

**GAP REGENERATION IN THE TSITSIKAMMA FOREST (EASTERN CAPE,
SOUTH AFRICA): THE EFFECT OF GAP SIZE AND ORIGIN**

BY GHISLAIN ELLA

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SUPERVISORS:

MR. DAVE PEPLER AND PROF. MELODIE A. MCGEOCH

**DEPARTMENT OF CONSERVATION ECOLOGY
FACULTY OF AGRICULTURAL AND FORESTRY SCIENCES**

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DECLARATION

I, the undersigned, hereby declare that the work contained in this assignment is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature:

Date:

Ghislain ELLA

ABSTRACT

Recognizing the biological significance of gaps, the South African Department of Water Affairs and Forestry (DWAF) in 1989 initiated a Gap Dynamics Project in the indigenous forests of Tsitsikamma (Eastern Cape, South Africa). This consists of three sub-projects: Koomansbos (9300 m²), created by a ground fire in 1989; Plaatbos (1600 m²), made by a *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) windfall in 1994; and nine gaps of different sizes, artificially created by selective tree felling in 1995: three small (100-150 m²), three medium (300-500 m²) and three large (800-1000 m²). All the gaps were surveyed after creation and permanent plots were established for subsequent monitoring. The current timber harvesting system practiced in South African indigenous forests attempts to minimize gap size. It has been proposed by Euston-Brown *et al.* (1996) that this practice is likely to benefit the more shade tolerant species, but may inhibit the regeneration of less shade tolerant plants in the forest. Therefore, the present study aimed to verify two hypotheses: gaps may close in a process that is determined by their size, their origin and the plant species characteristics; soil quality might change inside those gaps. For the purpose of the study, the gaps cited above were re-surveyed between 2002 and 2003. It was found that: 1) there was little clear difference in the community structure of plant species between gaps of different sizes and origins; as expected from the species-area relationship, large gaps had higher species richness, plant diversity and herbaceous percentage cover than medium and small gaps; diversity indices were higher in the large windfall gap than in the large fire and artificial gaps; generally, context and stochastic events were largely more important in determining gap diversity and regeneration than gap sizes and origins; 2) diversity indices in the gaps were higher than recorded previously; 3) soil pH and Electrical Conductivity were respectively lower and higher inside the gaps than adjacent to them; these variations were statistically significant. Present data on the vegetation in the gaps were compared to past measurements, and future vegetation structure has been predicted, as a function of current gap vegetation. Recommendations have been made for sustainable management of the indigenous forest of Tsitsikamma.

OPSOMMING

Voortspruitend uit die erkenning van die biologiese belang van gapings, het die Suid-Afrikaanse Departement van Waterwese en Bosbou (DWB) in 1989 'n projek oor gapingsdinamika in die inheemse woude van Tsitsikamma (Oos-Kaap, Suid-Afrika) geïnisieer. Dit bestaan uit drie subprojekte: die gaping in Koomansbos (9300 m²) wat in 1989 deur 'n grondvuur geskep is; die gaping in Plaatbos (1600 m²) wat veroorsaak is toe bome van die spesie *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) in 1994 omgewaai is; en nege gapings van verskillende groottes wat in 1995 kunsmatig deur geselekteerde boomkappery geskep is: drie is klein (100-150 m²), drie mediumgrootte (300-500 m²) en drie groot (800-1000 m²). Alle gapings is ná hulle ontstaan opgemeet en ondersoek en permanente terreine is vir daaropvolgende monitering gevestig. Die stelsel wat tans vir die oes van hout in Suid-Afrikaanse inheemse woude gebruik word, poog om die grootte van gapings te minimaliseer. Euston Brown *et al.* (1996) doen aan die hand dat hierdie praktyk spesies wat meer skaduweeverdraagsaam is waarskynlik sal bevoordeel, maar die regenerasie van plante in die woud wat minder skaduweeverdraagsaam is, kan inhibeer. Hierdie studie het dus ten doel gehad om twee hipoteses te verifieer: Gapings kan toegroei in 'n proses wat deur hul grootte, oorsprong en die eienskappe van die plantspesies bepaal word; en die gehalte van die grond binne daardie gapings kan verander. Die gapings waarna hierbo verwys is, is vir die doel van hierdie studie tussen 2002 en 2003 weer gemonitor. Daar is bevind dat: 1) daar min duidelike verskille was tussen die gemeenskapstruktuur van plantspesies tussen gapings van verskillende groottes en oorsprong; soos van die verhouding tussen spesies en area verwag kan word, het groter gapings 'n hoër spesierykheid, plantdiversiteit en persentasie niehoutagtige dekking as medium- en klein gapings gehad; diversiteitsindekse was hoër in die groot Plaatbosgaping as in die groot Koomansbosgaping of die kunsmatige gapings; in die algemeen was konteks en stochastiese gebeure grootliks belangriker in die bepaling van gapingsdiversiteit en -regenerasie as gapingsgrootte of -oorsprong; 2) diversiteitsindekse in die gapings was hoër as wat voorheen aangeteken is; en 3) grond-pH en elektriese geleidingsvermoë was onderskeidelik laer en hoër binne die gapings as neffens hulle; hierdie variasies was statisties beduidend. Huidige data oor die plantegroei in die gapings is met vorige metings vergelyk, en 'n toekomstige plantegroeistruktuur is as 'n funksie van huidige gapingsplantegroei voorspel. Aanbevelings is gemaak rakende die volhoubare bestuur van Tsitsikamma se inheemse woud.

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CHAPTER 1: GENERAL INTRODUCTION AND LITERATURE REVIEW

1.1. GENERAL INTRODUCTION

Species richness and diversity are considered to be amongst the highest in the indigenous forest biomes across various regions worldwide (Hocker 1979; Potts *et al.* 2002; Karnosky 2003). In many of these areas multiple use strategies are applied to meet both conservation requirements, industrial demands and social needs (Dasmann 1960; Dyck *et al.* 1994; Van der Merwe 1998). Ecological parameters and biodiversity indices in forests are changing as a result of plant species perturbation, therefore, forest gaps are significant areas for vegetation structure change (Jackson & Overpeck 2000; Ackerly 2003a, 2003b). Watt (1923) has primarily acknowledged the importance of gaps; he stated that: 1) regeneration occurs mainly within gaps, 2) regrowth process and corresponding recovery period are related to gap dimension and forest state before gap formation. The terms “regrowth” and “regeneration” are used interchangeably. Despite existing studies, our understanding of forest gap impacts on vegetation remains limited (Watt 1923; Jackson & Overpeck 2000; Ackerly 2003a). Therefore, more research on forest gap dynamics is needed to address issues dealing, for instance, with disturbances due to human demands (Dasmann 1960; Dyck *et al.* 1994; Grau 2002; Potts *et al.* 2002).

Natural resources needed by plants such as sunlight, humidity and soil nutrients vary according to gap characteristics (e.g. dimensions and origins), which may also modify other parameters controlling vegetation regrowth (Watt 1923; Grau 2002). For instance, windthrow causing gaps in an indigenous forest area may provoke the increase of specific soil minerals, which might lead to the growth of special plants using those particular resources (Watt 1923; Dyck *et al.* 1994; Grau 2002). The regeneration of juvenile woody species may be reduced by ground flora present in the gaps prior to creation and grow faster as nutrients increase within those gaps (Hocker 1979; Van Daalen 1980; DWAF 1995a). Gaps may modify the natural balance amongst species, while expanding nutrients momentarily as well as the number of certain plants, but bad weather or unsuitable site characteristics taking place in those openings may decrease the establishment of indicator species, which are important for the preservation of indigenous forest biodiversity (Van Daalen 1980; Tilman 1988a, 1988b; Geldenhuys & MacDevette 1989; Midgley *et al.* 1997).

