

LIGHT MICROSITE REQUIREMENTS OF SEEDLINGS OF SOME  
AFROMONTANE FOREST TREE SPECIES : THE ROLE OF CANOPY  
GAPS PROMOTING REGENERATION.

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BOTANY HONOURS : ECOLOGY PROJECT

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**ABSTRACT**

Predictions of microsite requirements for seven common Afromontane forest tree species were made by testing above ground relative growth rate (RGR) and photosynthetic response of seedlings of the respective species under different light intensities. Vigilia oroboides and Halleria lucida, with either a very high photosynthetic rate or RGR, were regarded to be pioneer species. Podocarpus latifolius was regarded to be a deep shaded species due to its low photosynthetic and RGR's. Rapanea melanophloeos, Ilex mitis, Olea capensis sub sp. macrocarpa and Kiggelaria africana either had a moderately high RGR or photosynthetic rate and were regarded to be light shaded species. Predictions were tested in Grootvadersbosch (34°05'S, 20°50'E) forest, where frequency of seedlings beneath the canopy and under a canopy gap were recorded and tested using a  $\chi^2$ - goodness of fit test, against the null hypothesis that there are equal frequencies of seedlings beneath the canopy and canopy gaps. Results confirmed predictions made for P. latifolius, O. capensis sub sp. macrocarpa, and R. melanophloeos. Low seedling frequencies for the other species, either due to a restricted distribution of adult trees (e.g. V. oroboides) or high levels of herbivore attack, made it difficult to test predictions. Significantly higher frequencies of seedlings of P. latifolius and O. capensis sub sp. macrocarpa beneath the canopy than in the gap of dry forest suggest that gaps in drier forests are stressful sites for regeneration. This led to the hypothesis of expecting a greater dominance of shade tolerant species in the canopy of dry forests than in moist forests. McKenzie's (1978) findings support this hypothesis. It was concluded that Afromontane forests are largely made up of deep or light shaded tree species, with pioneer species confined to forest margins. The role of canopy gaps can be seen to play a minor role promoting regeneration.

## INTRODUCTION

This paper addresses the question of whether there are tree species in Afromontane forests adapted to different microsites with regards to their light requirements, for successful regeneration. It is estimated that the majority of canopy trees in tropical forests require a light gap at some stage to successfully reach the canopy (Hartshorn 1980), however, little is known about the regeneration requirements of Afromontane forest tree species. Phillips (1931) looked at forest succession in the Knysna forests, and found that many species showed increased growth rates in disturbed areas, since then the topic has been neglected. The success of a species surviving after germination will largely be dependent on whether it is able to tolerate shade conditions if it germinates beneath the canopy, or its ability to utilise the favourable conditions of a canopy gap should it germinate in it or already be present when the disturbance opens the canopy. This study will therefore concentrate on the growth and light requirements of the seedling stage during regeneration. Although this is only one of many stages determining the regeneration success of a species, I regard it to be of vital importance and a good starting point for gaining insight into microsite requirements of a species.

Much debate surrounds the characterisation of forest species in terms of their growth and regeneration requirements. It is argued that, although tree species differ from one another in numerous ways, they can be classed into two distinct groups based on simple qualitative differences of profound ecological consequence, namely species which are totally dependent on light gaps for their regeneration (pioneer species) and those which are not (non-pioneer species) (Denslow 1980). Swaine and Whitmore (1988, also see Whitmore 1989) have extended this dichotomy in classing forest trees, to regarding pioneer species as those

which can germinate only in canopy gaps open to the sky, in which full sunlight reaches the ground level during part of the day. The other group of tree species are those whose seeds can germinate under a forest canopy, and whose seedlings are able to establish in forest shade. These are classed as the non-pioneer species (climax or shade tolerant). These shade species almost certainly fall along a continuum in their light requirements, from juveniles that grow slowly beneath the canopy but do not respond greatly to periodic openings, to juveniles that can persist beneath the canopy but show significant increase in growth following the formation of a gap and increased light intensity (Augspurger 1984, Canham 1989).

Characterising species in such a way however, suffers one setback in that it is obscured by circular reasoning (Liebermann et al 1989). By assuming that a species fits into a particular category, based only on observations in the field, it makes it difficult to assess from results how competent the characterisation of species was in the first place.

In this study I therefore adopt a slightly different approach in determining the response of seedlings to gap conditions, where first the growth and photosynthetic responses of seedlings to different light intensity is experimentally determined. This then allows predictions to be made about what category the species should fit into, which are then able to be tested in the field looking at gap and beneath canopy seedlings. Predictions however, should be made with some caution since physiological responses to light cannot necessarily be linked to the ecological success of a species (Bjorkman 1981). Nevertheless it does provide a starting point for understanding something about the regeneration requirements of the different species.

## STUDY SITE

Field studies were carried out in Grootvadersbosch (34°05'S, 20°50'E), one of the largest afro-montane forests west of the Knysna forest. This seemed an appropriate forest since it is probably well protected from fire, and from prior observations there appeared to be a high incidence of canopy gaps caused by tree and branch falls. Rainfall is fairly high in this region with an average of approximately 1000mm (Taylor 1955). Although rain falls regularly throughout the year, the rainfall is below average during autumn and winter (April to August) and is highest during the spring months of September, October and November. Most of the forest has developed on soils derived from Bokkeveld shale, although some of the south slopes are sometimes overlain with Table Mountain Sandstone boulder scree (Taylor 1955). Aspects of the forest are generally either north (dry) or south (moist) facing (see appendix A for moisture levels of the different forest regions).

