience* 32:198-206.
- Mooney HA, Field C, Gulmon SL, Rundel P and Kruger FJ. 1983. Photosynthetic characteristic of South African sclerophylls. *Oecologia* 53:398-401.
- Nicholson G. 1984. Methods of soil, plant and water analysis. FRI Bulletin No. 70, Forest Service, Rotorua New Zealand.
- Phillips JF. 1931. Forest succession and ecology in the Knysna region. *Memoirs of the botanical survey of South Africa* No.14.
- Proctor J, Anderson JM, Chai P and Vallack HW. 1983. Ecological studies in four contrasting lowland rainforests in Gunung Mulu National Park, Sarawak. *J. Ecol.* 71:237-260.
- Putz FE. 1983. Liana biomass and leaf area of a "Tierra firme" forest in the Rio Negro Basin, Venezuela. *Biotropica* 15:185-189.
- Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6):1713-1724.
- Putz FE and Chai P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *J. Ecol.* 75:523-531.
- Putz FE and Windsor DM. 1987. Liana phenology on Barro Colorado Island, Panama. *Biotropica* 19:334-341.
- Richards PW. 1952. *The tropical rain forest*. Cambridge University Press. Cambridge.

Schulze E-D. 1982. Plant life forms and their carbon, water and nutrient relations. Encyclopedia of plant physiology, NS Vol 12B. Springer Verlag, Berlin.

Smith GS, Johnston CM and Cornforth IS. 1983. Comparison of nutrient solutions for growth of plants in sand culture. *New Phytol.* 94:537-548.

Thompson WA, Stocker GC and Kriedemann PE. 1988. Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F.Muell., a rainforest tree with broad tolerance to sun and shade. *Aust. J. Plant Physiol.* 15:299-315.

Tieszen LL, Hein D, Qvotrup SH, Troughton JH and Imbamba SK. 1979. Use of  $\delta^{13}\text{C}$  values to determine vegetation selectivity in east African herbivores. *Oecologia (Berlin)* 37:351-359.

Van Daalen JC. 1984. Distinguishing features of forest species on nutrient-poor soils in the southern Cape. *Bothalia* 15(1&2):229-239.

White JW, Castillo JA and Ehleringer J. 1990. Associations between productivity, root growth and carbon isotope discrimination in *Phaseolus vulgaris* under water deficit. *Aust. J. Plant Physiol.* 17:189-198.

## Chapter Five

### **The impact of climbers on forest regeneration: Or do climbers inhibit forest regrowth?**

#### **Introduction**

The evergreen forests of southern Africa have been broadly categorised into two biogeographical groups, the upland Afromontane forests and the lowland Tongaland/Pondoland forests (White 1983; White and Moll 1978). The highland forests experience a cooler, more moist climate than the warmer and drier conditions of the lowland forests (Geldenhuys 1989). The soil substrate of sedimentary rock (Meadows and Linder 1989) with a low nutrient status in the highland forests differs from that of the lowland forests which is derived from uplifted sands and dunes (Moll 1980) and is more nutrient rich (see MacDevette 1989; Marker and Russell 1984). Does this grouping, based on floristic differences, reflect only the individual species response to climate and soil differences, past species migrations and shared histories or are there differences in the dynamics and the regeneration conditions (Grubb 1977) that may underlie the compositional shifts between the groups?

Forest dynamics and the regeneration of mature forest canopy trees by new growth has long interested forest ecologists (Phillips 1931; Watt 1947; Richards 1952; Whitmore 1982). The initial focus on the replacement patterns of trees after large scale disturbance of a forest (eg. Veblen 1979) has, in the last two decades, been replaced by an interest in the effects of smaller scale disturbances, in particular gaps in the forest canopy due to tree falls (Hartshorn 1978; Runkle 1985; Denslow 1987).

Many studies have been concerned with the description and quantification of the regeneration of mature forest trees and the successional pathways that are followed, after the formation of a treefall gap (see Phillips 1931; Swaine, Lieberman and Putz 1987). These studies include work on biotic factors such as seed bank dynamics (Schupp 1988), seed germination (Garwood 1983),

and seedling (Turner and Newton 1990) and sapling dynamics (Lang and Knight 1983). Other studies have concentrated on changes in environmental factors such as the increase in light intensity (Canham 1988a), the increase in air and soil temperatures (Denslow 1980) the increase in nutrient availability in larger gaps (Denslow 1987), and the effect that these changes have on the species composition and structure of the regenerating forest.

The most dramatic, and possibly the most important change that occurs when a gap forms in the canopy, is the change in the light intensity (Canham 1988a). The importance of the response of forest plants to light has led Swaine and Whitmore (1988) to suggest that two guilds, based on the plants light response, be named i.e. pioneer (shade intolerant) and climax (shade tolerant) guilds. Much of the literature on forest regeneration is concerned with the competitive interactions and differential survival of different light response guilds to different gap formation processes, gap frequencies and gap sizes (see Denslow 1987 for review), and how these interactions may influence community composition of a forest (Brokaw 1985; Connell 1989). Gaps in the forest canopy have become widely accepted as being important for the regeneration of canopy species (Whitmore 1989).

Different plants growing to different heights within a forest result in a layered structure developing between the ground and the canopy (Richards 1952; Smith 1973). Little work has been done on the interaction between the understory and the overstory and the effects that these interactions may have on the regeneration of canopy tree species. The inhibitory effects of shading by individual vegetation layers, for example the understory layer (Veblen 1979) and the lateral growth of the gap edge branches (Hibbs 1982), on regenerating individuals have been considered. However the influence of different layers within the same forest on the regenerating canopy tree species has not been studied. The impact of climbers on the regeneration of canopy trees in treefall gaps has been mentioned (Phillips 1931; Kochummen 1966; Putz 1984), but not quantified.

The treefall gap as a homogeneous entity has been challenged (Hallé *et al.* 1978), and differences in the distribution of species within treefall gap microsites have been shown (Brandani *et al.* 1988; Putz 1983). The orientation of the gap appears to effect the regeneration processes (Poulson and Platt 1989). These demonstrations suggest that gaps are not rigid entities which influence forests regeneration in set ways. There have been recent challenges of the universal validity of viewing

a forest as a series of gaps in an otherwise complete canopy, for understanding forests dynamics (the gap/non-gap paradigm) (Canham 1988b; Lieberman *et al.* 1989; Midgley *et al.* 1990). For the present study, however, the dichotomy is found to be a useful tool in investigating the differences in dynamics between the highland and the lowland forests.

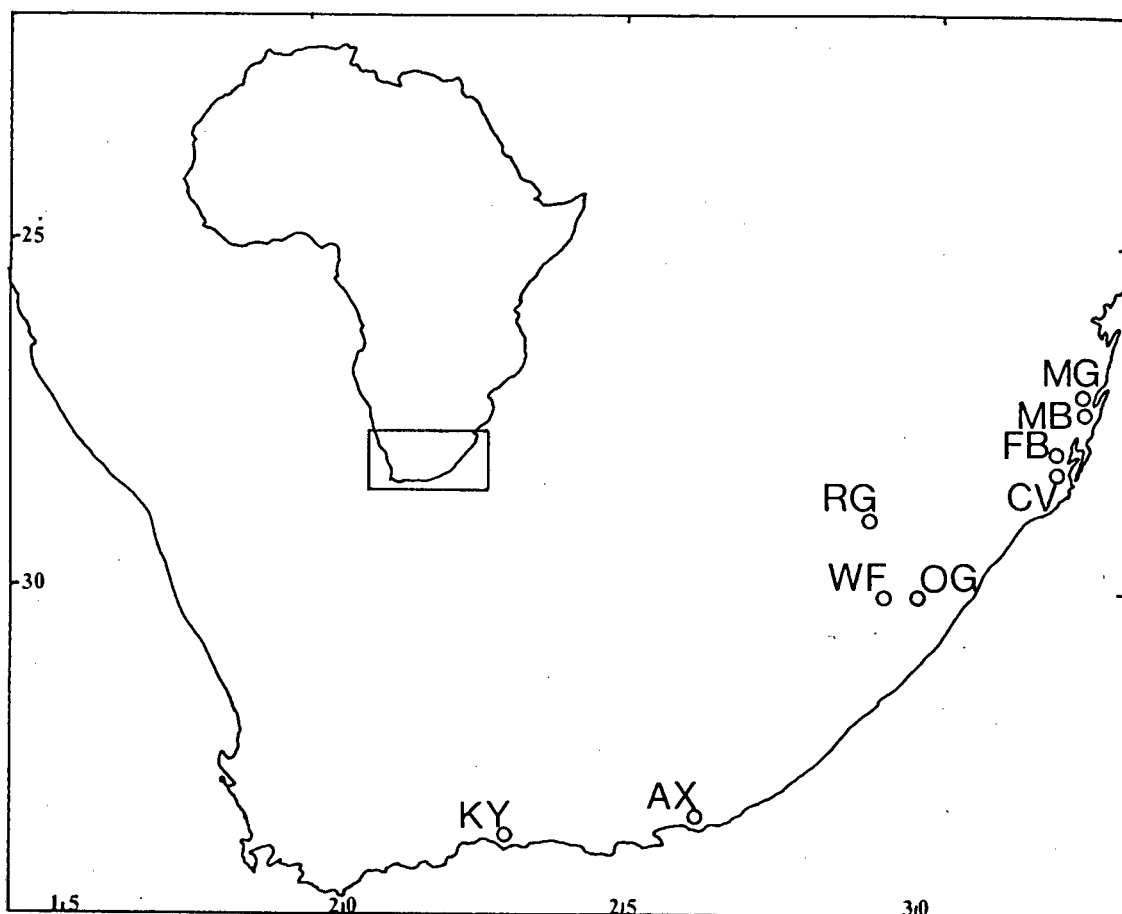
Little has been done on the dynamics of the forests of southern Africa. In the southern Cape, Phillips (1931) investigated broad forest succession, Geldenhuys and Maliepaard (1983) have examined the causes and nature of gaps, and Midgley *et al.* (1990) have looked at shade tolerance and species distribution patterns. A number of studies describe and discuss aspects of the successional dynamics of the forests of the Natal coastal belt (Huntley 1965; Breen 1971; Moll 1972; Weisser and Marques 1979; Moll 1980; Ward 1980). Understanding of the processes driving the regeneration dynamics of these forests is, however, weak.

