AN INVESTIGATION INTO FOREST MARGIN DYNAMICS AND THE ROLE OF LEGUMES ON FOREST MARGIN SUCCESSION TWO YEARS POST FIRE.

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CONTENTS

ABSTRACT :

The floristics and dynamics of Southwestern Cape forests and their forest edges are virtually unknown, particularly with respect to disturbance regimes and post-fire nutrient cycling. Legume plants are hypothesized as an important component of forest edge vegetation and may facilitate post-fire forest re-establishment through enhanced nitrogen enrichment of the soils.

Species, their growth form, height and cover abundance were recorded along four transects occurring between forest and fynbos for three forest patches in the Hermanus district. Each transect consisted of four quadrats. Total nitrogen in the soil and all legume plants were identified for each quadrat.

Ordination plots were used to describe the community structure of forest and forest edge vegetation. Analyses of variances and multiple range tests were used to determine relationships between total nitrogen and legume species.

Forest edge vegetation was most clearly identified in the largest and oldest forest patch, and the poorest descrimination occurred in the youngest and smallest forest patch. Legume species were found to be associated with forest margins. Total nitrogen in the soil increased with the development of the forests.' Results of this study were consistent with the hypothesis that legumes occurring in forest edges contribute to forest succession.

INTRODUCTION :

Afromontane forest in the Southwestern Cape is restricted to isolated patches surrounded by fynbos, which is subject to fairly frequent fires. Margins of these forest patches are periodically burnt and succession initiated. During fire, nutrients are released from the vegetation and litter, and with high temperatures, nitrogen is volatilized (Granger 1984). Legume species are often found to be associated with post-fire succession along forest margins and their role in forest regeneration was investigated in this study.

According to Finegan (1984), autogenic changes have been shown to be brought about by plant communities. Crocker and Major (1955) demonstrated that changes in pH, organic content and accumulation of mineral nutrients, particularly nitrogen occur during primary succession. However, Drury and Nisbet (1973) suggest that the development of soils is only associated with primary succession, and that during secondary succession, modifications to the soil by early successional stages may often have the effect of bringing about a delay in succession. They also suggest that plants dominating the later stages of succession were present from the beginning and that their dominance in later stages is probably due to their slow growth and/or suppression of their growth by other species, in which case the process taking place can be described as either "tolerance" or "inhibition". However, if autogenic changes are taking place to the benefit of plants dominating later stages of succession, "facilitation" occurs (Connell and Slatyer, 1977).

In this investigation, forest margins which had been burnt two years previously were selected and the dominance and growth form of those plants within the forest and adjacent vegetation was described. The relative cover of legume species was determined and their effect on the total nitrogen in the soil was investigated. The role of legume species in succession was then assessed in terms of the models put forward by Connell and Slatyer (1977).

Study site :

The forest margins investigated were from the Hermanus district. The forests are at Vogelgat Nature Reserve (34°23'S, 19°19'E), Fernkloof Nature Reserve (34°23'S, 19°16'E), called Boekenhoutbos, and the third forest was above Voelklip and situated between Vogelgat and Fernkloof (34°24'S, 19°18'E) and was called Priscilla for the purposes of this investigation. Both Boekenhoutbos and Priscilla are riverine forests, whereas Vogelgat is a scree forest growing on the western slope of the valley above the Vogelgat River. At Boekenhoutbos the margin studied was situated on the eastern slope of the valley, while at Priscilla, and at Vogelgat the margin was to the north of the forest. Boekenhoutbos was the most developed forest and covered the largest area. Structurally, it was a tall forest (Campbell et al. 1981) with Rapanea melanophloeos, Chionanthus foveolatus and Cunonia capensis the most dominant overstorey species. The understorey was sparse and included : Rumora adiantiformis, Blechnum puntulatum, Blechnum sylvaticum, Myrsiphyllum scandens, and the seedlings of many of the overstorey species. The vegetation beyond the forest margin, which is referred to in this paper as fynbos, showed a gradient from tall open scrubland with a closed graminoid scrub understorey adjacent to the forest edge, to very sparse mid-high shrubland with a mid-dense graminoid understorey (Campbell et al. 1981), further from the forest-edge. Close to the forest, the dominant overstorey species included Rhus lucida, Rhus tomentosa, Protea nitida and Chrysanthemoides monilifera, and further from the forest Thesium spicatum and Othona quinquedentata dominated. In the understorey, both restioid and grassy components were present with the dominant species including Restio trilicens, Ficinia ramosissima and Pentaschistis curvifolia. Legume species found in the understorey included Indigophera augustfolius and Hypocalptus oxalidifolius.

The Priscilla forest consisted of a low forest with a very sparse understorey. This was the smallest forest patch and was restricted to the bottom of a narrow, steep-sided valley. The dominant overstorey species were Rapanea melanophloeos, Olea capensis ssp. capensis, Chionanthus foveolatus and Brachylaena neriifolia. The fynbos vegetation adjacent to the forest edge was structurally tall mid-dense shrubland with a closed graminoid shrub understorey (Campbell et al. 1981). The dominant overstorey species were Thesium spicatum, Chrysanthemoides monilifera and Protea nitida. The understorey species included Pentaschistis curvifolia, Protasparagus compactus and Muraltia heisteria. Legume species which occurred here were Hypocalyptus oxalidifolius, Indigofera augustifolius and the creeper Dipogan lignosus Further from the forest edge the understorey became a mid-dense graminoid shrubland with a very sparse mid-dense cyperoid shrub overstorey (Campbell et al. 1981) composed of Othona quinquedentata, Thesium spicatum and Tetraria thermalis. Dominant species in the understorey were Pentaschistis curvifolia, Protasparagus compactus and the legumes Aspalanthus serpens and Indigofera augustifolia.

In terms of structural classification of Campbell et al. (1981), the forest at Vogelgat was a closed woodland, with trees 10 metres or less in height, and much younger in age than those in the other forest sites. The dominant species were Olea capensis ssp capensis, Cunonia capensis and Maytenus accuminata. The understorey was sparse and comprised mainly of seedlings and saplings of the overstorey species. Two legume species were also present : the 1.5m shrub Indigofera filifolia and Dipogon lignosus. The adjacent vegetation contained no proteoid or restioid elements, but is still referred to here as fynbos, and there was no gradient similar to those observed at the other forest sites. Strucutrally it was a mid-high, mid-dense shrubland with a closed grassy shrub understorey (Campbell et al. 1981). The dominant overstorey species were Indigofera superba, Othona quinquedentata and Widdringtonia nodiflora. Understorey dominants included Ficinia cappillaris, Thesium spicatum and Ursinia chrysanthemoides.