1.1.1. Presentation of the study

The Tsitsikamma State natural forests (Fig. 1) that form part of the Southern Cape indigenous forests are situated within the Western and Eastern Cape forestry regions. They are located along the coasts over a distance of 225 km near to the Outeniqua and Tsitsikamma mountains (Van Daalen 1980; Vermeulen 1994; Van der Merwe 1998; Vermeulen 1999). The Southern Cape forests cover about 60500 ha and DWAF manages at least 35760 ha (Van Daalen 1980; Van der Merwe 1998; Vermeulen 1999). They are divided into areas of different dimensions, usually smaller than 5000 ha, and are separated by farms, exotic plantations and topography (Van Daalen 1980; Vermeulen 1994; Vermeulen 1999).

As practiced by DWAF, the present timber harvesting system conducted in the South African indigenous forests attempts to reduce forest gap dimension (Vermeulen 1994; Euston-Brown *et al.* 1996; Van der Merwe 1998). It has been suggested that this practice would increase the growth of less sunlight tolerant forest species, but may reduce the re-establishment of plants having opposite characteristics (DWAF 1995a; Euston-Brown *et al.* 1996). This suggestion and other concerns have generated an interest in understanding the impacts that forest gaps would have on the plant species regeneration (Everard 1994; DWAF 1995a; Euston-Brown & Geldenhuys 1997). As a result, the role of gaps in the Southern Cape indigenous forests was identified as an important research area by DWAF (Everard 1994; DWAF 1995a; Euston-Brown *et al.* 1996).

From 1989, a Gap Dynamics Project was initiated in the Tsitsikamma indigenous forests by DWAF (Everard 1994). Three areas are included in the project: 1) Koomansbos (9300 m²), created by a ground fire in 1989; 2) Plaatbos (1600 m²), made by a *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) windfall in 1994; 3) nine gaps of different sizes - three small (100-150 m²), three medium (300-500 m²), three large (800-1000 m²) - artificially created by selective tree felling by the Council for Scientific and Industrial Research (CSIR) in 1995 (Everard 1994; DWAF 1995a; Euston-Brown *et al.* 1996). All the gaps were surveyed after creation and permanent plots were established for subsequent monitoring (Everard 1994; DWAF 1995a; Euston-Brown *et al.* 1996). The main conclusion from these previous surveys was that forest regeneration will take time (DWAF 1995a; Euston-Brown *et al.* 1996). These gaps, aged between eight and fourteen years, were re-surveyed between 2002 and 2003 as part of the research presented here.

As already mentioned, this study aimed to verify the hypothesis that gaps may close in a process that is determined by their size, their origin and the plant species characteristics. The closure might be coupled with soil quality change inside these gaps (Tilman 1988a, 1988b).

The specific objectives of this study were to investigate if gap regeneration patterns were uniform across gaps and to predict future community structure of plant species inside the gaps. To achieve these objectives, the key questions were: was there a significant difference in the community structure of plant species between gaps of different sizes and origins? how were species diversity and richness in the gaps different from that recorded previously for the same gaps?

Present data on the vegetation in the gaps were compared to past measurements (Everard 1994; DWAF 1995a; Euston-Brown *et al.* 1996). Future vegetation structure was predicted as a function of current gap vegetation, and changes in diversity indices over time were assessed using a simple growth rate model (Philip 1994). The methods used during the study include: 1) vegetation surveys in all plots, Diameter at Breast Height (DBH) and height of woody plants, identification and percentage cover of each species using Braun-Blanquet ground cover values; 2) soil samples analysis based on pH measurements and Electrical Conductivity (Philip 1994; Sutherland 1999). Concerning soil assessments, a bioassay experiment (employ of plants in the determination of soil quality) using radishes was also conducted. The results of the test were inconclusive. This highlighted the point that perhaps indigenous or pioneer species should also have been tested (Keddy *et al.* 1995; Venter & Venter 1996). Recommendations, based on the current results, have been made as a contribution to improve the sustainable management of the Tsitsikamma indigenous forests.

1.1.2. Outline of the study

The present study was based on the long-term monitoring plots of Everard (1994), DWAF (1995) and Euston-Brown *et al.* (1996) at Koomansbos, Plaatbos, Lottering (six gaps) and Kleinbos (three gaps) in Tsitsikamma indigenous forests. These plots were re-surveyed using the same methods to facilitate the comparison of the study's results with the results of previous investigations conducted in 1989, 1994 and 1995.

Chapter one presents also an overview of the Southern Cape indigenous forests. It focuses on their history, ecology and management (Geldenhuys 1982; Geldenhuys & MacDevette 1989; Seydack *et al.* 1990; Seydack 1991; Vermeulen 1994; Van der Merwe 1998; Vermeulen 1999). In these forests, which were extensively harvested, a multiple use management strategy has been implemented and regularly improved towards conservation issues (Von Dem Bussche 1975; Geldenhuys 1982; Van Dijk 1987; Seydack *et al.* 1990; Vermeulen 1999). It also describes the current commercial timber harvesting system practiced in these forests, which attempts to reduce gap sizes (Seydack 1991; Euston-Brown *et al.* 1996; Vermeulen

1999).

Chapter two explores the plant community structure in forest gaps of different sizes and origins (Geldenhuys & Maliepaard 1983; Everard 1994; DWAF 1995a; Euston-Brown & Geldenhuys 1997). It provides insight into the mechanisms underlying plant community configuration and regeneration (Tilman 1988a, 1988b; Dyck *et al.* 1994; Jackson & Overpeck 2000) in the Tsitsikamma indigenous forests.

Chapter three examines how species diversity and richness in the artificially created gap sizes are different from that recorded previously for the same gaps (Euston-Brown & Geldenhuys 1997; Tilman 1988a, 1988b). Changes in diversity indices over time were assessed using a simple growth rate model (Philip 1994). It also investigates whether or not the subsequent growth inside the gaps is associated with a change in the soil quality (Tilman 1988a, 1988b). It examines if there is a relationship between soil change and gap sizes.

Chapter four synthesizes the main findings of this study. It recommends strategies to improve the sustainable management of the Tsitsikamma indigenous forests (Geldenhuys 1982; Van Dijk 1987; Seydack 1991; Vermeulen 1994; Van der Merwe 1998; Vermeulen 1999). Recommendations are based mainly on the results of this study.

1.2. LITERATURE REVIEW OF FOREST DISTURBANCES

1.2.1. Disturbance factors in general

Gap creation may change future vegetation structure because the growth of sunlight tolerant plants might increase while other species may be restricted due to factors such as increasing competition and other inappropriate ecological conditions (Bush & Van Auken 1990; Huston 1994; Brown *et al.* 1998; Ackerly 2003a, 2003b). Small and unusual climatic variations can cause biological changes within a specific forest ecosystem; these changes might be unpredictable, and may have a significant impact on the entire forest vegetation structure; therefore, the characteristics of forest plants are studied to minimize the negative ecological effects of these changes (Huston 1994; Jackson & Overpeck 2000; Ackerly 2003b).