In this study I attempt to quantify the regeneration dynamics of a number of highland and lowland forests by comparing the regeneration of canopy species in gaps and non-gaps. I aim to determine whether any differences in the regeneration dynamics between upland and lowland forests can be detected and whether these can be attributed to the shading effects of different vegetation layers within the forests.

### **Study area**

I selected nine forests from the mixed evergreen forests of Natal and the southern and eastern Cape (Fig. 1). Rainbow Gorge, Wesa forest and Knysna forest represent a range of Afromontane forests of the highlands and Mist Belt of Natal and the southern Cape (White 1978). Mangusi, Mabibi, False Bay and Cape Vidal represent lowland forests of the Tongaland/Pondoland region (White and Moll 1978); (for a detailed report of the indigenous forests of Natal see Gordon (1989)). Oribi Gorge and Alexandria Forest do not fit neatly into the Afro-Montane or the Indian Ocean Coastal Belt phytochoria and can be considered to be transition (or linking) forests between the above two groupings (Phillipson and Russell 1988; Cooper 1985) (see Table 1). Although there are floristic links between the Afromontane and the Tongaland/Pondoland forests there are structural differences (particularly in the number of climbers) between the two regions and the

growth rates are generally higher in the Tongaland/ Pondoland forests (White and Moll 1978). While the majority of forest patches in southern Africa cover less than 1 km<sup>2</sup> (Geldenhuys 1989), the forests chosen for this study were all sufficiently large to enable edge effects to be avoided.



**Figure 1.** Map of southern African showing the location of the forests. MG = Mangusi forest, MB = Mabibi forest, FB = False bay forest, CV = Cape Vidal forest, RG = Rainbow Gorge forest, WF = Wesa forest, OG = Oribi Gorge forest, AX = Alexandria forest and KY = Knysna forest.

**Table 1.** The forests that were surveyed in this study, their abbreviations in brackets, the number of gap and sub-canopy plots surveyed in each forest, their elevation above mean sea level and their phytogeographical affinities. T/P = Tongaland Pondoland Forest.

Forest	Plot Number	Elevation	Affinity
Mangusi (MG)	10	< 100 m	T/P (Lowland)
Mabibi (MB)	9	< 100 m	T/P (Lowland)
False Bay (FB)	6	< 100 m	T/P (Lowland)
Cape Vidal (CV)	6	< 100 m	T/P (Lowland)
Alexandria (AX)	6	200 m	Transition (linking)
Oribi Gorge (OG)	6	400 m	Transition (linking)
Rainbow Gorge (RG)	10	2000 m	Afromontane (Highland)
Wesa Forest (WF)	6	750 m	Afromontane (Highland)
Knysna (KY)	5	250 m	Afromontane (Highland)

## Methods

Field surveys were carried out between April and June 1990. Although in Natal closed canopy woody communities greater than five meters high are often classified as forest (MacDevette *et al.* 1989), I restricted all sampling to forest with a canopy at least ten meters high.

To establish where the canopy species were regenerating and to assess the structural attributes of the forest, I surveyed between five and ten gaps and neighbouring sub-canopy plots within each forest (Table 1). I defined a gap as an opening in the canopy where there was evidence of at least one fallen tree. In each case the gaps were situated well away from the forest margin. Sub-canopy plots, defined as plots below intact forest canopy, were sited in a random direction from the centre of the gap and initiated five meters from the base of a gap edge tree so as to avoid the influence of the gap light conditions on the sub-canopy vegetation (Canham 1988a). The sub-canopy plots were of the same area and dimensions as the adjacent canopy gap.

To determine the regeneration patterns of the different forests I recorded the presence of each seedling having a height of 1 - 2m; each sapling between 2 and 5 m tall; and all sub-canopy trees greater than 5 m in height but not yet in the canopy, in the gap and sub-canopy plots. In the context of the results of this study the words seedling, sapling and sub-canopy tree refer to the size classes indicated above.

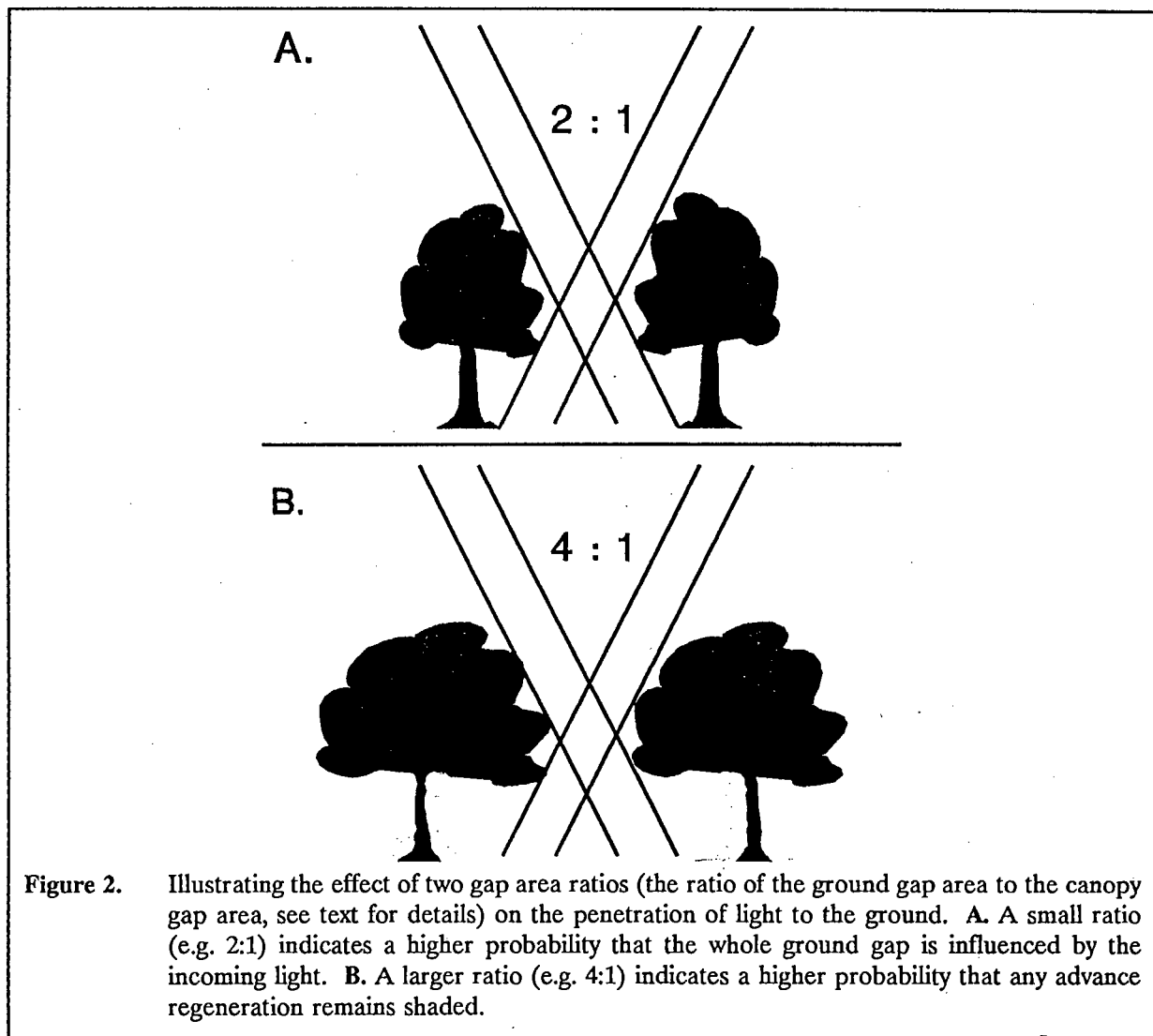
I classified the regenerating trees into canopy species (species that frequently attained the canopy) and sub-canopy species (those that seldom or never reached the canopy). This classification was not entirely consistent for all forests as in a few cases the same species would occupy the canopy in one forest but remain in the sub-canopy in other forests. Species were thus classified according to the dominant position that they took in the forest under consideration.

For each gap the length and breadth of the canopy gap (i.e. the gap created in the canopy of the forest (see Brokaw 1982) and the ground gap (i.e. the distance to the base of the gap forming trees (see Runkle 1982) was recorded. Gap areas were calculated using the formula for the area of an ellipse ( $\text{Area} = \pi * \text{length} * \text{breadth} / 4$ ).