## STUDY SPECIES

The seven species studied were selected firstly because they were all common in Grootvadersbosch, and secondly because they were easily available. They are Podocarpus latifolius, Olea capensis sub sp. macrocarpa, Rapanea melanophloeos, Kiggelaria africana, Ilex mitis, Halleria lucida, and Virgillia oroboides, all of which are evergreen canopy trees.

## MATERIALS AND METHODS

### Growth experiments:

Seedlings of the study species were germinated and grown in standard potting soil in black plastic bags. In a sunny glass

house the different species were grown under different shade conditions; 0% shade (i.e. in the open, equal to approx.  $800 \mu \text{mol.m}^{-2}.\text{s}^{-1}$  under full sunlight which roughly simulates light conditions in an open clearing), 40% shade cloth (equal to approx.  $180 \mu \text{mol.m}^{-2}.\text{s}^{-1}$  under full sunlight, this roughly simulates light conditions in an average size gap of  $100\text{m}^2$ ), and 80% shade cloth (equal to approx.  $60 \mu \text{mol.m}^{-2}.\text{s}^{-1}$  under full sunlight, which roughly simulates understory light conditions). Plants in replicates of between five and eight for each species under their different shade conditions were randomly positioned and rotated on a monthly basis to avoid a bias in the results. Each plant was watered with approximately 500 ml every two to three days. Only above ground biomass was measured by counting the number of leaves at the start of the experiment and then again at the end. Dry weight per leaf was worked out at the end of the experiment by taking a sample of 60 leaves (20 mature, 20 intermediate and 20 young) from a number of plants and drying them in an  $80^\circ\text{C}$  oven for 24h. Relative growth rate was calculated according to the formula (Hunt 1978, in Pompa and Bongers 1988):

$$\text{RGR} = \frac{\text{Ln}W_2 - \text{Ln}W_1}{T_2 - T_1}$$

(W = dry weight (g) = leaf number x average dry wt/leaf, T= time in days).

Growth was recorded over a 105 days between the 18th of May and the 1st of September 1989.

Unfortunately Virgillia oroboides suffered a fungal attack and so had to be discarded from growth experiments. Likewise many of the seedlings of Olea capensis sub sp. macrocarpa suffered from some root disease and so was discarded due to lack of enough replicates.

## Photosynthetic experiments

After growth experiments, plants that had been growing in the open condition (i.e. 0% shade) were transferred to a controlled light room, that had a similar maximum light intensity to their growth conditions (also 10h day following simulated cycle of sunrise to sunset/14h night, 22°C, 50% RH). Plants were thus already well acclimatised to these light conditions and so were only given a week to acclimatise before starting the experiments.

Five plants of each species were used for photosynthetic measurements. Photosynthetic readings were taken using an infra-red-gas analyser (IRGA, make **DCA**, model **LCA2**), and photosynthetic rates were recorded and calculated using a database logger (make **AOC**, model **LC2**). Photosynthetic response curves were determined by taking readings at four successive light intensities ( $\pm 600$ ,  $\pm 400$ ,  $\pm 200$  and  $\pm 50 \mu\text{E}$ )

starting from the highest and then to the lower light intensities. These different light intensities are quite similar to what one would find moving from an open clearing to a large gap to beneath the canopy (see Chazdon and Fetcher 1984). These light intensities were obtained by using various levels of shading. In all cases a power curve was a best fit for the photosynthetic response curves.

## Field study

Fifteen canopy gaps were located in the forest, 4 in the drier parts of the forest (north facing) and 11 in the moist regions of the forest (south facing), (see Appendix A). Frequencies of seedlings of the study species were taken in the gap and beneath the adjacent canopy. A seedling was regarded as any plant 35cm. Frequencies were obtained by randomly taking four 2m x 2m plots in both sites. This proved difficult in the gap due to the