METHODS :

Four replicate transects were taken across the gradient from within the forest and into the surrounding fynbos vegetation at each forest site. Along each transect, four circular quadrats were placed, each with an area of $4m^2$. One quadrat was placed within the forest 10m from the forest edge, another outside the forest, also 10m from the edge, and the next two at 10m intervals along the transect.

Each quadrat was marked and the following information was determined : a) the species present, b) the estimated abundance of each species as a percentage cover, c) the origin of each species (resprouter or reseeder), d) the growth form (herbaceous, woody or climber). In September 1988 each site was revisited and a soil sample was taken at each quadrat from the A_1 horizon. The soil samples were air dried and sieved through a 2mm mesh. Total nitrogen was then found for 1.0000g of soil from each sample using the standard Kjeldahl digestion and phenol-hypochlorite method for the determination of nitrogen.

STATISTICAL ANALYSIS :

For each set of replicates an ordination was carried out using correspondence analysis, also known as reciprocal averaging, to delimit and describe the forest and fynbos communities. Reciprocal averaging was used as it has been shown to be one of the more discriminating methods for showing succession (Knight 1988). Relative cover was calculated for legume species, those species which had resprouted after fire and for climbing and woody species. The relative cover of the legume species was arcsin transformed and one-way analysis of variance was then used to compare variations in relative cover of these species in forest and fynbos communities revealed by the ordination and also for the mean of the quadrats along the transects at each site. Multiple range tests were then carried out to locate significance. One-way analysis of variance and multiple range tests were also used to investigate differences in the total nitrogen in soils beneath forest and fynbos communities and along the transects, total cover was treated in the same way. The average number of species per $4m^2$ quadrat, (species richness) and the mean height of the canopy was calculated for forest and fynbos communities, and along the transects. One-way analysis of variance and multiple range tests were carried out using the Statsgraphics computer package (Anon,1986).

RESULTS :

Using the coordinates on axis 1 and 2 for quadrats the ordination for Boekenhoutbos (Figure 1) revealed that in floristic terms, the forest community was distinct from the fynbos community and that the ecotone did not extend across the 10m distance between the forest edge and the first quadrat. Furthermore, the fynbos community was composed of two sub-communities which have been called fynbos 1 and fynbos 2. The ordination for quadrats at Priscilla (Figure 2) also using axis 1 and 2 shows a less homogeneous forest community with the fynbos once again distinct from forest. For the Vogelgat quadrats the ordination (Figure 3) illustrates a far more heterogenous forest community than at the other sites , but the fynbos community was more homogeneous. From the ordination of quadrats at all the forest sites using axes 1 and 4, (Figure 4) the fynbos communities are shown to be very much more heterogeneous than the forest, and that the fynbos community at Vogelgat is unlike that at the other two sites.

Species richness in the three forest communities was predicatably much lower than for the fynbos communities. The lowest value for the forest communities was recorded at Priscilla, and the lowest for fynbos communities was at Vogelgat (Figure 5). Total cover was greatest for the forest community at Boekenhoutbos, and decreased from the fynbos 1 to the fynbos 2 community (Figure 6). The forest community at Boekenhoutbos also had the highest canopy of the three forest sites investigated (Figure 7), with the Priscilla forest community having the lowest canopy. There was little difference in canopy height for the two fynbos communities at Boekenhoutbos.

The relative cover of woody species at Boekenhoutbos was lower than at the other forest communities (Figure 8), and a decrease in relative cover from the fynbos 1 to the fynbos 2 community. Fynbos 1 had a higher relative cover of woody species than the fynbos at the other two sites, and there was also a higher relative cover for species having resprouted after the fire in this community compared with the other communities (Table 1). Relative cover for climbers did not show any particular trend (Table 1). At both Vogelgat and Priscilla, the relative cover of legume species was higher in the fynbos communities than in the forests, but not significantly so (at Vogelgat $F = 0.24$, $P > 0.05$; and at Priscilla $F = 4.25$, $P > 0.05$). Relative cover was also greater at these sites than at Boekenhoutbos, where there was a gradient from the fynbos 1 to fynbos 2 community and no legumes are found in the forest (Figure 9).

Total nitrogen in the soil under the two fynbos communities at Boekenhoutbos decreases with increasing distance from the forest edge (Figure 10), but multiple range testing showed this difference to be insignificant. The total nitrogen in soils beneath forest communities at all three sites was significantly higher than beneath the surrounding fynbos communities (Vogelgat $F = 11.64$, $P<0.001$; Priscilla $F = 5.32$, $P<0.05$; Boekenhoutbos $F = 20.80$, $P<0.001$).

Gradients were observed within the fynbos communities at Boekenhoutbos and Priscilla, which did not occur at Vogelgat. Illustrating these gradients are the trends towards lower total cover with distance from the forest edge (Figure 11). At Priscilla, the total cover at 10m was much higher than at 20m and 30m, and at Boekenhoutbos total cover was much greater at both 10 and 20m than at 30m. Although the differences between the points along the transects were not statisically significant (Boekenhoutbos $F = 3.01$, $P>0.05$; Priscilla $F = 1.46$, $P>0.05$). Ten metres from the forest edge at Priscilla, the relative cover of woody species was also much higher than further along the transect, and at Boekenhoutbos both at 10m and 20m from the forest edge there was a much higher relative cover of woody species than at 30m (Figure 12). The relative cover of legume species (Figure 13) at Boekenhoutbos was highest at 20m from the forest edge and at Priscilla at was highest at 10m, although these differences were also not statistically significant (at Boekenhoutbos, multiple range teat shows no difference between fynbos quadrats and at Priscilla $F = 2.71$, $P>0.05$). Twenty metres from the forest edge at Vogelgat the highest relative cover of legume species occurred, and at this distance the total cover was lowest as was the total soil nitrogen (Figure 14). However, at Boekenhoutbos and Priscilla there was a gradient of decreasing total nitrogen along the transect from the forest.