I used the lateral growth of branches into a canopy gap as a measure of the shading effect of the canopy on the gap. The extent of the lateral infill of the canopy trees surrounding a gap was calculated as the mean width of the doughnut shape resulting after the canopy gap area has been subtracted from the ground gap area. To minimise the effect of tree size the ratio of the ground gap area to the canopy gap area (gap area ratio) was used as an index of canopy infill that is comparable between forests (Fig. 2). Unless otherwise stated in the text I use the word "gap" to refer to a canopy gap.

I measured the shading effect of the understory layer (0.5 - 3.5 m) on newly germinated seedlings by establishing a foliage density profile (MacArthur and MacArthur 1961) for each gap and sub-canopy plot (except for those at Rainbow Gorge and three plots at Mabibi where these measures were not made). Eight alternate readings were taken to the left and the right of a transect along the mid-line of the long axis of the plot. Each reading consisted of recording the distance from the transect line at which half of a 10 cm by 10 cm white board was obscured from vision by the intervening vegetation (vision distance). At each of the eight points readings were taken at 0.5 meter height intervals from ground level to the height of the undergrowth (maximum of 3,5 m) or at least to a height of two meters. Where the forest was very open and readings were greater

than ten meters I recorded the vision distance as ten meters. The inverse of the vision distances at each height were calculated and joined using a best fit line. The integral of the best fit line was used as a measure of foliage density. A foliage density index for each plot was calculated as the mean area of the eight reading points.



**Figure 2.** Illustrating the effect of two gap area ratios (the ratio of the ground gap area to the canopy gap area, see text for details) on the penetration of light to the ground. **A.** A small ratio (e.g. 2:1) indicates a higher probability that the whole ground gap is influenced by the incoming light. **B.** A larger ratio (e.g. 4:1) indicates a higher probability that any advance regeneration remains shaded.

Ground cover was recorded in each plot as a measure of the shade environment of germinating and newly establishing seedlings. Ground cover categories comprised grasses and ferns, seedlings of herbaceous Acanthaceae species e.g. *Isoglossa woodii*, fallen liana (woody climber) mats and bare ground. Cover values were recorded only for individuals less than 30 cm in height.

I recorded the presence of woody climbers for each plot. Lianas were classified into small (< 1 cm); medium (1 - 2 cm) and large (2 - 5 cm) size classes. Abundance ratings of 1 - 10 (5); 11 - 20 (15); or 21 - 50 (35) were made. The figure in brackets is the weighting given to each abundance group in the results. The presence of liana curtains was noted.

## Results

### Regeneration Dynamics

The percentage of canopy species regenerating in the highland forests was two times higher than in the lowland forests, both in the gaps and the sub-canopy plots; 51% and 56% for the highland and 29% and 25% for the lowland gaps and sub-canopy plots, respectively (Table 2). The highest mean number of seedlings of a canopy species regenerating in any of the forests was 8.3 individuals from the gap plots in the False Bay forest while the lowest is zero for the Cape Vidal forest (Table 2). There were no significant differences between the number of canopy seedlings, saplings or sub-canopy trees regenerating in the gap and the sub-canopy plots for any of the forests (Table 2).

For the forests grouped into highland and lowland forests, excluding the transitional forests, there were no significant differences between the number of canopy seedlings, saplings or sub-canopy trees in the gap and the sub-canopy plots for the highland or the lowland forests. However, for each of the size classes there was a clear trend with the lowland forests having more canopy individuals regenerating in the gaps than in the sub-canopy plots while in the highland forests more canopy individuals regenerated in the sub-canopy plots than in the gaps (Table 3).

For the grouped data there were significantly fewer ( $p < 0.001$ ) (Anova) seedlings (1 - 2 m) of canopy species, regenerating in the sub-canopy of the lowland forests ( $1.7 \pm 0.4$ ) than in the sub-canopy of the highland forests ( $7.2 \pm 1.7$ ) (Table 3). There were also significantly fewer sub-canopy trees of canopy species regenerating in the sub-canopy plots of the lowland forests ( $1.4 \pm 0.3$ ) than in the highland forests ( $3.2 \pm 0.7$ ) ( $p < 0.05$ ). This trend is not apparent for the saplings (2 - 5 m). There were no differences in canopy species regenerating between the gaps of the lowland and highland forests, in any of the three size classes (Table 3).

**Table 2.** The mean number of seedlings (1-2 m), saplings (2-5 m) and sub canopy trees (>5 m but not in the canopy) in each of the forests ( $\pm$  SE) for the gap and sub-canopy plots (S-C), and the percentage of the total stems that are canopy species in each class.

Size Class	Forest								
	Lowland				Transition		Highland		
	MG	MB	FB	CV	AX	OG	RG	WF	KY
<b>1-2 Gap</b>	1.7	1.2	8.3	0.0	2.7	1.5	4.2	5.3	5.2
<b>SE</b>	1.2	0.7	4.2	0.0	1.0	0.2	2.1	2.0	3.9
<b>%</b>	19	21	53	0	33	24	49	40	63
<b>1-2 S-C</b>	2.9	1.2	1.7	0.2	2.7	2.8	9.6	7.0	5.2
<b>SE</b>	1.3	1.0	0.8	0.2	1.2	1.0	3.7	1.9	3.7
<b>%</b>	33	15	52	2	25	40	62	56	72
<b>2-5 Gap</b>	5.4	4.7	3.8	0.7	0.0	2.0	4.7	2.3	1.2
<b>SE</b>	2.7	2.0	2.7	0.3	0.0	0.6	1.2	0.8	0.6
<b>%</b>	43	33	44	8	0	29	60	21	30
<b>2-5 S-C</b>	6.6	2.0	1.2	4.2	1.3	3.5	4.8	2.0	2.4
<b>SE</b>	2.1	0.6	0.5	1.5	0.8	1.6	1.5	0.8	1.2
<b>%</b>	52	15	26	24	21	29	59	11	75
<b>&gt;5 Gap</b>	2.3	1.0	0.8	0.2	4.3	1.0	2.1	1.5	2.8
<b>SE</b>	1.0	0.6	0.3	0.8	1.4	0.5	0.7	0.6	1.0
<b>%</b>	57	56	30	4	86	44	81	35	78
<b>&gt;5 S-C</b>	2.0	0.8	0.5	2.3	2.2	2.7	4.0	2.3	3.4
<b>SE</b>	0.6	0.3	0.3	1.1	0.7	1.3	0.9	1.2	1.4
<b>%</b>	40	15	10	25	40	33	80	24	74

**Table 3.** The mean number of canopy species individuals ( $\pm$  SE), regenerating in the different size classes, for the gaps and the sub-canopy plots (S-C) of lowland and highland forests. Lowland includes Mangusi, Mabibi, False Bay and Cape Vidal forests; Highland includes Rainbow Gorge, Wesa and Knysna forests.

Size Class		Highland	Lowland
1-2 m	Gap	4.8 $\pm$ 1.4	3.5 $\pm$ 1.4
	S-C	7.2 $\pm$ 1.7	1.7 $\pm$ 0.4
2-5 m	Gap	3.0 $\pm$ 0.6	5.8 $\pm$ 1.2
	S-C	3.2 $\pm$ 0.6	3.3 $\pm$ 1.0
> 5 m	Gap	2.1 $\pm$ 0.4	1.8 $\pm$ 0.4
	S-C	3.2 $\pm$ 0.7	1.4 $\pm$ 0.3

There appears to be a consistent self thinning effect shown by the reduction in the number of individuals with increasing size classes in both the gaps and the sub-canopy plots in the highland forest (Table 3), while there is no clear pattern for the lowland forests.

The highland forests had a consistently higher percentage of canopy seedlings regenerating in both the gaps and the sub-canopy (Fig. 3a) than the lowland forests where there was great variability in the regeneration patterns. No clear pattern is evident for the larger size classes although the differences between the lowland and the highland forests become less clear (Fig. 3b,c). These results suggest that there is greater predictability in the regeneration of the highland forests while the lowland forests have episodic regeneration.

## Structure

### Ground cover

Newly germinated seedlings may be excluded by competitive interactions with the ground layer of a forest. However in the present study there was a high percentage of bare ground recorded in all the forests. The ground cover for the gap and sub-canopy plots in all of the forests was less than 30% except in Wesa Forest (67% in gap; 69% in U/S) and Rainbow Gorge (58% in gap; 35% in U/S) (Table 4). There was significantly more grass and fern cover in the gaps of the highland forests than in the gaps of the transitional and lowland forests ( $p < 0.05$ ). The Acanthaceous layer (often largely comprising *Isoglossa woodii*) never occupied more than 30% of the cover at this level. Liana mats, were only found in the gaps and were more common in the highland forests (Table 4), however they provide very little of the cover, being greatest at Alexandria (12%), and were absent in most forests. The cover values shown in Table 4 do not always total 100% as other categories such as the presence of boulders and treefall logs have not been included in the table although they always represented less than ten percent of the cover. These results suggest that the influence of the ground layer on germinated seedlings is probably slight.