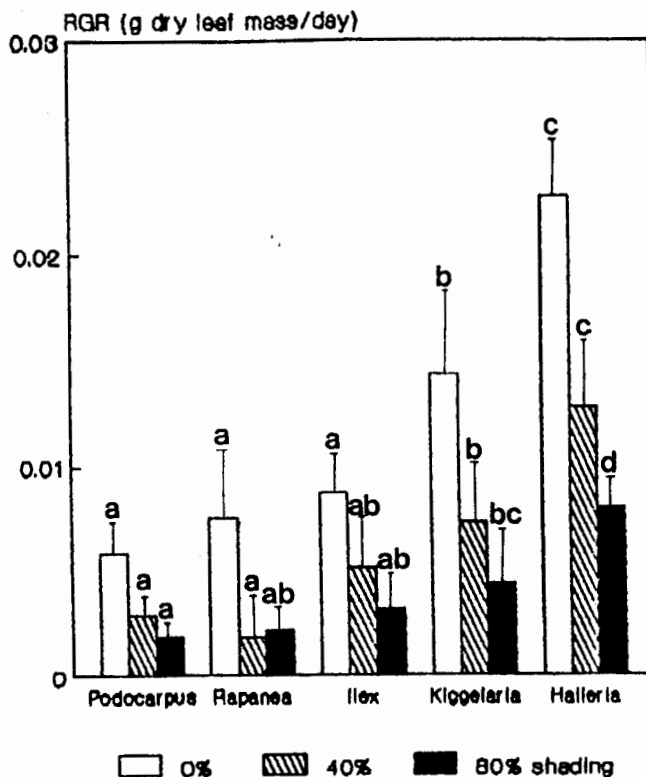


tremendous heterogeneity. Gaps were demarcated using Brokaw's (1982) definition of a gap; a 'hole' in the forest extending through all levels down to an average height of two meters above ground. Although this has been heavily criticised as being inaccurate (Pompa et al 1988), I see no better alternative. To test the null hypothesis that equal numbers of seedlings would be expected in gaps and beneath the canopy, frequency of seedlings were compared using a  $\chi^2$  goodness of fit test. Gap size was also measured by taking eight transects from the centre of the gap to the edge each at  $45^\circ$  intervals, and then working out the area on graph paper. Frequencies of seedlings in small ( $>40\text{m}^2$ ) and large gaps ( $<140\text{m}^2$ ) were compared. Frequencies of sapling (any plant  $>35\text{m}$  but  $<250\text{cm}$ ) of the study species were also recorded in the same  $2\text{m} \times 2\text{m}$  plots to gain some idea of mortality from the seedling to the sapling stage.

## RESULTS

### Growth rates:

There was an increase in relative growth rate (RGR) with an increase in light for all species. A one way ANOVA showed that there were significant differences ( $p < 0.05$ ) in RGR among all species for the different light conditions. Podocarpus latifolius and Rapanea melanophloeos had the slowest growth rates under all light conditions, while Halleria lucida and Kiggelaria africana grew the fastest under all light conditions, especially in the case of H. lucida (Figure 1). Ilex mitis showed a growth response intermediate between these two extremes at 40% and 80% shading, but had a similar slow RGR as P. latifolius and R. melanophloeos under 0% shading (Figure 1).



**Figure 1.** Relative growth rate of five of the study species under the respective light conditions. Standard errors are shown, one sided only. Bars with the same letter are not significantly different between species of the same shade condition (ANOVA and Tukey's multiple range test,  $P < 0.05$ ).

### Photosynthetic response

At a light intensity of 600  $\mu\text{E}$ , none of the species had reached light saturation level in their photosynthetic response, except for P. latifolius which was nearing saturation at this level with the lowest photosynthetic rate of  $3.8 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . I. mitis and H. lucida also had high photosynthetic rates at 600  $\mu\text{E}$ , of  $7.8 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  and  $6.7 \mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  respectively. Olea capensis sub sp. macrocarpa, R. melanophloeos and K. africana showed an intermediate response between these high and low extremes (Figure 2).

### Field results

In the dry forest regions O. capensis sub sp. macrocarpus and P. latifolius had significantly fewer seedlings in the gap than beneath the canopy, while R. melanophloeos had significantly more seedlings in the gaps than beneath the canopy (Table 1a). In the moist forest regions there were again significantly many more seedlings in the gaps than beneath the canopy for R. melanophloeos (Table 1b). However there was no significant difference between frequency of seedling in the gap and beneath the canopy for P. latifolius and O. capensis sub sp. macrocarpus. Frequencies of the other species were all too low to perform any statistical tests (see appendix B). It is however interesting to note that both V. oroboides and I. mites were only found in gaps. No seedlings of H. lucida were found.

Large gaps had significantly more seedlings than small gaps, for both O. carpensis sub sp. macrocarpa and R. melanophloeos (Table 1c).