Table 1 :

The relative cover of species wich have resprouted two years post-fire, and climbers in the different communities at Vogelgat, Priscilla and Boekenhoutbos forest sites ($\pm$ the standard error)

	n	Rel. cover of post-fire resprouters	Rel cover of climbers
Vogelgat Forest	4	0	0.165 $\pm$ 0.15
Vogelgat Fynbos 1	12	0.358 $\pm$ 0.06	0.020 $\pm$ 0.01
Priscilla Forest	4	0	0
Priscilla Fynbos 1	12	0.450 $\pm$ 0.07	0.020 $\pm$ 0.02
Boekenhoutbos Forest	4	0	0.350 $\pm$ 0.01
Boekenhoutbos Fynbos 1	7	0.563 $\pm$ 0.04	0.002 $\pm$ 0.001
Boekenhoutbos Fynbos 2	5	0.496 $\pm$ 0.04	0

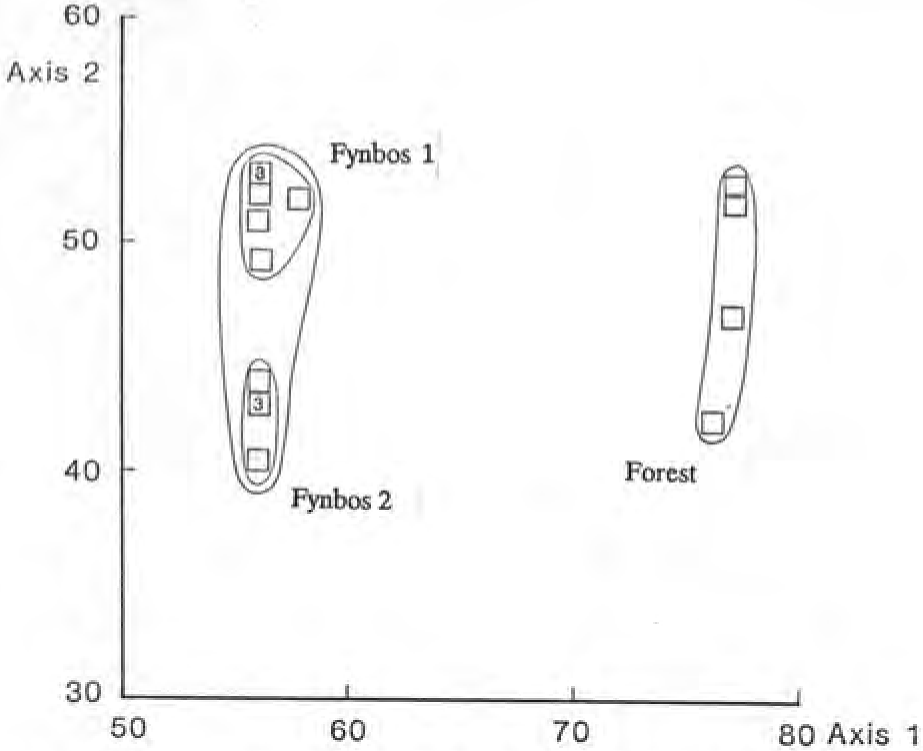

FIGURE 1 : Correspondence analysis for quadrats at Boekenhoutbos using axes 1 and 2. The number in the symbol represents the number of quadrats occupying the same position.

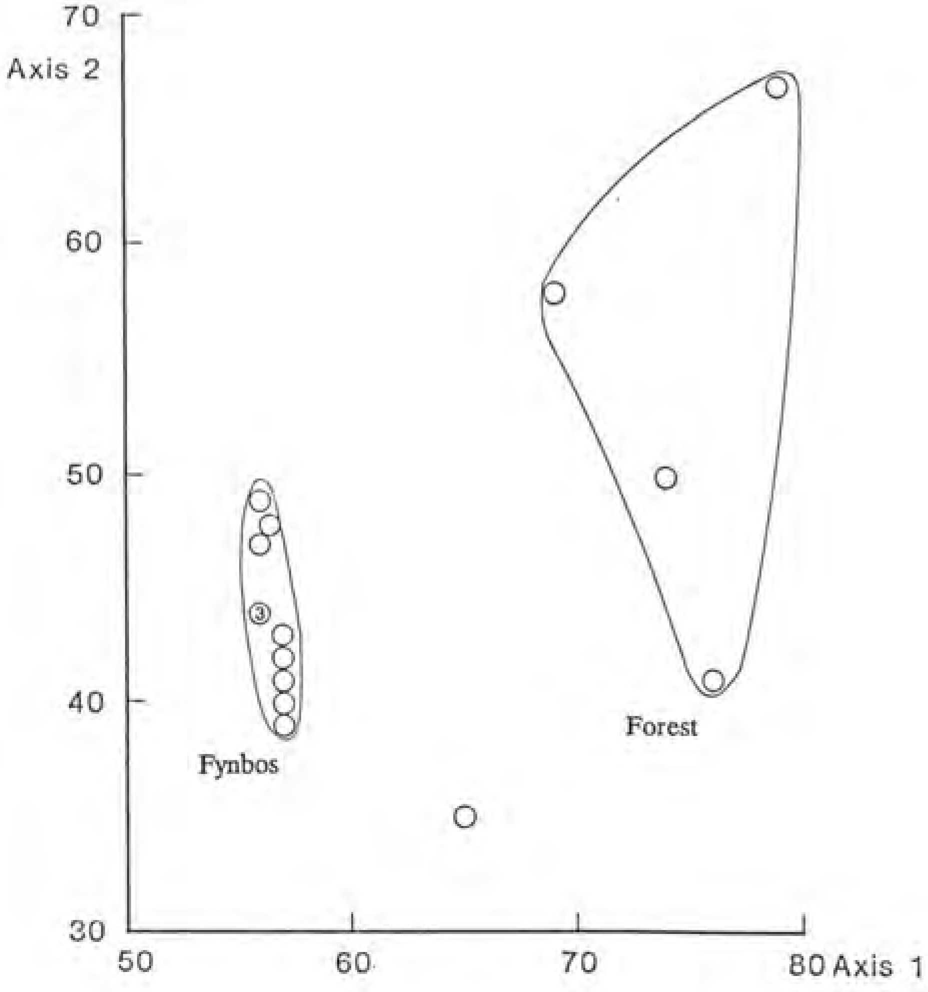

FIGURE 2 : Correspondence analysis for quadrats at Priscilla using axes 1 and 2. The number in the symbol represents the number of quadrats occupying the same position.