Perturbations may increase plant species extinction and establishment; relative population abundances might change, which may impact diversity at a local scale (Rosenzweig 1995; Meffe & Carroll 1997; Lassig & Macalov 2000). Usually, the impacts of these perturbations are amplified by their size, intensity, and frequency (Meffe & Carroll 1997; Grau 2002). For instance, the growth of various woody species are related to fungi (Creber & Ash 1990; Huston 1994; Spence 2001), and when these fungi are not present in the ground, the seedlings

of those plants would not grow or resist competition (Jackson & Overpeck 2000; Spence 2001; Wilson & Tilman 2002). In a specific area, if a slight ground perturbation arises, such as a fallen tree, the original fungi amount can be kept or rapidly recovered, while the opposite can happen when a large ground perturbation takes place (Huston 1994; Spence 2001). Consequently, species diversity is conserved within sites where slight ground perturbations occur, and is decreasing as perturbation intensities increase (Majer 1990; Meffe & Carroll 1997; Grau 2002). However, when a low intensity and small frequency of perturbation happens, local plant diversity is reduced, and the seeds of gap edge trees might invade indigenous forest gaps for instance (Majer 1990; Euston-Brown & Geldenhuys 1997; Meffe & Carroll 1997).

A general view of natural perturbations in various forests of Europe shows that strong winds caused most damage, followed by fire, snow and other abiotic sources of disturbances (Lekes & Dandul 2000; Lassig & Mocalov 2000; Jalkanen & Mattila 2000; Spence 2001; Schelhaas *et al.* 2003). Nevertheless, biotic sources caused the same level of damage as fire did, and half of this was due to insects such as bark beetles, while most types of damage seem to be increasing in those forests of Europe (Dasmann 1960; Spence 2001; Schelhaas *et al.* 2003).

Variations in forest planning strategy may also cause the increase of ecological damages (Dasmann 1960; Geldenhuys & MacDevette 1989). In Europe, several years of extensive forest plantations had a negative impact on forest soils and this provoked the alteration of sites by increasing soil pH and detritus, reducing nutrient transfer, which facilitated insect invasion and wind damage (Dasmann 1960; Knapp & Seastedt 1986; Meffe & Carroll 1997; Emmer *et al.* 1998; Lekes & Dandul 2000). In those plantations, to ensure larger trees, the cycle that comprises planting, felling and replanting was extended, and therefore as these woody plants were growing higher, forests were further exposed to wind effects (Lohmander & Helles 1987; Dyck *et al.* 1994; Lekes & Dandul 2000; Schelhaas *et al.* 2003). That is why, following a considerable time of excessive forest harvesting, reforestation and new plans regulating forest utilization were implemented (Dasmann 1960; Schelhaas *et al.* 2003).

Other factors that augment forest's vulnerability to wind impacts include recently harvested areas and human constructions on forest sites such as waterways, power lines and roads (Lohmander & Helles 1987; Lassig & Mocalov 2000; Jalkanen & Mattila 2000; Lekes & Dandul 2000; Schelhaas *et al.* 2003). Furthermore, contamination of the atmosphere may also be cited amongst reasons contributing to root injury, which increases woody plant vulnerability (Lekes & Dandul 2000; Karnosky 2003). Diseases due to fungi are also counted as another reason that impacts negatively on racine growth (Hocker 1979; Creber & Ash

1990; Spence 2001). Injuries occurring from harvesting of bark may also augment tree infection by fungi (Creber & Ash 1990; Dyck *et al.* 1994; Schelhaas *et al.* 2003). Global warming and related weather variations would also have various impacts on forest perturbations: 1) direct influence on the wind period and force, and increase of forest fires occurrence by augmenting ecosystem dryness; or 2) indirect influence on weather patterns increasing insect invasions (Lekes & Dandul 2000; Karnosky 2003).

1.2.2. Disturbances and regeneration in the Southern Cape indigenous forests

Forests of the Southern Cape experience perturbations that take place mostly as: 1) single tree windthrow; 2) lightning, destroying woody plants and being fire starter; 3) minor avalanches on vertical slopes; and 4) sporadic severe weather conditions (Geldenhuys & Maliepaard 1983; Vermeulen 1994; Grau 2002). In general, along the forest boundaries, appropriate pioneer woody plants do not occur in large numbers following a single perturbation such as fire (Van Daalen 1980, 1981; Trollope 1984). For instance, the tree species *Virgilia oroboides* (Berg.) Salter (Fabaceae) is said to be a suitable pioneer plant following forest fire perturbations that occur particularly in the humid mountain sites, but it reduces the regrowth of other woody plants (Van Daalen 1980, 1981). Species such as *Cunonia capensis* L. (Cunoniaceae) and *Rapanea melanophloes* (L.) (Myrsinaceae) may also act like pioneer plants (Van Daalen 1980, 1981; Geldenhuys 1994b; Geldenhuys *et al.* 2003).

Negative impacts on woody species regrowth can occur within large forest gaps (Laughton 1938; Geldenhuys & Maliepaard 1983; Midgley *et al.* 1992; Everard 1994; DWAF 1995a; Euston-Brown & Geldenhuys 1997). In forest areas where the windfall intensity and frequency is low, trees are generally and naturally dying standing (Geldenhuys & Maliepaard 1983; DWAF 1995a; Euston-Brown & Geldenhuys 1997). Forest regeneration studies conducted near to roads as well as within canopy openings greater than 0.1 ha, have shown that an altered environment takes place (Van Daalen 1980; Geldenhuys & Maliepaard 1983; DWAF 1995a; Van Wyk & Netshiluvhi 1997). In those study sites, juvenile woody plants do not establish themselves in quantities due to a lack of suitable microclimate and competition from herbaceous species (Geldenhuys & Maliepaard 1983; Knoop & Walker 1985; Everard 1994; DWAF 1995a; Van Wyk & Netshiluvhi 1997).

Acacia melanoxylon R. Br. (Fabaceae), which imported from Australia in 1909, was heavily sowed in the South African natural forest gaps (Vermeulen 1994; Geldenhuys 1996; Vermeulen 1999), as a consequence, various cleared and perturbed sites were highly colonized by this species (Van Daalen 1980; Lubbe & Geldenhuys 1991). It is considered to

be a worthy woody species that generates significant income for the indigenous forest industry (Geldenhuys 1982; Vermeulen 1994). Numerous indigenous forest species such as *Ocotea bullata* (Burch.) E. (Lauraceae), *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) and *Podocarpus latifolius* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) may grow adequately under the shade of *Acacia melanoxylon* R. Br. (Fabaceae), which is a rapid growing pioneer species tolerant of sunlight and occurring mostly within large forest gaps; as a result of a superficial root structure, adult trees of this invasive plant are more vulnerable to powerful winds (Geldenhuys 1996). In general, the distribution of this species may be regulated by minimizing forest gap dimensions (Van Daalen 1980; Geldenhuys 1996; Van Wyk & Netshiluvhi 1997).