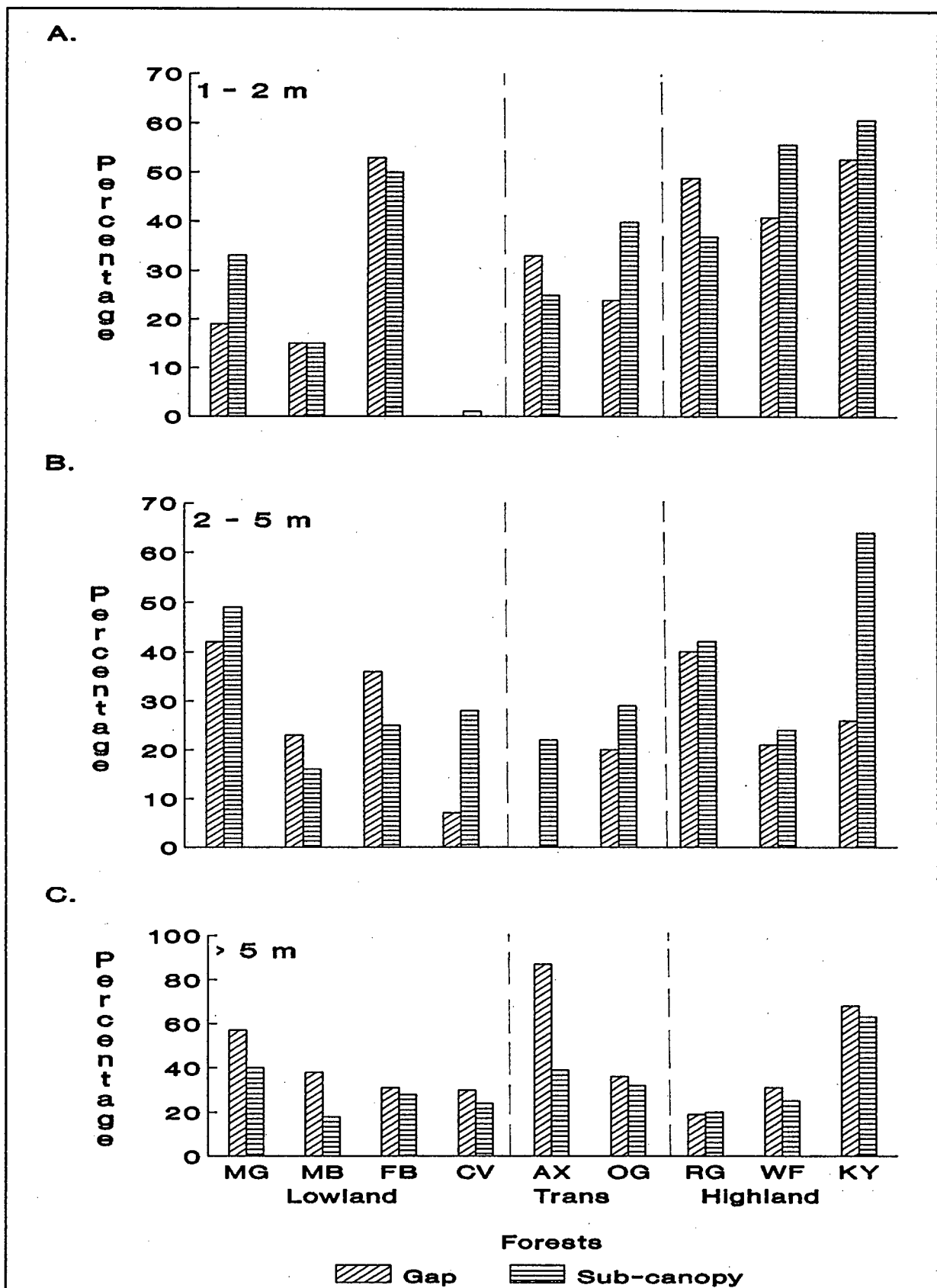


Figure 3.

The percentage of the regenerating individuals that are canopy species in the gap and the sub-canopy plots of each forest. A. Seedlings, B. saplings and C. sub-canopy trees.

**Table 4.** The composition and mean percentage of the ground cover in the gap and sub-canopy (S-C) plots for all of the forests surveyed.

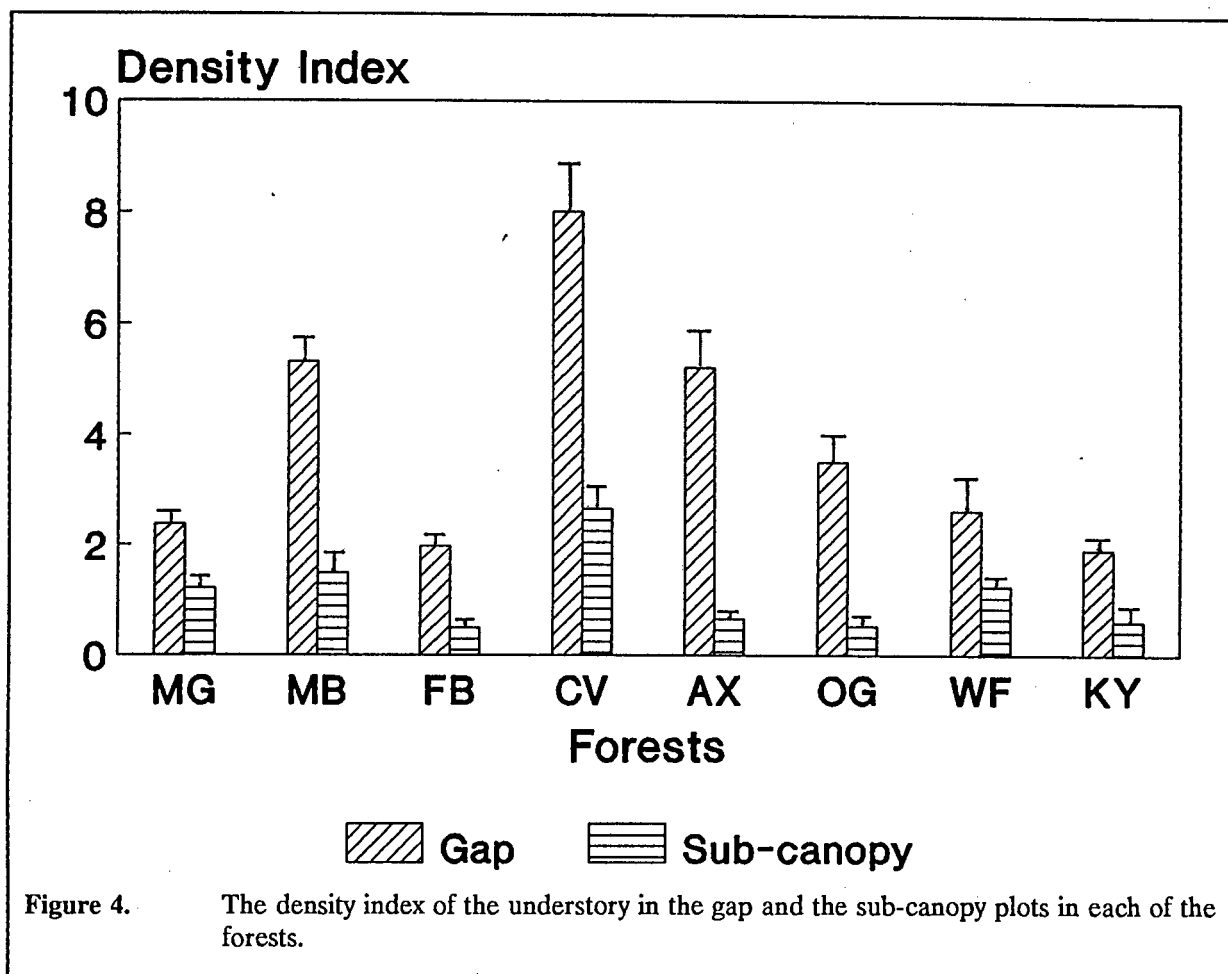
		Forest								
		Lowland				Transition		Highland		
Forest		MG	MB	FB	CV	AX	OG	RG	WF	KY*
<i>I. woodii</i>	Gap	14	28	0	29	0	0	0	0	6
	S-C	15	0	0	28	2	0	0	0	2
Grass/Ferns	Gap	3	0	3	2	6	12	58	67	14
	S-C	5	0	0	0	17	0	32		1
Liana mat	Gap	1	0	0	5	12	0	8	7	3
	S-C	0	0	0	0	0	1	0	0	0
Bare ground	Gap	83	80	95	63	78	65	28	13	75
	S-C	80	100	100	72	81	91	60	14	96

\* The understory in this forest is not largely represented by *Isoglossa woodii* but by a woody shrub, *Trichocladus crinitus*.