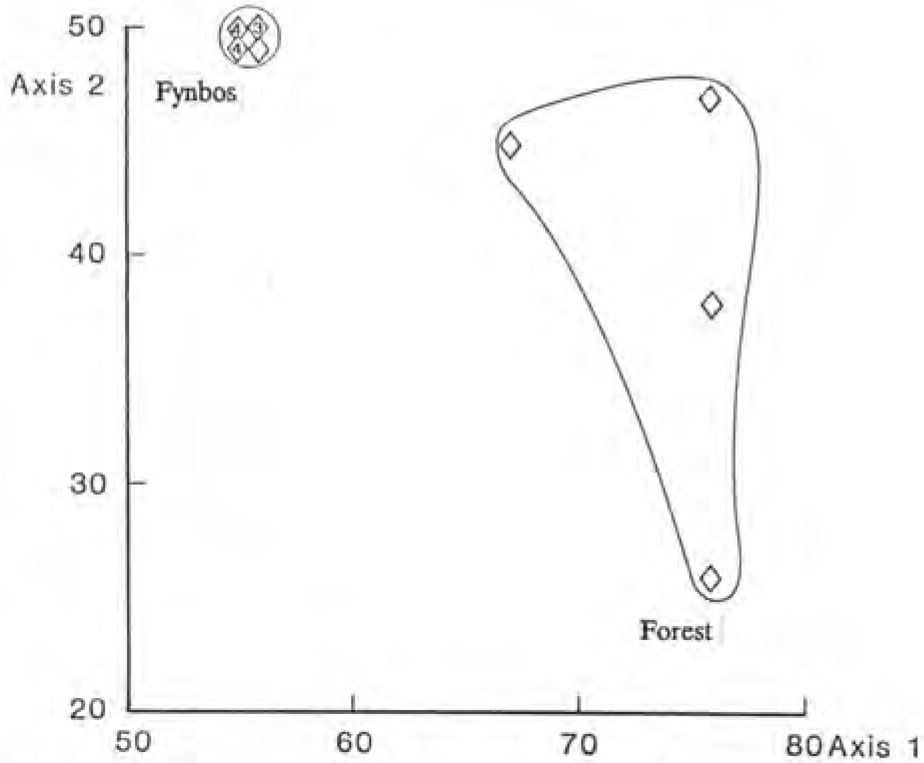

FIGURE 3 : Correspondence analysis for quadrats at Vogelgat using axes 1 and 2. The number in the symbol represents the number of quadrats occupying the same position.

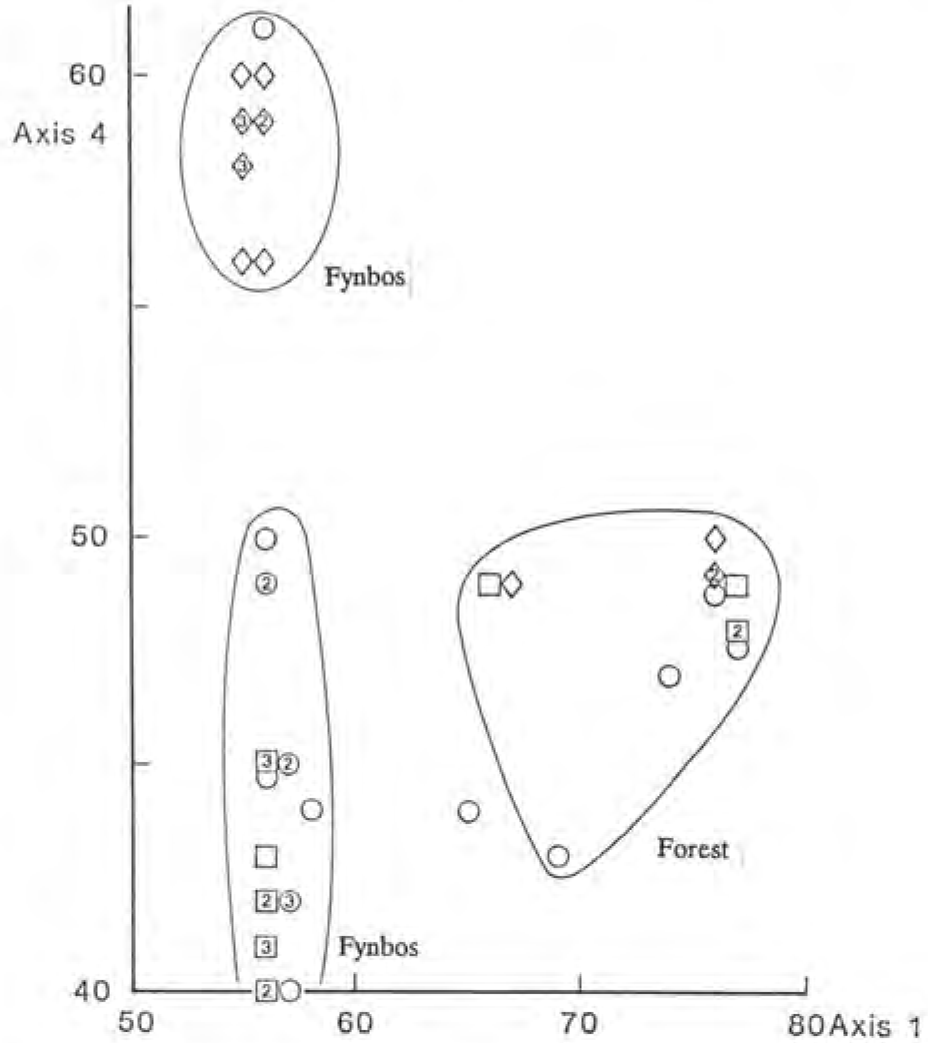

FIGURE 4 : Correspondence analysis for quadrats at Vogelgat, Priscilla and Bockenhoutbos forest sites using axes 1 and 4. The number in the symbol represents the number of quadrats occupying the same position.

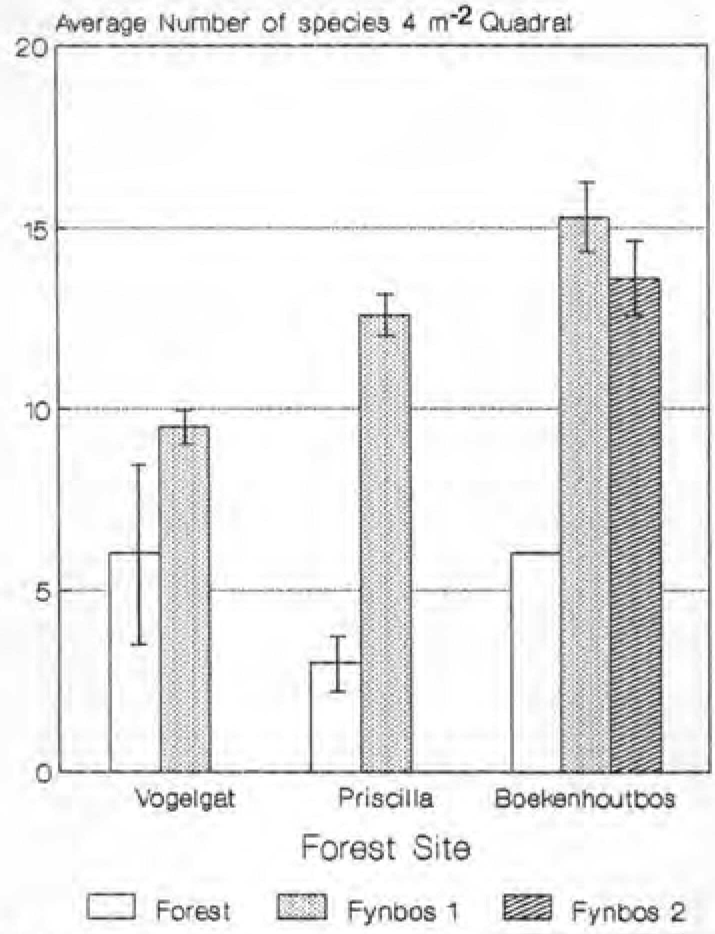

FIGURE 5 : The average number of species per $4m^2$ quadrat(species richness) in the forest and fynbos communities at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