Various other exotic species, such as pine and eucalyptus, were planted amongst fynbos vegetation, close to forest boundaries as well as within cleared sites (Van Daalen 1980; Seydack 1991; Van der Merwe 1998). In those sites, forest regrowth did not progress as well as expected, and this was explained by the incapacity of newly planted species to resist periodic fynbos fires and unpredictable weather events (Van Daalen 1980, 1981).

The majority of commercially valuable trees are gap invaders; however, after a certain period, some of them would not be able to grow adequately in the openings due to an increasing competition for sunlight and space from other trees (Lubbe & Mostert 1991; Lubbe & Geldenhuys 1991). The youngest plants of those trees are growing under the shadow of older woody plants, and they do not usually develop as adults prior to gap creation (Lubbe & Mostert 1991; Lubbe & Geldenhuys 1991; Euston-Brown & Geldenhuys 1997). Even if certain trees can grow to maturity, they are not able to tolerate greater sunlight after almost a decade of growth, however when seedlings of these same trees are still healthy during gap creation they may simply grow quickly to reach a mature stage (Lubbe & Mostert 1991; Lubbe & Geldenhuys 1991). Moreover, when these seedlings are at an early stage and a gap is too wide they disappear due to competition by invasive species, animal interactions and other woody plants (Bush & Van Auken 1990; Lubbe & Geldenhuys 1991; Euston-Brown & Geldenhuys 1997; Van Wyk & Netshiluvhi 1997; Brown *et al.* 1998). Species such as *Ocotea bullata* (Burch.) E. (Lauraceae) regenerate mainly by means of coppice, meaning seedlings growing from the base of mature trees (Wilson 1988; Lube & Mostert 1991; Van der Merwe 1998; Coates Palgrave 2002). This system of regeneration enables species to survive fires besides having a solid protective bark (Lubbe & Mostert 1991; Van der Merwe 1998).

As indigenous tree species are generally slightly more shade tolerant than the shrubs, and shrubs a little more than the invasive species, regeneration in large gaps progresses often from

the edges toward the centre (Lubbe & Geldenhuys 1991; Van Wyk & Netshiluvhi 1997). During this closing process, branches of the gap edge trees are leaning toward the openings, contributing therefore to the gradual reduction of invasive species and shrubs by decreasing sunlight availability within the gaps (Lubbe & Geldenhuys 1991; Van Wyk & Netshiluvhi 1997).

Generally, in the tropical indigenous forests, the regeneration process generates an heterogeneous species configuration. This means that many plants might coexist, even if particular tree species may seem to form their own uniform structure (e.g. *Podocarpus latifolius* and *Ocotea bullata*) (Lubbe & Geldenhuys 1991; Philip 1994; Meffe & Carroll 1997; Grau 2002; Potts *et al.* 2002). The regeneration process may occur at specific periods or be continuous (Hocker 1979; Philip 1994; Meffe & Carroll 1997), as in some areas where regrowth of one species may decrease while regeneration of another species can increase highly (Hocker 1979; Lubbe & Mostert 1991; Lubbe & Geldenhuys 1991). Depending on the level of disturbance, species diversity may be highest in some recently disturbed areas (Majer 1990; Rosenzweig 1995; Grau 2002; Potts *et al.* 2002), and trees of all age classes might not be equally distributed throughout the areas, but spread in small and large groups (Philip 1994; Potts *et al.* 2002).

Indigenous forests have rapid growth rates that occur firstly in height and then in volume. These fast increases happen during the regeneration stage (Laughton 1938; Von Breitenbach 1968, 1974). However, when reaching the climax, the forest growth rate decreases significantly (Von Breitenbach 1968, 1974). And at this stage, a forest area may have a minimum number of individual trees but a maximum in basal area and volume, thus the growth rate might be regulated by tree death (Hocker 1979; Seydack *et al.* 1990; Philip 1994). This regulation through mortality may exist until a new canopy gap appears, causing the end of the climax stage and the beginning of another process of regeneration (Van Daalen 1981; Tilman 1988a, 1988b; Majer 1990).

Perturbations by fire may also have a significant impact on plant recolonization (Van Daalen 1981; Everard 1994; Bradstock & Auld 1995), on young tree development, and on mature individual tree existence (Everard 1994; Ben-Shahar 1996). For instance, *Acacia* plant growth may be facilitated by fire (Everard 1994; O'Connor 1995; Mucunguzi & Oryem-Origa 1996). Fire decreases soil humidity due to a significant increase of the heat and considerable soil water evaporation (Savage 1980; Everard 1994). In fact, greater heat that occurs after fire and before plant regeneration may momentarily provoke a dryness of the top soil (Everard 1994; Bradstock & Auld 1995; Ben-Shahar 1996; Mucunguzi & Oryem-Origa 1996). Species loss

as a consequence of heat is associated with fire intensity and plant characteristics (Trollope 1984; Everard 1994). Generally, rapid species growths after a heat event can be caused by: 1) better weather patterns at the small and local scales; 2) woody species detritus conversion in nutrients; 3) increase in resources such as nitrogen, phosphorous as well as salts; and 4) momentary reduction of ground flora species cover (Knapp & Seastedt 1986; Bush & Van Auken 1990; Dyck *et al.* 1994; Everard 1994; Brown *et al.* 1998).

Parameters that reduce ground flora competition might facilitate tree increase (Knoop & Walker 1985; Van Wyk & Netshiluvhi 1997; Brown *et al.* 1998) and encourage young tree development because ground flora impact negatively on juvenile tree existence by reducing their growth rate (Bush & Van Auken 1990; DWAF 1995a). If water and other resources are abundant, above-soil species rivalry, mostly over sunlight, becomes considerable (Knoop & Walker 1985; Bush & Van Auken 1990; Brown *et al.* 1998). If resources are reduced, below-soil plant rivalry becomes more significant (Knoop & Walker 1985; Wilson 1988).

Vegetation and soil changes occur as a result of space and time variations, which modify conditions for woody species development (Everard 1994; O'Connor 1995; Rosenzweig 1995). For example, an increase in height following a reduction in sunlight intensity is a strategy adopted by plants in order to have an adequate height to gain more luminosity for photosynthesis (O'Connor 1995; Rosenzweig 1995).

Soil compaction may be significantly greater on forest sites where activities occur compared to more pristine forests (Dasmann 1960; Fuls 1992; Dyck *et al.* 1994; Van Wyk & Netshiluvhi 1997). Animal actions and pressure on the ground might have an effect on woody species regrowth (Fuls 1992; Ben-Shahar 1996; Venter & Venter 1996; Vera 2000). For instance, dung and urine produced by animals are rich in nitrogen, and may therefore play a significant role in nutrient cycling as well as the development of plant communities (Lutge *et al.* 1995; Venter & Venter 1996).

Forest perturbations may both increase and decrease plant species richness, depending on whether abundant or rare species are more affected (Everard 1994; Huston 1994; DWAF 1995a; Rosenzweig 1995; Euston-Brown & Geldenhuys 1997). Models predicting maximum diversity at intermediate levels of perturbation might help to explain how species richness varies with ecological conditions (Rosenzweig 1995; Meffe & Carroll 1997). A more heterogeneous vegetation structure may increase diversity, variation in resources availability (Tilman 1988a, 1988b), or change in the significance of above-soil and below-ground competition (Wilson 1988; Van der Merwe 1998). The relationship between diversity, soil quality and forest disturbances might continue to vary through time within created gaps

(Everard 1994; Rosenzweig 1995).