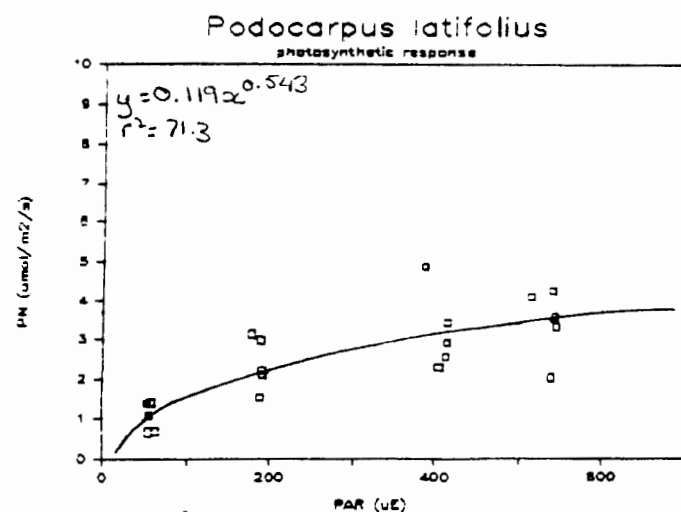
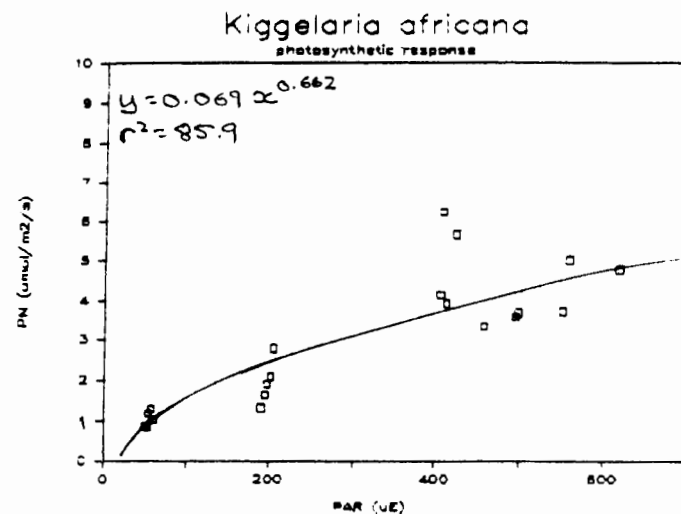
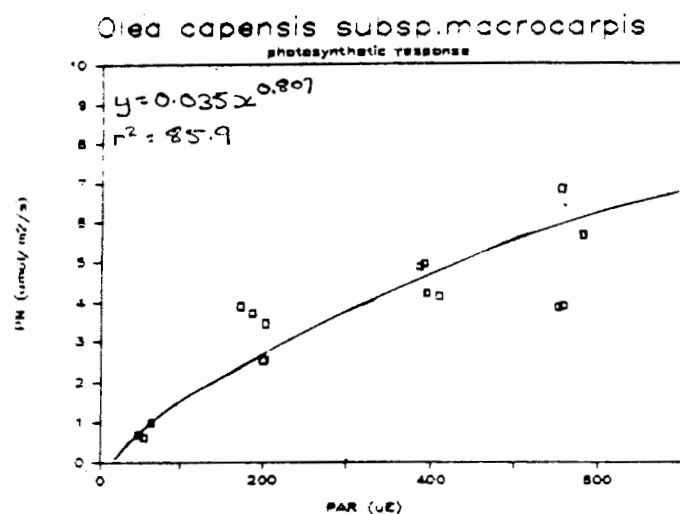
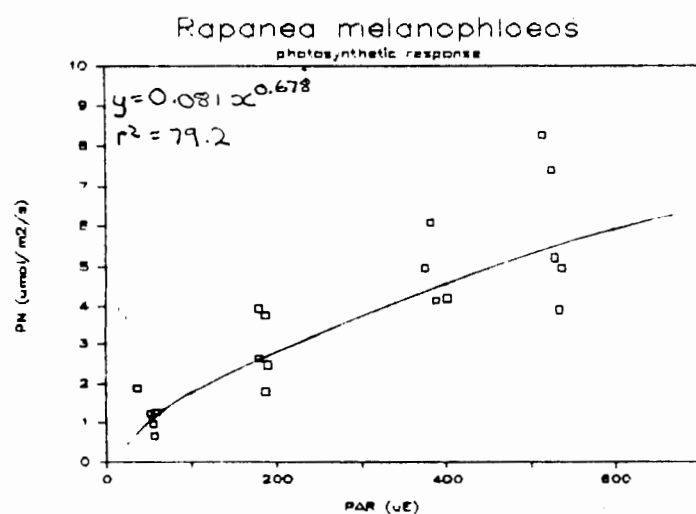
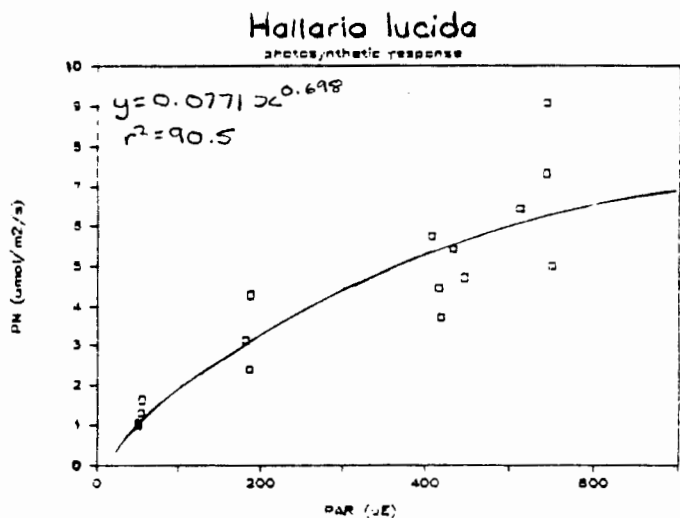
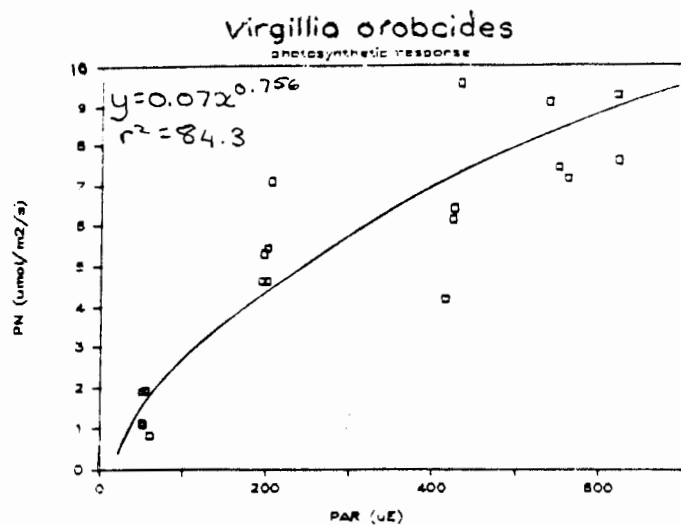
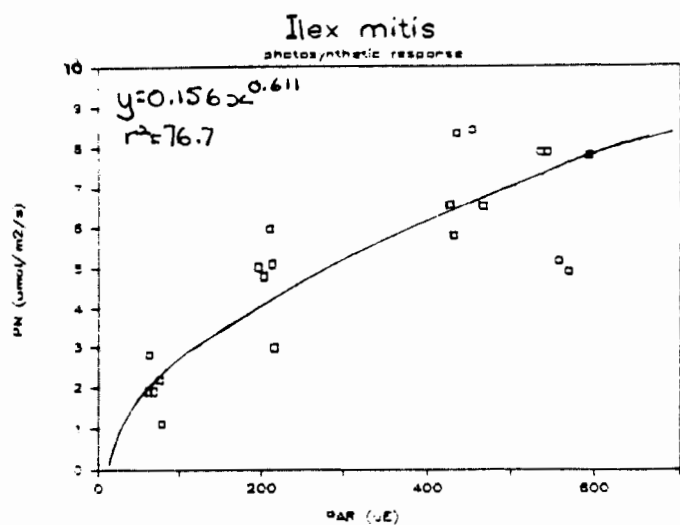