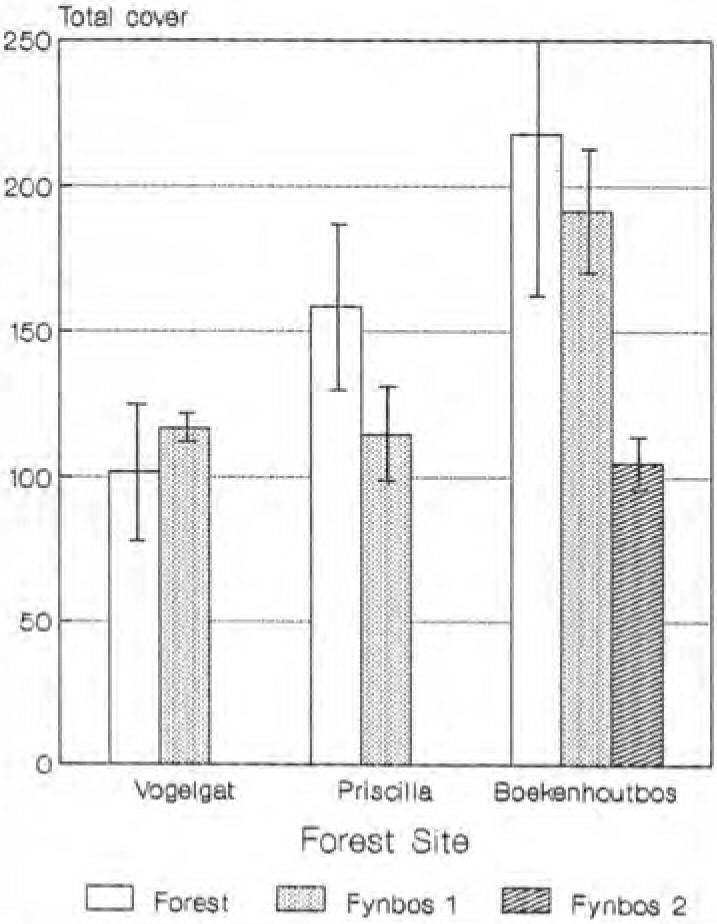

FIGURE 6 : The total cover per $4m^2$ quadrat in the forest and fynbos communities at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

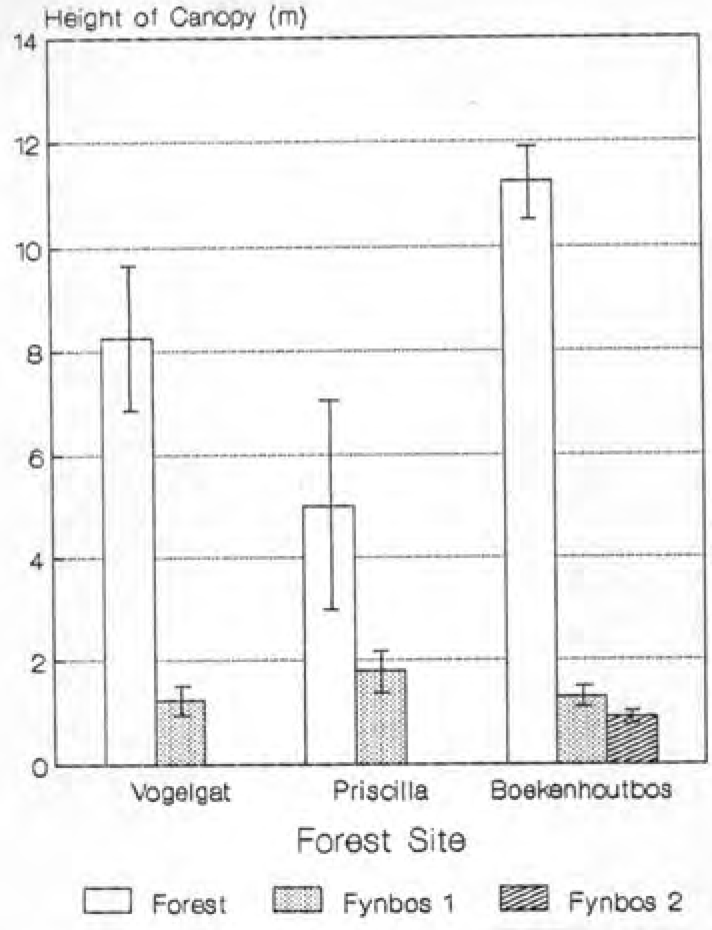

FIGURE 7 : The height of the canopy at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

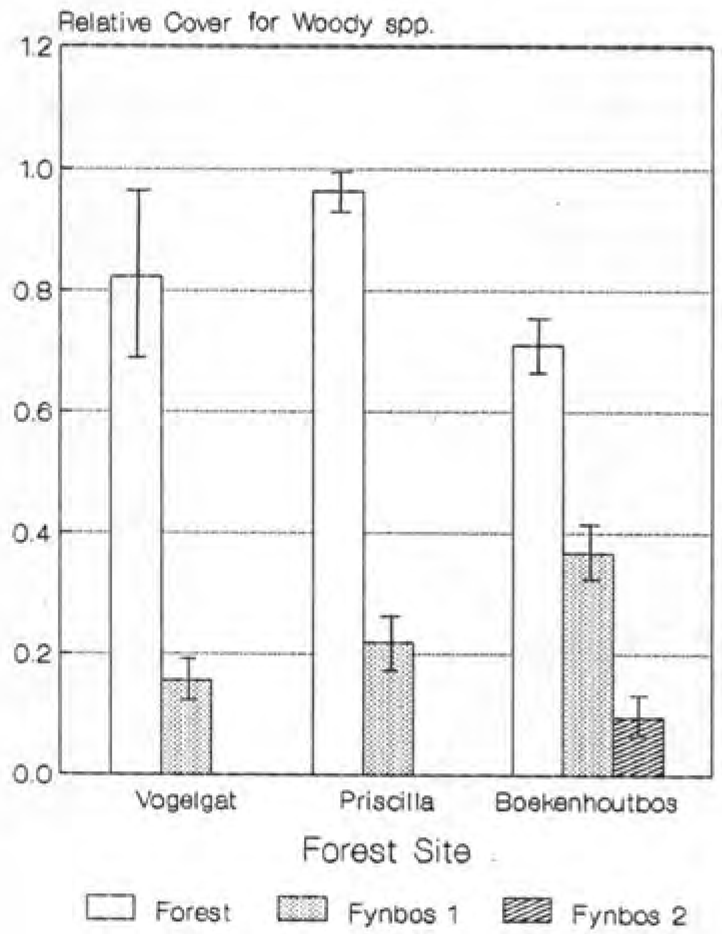

FIGURE 8 : The relative cover for woody species at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