1.3. THE SOUTHERN CAPE INDIGENOUS FORESTS

1.3.1. History

The intensive harvesting of indigenous forest species, which has been practiced since 1776 (Von Breitenbach 1968; Von dem Bussche 1975; Van Daalen 1980), was replaced in 1847 by a program that still promotes the sustainable utilization of forest products in the Southern Cape forestry regions (Von Breitenbach 1968; Von dem Bussche 1975; Geldenhuys 1982; Van Dijk 1987; Seydack *et al.* 1990).

Prior to 1652 and the coming of J. Van Riebeeck, these regions were inhabited by local tribes (Phillips 1963; Van Daalen 1980). In the 1700's, these areas had abundant and pristine forests, particularly from George to Knysna. This was the case for no less than half a century (Phillips 1931, 1963; Hartwig 1973). Intensive forest harvesting started between 1776 and 1778 at George during Governor J. Van Plettenberg's visit (Phillips 1931, 1963; Von Breitenbach 1974; Van der Merwe 1998), who made an attempt to reduce tree cuttings by appointing J. Meeding in the area (Phillips 1931, 1963; Von Breitenbach 1974). In 1788, trees were reported to be traded between Plettenberg and Cape Town (Phillips 1963; Von Breitenbach 1974; Van der Merwe 1998). During 1811, when George was developing as a town, the woody plant trading was already significant and forest damage was also significant; in 1812, the Royal British Navy also began the exploitation of woody species (Phillips 1931, 1963).

During 1836, harvesting was practiced in the Tsistikamma forests due to industrial needs mainly related to the establishment of railways (Phillips 1931, 1963). In 1846, cuttings were stopped by the Governor and various parts of these forests were bought by private foresters. However the other areas were conserved and managed by judicial officers who regulated harvesting permits (Phillips 1931, 1963; Von Breitenbach 1974). During 1847, L. Haswell was chosen as conservator officer in order to close these forests because of the increasing exploitation (Phillips 1931, 1963; Von Breitenbach 1974). In 1856, those forests were re-opened to respond to the lack of timber in the market, while C. Harrison was designated as the next conservator for the Tsitsikamma region (Phillips 1931, 1963; Von Breitenbach 1974). However, during 1869, forests were burnt between Humansdorp and Riversdale (Phillips 1931, 1963; Von Breitenbach 1974). In 1874, C. Harrison was re-appointed as conservator officer, but for the entire forest areas. However intensive public demands (e.g. Kimberley

diamond and Millwood gold) limited his actions toward the implementation of conservation laws (Phillips 1931, 1963; Von Breitenbach 1974). Between 1880 and 1888, M. de Vasselot de Règne was designated as supervisor of forest for the entire Cape region. This appointment was the most significant step toward forest conservation, because during this period the selective harvesting method was applied by C. Harrison (1884) and the Cape Forest Act was adopted (1888) (Phillips 1931, 1963; Von Breitenbach 1974). In 1906, the first management strategy was designed by McNaughton, but it was not applied because forest harvesting was still intensive in order to meet increased industrial needs, even though the selective method was still practiced (Phillips 1931, 1963; Von Breitenbach 1974).

During 1936, forest harvesting was definitely stopped by the Department of Forestry, only dying trees were cut, and this situation led to small scale forest exploitation between 1940 and 1964 (Phillips 1931, 1963; Von Breitenbach 1974; Vermeulen 1999). The indigenous forest research station was established at Saasveld (George) in 1964 (Van der Merwe 1998; Vermeulen 1999). During 1966, a multiple forest utilization plan toward conservation was developed and implemented (Von dem Bussche 1974, 1975). From 1985 to 1991, two selective harvesting methods, based on basal area, were initiated: 1) OPH (Optimum Productivity Harvesting); and 2) MRH (Mortality Retrieval harvesting) (Van der Merwe 1998; Vermeulen 1999). Momentary and permanent quadrats were laid out within indigenous forests in order to assess the increasing reserve of trees to be cut, and removal was based on growth speed as well as the mean ingrowth or mortality rate (Van der Merwe 1998; Vermeulen 1999). During 1992, a Senility Criteria Harvesting method (SCH) was introduced as part of the selective cutting plan (Van der Merwe 1998; Vermeulen 1999). After a considerable period of destructive tree extraction, the Southern Cape indigenous forests are currently managed in order to comply with relevant conservation issues (Von Breitenbach 1968; Midgely *et al.* 1997; Van der Merwe 1998; Vermeulen 1999).

1.3.2. Ecology

i. GEOGRAPHICAL CHARACTERISTICS

Located along the eastern coasts and next to the Outeniqua and Tsitsikamma mountains, the indigenous forests managed by DWAF are at an altitude ranging from 200 to 500 m (Geldenhuis 1991; Seydack *et al.* 1995; Theron 1998; Vermeulen 1999). The weather is to be mainly humid and warm like in similar forest regions. The annual average temperature of 15.6⁰ C, and annual rainfall ranges from 500 (in the west) to 1200 mm which falls mainly in autumn and summer (Geldenhuis 1991; Seydack *et al.* 1995; Theron 1998; Vermeulen 1999).

Generally, these forests grow optimally if the rains exceed 1500 mm (in the deep forest), while having negative increase rates with less than 500 mm (Geldenhuis 1991; Seydack *et al.* 1995; Theron 1998; Vermeulen 1999). However, when the rains go beyond 500 mm, heat, humidity and mineral resources are favourable to tree regeneration (Geldenhuis 1991; Seydack *et al.* 1995; Theron 1998; Vermeulen 1999). In these forests, cool rains, snowfall and storms are uncommon weather events, nevertheless warm and dry winds may occur especially between the fifth and eighth month of the year (Geldenhuis 1991; Seydack *et al.* 1995; Theron 1998).

Forest structure is affected by soil characteristics, particularly humidity and mineral resources (Theron 1998; Van der Merwe 1998). For instance, approximately 73 % of forest develops on sandstones, 21 % on shales and schists, and the remaining percentage on sands (deposited by winds), granite and other formations (Geldenhuis 1982; SCWG 1991; Theron 1998; Van der Merwe 1998). Soils are acid, not rich in phosphate and might be suitable to fynbos; trees, which are growing on humid soils and have shallow roots, are affected by windthrown (Donald & Theron 1983; SCWG 1991; Kotze & Geldenhuis 1992).

ii. VEGETATION

In the Southern Cape, plant species can be classified as follows: trees and shrubs (137 species), graminoids (25 species), bulb plants (11 species), orchids (14 species), lianas (47 species), climbers and ground flora (89 species) (Gledhill 1981; Midgley *et al.* 1997; Van der Merwe 1998; Coates Palgrave 2002). However, species diversity, distribution and characteristics change a lot, particularly in the northern direction (Geldenhuis 1982, 1991, 1994; Van der Merwe 1998; Theron 1998). Certain plants in the south have properties that are similar to some in the north (Geldenhuis 1982, 1994; Midgley *et al.* 1997; Van Wyk & Van Wyk 1997). Shallow and thick roots (at least 200 mm) are a characteristic of various mature woody species such as *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. (Podocarpaceae) (Kotze & Geldenhuis 1992; Van der Merwe 1998). Insects (e.g. bees) and other animals (e.g. birds and mammals for *Podocarpus falcatus*) are significant in the fertilization and distribution process of plants (Koen 1983; Geldenhuis 1994a; Venter & Venter 1996; Van der Merwe 1998). The Southern Cape elephants are surprisingly not playing a considerable role in the distribution of seed plants (Koen 1983; Van der Merwe 1998).