#### Understory layer

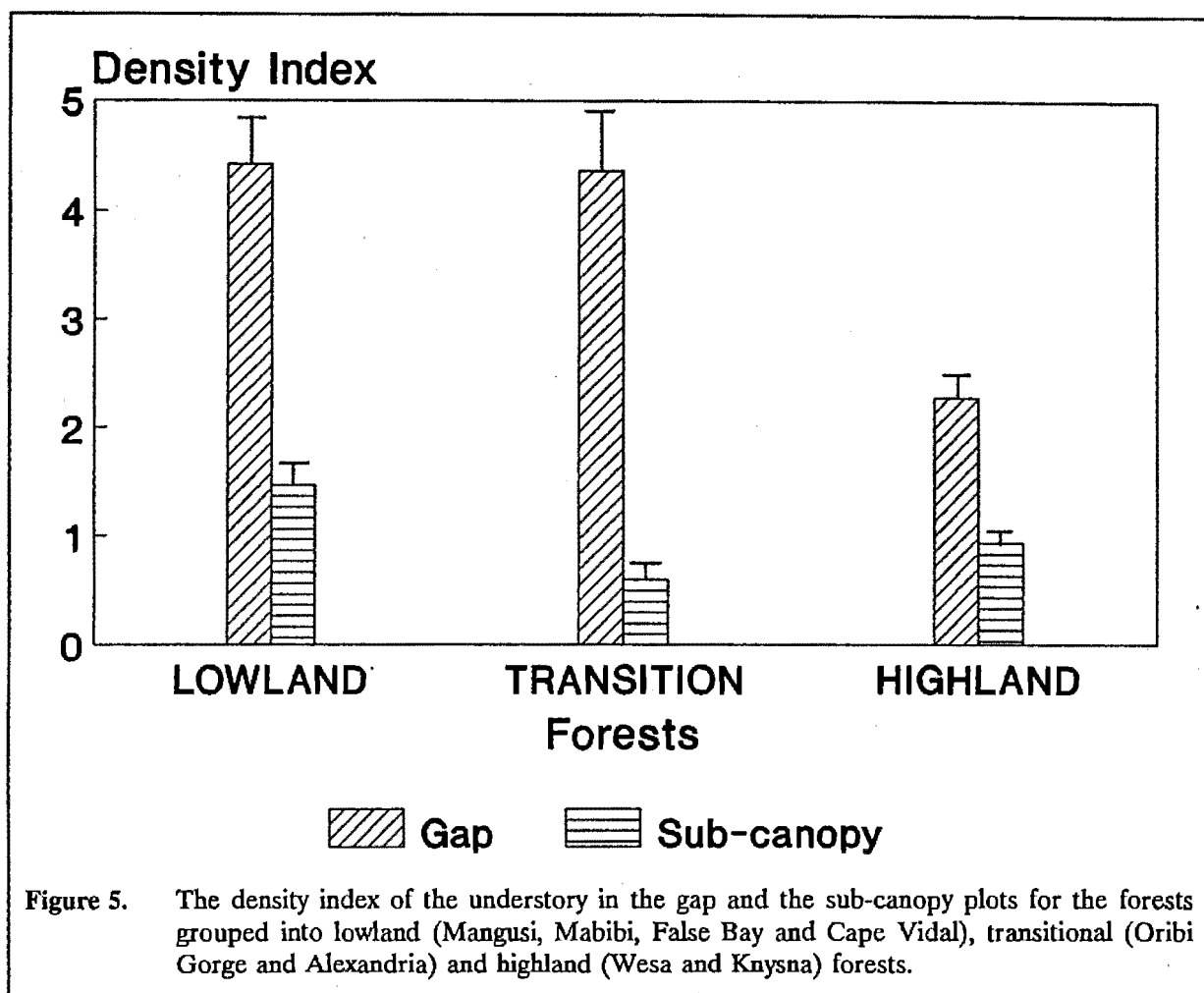
The foliage density of the understory was measured as an index of the light environment experienced by seedlings. The density of the gap understory was highest at Cape Vidal ( $8.01 \pm 0.87$ ) and lowest at Knysna ( $1.92 \pm 0.22$ ). The density of the sub-canopy understory was highest at Cape Vidal ( $2.65 \pm 0.28$ ) and lowest at False Bay ( $0.49 \pm 0.14$ ) (Fig. 4).

There was a significant difference ( $p < 0,001$ ) between the density of the gap understory and the sub-canopy understory in each of the eight forests where density was measured (Rainbow Gorge excluded). The forests were grouped into highland, transitional and lowland forests to determine whether there was a difference in the mean densities of the understory between the groups. The density of the understory in lowland gaps ( $4.19 \pm 0.27$ ) was significantly higher than under the sub-canopy ( $1.43 \pm 0.12$ ) ( $p < 0.001$ ), and the density of the understory in highland gaps ( $2.3 \pm 0.19$ ) was significantly greater than the density of the understory under the forest canopy ( $0.96 \pm 0.07$ ) ( $p < 0,001$ ) (Fig. 5).



The understory density of the gaps in lowland forests was significantly greater ( $4.19 \pm 0.27$ ) than highland forests ( $2.3 \pm 0.19$ ) ( $p < 0.01$ ) (Fig. 5). The same is true for below the canopy where the lowland understory ( $1.43 \pm 0.12$ ) was significantly more dense than the highland ( $0.96 \pm 0.07$ ) ( $p < 0.05$ ).

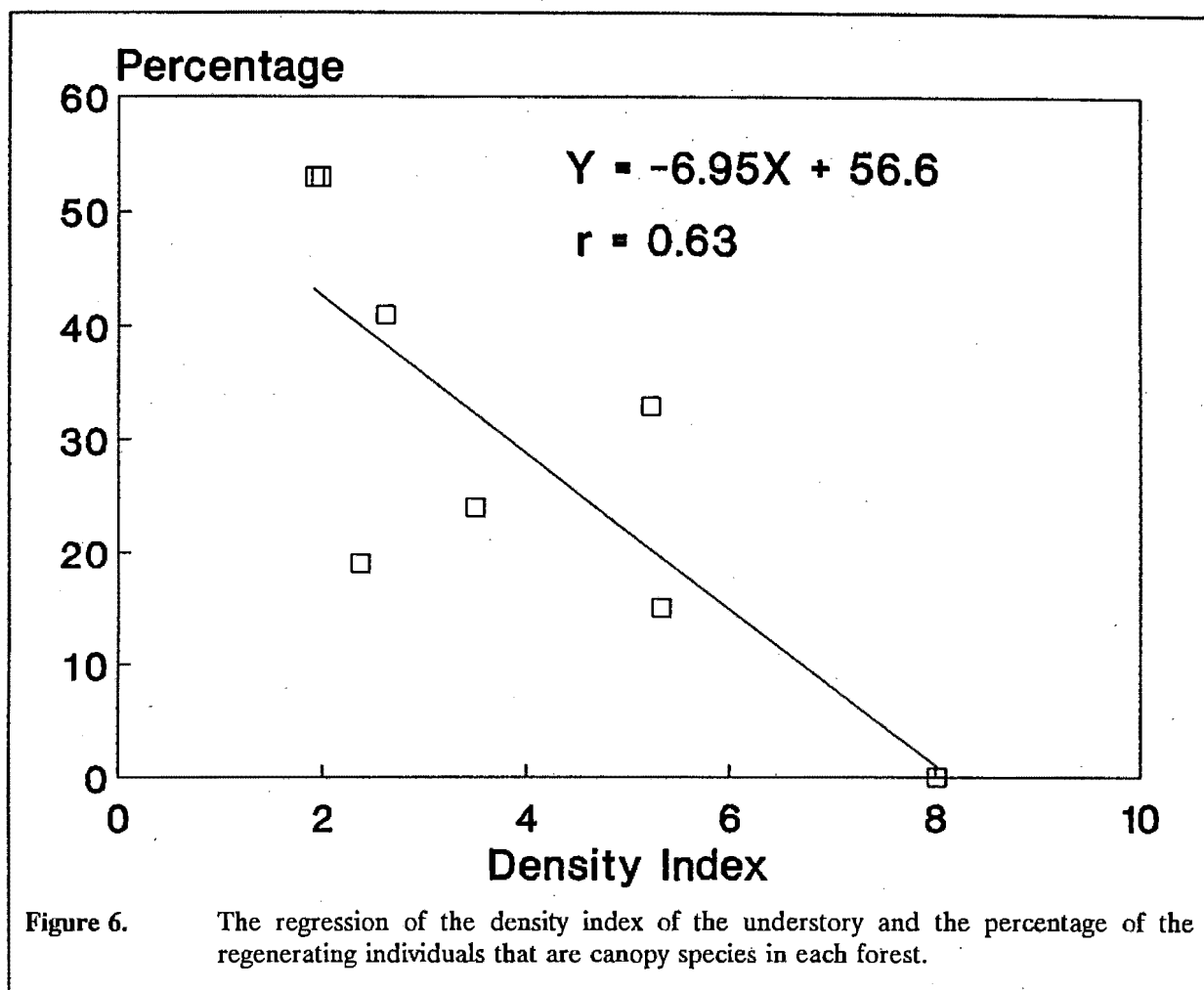
There was a significant negative correlation between the number of canopy seedling regenerating in the gaps of the different forests and the density of the associated understory ( $r^2 = 0.523$ ;  $Y = -0.94 X + 6.9$ ;  $p < 0.05$ ), as well as between the percentage of canopy species and the density of the herbaceous layer in the gaps of the different forests ( $r^2 = 0.63$ ;  $Y = -6.95 X + 56.6$ ;  $p < 0.05$ ) (Fig. 6). This suggests that the density of the understory layer negatively influences the regeneration of canopy species in these forests.



There was a greater range in understory density of the lowland forests, both in the gap and the sub-canopy plots, than in the highland forests (Fig. 4). To ascertain if any of the forests had particularly patchy understory, I considered the degree of heterogeneity of the understory density by calculating the coefficient of variation of the density indices (Table 5). There was no significant difference in the coefficients of variation of the gap or sub-canopy understory density indices between the forests.

**Table 5.** The coefficient of variation of the density indices of the gap and the sub-canopy understory layers for the forests measured. The results suggest that the understory layer has an impact on the regeneration of canopy species and may influence where seedlings can establish.