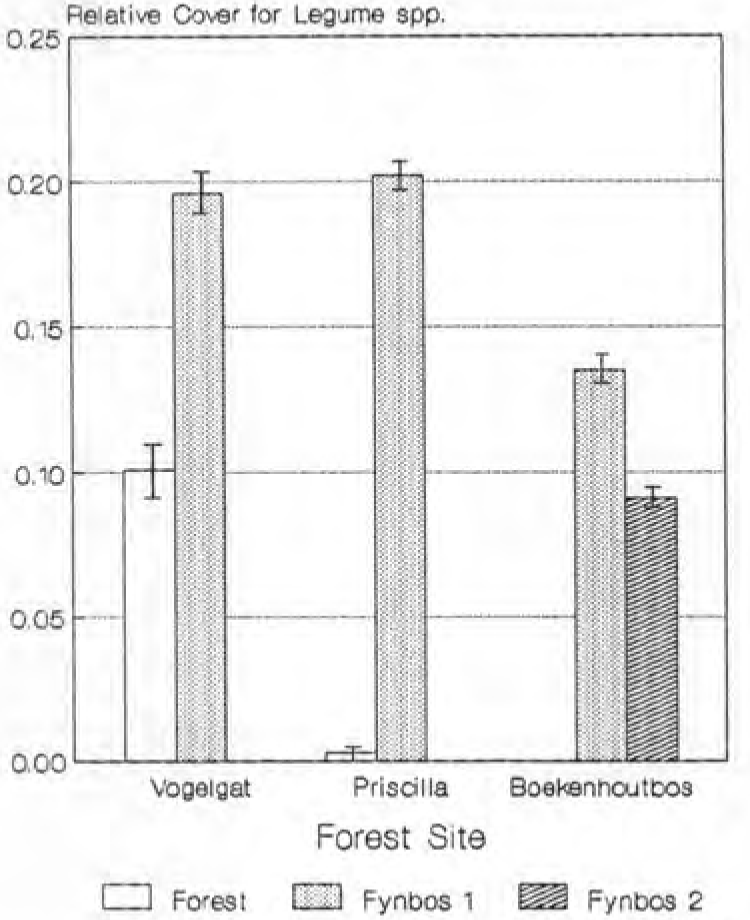

FIGURE 9 : The relative cover for legume species at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

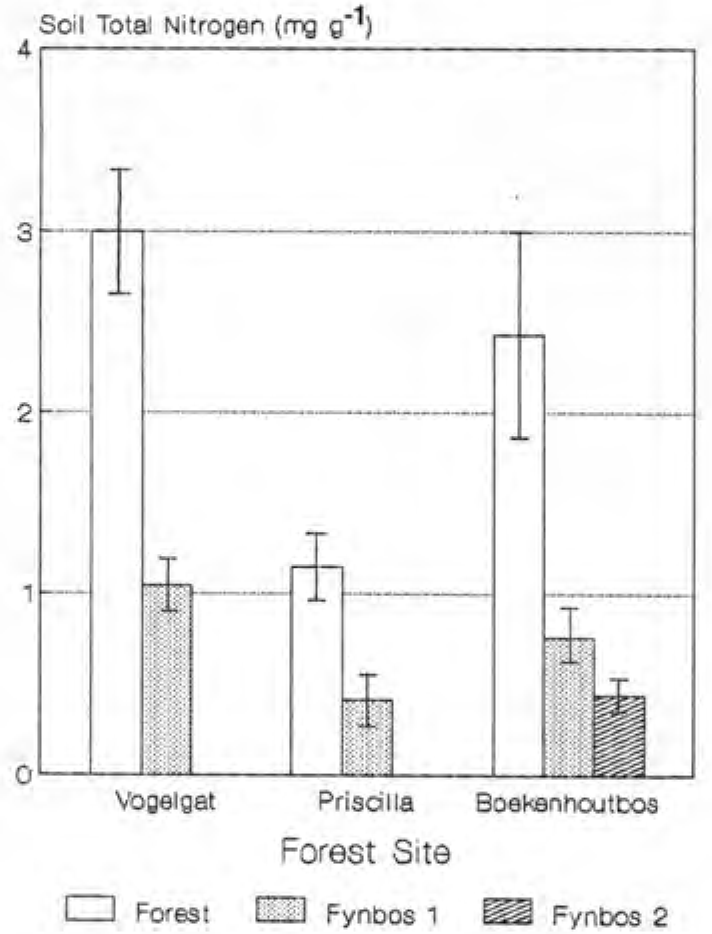

FIGURE 10 : Soil total nitrogen (mg g^{-1}) at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