Components of Afromontane plant communities (e.g. epiphytic lichens, bryophytes, ferns, orchids) as well as humidity are used as indicators to divide these forests into three specific sectors: 1) areas covered by more than 80% of *Cunonia capensis* L. (Cunoniaceae) and

Ocotea bullata (Burch.) E. (Lauraceae), with herbaceous plants mostly composed of ferns such as *Blechnum sp.* (Blechnaceae); 2) forests of the coast sides, which are generally arid, but with a high plant richness; and 3) areas specifically humid, which have mostly mountaineous plants (Koen 1983; Kotze & Geldenhuys 1992; Geldenhuys 1994a, 2000; Theron 1998; Van der Merwe 1998).

In general, the Southern Cape Afromontane forests comprise: 1) very dry and dry (36%); 2) moist and medium moist (48%); 3) wet and very wet areas (16%) (Geldenhuys 1994a; Theron 1998; Vermeulen 1999). To facilitate foresters' work, these forests are subdivided in six forest categories: 1) very dry scrub forest: located on superficial, warm and arid grounds, has a significant density of shrubs (3-6 m high) and dwarf woody species (up to 9 m high), different plant regrowth between species, and existence of massive woody plants (e.g. *Podocarpus falcatus*) as well as various plants from the arid and humid forests; 2) dry high forest: located on well-drained or superficial and warm grounds, considerable tree density (10-18 m high), woody species regrowth not significant but, more herbaceous species and more shrubs such as *Trichocladus crinitus* (Thunb.) Pers. (Hamamelidaceae), existence of many plants from the humid forests; 3) medium moist high forest: located on various and poorly-drained grounds, has two ranges of tree height (6-16 m, 6-22 m), significant shrub species density such as *Trichocladus crinitus* (up to 6 m high), considerable woody plant regrowth and few herbaceous species; 4) moist high forest: located on humid and thick mud grounds, has three ranges of tree height (6-12 m, 12-20 m, 20-30 m); many woody plants from the medium moist forest with a bigger DBH, density of *Trichocladus crinitus* not significant, considerable woody species regrowth, although the density of herbaceous plants is important; 5) wet high forest: located on colder areas with humid, usually superficial and poorly-drained grounds, forests next to structures such as rivers, range of tree height 12-30 m; existence of few plants, *Cyathea capensis* (L.f.) Sm. (Cyatheaceae) proper to humid forest (up to 6 m high), woody species regrowth not considerable compared to ferns that are well distributed, rare *Trichocladus crinitus*; 6) very wet scrub forest: located on humid and shallow soils, tree heights' range between 6-10 m (Van Dijk 1987; Vermeulen 1994; Theron 1998; Van der Merwe 1998).

1.3.3. Management

Studies done on the Southern Cape forests were taken into account when designing a strategy to comply with ecosystem preservation, harvesting and recreational activities (Seydack 1991; Geldenhuys 1994a; Seydack *et al.* 1995; Theron 1998; Vermeulen 1999). This strategy,

mainly set for the benefit of forest biodiversity, was not difficult to implement and complies with needed transformations (Seydack *et al.* 1995; Theron 1988; Vermeulen 1999). Some forests were divided in large and smaller compartments that have been reclassified in five groups, according to forest categories, conservation priorities, industrial and human demands: 1) tree harvesting (26%) where it has less damage for the environment; 2) ecosystem preservation (45%) in areas defined as biologically sensitive; 3) Nature Reserves (27.6%), which comprise various forest categories; 4) recreational activities (0.4%); 5) long term scientific studies (1%) (Seydack 1991; Geldenhuys 1994a; Seydack *et al.* 1995; Van der Merwe 1998; Vermeulen 1999).

i. THE SELECTIVE HARVESTING SYSTEM

Indigenous tree harvesting is done sustainably and differently to plantations (Theron 1988; Vermeulen 1999). In a particular area, not every tree is harvested, but a selection of various individual species occurs after a period of ten years (Van Dijk 1987; Seydack *et al.* 1990; Vermeulen 1999). Tree removals are done to comply with normal processes of plant regeneration, meaning that regrowth after harvesting has to take place without negative impacts on a particular species survival (Seydack *et al.* 1990; Midgley *et al.* 1997; Vermeulen 1999).

The current trees are harvested according to senility conditions, which imply that the less healthy trees are periodically removed based on different physiological aspects (Geldenhuys 1982; Seydack *et al.* 1990; Van der Merwe 1998; Theron 1998) such as proportion of crown dying (best sign of senility), stem decay, agony shoots as well as various injuries. Past harvesting methods were mainly based on the removal of a predetermined proportion of trees (Geldenhuys 1982; Seydack *et al.* 1990).

ii. MONITORING

Forest ecosystem monitoring is part of the yield regulation system (Seydack 1991; Vermeulen 1999). Surveys of trees and fern species such as *Rumohra adiantiformis* (G. Forst.) Ching (Dryopteridaceae), are done in specific sites to look at vegetation responses to wood and fern removals (Van der Merwe 1998; Vermeulen 1999). These assessments are undertaken mostly in nature reserves and comprise the entire study of plant and wild animal characteristics (Geldenhuys 1982; Van der Merwe 1998).

The indigenous forest management of the Southern Cape has changed to be in line with

biodiversity conservation requirements (Von Breitenbach 1968; Von dem Bussche 1975; Vermeulen 1994; Van der Merwe 1998). Past negative impacts on forest resources have showed that regulations were needed in order for forest products to be harvested with less ecological problems (Seydack *et al.* 1990; DWAF 1995b; Theron 1998). Thus, these regulations would guarantee forest ecosystem survival as long as all the principles, criteria and indicators that were defined are implemented (DWAF 1995b; Van der Merwe 1998).