Forest	Lowland				Transition		Highland	
	MG	MB	FB	CV	AX	OG	WF	KY
Gap Coef. var.	.53	.53	.52	.75	.93	.97	.79	.73
S-C Coef. var.	.84	1.39	2.04	0.74	0.72	1.32	.39	1.19



### Canopy lateral growth

I quantified canopy gap lateral growth to determine whether patterns of regeneration could be explained by the shading effect of this lateral growth. There was no significant difference in the size of the mean canopy gaps between forests although Cape Vidal has a significantly larger mean ground gap area than the other forests ( $p < 0.01$ ). There was also no significant difference between the extent of lateral infill of the gap edge trees between forests except between that of Alexandria (6.9 m) and Oribi Gorge (2.2 m) ( $P < 0.05$ ) (see Table 6). There were no significant differences in the extent of lateral infill between the lowland and the highland groupings of the forests.

The gap area ratio (ground gap area : canopy gap area), was remarkably similar between the forests with a ratio value of approximately 2.5 for most forests (Table 6), the exceptions being False Bay (8.3) and Mangusi (6.2). There was no significant correlation between the height of the

forest and the extent of the lateral canopy infill. Taller trees did not appear to have a greater lateral infill distance than shorter trees as there was no pattern between the lowland and highland forests if the gap area ratio is divided by the mean height of the forest (Table 6).

**Table 6.** The mean lateral infill distance ( $\pm$  SE) of the trees surrounding the gaps, the ratio of the area of the ground gap to the area of the canopy gap (Gap Area Ratio - GAR; see Figure 2) and the GAR divided by the height of the tree.

Forest	Lowland				Transition		Highland		
	MG	MB	FB	CV	AX	OG	RG	WF	KY
Infill (m)	5.3	3.4	6.5	5.3	6.9	2.2	5.8	2.6	2.5
SE ( $\pm$ )	0.9	0.4	1.2	0.9	1.5	0.3	1.5	0.2	0.2
Gap area ratio	6.2	2.0	8.3	2.3	2.5	2.2	3.3	2.2	3.1
GAR/Tree Hgt.	0.35	0.11	0.53	0.11	0.16	0.13	0.16	0.09	0.15

There was no significant correlation between the number of canopy species or regenerating canopy seedlings, saplings or sub-canopy trees in the gaps of the 2 - 5 m and the > 5 m size classes and the lateral infill or the gap area ratio. These results suggest that the extent of canopy infill does not influence the regeneration of canopy trees in these forests

#### Climber infestation

I established the abundance of lianas to determine if the regeneration of canopy trees was influenced by liana density. There were fewer large lianas than medium and small lianas (Table 5). For the small and medium lianas in all forests except for Alexandria and for the small lianas in Mabibi there was a higher mean number in the gaps than in the sub-canopy plots. This trend was reversed when the large lianas were considered and in six of the nine forests there were either more or the same number of lianas in the sub-canopy plots than in the gaps (Table 5). A number of plots had no lianas at all. It appears that climbers have little influence on the regeneration of canopy trees.

**Table 7.** The weighted mean number of lianas in the gap and sub-canopy plots (S-C) of the different forests. HLM is the mean for the highland forests, TM is the mean for the transition forests and LLM is the mean for the lowland forests.

Stem Site	FOREST											
	MG	MB	FB	CV	LLM	AX	OG	TM	RG	WF	KY	HLM
<b>&lt; 1cm</b>												
Gap	24.0	5.5	3.3	0.0	8.2	8.3	13.3	10.8	18	5.0	1.8	8.3
S-C	7.8	7.7	0.0	0.0	3.9	11.6	0.0	5.8	0.0	0.0	1.2	0.4
<b>1-5cm</b>												
Gap	11.3	7.5	8.3	8.3	8.9	3.3	13.8	8.6	11.7	28.0	3.8	14.5
S-C	5.8	4.8	5.0	3.2	4.7	10.8	3.3	7.1	4.8	6.7	1.6	4.4
<b>&gt; 5cm</b>												
Gap	7.2	1.4	1.2	1.8	2.9	0.0	1.7	0.8	1.8	1.8	0.8	1.5
S-C	3.9	1.7	1.2	3.3	2.5	5.8	1.7	3.8	5.6	1.0	0.4	2.3

## Discussion

The comparison of the patterns of regeneration of canopy trees between the lowland and the highland forests shows clear differences. Firstly, the highland forests are characterised by a greater percentage of canopy species regenerating as seedlings and saplings than the lowlands (Table 2). Secondly, at the sampling scale used in the study, lowland forests show great variability in the regeneration patterns of canopy seedlings between forests, while highland forests show greater consistency of pattern (Fig. 3a). If the different size classes are taken to reflect the different ages of individual plants, then variability in the success of establishment of canopy species over a time period, can be seen. Under equilibrium conditions with consistent annual recruitment and subsequent self thinning (Meyer 1952), there would be fewer canopy individuals as the plants get larger. The highland forests display this pattern (Tables 2 & 3) suggesting a high degree of predictability in the regeneration dynamics (see also Midgley *et al.* 1990). Recruitment of canopy species in the lowland forests, on the other hand, appears to be episodic and with a low degree of predictability. Thirdly, there are differences in the sites of canopy species regeneration between highland and lowland forests. Sub-canopy plots are the main sites of canopy regeneration in the highland forests, while treefall gaps appear to suppress much of this regeneration. In the lowland

forests, on the other hand, the gaps are the main sites of canopy regeneration with little canopy regeneration in the sub-canopy plots.

Can the differences in regeneration dynamics between lowland and highland forests be explained in terms of competitive interactions between different growth forms? The competitive dominance of tree seedlings by perennial herbs and shrubs has been well documented (see Grime 1979; Maguire and Forman 1983; Bond 1989). Different layers of the vegetation within a forest have been shown to have a negative influence on the regeneration of forest plants with smaller stature by shading (Veblen *et al.* 1977; Veblen 1979; Hibbs 1982).

Dealing first with the ground layer, its near absence in the lowland forests, suggests that the shading effect of this layer provides little or no obstacle to the germination and establishment of canopy tree seeds. The reasons for the low ground cover are not clear, but may be due to the already dense shade provided by the sub-canopy layer of *Drypetes* and *Cola* spp. found in the sub-canopy. A second possibility is that much of the growth at this level is reduced by heavy browsing of ungulates of which there was much evidence. Both False Bay and Cape Vidal are in fenced reserve areas where browsing ungulate numbers are manipulated and have recently been high (Personal communication with reserve staff). The dwarf antelope *Neotragus moschatus* (Heinichen 1972) and other antelope (see Smithers 1983) are recorded as eating small forest plants in this area.

The higher percentage of grass and fern ground cover in the highland forests, particularly in Rainbow Gorge and Wesa Forest, do not appear to inhibit seedling regeneration of canopy species significantly as evidenced by the high number of seedlings regenerating in the sub-canopy of the highlands (Table 2). This result is surprising in the light of the work by Maguire and Forman (1983) showing the negative impact of the herb layer on tree regeneration. The cover value does not exceed 70% in this study which may be insufficient to suppress seedling regeneration. The impact of liana mats, through shading, on the regeneration of canopy species appears to be minimal as they never cover more than a mean of 12 % of the gap ground area.

The lack of a significant correlation between the number of regenerating saplings or sub-canopy trees and the infill distance or the gap area ratio for the forests suggests that shading effects of the gap edge trees do not influence the regeneration of the canopy species (see Table 6). Hibbs (1982), in a study on small canopy gaps showed a negative influence of lateral canopy growth on

tree reproduction in a hemlock-hardwood forest. However this situation differs from that described by Hibbs (1982) where the size of the gaps concerned were much smaller. I have no measure of the foliage density of individual tree species but suggest that it could play an important role in altering the shade environment of the gap understory (cf. Horn 1971; Halle *et al.* 1978).

Lianas are frequently associated with gaps where they are found drooping from gap edge trees as well as being concentrated within the gaps (Richards 1952; Putz 1984). In this study the two smaller size classes of liana were more abundant in gaps than in the sub-canopy plots (Table 7). The greater abundance of larger climbers in the sub-canopy plots is possibly a result of the poor light conditions and the absence of trellises by which young lianas can reach the canopy (Putz 1984; see also Chapter 2 this thesis). In the gaps on the other hand there is a higher light level as well as there being more trellises for young lianas to gain access to the canopy. I found no association between liana abundance and reduced canopy species regeneration, suggesting that they do not impact on southern African forests in this way. This is contrary to the commonly published view that they negatively impact forests regeneration in tropical forests (Kochummen 1966; Fox 1968; Neil 1984).

Shading, due to the density of the understory, appears to provide the largest obstacle to the establishment of canopy species in the forests considered here. In highland forests the density of the understory layer is greatly reduced in the sub-canopy relative to the gaps (Figs. 4 & 5). I suggest that release from the suppressive effect of understory vegetation accounts for the improved canopy regeneration in the sub-canopy. The significant negative correlation between the number of canopy seedlings and the density of the understory as well as the percentage of canopy species regenerating in the gaps of the forests and the density of the gap understory (Fig. 6) supports this argument. Community control of vegetation in this manner has been reported for temperate *Nothofagus* forests in south-central Chile (Veblen 1979; Veblen *et al.* 1977), where the regeneration of canopy trees is inhibited by the understory bamboo *Chusquea tenuiflora*, and appears to be an important influence in the regeneration of the forests.