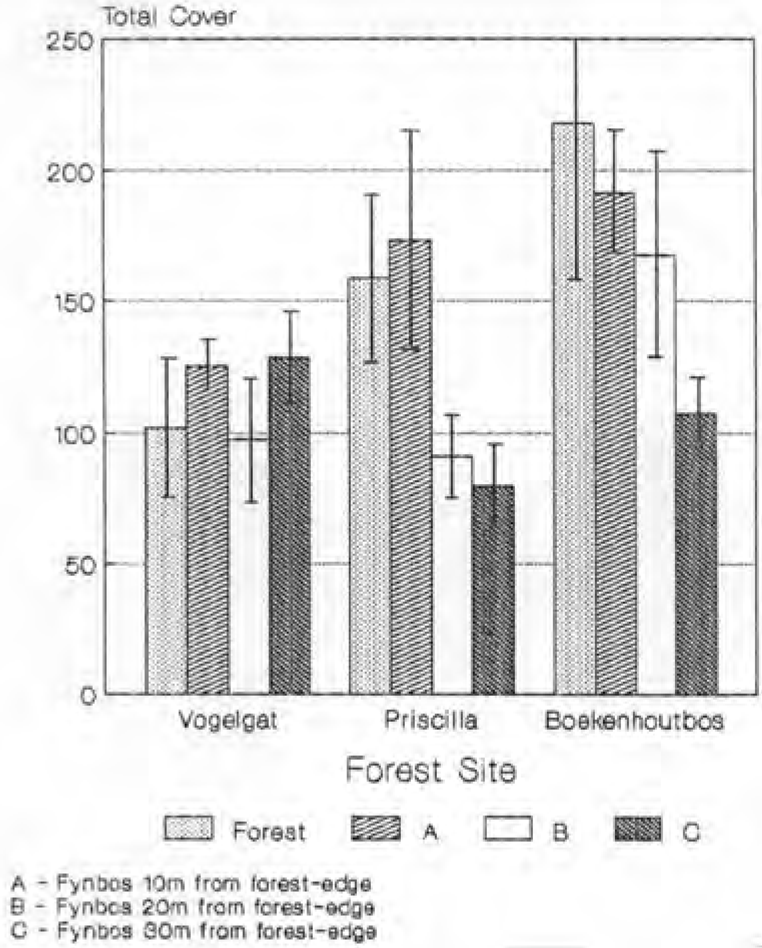

FIGURE 11 : Total cover at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

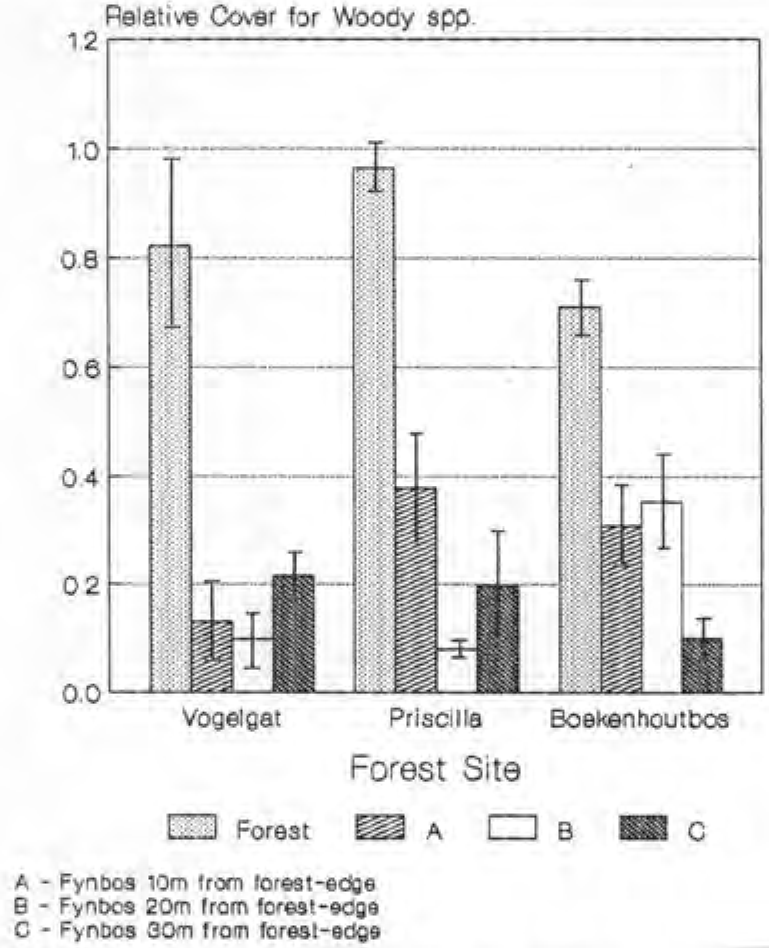

FIGURE 12 : Relative cover for woody species at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

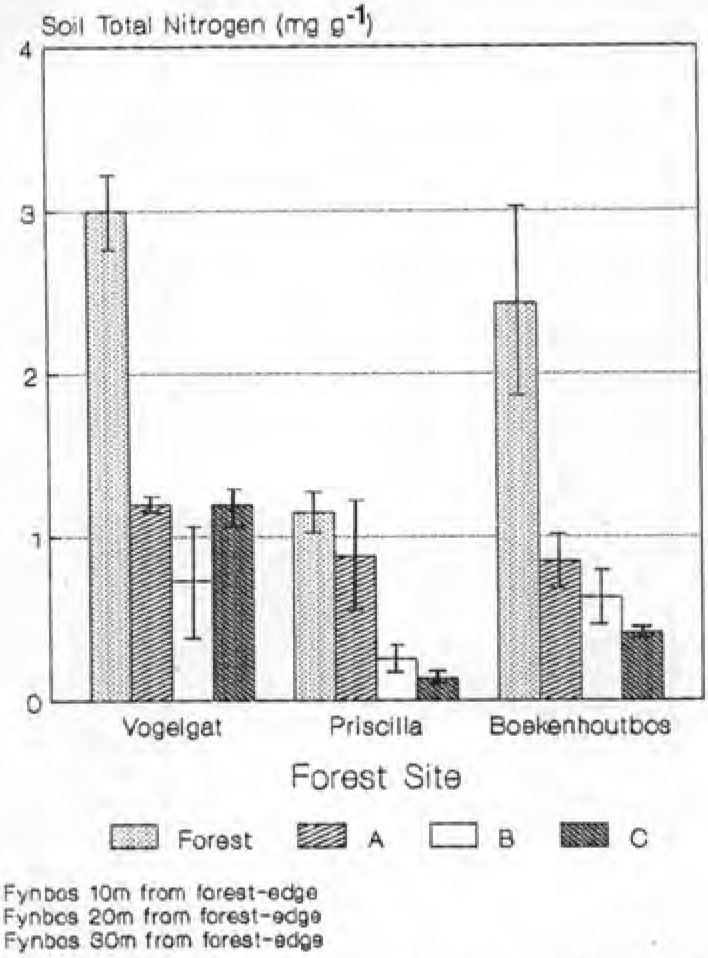

FIGURE 14 : Soil total nitrogen (mg g^{-1}) at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