FIGURE 2 : Photosynthetic rate as a function of irradiance for the seven study species. The light intensity range simulates intensities of beneath a canopy to the intensity found in a large gap.

a) **Dry forest**

Species	Beneath canopy	Gap	$\chi^2$	p
<u>Rapanea melanophloeos</u>	4	53	41.1	0.0001
<u>Olea capensis</u> sub sp. <u>macrocarpa</u>	34	9	14.5	0.0001
<u>Podocarpus latifolius</u>	17	0	17	0.0001

b) **Moist forest**

Species	Beneath canopy	Gap	$\chi^2$	p
<u>Rapanea melanophloeos</u>	114	410	167	0.0000
<u>Olea capensis</u> subsp. <u>macrocarpa</u>	38	55	3.10	0.078
<u>Podocarpus latifolius</u>	7	5	0.33	0.564

c) **Gap size (in moist forest)**

Species	Small Gaps 40m <sup>2</sup>	Large Gaps 140m <sup>2</sup>	$\chi^2$	p
<u>Rapanea melanophloeos</u>	78	113	6.41	0.011
<u>Olea capensis</u> subsp. <u>macrocarpa</u>	11	16	5.76	0.016

**Table 1.** Frequencies of seedlings in canopy gaps and beneath the adjacent canopy (four 2m x 2m random plots); a) the dry regions of the forest (4 samples), b) the moist regions of the forest (11 different samples), and c) the different size gaps of the moist regions of the forest (samples of 2 small and 2 large gaps). Frequencies of other species were too low for analysis (see Appendix B).

## DISCUSSION

### Growth, Photosynthesis and Predictions:

All five species in the growth experiments showed a highest RGR in the open sunlight treatment, and thus would all benefit from increased light found under canopy gaps. This was especially true for Halleria lucida and Kiggelaria africana which showed very high above ground RGR under 0% shade (see Figure 1). An interesting feature was that these two species also exhibited high RGR under increased shade conditions, possibly indicating that their growth rate is intrinsically determined. This might be due to higher respiration rates or an inability to lower their respiration rate under shaded conditions. Field (1988) found this to be true for a pioneer forest species (Piper auritum) where, with a decrease in the photosynthetic capacity (with an increase in shaded conditions), the plant was unable to lower its dark respiration rate. This might have important ecological implications, in that although H. lucida and K. africana have high RGR in the shade, the ability to tolerate shade might decline as an individual grows if ratios of photosynthetic to non-photosynthetic tissues decline as the height and size crown increase (Canham 1989). This might result in stress to the plant making it more vulnerable to disease or episodic drought. Hence a high mortality rate of these individuals beneath the canopy after a certain age might be predicted and greater frequency of individuals surviving under canopy gaps.

On the other hand the very slow above ground RGR exhibited by Podocarpus latifolius and Rapanea melanophloeos in both high light and deeply shaded conditions would seem to indicate an adaptation to tolerating understory environment. Ilex mitis shows intermediate RGR between these two extremes, and might thus be expected to show some degree of adaptation to shade conditions, but at the same time respond quite well to gap openings. There

thus appears to be a continuum in above ground RGR's of the different species under all three growth conditions. A similar continuum might be expected in the forest where species such as H. lucida, K. africana and I. mitis occur in greater frequencies under canopy gaps than R. melanophloeos and P. latifolius.