The mean density of the understory in lowland forests was double that of highland forests but little regeneration of canopy species occurs in the understory of the lowland forests. How then do canopy trees regenerate in the crowded gaps of the lowland forests? The answer is not clear and more research is needed. However, in the light of observations made in the field I suggest a few possible solutions.

If regeneration of the canopy species is dependent on the release from the suppressive competitive effects of the understory this release could occur in a number of ways. Firstly, heterogeneity in the density of the understory could provide less dense "gaps" in this layer through which regeneration of canopy species could occur. The results suggest that this is not the case. The coefficient of variation of the density of the gap understory is lower in the lowlands than in the highlands where the understory appears to inhibit regeneration. Further, heterogeneity in the understory layer would not explain the episodic nature of the recruitment of canopy species in the lowland forests.

Secondly, die back every seven to ten years of the semelparous dominant understory herb *Isoglossa woodii* (Acanthaceae) (Ward 1980), could provide a temporary release of one to two years within which less vigorous or shade intolerant canopy species can establish. The establishment of tree species in the die back period of semelparous bamboo of the genus *Chusquea* has been reported for near timberline *Nothofagus* forests in Chile (Veblen 1979). Recruitment in this manner would result in a pulsed regeneration pattern of canopy species in lowland forests such as is seen in Table 3. The age of the seedlings in this study is not known but a prediction arising from this idea is that there would be pulses of even aged cohorts of canopy species in the lowland forests, correlated with the time of the last die back of *I. woodii*.

Thirdly, population eruptions by ungulates such as the nyala (*Tragelaphus angasii*) and other antelope may result in large scale browsing of the understory. This could be partially responsible for the episodic recruitment of canopy species in lowland forests. There were signs of recent heavy browsing in the False Bay forests attributed to a recent nyala outbreak which could explain the low density of the understory recorded there. The role of large mammals such as the elephant may be particularly important in forests such as Alexandria where the understory is not herbaceous, but a woody shrub *Grewia occidentalis*, which can become particularly dense. Historical records (Skead 1980) suggest that elephant were common in the area of the Alexandria forests and that they fed on the fruit and foliage of *Grewia* spp. In the last one hundred years however, elephant numbers have declined substantially with no elephant being recorded in the area for at least fifty years (Skead 1980). I suggest that the destructive effect of elephant walking through treefall gaps and feeding on the dense growths of *Grewia* would have opened sufficient space to allow the release of canopy seedlings, an event that has not happened in the recent past. This would be consistent with regeneration failure of canopy dominants such as *Podocarpus*, *Celtis* and *Erythrina* species in this forest.

## Conclusions

The southern African highland and lowland forest regions differ in their regeneration dynamics. The importance of gaps for the regeneration of forest canopy tree species is recognised for the lowland forests while highland forests regenerate predominantly in the sub-canopy.

While the ground layer appeared to have little impact on the regeneration of the canopy species and evidence for the impact of the canopy lateral growth was inconclusive, the understory appears to negatively influence the regeneration of canopy tree species. There is a negative correlation between the density of the understory and the ability of the canopy species to regenerate. Thus in the highland forests, canopy species regenerate more in the sub-canopy while regeneration is weaker in the gaps. Lowland forests, on the other hand, experience particularly dense understories which suppress canopy species regeneration in both the gaps and the sub-canopy. They do however appear to experience periodic release from this condition allowing episodic regeneration of forest trees in the treefall gaps. The impact of climbers on the regeneration of canopy trees appears to be minimal.

There are a number of implications for the management of these forests. The highland forests experience predictable and continuous regeneration of canopy trees in the sub-canopy regions while regeneration is impeded in the treefall gaps. The felling of any tree thus needs to take this into account and to disturb the canopy as little as possible, minimizing the size of the canopy gap that is formed. Secondly, attempts should be made to do as little damage to the advanced tree regeneration as is practical to allow the closure of the canopy gap by these individuals. The results of this study essentially agree with those of Geldenhuys and Maliepaard (1983).

In the lowland forests vertebrates could have an important impact on forest dynamics a) by influencing the frequency and size of gaps and b) by influencing the density of the understory and therefore its capacity to suppress canopy regeneration. The regeneration of forest trees is dependent on the formation of gaps and any natural gap forming processes. The role of elephants in toppling old or dead trees, may be essential for the functioning of the forest. However within a gap the regeneration of canopy species is dependent on a reduction in the density of the understory. This can be achieved by managing the density and nature of vertebrate herbivores as well as events such as the die back of semelparous herbaceous vegetation. If large herbivores are excluded, for example at Mangusi where the forest is fenced off, special compensatory management may be needed to ensure the continual regeneration of canopy species. Clearly more work is needed on these aspects of forest dynamics.

## References

- Brandani A, Hartshorn GS and Orians GH. 1988. Internal heterogeneity of gaps and tropical tree species richness. *J. Tropical. Ecol.* 4:99-119.
- Breen CM. 1971. An account of the plant ecology of the dune forest at lake Sibayi. *Trans. roy. Soc. S. Afr.* 39:223-235.
- Brokaw NVL. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158-160.
- Brokaw NVL. 1985. Gap-phase regeneration in tropical forest. *Ecol.* 66:682-687.
- Bond WJ. 1989. The tortoise and the hare: ecology of angiosperm dominance and gymnosperm persistence. *Biol. J. Lin. Soc.* 36:227-249.
- Canham CD. 1988a. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. *Ecol.* 69(3):786-795.
- Canham CD. 1988b. An index for understory light levels in and around canopy gaps. *Ecol.* 69(5):1634-1638.
- Connell JH. 1989. Some processes affecting the species composition in forest gaps. *Ecol.* 70:560-562.
- Cooper KH. 1985. The conservation status of indigenous forests in Transvaal, Natal and O.F.S., south Africa. *Wildlife Society of South Africa.* Durban.
- Denslow JS. 1980. Gap partitioning among tropical rainforest trees. *Tropical Succession* 47-55.
- Denslow JS. 1987. Tropical rainforest gaps and tree species diversity. *Ann. Rev. Ecol. Syst.* 18:431-451.
- Fox JED. 1968. Logging damage and the influence of climber cutting prior to logging in the lowland dipterocarp forest of Sabah. *The Malayan Forester* 31:326-347.
- Garwood NC. 1983. Seed germination in a seasonal tropical forest in Panama: a community study. *Ecol. Mono.* 53(2):159-181.
- Geldenhuys GC. 1989. Richness, composition and relationships of the floras of selected forests in southern Africa. In: Geldenhuys CG (Ed) *Biogeography of the mixed evergreen forests of southern Africa* Foundation for research development occasional report. No. 45. pp 208.
- Geldenhuys CG and Maliepaard W. 1983. The causes and sizes of canopy gaps in the southern Cape forests. *S. Afr. For. J.* 124:50-55.
- Gordon IG (Ed). 1989. *Natal indigenous forests: A preliminary collection of reports on indigenous forests in Natal.* Natal Parks Board Publication, Pietermaritzburg. 195 pp.

- Grime JP. 1979. Plant strategies and vegetation processes. John Wiley & Sons. Chichester, England.
- Grubb PJ. 1977. The maintenance of species-richness in plant communities the importance of the regeneration niche. *Biol. Rev. Cambridge Philos. Soc.* 52:107-145.
- Halle F, Oldeman RAA and Tomlinson PB. 1978. Tropical trees and forests: An architectural analysis. Springer-Verlag, Hiedelberg, Germany.
- Hartshorn GS. 1978. Treefalls and tropical dynamics pp 617-638. In: Tomlinson PB and Zimmermann MH (Eds). Tropical trees as living systems. Cambridge University Press, New York.
- Heinichen IG. 1972. Preliminary notes on the suni *Neotragus moschatus* and red duiker *Cephalophus natalensis*. *Zool. Afr.* 7:157-165.
- Hibbs DE. 1982. Gap dynamics in a hemlock-hardwood forest. *Can. J. For. Res.* 12:522-527.
- Horn HS. 1971. The adaptive geometry of trees. Monographs in Population Biology Number 3. Princeton University Press, Princeton, New Jersey, USA.
- Huntley BJ. 1965. A preliminary account of the Ngoye forest reserve, Zululand. *J. S. Afr. Bot.* 31:177-205.
- Kochummen KM. 1966. Natural plant succession after farming in Sg. Krog. *The Malayan Forester* 29:170- 181.
- Lang GE and Knight DH. 1983. Tree growth, mortality, recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. *Ecol.* 64(5):1075-1080.
- Lieberman M, Lieberman D and Peralta R. 1989. Forests are not just swiss cheese: canopy stereogeometry of non-gaps in tropical forests. *Ecol.* 70:550-552.
- MacArthur RH and MacArthur JW. 1961. On bird species diversity. *Ecol.* 42:594-598.
- MacDevette DR. 1989. The vegetation and conservation of the Zululand coastal dunes. In: Gordon IG. (Ed). Natal indigenous forests: A preliminary collection of reports on indigenous forests in Natal. Natal Parks Board Publication, Pietermaritzburg. 195 pp.
- MacDevette DR, MacDevette DK, Gordon IG and Bartholomew RLC. 1989. The floristics of the Natal indigenous forests. In: Gordon IG. (Ed). Natal indigenous forests: A preliminary collection of reports on indigenous forests in Natal. Natal Parks Board Publication, Pietermaritzburg. 195 pp.
- Maguire DA and Forman RTR. 1983. Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecol.* 64:1367-1380.
- Marker ME and Russell S. 1984. The application of biogeographical techniques to forest site-factor analysis. *South African Geographical Journal.* 66:65-78.