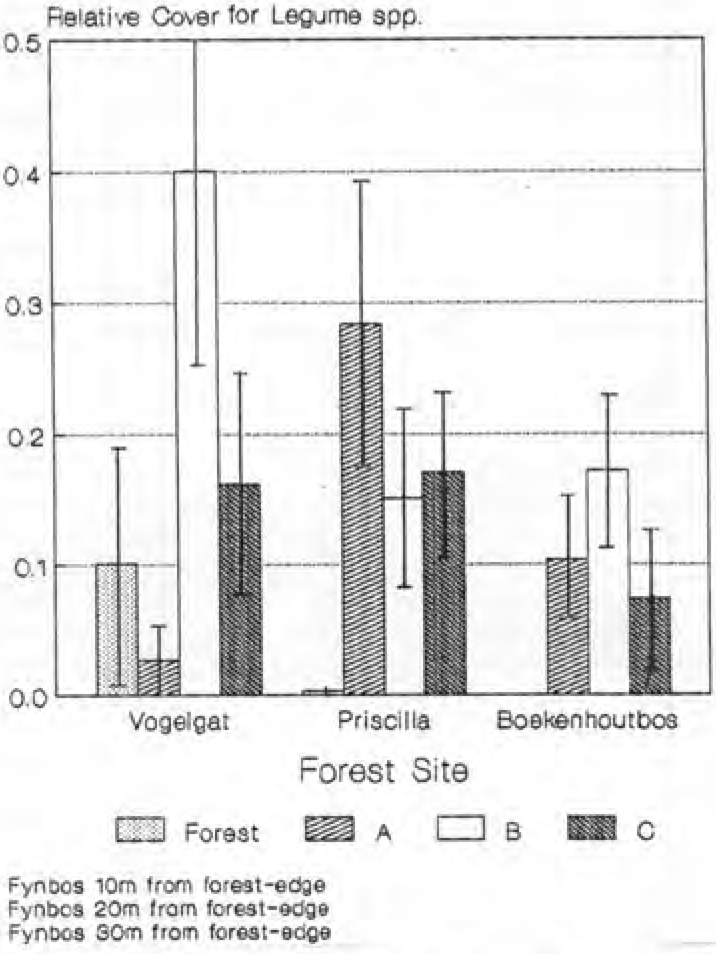

FIGURE 13 : Relative cover for legume species at the Vogelgat, Priscilla and Boekenhoutbos forest sites. (Vertical bars represent S.E.M.)

DISCUSSION :

The ordination of the three forest sites illustrated that in none of these forests had the ecotone extended across the 10m gap between the forest edge and the first fynbos quadrat during the two years since the last fire. However, at Boekenhoutbos, the separation of the fynbos community into two sub-communities would indicate that a margin community was probably developing. The ordination also shows that the Priscilla forest community was less homogeneous than at Boekenhoutbos. This may be accounted for by the size of the Priscilla forest. At Boekenhoutbos the forest covers a larger area, is well established and is much older. The forest at Vogelgat was less homogeneous than the other two forests, due largely to its age and although larger than the forest at Priscilla, the tree species were shorter, with narrower trunks and the forest was less dense. The fynbos community at Vogelgat differed significantly from those at Boekenhoutbos and Priscilla, and this was illustrated by the ordination in which axes 1 and 4 were used, and from its species composition it is probably less advanced in successional terms.

Species richness appears to be directly related to the size and age of the forest. Boekenhoutbos, the largest and oldest forest, has the greatest species richness, with the lowest recorded at Priscilla, the smallest forest. In the fynbos communities, species richness is one of the factors which differentiates the Vogelgat community from those at the other two sites and indicates its low level of development. The high total cover at the Boekenhoutbos forest was also related to the age and size of the community, a well developed understorey comprising ferns, climbers and the seedlings of the canopy species was well established, a situation which had not occurred at the other forests. The difference in total cover of the two fynbos communities at Boekenhoutbos also suggests that a margin community was developing, and the age of the forest accounts for the higher canopy. Age does not account for the differences in canopy height between the forests at Vogelgat and Priscilla. At Priscilla, the forest is not as clearly defined and forest margin species like Podylaria calyptrata were found growing amongst the forest species.

The low relative cover of woody species at the Boekenhoutbos forest was due to the establishment of an understorey, but at Priscilla this understorey was not as well developed and a higher relative cover of woody species was recorded. The difference in relative cover of woody species in the fynbos community at Boekenhoutbos is further evidence for the hypothesis that a margin community is developing and the higher relative cover of species which have resprouted after the fire would indicate that a margin community had existed along the edge of the forest before the fire. Furthermore, among those species forming the overstorey in this community was Chrysanthemoides monilifera, a bird dispersed species which has been associated with forest succession (Knight et al 1988). The absence of legume species in the forest community at Boekenhoutbos is a reflection of the age and degree of establishment of this forest. At both Priscilla and Vogelgat, legumes were found and at Vogelgat where the forest community was no more than a closed woodland, Dipogon lignosus was abundant. The relative cover for legumes in the fynbos community at Boekenhoutbos indicated a clear association with the developing margin community, and the difference in total nitrogen in the soil under these communities would suggest that these species were playing some role in the development of the soil. However at the Priscilla site the highest relative cover for legume species in the fynbos community was recorded, but the soil under this community had the lowest total nitrogen. This may indicate that a simple relationship in which a facilitation model can be applied did not exist.

From the total cover calculated for the points along the transect at Boekenhoutbos it was apparent that the margin community which was developing extended up to 20m from the forest edge. Thus, at Boekenhoutbos, which is the larger and more established forest the margin community extends further from the forest edge. At Priscilla, where a similar margin community appears to be developing, it is narrower, only extending 10m from the forest edge. At Vogelgat where the forest community was poorly developed, no margin community seems to be developing. Results for the relative cover of woody species supports this finding.

The distribution of legume species along the transect suggests that at Boekenhoutbos they are associated with the outer edge of the margin community, and play a role in early succession, as they are at a competitive advantage in soil with a low nitrogen content. As they are short-lived, their decay may lead to an increase in the soil nitrogen level, and their competitive advantage is lost particularly to the resprouting woody species. At Priscilla a similar situation was seen, with legume species found predominantly along the developing margin. However trends in the total nitrogen in the soils along the transect are unrelated to those trends observed for the relative cover of legume species, and at Vogelgat, where no forest margin community was identified the relative cover for legume species was highest where the lowest levels of total nitrogen were recorded. There appears to be closer link between total cover and soil nitrogen levels; as the total cover increases along the transect so soil nitrogen levels increase.

These findings conflict with those of van Daalen (1984) who found no difference in the total nitrogen in forest soils in the Southern Cape and adjacent fynbos soils. However, the differences in these results are best accounted for by the fact that in the study by van Daalen, the forest-fynbos edges were artificially induced, whereas, in this study the edges have long been established. The total cover measured here is an indication of the total biomass, and it seems likely that as the biomass increases along the gradient towards the forest, the organic content of the soil also increases. With greater organic content, nitrogen, which was incorporated into the system by legume species, is not as readily leached from the soil, accounting for the higher total nitrogen along the gradient. Organic material also increases the water retaining capacity of the soil and, as was suggested by Knight et al. (1988), seed germination will be enhanced, ultimately leading to the development of a forest community.

It is not possible to assess the role of legume species in succession simply in terms of the three models suggested by Connell and Slatyer (1977). The mechanisms involved are considerably more complex. (Finegan, 1984; Pickett, Collins and Armesto, 1987). Although legume species have been shown to play a role in forest succession, models like facilitation, tolerance and inhibition are not appropriate as they describe mechanisms which can occur simultaneously and with varying degrees of importance (Huston and Smith 1987). Edaphic factors such as parent rock material, the rockiness of the soil and the soil moisture have also been shown to be of considerable importance in determining the colonisation of areas by forest species (Masson and Moll, 1987) and must play a significant role in determining both the rate and extent to which forest succession can take place.

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