One would expect these contrasting growth rates to be reflected by their photosynthetic rates (Pickett 1983), however this was not the case for all of the species. R. melanophloeos ( $6.2 \mu \text{ mol CO}_2/\text{m}^{-2}\cdot\text{s}^{-1}$  at  $600 \mu\text{E}$ ) had a much higher photosynthetic rate than P. latifolius ( $3.8 \mu \text{ mol CO}_2/\text{m}^{-2}\cdot\text{s}^{-1}$  at  $600 \mu\text{E}$ ) in spite of their similar growth rates. In fact, R. melanophloeos showed very similar photosynthetic rates to H. lucida ( $6.7 \mu \text{ mol CO}_2/\text{m}^{-2}\cdot\text{s}^{-1}$  at  $600 \mu\text{E}$ ) which had the highest RGR. Also K. africana with its high RGR showed a surprisingly low photosynthetic rate ( $4.8 \mu \text{ mol CO}_2/\text{m}^{-2}\cdot\text{s}^{-1}$  at  $600 \mu\text{E}$ ). The reason for such peculiar contrasts between growth and photosynthetic results in some species is because photosynthetic rates do not describe resource allocation to different parts of the plant. The fact that only above ground RGR's were measured and not below ground parts as well limits the interpretations of results. For example the fact that R. melanophloeos had a high photosynthetic rate but low above ground RGR is probably due to the plant allocating more of its resources to its roots. This is supported by the fact that R. melanophloeos tends to be a root resprouter (pers obs). Likewise the high above ground RGR of K. africana in comparison to its low photosynthetic rates might be due to there being a low allocation of resources to either the roots or antiherbivore defences or both, since this species is known to suffer heavy attacks from the host specific larvae of Acraea horta (Lepidoptera) (Raubenheimer 1987, also pers obs on some of my seedlings). Givinish (1988) stresses the need for a greater understanding of resource allocation in sun and shade plants, with more of a whole plant perspective. This is true for these results, where a knowledge of root growth and

morphology would increase our understanding of the response of these plants to different light conditions.

A further limitation of only knowing the photosynthetic response is that it does not tell us whether photosynthesis in the leaf is being limited by biochemical or physical factors. For example nitrogen content of the leaf is known to be one of the most limiting factors to the leaf's photosynthetic ability. I would suspect that the reason why Virgillia oroboides had the highest photosynthetic response ( $9.1 \mu \text{mol CO}_2/\text{m}^{-2}/\text{s}^{-1}$  at  $600 \mu\text{E}$ ) is due to a high leaf nitrogen content, since this species is known to be a nitrogen-fixing plant. The extremely low photosynthetic response found in P. latifolius is possibly due to the thick sclerophyllous nature of the leaf or an inability to produce enough of the enzyme RuBP carboxylase.

Nevertheless, these photosynthetic responses do give some indication of the potential for total net carbon gain in the plant. In the case of V. oroboides, even though its RGR was unknown, the very high photosynthetic rate ( $9.1 \mu \text{mol CO}_2/\text{m}^{-2}/\text{s}^{-1}$  at  $600 \mu\text{E}$ ) of the individual leaves would seem to indicate that this plant is an open site specialist. One can almost certainly predict for H. lucida, with both high photosynthetic and RGR's, that it is more of a gap specialist. I. mitis, R. melanophlocos, K. africana and possibly even Olea capensis subsp. macrocarpa might all be predicted to be light shaded species as they either have a moderately high photosynthetic response or moderately high RGR's (e.g. K. africana), and thus are probably partially dependent on gaps for successful regeneration. P. latifolius on the other hand has all the characteristics of being a deep shaded species (low photosynthetic and RGR). One would expect to find this species surviving well beneath the canopy, where most of its photosynthetic energy comes from short duration, direct beam radiation in the form of sunflecks (Denslow 1987).



### Seedling distribution in the forest:

The distribution of seedlings of these species in Grootvadersbosch (Table 1) supported a number of the predictions made from their photosynthetic responses and relative growth rates. In the moist forest regions, no significant difference ( $P = 0.56$ ) found between the frequency of seedlings of P. latifolius beneath the canopy and in the gap supports the idea of this species being a deep shaded plant that is able to maintain relatively slow growth rates beneath the canopy. Brief sunflecks of light through small openings in the canopy probably provide enough photosynthetic energy for this species to reach the canopy successfully. This idea is strongly supported in the drier regions of the forest where there were significantly more seedlings of P. latifolius beneath the canopy than in the gaps ( $P = 0.0001$ ), in fact no seedlings were found in the gaps. The stressful conditions found in a dry gap compared to a more mesic gap, appears to be acting as a selective force on the seedlings of P. latifolius. This was also true but to lesser degree for O. capensis sub sp. macrocarpa, where there was no significant difference between beneath canopy and gap seedling frequencies in the moist region ( $P = 0.07$ ), while in the dry regions there were significantly more seedlings beneath the canopy ( $P = 0.0001$ ). So even though O. capensis sub sp. macrocarpa exhibits a relatively high net photosynthesis it shows a similar response to P. latifolius of tolerating understory shaded conditions. O. capensis subsp. macrocarpa, however, did show a significantly greater frequency of seedlings in large gaps (Table 1c) indicating some positive response to gap conditions.