- Meadows M and Linder HP. 1989. A reassessment of the biogeography and vegetation history of the southern Afromontane region. In: Geldenhuys GC (Ed) Biogeography of the mixed evergreen forests of southern Africa. Foundation for research development occasional report. No. 45. pp 208.
- Meyer HA. 1952. Structure, growth and grain in balanced uneven aged forests. *J. For.* 50:85-92.
- Midgely J, Seydack A, Reynell D and McKelly D. 1990. Fine-grain pattern in southern Cape plateau forests. *J. Veg. Sci.* 1:539-546.
- Moll EJ. 1972. The current status of mistbelt mixed podocarp forest in Natal. *Bothalia* 10:595-598.
- Moll EJ. 1980. Terrestrial plant ecology. In: Bruton M and Cooper K. (Eds.) Studies on the ecology of Maputaland. Rhodes University and the Natal branch of the Wildlife society of southern Africa.
- Neil PE. 1984. Climber problems in Solomon Islands forestry. *Commonw. For. Rev.* 63:27-34.
- Phillips J. 1931. Forest succession and ecology in the Knysna region. *Memoirs of the botanical survey of South Africa* No.14.
- Phillipson PB and Russell S. 1988. Phytogeography of the Alexandria forest (southeastern Cape province). *Monogr. Syst. Bot. Missouri Bot. Gard.* 25:661-670.
- Poulson TL and Platt WJ. 1989. Gap light regimes influence canopy tree diversity. *Ecol.* 70:553-555.
- Putz FE. 1983. Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecol.* 64(5):1069-1074.
- Putz FE. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6):1713-1724.
- Richards PW. 1952. *The tropical rain forest.* Cambridge University Press, Cambridge.
- Runkle JR. 1982. Patterns of disturbance in some old-growth forests of eastern North America. *Ecol.* 63:1533-1546.
- Runkle JR. 1985. Disturbance regimes in temperate forests. In: *The ecology of natural disturbance and patch dynamics.* Eds. Pickett STA and White PS. Academic Press Inc.
- Schupp EW. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51:71-78.
- Skead DM. 1980. *Historical mammal incidence in the Cape province.* Cape Town, Department of Nature Conservation.
- Skinner RHN. 1983. *The mammals of the southern African subregion.* University of Pretoria, Pretoria, South Africa.

- Smith AP. 1973. Stratification of temperate and tropical forests. *Am. Nat.* 107:671-683
- Swaine MD, Lieberman D and Putz FE. 1987. The dynamics of tree populations in tropical forest: a review. *J. Tropical Ecol.* 3:359-366.
- Swaine MD and Whitmore TC. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81-86.
- Turner IM and Newton AC. 1990. The initial responses of some tropical rain forest tree seedlings to a large gap environment. *J. Appl. Ecol.* 27:605-608.
- Veblen TT, Ashton DH, Schlegel FM and Veblen AT. 1977. Distribution and dominance of species in the understory of a mixed evergreen-deciduous *Nothofagus* forest in south-central Chile. *J. Ecol.* 65:815-830.
- Veblen TT. 1979. Structure and dynamics of *Nothofagus* forests near timberline in south-central Chile. *Ecol.* 60:937-945.
- Ward CJ. 1980. The plant ecology of the Isipingo beach area, Natal, South Africa. *Memoirs of the Botanical Survey of South Africa No. 45.* Botanical Research Institute. South Africa.
- Watt AS. 1947. Pattern and process in the plant community. *J. Ecol.* 35:1-22.
- Weisser PJ and Marques F. 1979. Gross vegetation changes in the dune area between Richards Bay and the Mfolozi river, 1937-1974. *Bothalia.* 12,4:711-721.
- White F. 1978. The afro-montane region. In: Wergner M.J.A. (Ed). *Biogeography and ecology of southern Africa.* W.Junk, The Hague, pp 436 - 513.
- White F and Moll EJ. 1978. The Indian ocean coastal belt. In: Wergner M.J.A. (Ed). *Biogeography and ecology of southern Africa.* W. Junk, The Hague, pp 563 - 598.
- White F. 1983. The vegetation map of Africa: a descriptive memoir to accompany the UNESCO/AETFAT/UNSO map of Africa. *Natural resources Research* 20, UNESCO, Paris 356 pp.
- Whitmore TC. 1982. On pattern and process in forests, pp 45-59. In: Newman EI. (Ed). *The plant community as a working mechanism.* Blackwell Scientific, Oxford.
- Whitmore TC. 1989. Canopy gaps and two major groups of forest trees. *Ecol.* 70:536-538.

## Chapter Six

### Conclusion

In this study I set out to answer two questions. Firstly, what limits the abundance of climbers and why? Secondly, do climbers influence the regeneration of forest trees? My intention in this chapter is to consider the extent to which I have answered these questions and to consider beneficial directions for future research to follow.

#### What limits the abundance of climbers and why?

I show that there is variation in the abundance of climbers over a soil nutrient gradient. Under standardised light conditions there is a positive correlation between climber abundance and the potassium concentration and the S - value of the soil, but not the nitrogen concentration. There is thus no positive correlation between all soil nutrients and climber abundance suggesting that there is no causative relationship between them. The positive results may merely be reflecting the altitudinal gradient. There is also little difference between the growth response of climbers and trees to increased nutrient availability. I thus question the link between climber abundance and soil nutrient status.

Instead I suggest that the role of tree canopy architecture and trellis availability, may be important in determining the distribution and abundance of climbers. As few climbers enter their host trees via the trunk, tall trees with high canopies tend to avoid climber occupation except for those that enter the tree canopy horizontally from neighbouring trees. Also, trees with lower canopies have more climbers which enter the canopy vertically via available trellises. There is thus a positive correlation between aspects of tree canopy architecture and climber abundance. The role of trellises is highlighted by the apparent facilitatory role whereby the presence of one climber species enhances the chances of another species gaining access to the canopy of a host tree. I suggest that climber abundance and distribution may be controlled by interactions between the tree and climber growth forms rather than by the abiotic environment. This idea needs to be tested over a wider range of forests, while further attention needs to be paid to the relationship between climber abundance and specific soil nutrient levels e.g. potassium. An interesting study would be to determine the relationship, if any, between the availability of trellises (tree architecture) and soil nutrient levels.

Climbers differ from trees in that they fail to allocate resources to the formation of a rigid woody support. In this study I show that they possibly also differ in aspects of their physiology related to carbon gain, although these differences are small. I present contradictory evidence which suggests that climbers may be able to photosynthesize at higher rates than trees while other evidence indicates that there are no differences between the maximum photosynthetic rates of the two growth forms. There appears to be minimal difference in water use efficiency between trees and climbers. Clear increases in the carbon gain capacity of climbers compared with trees would support the argument that climbers are reliant on high nutrient levels to be competitive. While evidence presented here suggest that climbers may have a higher carbon gain capacity than trees the difference appears to be small and insufficient to justify the apparent association between climbers and high soil nutrient levels. This further supports the earlier questioning of the relationship. The implications of these differences for the ecology of climbers, are that climber distribution and abundance may be independent of soil nutrients. Further studies that consider both the carbon allocation patterns and the carbon gain mechanisms of trees and their hosts in the wild as well as their growth phenologies will greatly enhance our understanding of climber ecology. Such understanding will be of use to both tropical foresters concerned with the regeneration of logged trees as well as to conservationists concerned with the invasive ability of exotic climbers.

#### Do climbers influence the regeneration of forest trees?

Contrary to widely documented reports that climbers in tropical forests swamp gaps and disturbances in a forest canopy and inhibit the regrowth of canopy tree species, little evidence of this was found in southern Africa. I suggest that the climber growth form does not influence the dynamics of forests at the level of seedling and sapling regeneration. Instead the impact of other vegetation layers, such as the herbaceous and shrub understory layer, play an important role in influencing the regeneration of canopy trees after a treefall. This is apparent in highland forests where canopy species tend to regenerate below intact canopies where the density of the understory is low compared with the gaps. There are implications of this for lowland forests where the understory density is on average double that in highland forests. Many canopy species in lowland forests are shade intolerant and are dependent on gaps to regenerate. However they are also dependent on disturbance to the understory layer to release them from the suppressive influence of the dense understory. I suggest this release can occur through natural processes such as die back of the semelparous acanthaceous herbs, but can also occur through the effects of browsing by large ungulates. Management of browsing pressure on the understory may provide

the necessary release for seedlings of canopy species to establish and to ensure the regeneration of canopy trees in these forests.

Observation in the field suggests that the largest impact of lianas is by inducing early adult mortality of the host trees, through shading, and thus increasing gap formation rates. I suggest that in lowland forests where herbivores are prevented from providing the release that canopy seedlings need to regenerate, and where lianas are maintaining high adult mortality rates, the forest dynamics may alter to the extent where there is virtually no replacement of canopy trees leading to the gradual stagnation and collapse of the forest ecosystem. Further research needs to focus on the dynamics of the understory layer in southern African forests and the interaction between this layer and both large herbivores and regenerating canopy seedlings. The role of climbers (particularly lianas) needs to be investigated particularly at the level of inducing adult tree mortality.