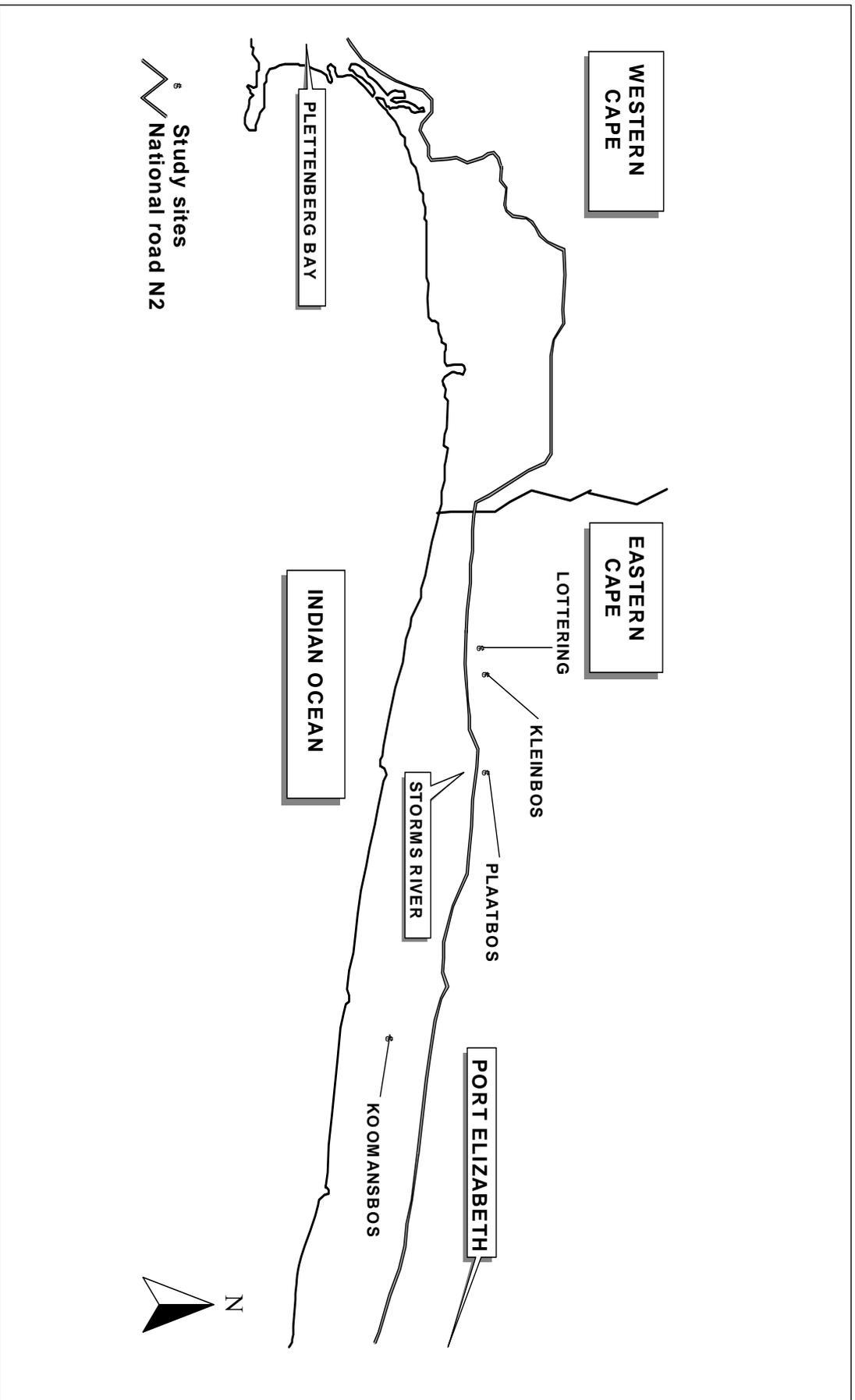


Fig. 1.1 Locations of the study sites in the Tsitsikamma State indigenous forests.

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CHAPTER 2: PLANT COMMUNITY STRUCTURE IN FOREST GAPS OF DIFFERENT SIZES AND ORIGINS

2.1. INTRODUCTION

As stated previously, forest disturbances leading to the death and regrowth of plant species are major factors of variability in vegetation community arrangement (Petraitis *et al.* 1989; Martin & Gower 1996; Van Wyk & Netshiluvhi 1997; Potts *et al.* 2002). Seen as the more diverse ecosystems worldwide, forests are either strictly protected or sustainably used in many regions (Seydack 1991; Dyck *et al.* 1994; Potts *et al.* 2002). Since a significant understanding of the effect of forest perturbations is gradually available, activities of men may be changed to mimic natural disturbances occurring in forests (Dyck *et al.* 1994; Euston-Brown *et al.* 1996). Therefore, knowledge of forest gaps that control the natural regrowth of plant species is specifically necessary (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996). Natural substances, which forest plants need in order to live and grow are linked to gaps and may vary (Watt 1923; Everard 1994), like other factors controlling forest regrowth (Dyck *et al.* 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997).

Before gap opening, herbaceous plants may exist as seedlings and seedbanks; they might develop with the increasing availability of nutrients in the openings, decreasing the regrowth of young woody species (Everard 1994; DWAF 1995; Potts *et al.* 2002). Generally, the creation of forest gaps changes the natural competition amongst plants, momentarily augmenting important nutrients and favouring the abundance of certain species (Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997).

As already mentioned, the ongoing wood harvesting method applied in South African natural forests tries to reduce gap dimension (DWAF 1995; Euston-Brown *et al.* 1996). Hypotheses suggest that this method is expected to be of advantage to the most shade sensitive plants, and might slow down the regrowth of less shade sensitive ones (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). This concern generated an interest in investigating the impacts that gap sizes and origins have on the plant species regeneration (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996). Therefore, the role of gaps in the Southern Cape natural forests was identified as an important research focus by the Department of Water Affairs and Forestry (DWAF 1995; Van der Merwe 1998; Euston-Brown *et al.* 1996). This Department initiated a Gap Dynamics Project in the Tsitsikamma indigenous forests in 1989 (Everard 1994).

This chapter tests the hypothesis that gaps may close in a process that is determined by their sizes, origins and the plant species characteristics adjacent to the gap (Everard 1994; DWAF 1995; Euston-Brown & Geldenhuys 1996; Van Wyk & Netshiluvhi 1997). The aim of the present chapter was therefore to examine variations in plant species assemblages between gap sizes and amongst gap origins. The specific objectives of this chapter were: 1) to compare the community structure of plant species between gaps of different sizes, and 2) to compare plant community structure in artificially created gaps with those of two naturally created gaps.

2.2. STUDY SITES AND METHODS

The methods used comprise vegetation surveys of all plots, including measures of Diameter at Breast Height (DBH), height of woody plants, and the identification and percentage cover of each species using Braun-Blanquet ground cover values (Philip 1994; Sutherland 1999). This study was based on the long-term monitoring plots of Everard (1994), DWAF (1995) and Euston-Brown *et al.* (1996) at Koomansbos, Plaatbos, Lottering (six gaps) and Kleinbos (three gaps), located in Tsitsikamma indigenous forests. These plots, aged between eight and 14 years, were then resurveyed between 2002 and 2003 using the same methods to facilitate the comparison of this study's results with the results of the previous surveys conducted in 1989, 1994 and 1995.

2.2.1. History of gaps included in this study

i. ARTIFICIALLY CREATED GAPS

The Department of Water Affairs and Forestry initiated a study in 1995 to understand the effect of gap size on plant species regeneration and rate of canopy re-establishment in the Southern Cape natural forests (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Artificial gaps were created in two regions, which are representative of the areas where timber harvesting occurs, and three gap sizes were replicated three times within these areas (Euston-Brown *et al.* 1996). The gap sizes ranged between 100-150 m² (small) - average gap size resulting from trees dying standing and current harvesting - (DWAF 1995), 300-500 m² (medium) - occasional size of a gap caused by a windthrow or tree breaking - and 800-1000 m² (large) - gap size occurring after an extensive harvesting - respectively (Euston-Brown *et al.* 1996). Nine gaps were created at Tsitsikamma State Forest and a further nine at Diepwalle State Forest (Van Wyk & Netshiluvhi 1997). Only those located at Tsitsikamma were considered in this study (Figs 2.1-2.2; Table 2.1).