The highly significant positive response of R. melanophloeos to gap conditions in both the mesic and the dry regions correlates well to the relatively high net photosynthesis found in this species. Also the significantly higher frequency of seedlings found in larger gaps (Table 1c) indicates a favourable response

to canopy gaps. This pattern found is either due to higher mortality rates of this seedling beneath the canopy due to an inability to tolerate shaded conditions, or higher germination rates under gaps due to the increased light and temperature conditions. Phillips (1931) in his studies on succession in the Knysna forests, found this species to be vigorous on first appearance, but developed badly shaped stems and rooted systems, and were found to be liable to early fungus attack, thus suffering a high degree of mortality. These high mortality rates are evident if one looks at the frequency of saplings present (see appendix C) where in both beneath the canopy and in gaps there were close to no saplings. I suspect that most of these that were present were probably root resprouters from adult trees (persobs). I therefore suggest that although this species on first appearance would seem to indicate a favourable response to gap conditions, most of the juveniles that reach the canopy probably originate as root resprouters from adult trees. It would be interesting to test whether there are more resprouters in gaps than beneath the canopy.

The extremely low frequencies of V. oroboides, I. mitis, and K. africana, and the absence of H. lucida makes it difficult to test any of the predictions made for these species. The possibility of this being due to a low seed set cannot be considered since all of these species are known to have a very large seed set (Phillips 1931). One possible reason might be that the abundance of these particular tree species in the canopy is very low in Grootvadersbosch, thus resulting in a low total seed set. This would appear to be true for V. oroboides which rarely occurs in the forest interior, but tends rather to be confined to the forest margins (Taylor 1955, von Breitenbach 1976). Phillips (1931) noted that the seeds of V. oroboides will only germinate if stimulated by heat or bruising, thus further lowering chances of ever germinating in the interior of the forest since seeds

would only experience this condition in a gap. This species can therefore strongly be regarded to be a pioneer species under Swaine and Whitmore's (1988) definition. I. mitis, although fairly common in this forest, is restricted to very moist microsite conditions such as close to river streams (Taylor 1955, con Breitenbach 1976), which would explain the low frequency of seedlings found, since very few of the plots were situated in such microsites. K. africana and H. lucida however were both fairly common canopy trees throughout the forest, except in the very dry regions (Taylor 1955, also pers obs), and yet very few, if any seedlings of these species were found. As already mentioned, K. africana suffers heavy herbivore attacks from the larvae of Acraea horta (Lepidoptera) (Raubenheimer 1987), which might reduce number of seedlings substantially. Likewise, Phillips (1931) noted that H. lucida tends to be heavily browsed by buck in the Knysna forests. Grootvadersbosch appeared to have a fairly large population of bushbuck (pers obs), and thus might be suspected to be playing an important role in limiting the abundance of H. lucida seedlings.

The most significant finding appears to be the highly stressful conditions created by a gap in drier forest regions (mostly north facing slopes). Unfortunately water content of the soil beneath the canopy and in the gap was not measured, but from observation the soil in the gaps was much drier than beneath the canopy. In studies on tropical forests, moisture content has never been an issue since the high rainfall received by these regions always maintains more favourable conditions in a gap (there is no canopy to trap water). However in these Afromontane forests moisture appears to be of vital importance where it is more advantageous for a seedling in drier forests to germinate beneath the canopy. This has bearing on the south western Cape forest which suffers long summer drought periods. Lieberman et al (1989) suggests that forest ecologists need to shift away from viewing forests as gap

and non-gap situations and rather view them as a continuum based on light level. I would however, suggest that based on moisture content of the soil there is a marked difference between gaps and non gap environments in drier regions of Afromontane forests. Most of these gaps can therefore be predicted to fill, not by rejuvenation of young plants, but rather by the lateral ingrowth of the surrounding canopy trees. Knight (1989, pers com) noted that these drier forest regions are marked by much smaller gaps due to branchfalls being the source of the gap rather than treefalls, which would also reduce any chances of gap colonists being able to reach the canopy. One might therefore suspect that most of these drier forests are marked by a greater dominance of shade tolerant species such as P. latifolius and O. capensis sub sp. macrocarpa, compared to more mesic parts of the forest where species dependent on gaps at some stage of their life should be more abundant. McKenzie's (1978) findings, in comparing species densities in moist and dry forests would seem to support this hypothesis for the relevant species. In the dry forests, P. latifolius was found to have a high density in the canopy, subcanopy and understory (55/ha, 60/ha, and 83/ha respectively), while in the more mesic forests, densities were low in both the canopy and subcanopy (22/ha and 27/ha respectively) and were only high in the understory (77/ha), indicating an outcompeting of this species by other species in the moist forests. Likewise R. melanophloeos, which was predicted to be a light shaded species, was the most dominant species in the canopy of dry forests (168/ha), while in the moist forest it had a low density in the canopy (36/ha). H. lucida, which was predicted to be a gap species, was only found to occur in the moist forests.

These predictions made would need to be tested more rigorously in the future since this study was too brief to gain a true understanding of response of these species to light gaps. Age of gaps would need to be known, with a year round monitoring of

recruitment and growth of all tree species in the gap. Also of vital importance is a better understanding of the germination requirements and soil seed storage ability of these species.

I, therefore, conclude that even though these results have their limitations, the role of canopy gaps in Afromontane forest can be seen to play a minor role in the driving of the forest cycle. The bulk of these forests appear to be dominated by deep or light shaded species with pioneer species such as V. oroboides being confined to the fringes of the forest.

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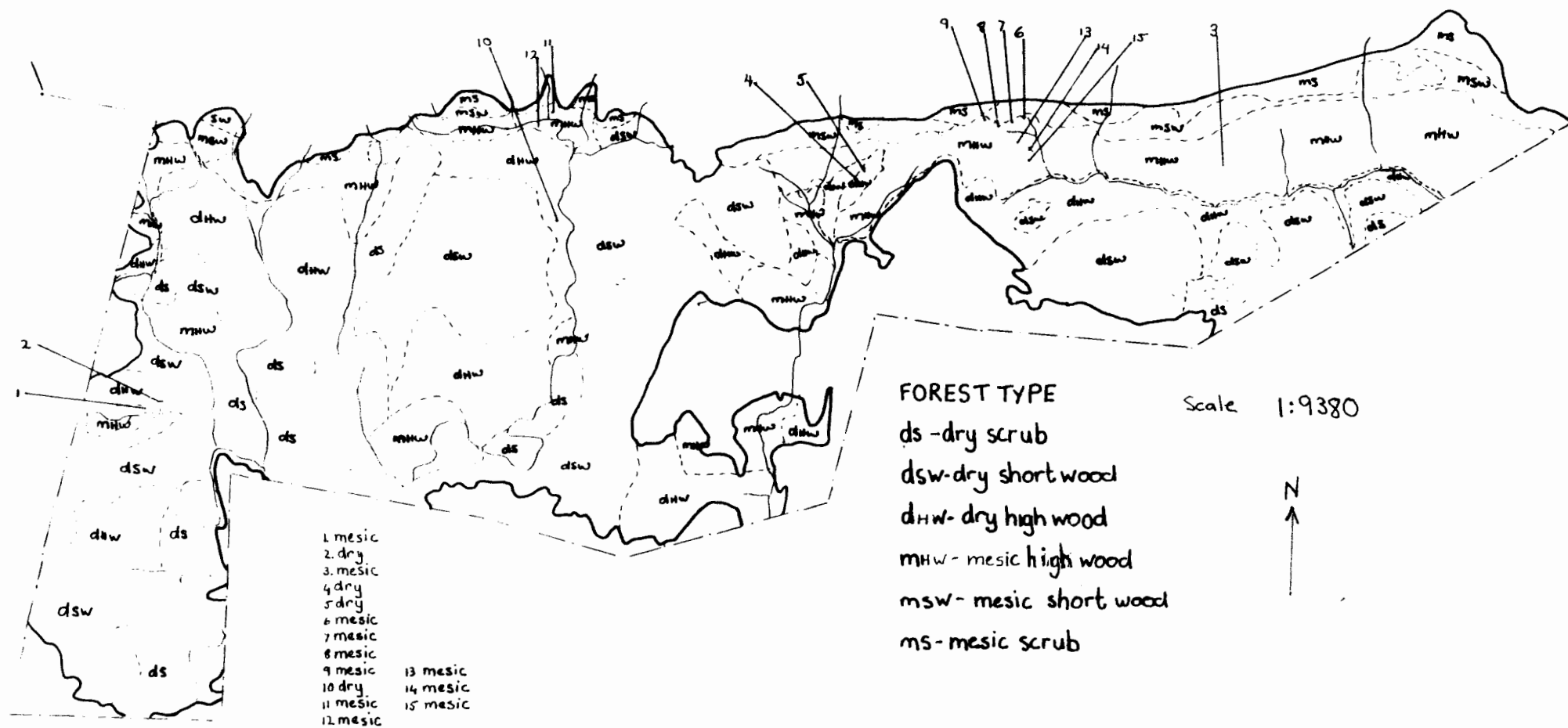
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APPENDIX A - The forest of Grootvadersbosch, showing the different forest types as well as the 15 sites where gaps were located.





### Moist forest

Species	Beneath canopy	Gap
<u>Kiggelaria africana</u>	2	8
<u>Ilex mitis</u>	0	2
<u>Virgillia oroboides</u>	0	1

**APPENDIX B.** Frequencies of seedlings in the gap and beneath the adjacent canopy (four 2m x 2m plots) in the moist regions of the forest (11 samples).

#### a) Dry forest (saplings)

Species	Beneath canopy	Gap	$\chi^2$	p 0.05
<u>Rapanea melanophloeos</u>	1	2	-	-
<u>Olea capensis</u> subsp. <u>macrocarpa</u>	10	12	0.181	X

#### b) Moist forest (saplings)

Species	Beneath canopy	Gap	$\chi^2$	p 0.05
<u>Rapanea melanophloeos</u>	3	6	-	-
<u>Olea capensis</u> subsp. <u>macrocarpa</u>	9	15	1.5	X
<u>Kiggelaria africana</u>	0	2	-	-
<u>Podocarpus latifolius</u>	3	6	-	-

**APPENDIX C** Frequencies of sapling species in the gap placed and beneath the adjacent canopy (four 2m x 2m plots) in a) dry forest (4 samples) and b) moist forest (11 samples).