When creating the artificial gaps, the following criteria were respected: 1) selection of flat sites; 2) three different gap sizes were created in nearest locations (Fig. 2.1); 3) sites with a closed canopy were selected; 4) while creating the gaps, a immense *Olea capensis* subsp. *macrocarpa* (L.) C. H. Wright (Oleaceae) was taken as the center tree; 5) the openings were as round as feasible; 6) all woody plants, which have been cut, were removed from the gaps; 7) in the east or west part of the openings, all the *Trichocladus crinitus* (Thunb.) Pers. (Hamamelidaceae) were cut at ground level, and other species seedlings were not damaged; 8) the maximum and minimum length of the openings were averaged when calculating gap dimension; 9) measurements of woody species cutted in the gaps were taken; 10) adult and young woody species shorter than ten meters were left intact and their measurements were registered; 11) an angle to the horizon (canopy) was recorded for every twenty degree direction (i.e. 18 records), in order to evaluate at particular spots the sun infiltration into the opening (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997).

ii. PLAATBOS WINDFALL GAP

In December 1994, a forest gap was created by the fall of an enormous *Podocarpus falcatus* (Thunb.) R. Br. Ex Mirb. (Podocarpaceae) (DWAF 1995). The fall of the tree created a gap of about 1600 m² (33°58'S, 23°54'E) (Fig. 2.3; Table 2.1). The opening is situated inside the Tsitsikamma Big Tree leisure site, which is a component of Plaatbos Nature Reserve (PNR), Storms River compartment F14b (DWAF 1995). The National Road (N2) is at about 100 m south of the gap location, Storms River settlement is in the west, and Storms River Bridge in the east (DWAF 1995). The weather is relatively warm and humid with a mean yearly precipitation around 900 mm (DWAF 1995; Van der Merwe 1998).

iii. KOOMANSBOS FIRE GAP

Koomansbos is located at an altitude of about 190 m, and it is described as dry forest (Everard 1994). The weather is moderately warm and humid with an average annual rainfall of approximately 900 mm, the Elands River is located in the east, and the Kruis River in the west (Everard 1994; Van der Merwe 1998). In this region, a natural forest area of 9300 m² was burnt in 1989 (34°01'S, 24°03'E) (Fig. 2.4). Acknowledging the significance of gaps in natural forests (DWAF 1995; Euston-Brown *et al.* 1996; Euston-Brown & Geldenhuys 1996), the Department of Water Affairs and Forestry decided that this gap was an occasion to assess forest dynamics after fire, and therefore Koomansbos was included as a component of the

studies on gap effects (Everard 1994).

2.2.2. Description of previous surveys of the gaps

i. ARTIFICIALLY CREATED GAPS

These gaps were first surveyed in 1995, and then re-surveyed after six months of gap establishment, and again one year later after gap creation (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). In January 1997 and February 1998, the DBH of trees surrounding gaps were measured as well as their canopy expansion toward the gaps, in order to evaluate the impact of these trees on the regeneration of gaps (Euston-Brown & Geldenhuys 1996; Van Wyk & Netshiluvhi 1997). Preliminary findings indicated that young woody species which existed prior to gap opening would re-colonize these gaps, and that bordering trees would close the smaller openings (Van Wyk & Netshiluvhi 1997). Another finding was that ground flora species in the gaps have increased in cover and appeared to negatively affect the growth and establishment of seedlings, therefore it was advised that these gaps should be re-surveyed every five years. Changes in vegetation structure may be shown in a five year period for many shrub and ground flora species (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997).

ii. PLAATBOS WINDFALL GAP

The Plaatbos opening offered an opportunity to examine the effects that such a kind of perturbation would have on vegetation structure (DWAF 1995; Martin & Gower 1996; Potts *et al.* 2002). In March 1995, three months following this gap formation, a first monitoring of the site was conducted and permanent sampling plots were set up for future measurements (DWAF 1995). The finding of this initial monitoring was that regeneration of trees would be slow as a negative consequence of *Hypolepis sparsisora* (Schrad.) Kuhn. (Hypolepidaceae) (DWAF 1995; Van Wyk & Netshiluvhi 1997). To evaluate the regeneration process, a yearly survey of this gap was suggested. Unfortunately these annual assessments were not conducted since the first survey.

iii. KOOMANSBOS FIRE GAP

This site was surveyed in May 1990 and September 1992 (Everard 1994). From these surveys it appeared that there was a loss of roughly 86% of the young woody species, and about 82% of adult trees and seedlings combined (Everard 1994). These previous surveys showed also

that the complete soil seed bank was damaged (Everard 1994). However, a later survey was conducted at Koomansbos between 1992 and 1993, and this survey revealed that the entire burnt area had become almost completely covered by *Pteridium aquilinum* (L.) Kuhn. (Dennstaedtiaceae) (Everard 1994). This fern species formed a mass of vegetation about 1.5 m in height, and the density was such that it was not possible to locate all the plots, therefore only a portion of the plots was remeasured, resulting in a total area surveyed of 1000 m² (5 plots of 20m×10m) instead of 3600 m² (18 plots of 20m×10m) (Everard 1994). It was thus predicted that forest closure would be slow, and suggestions were made to survey the site every five years (Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997). For the 2003 study, the same abovementioned 5 plots were surveyed.

2.2.3. Description of plots and plot layout used in previous surveys and for 2003 study

i. ARTIFICIALLY CREATED GAPS

For every gap, plots measuring 3m×3m were established: 1) small gaps: two plots; 2) medium and large gaps: four plots; 3) under forest canopy adjacent to gap: two plots (Fig. 2.2) (Euston-Brown *et al.* 1996). In the openings, initial plots were placed in locations having less damage after gap creation, and the canopy quadrats were placed under closed canopy forest (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Along each plot a two-meter empty space was created, the north-east corner of every quadrat was labeled with a wooden peg, and the other angles with red wire sticks (Euston-Brown *et al.* 1996).

ii. PLAATBOS WINDFALL GAP

Forty four plots measuring 5m×10m each were established in the open area (Fig. 2.3). The first quadrat was established in the north-eastern angle of the gap and other plots were placed next to the quadrat (DWAF 1995). Those plots were separated by using a wooden peg in each corner of the plot, and linked with nylon rope (DWAF 1995). Each plot was numbered on the north-eastern angle (DWAF 1995): 1) in alphabetical order from north to south; 2) in numeral order from east to west.

iii. KOOMANSBOS FIRE GAP

In the south-easterly direction of this gap, four strips were established on the burnt surface (Fig. 2.4). These strips were separated into 18 plots measuring 20m×10m each. Six of the

quadrats being out of the damaged surface, and the other 12 plots were located in the inflamed area (Everard 1994).

2.2.4. Description of measurements done previously in the gaps for 2003 study

i. ARTIFICIALLY CREATED GAPS

The following survey method was conducted within each plot: 1) the height of plants taller than 30 cm was recorded, the DBH was taken for individuals higher than 2 m, and these plants were numbered using metallic tags and strings; 2) tree injuries which occurred during gap creation were registered, and individuals between 10 cm and 30 cm tall were counted as seedlings (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Outside the plots but within the openings, only trees taller than 2 m were measured in the same manner as those in the plots (Euston-Brown *et al.* 1996). The percentage cover of each herbaceous species was visually rated in every plot (Van Wyk & Netshiluvhi 1997; Sutherland 1999).

ii. PLAATBOS WINDFALL GAP

Woody plants with a DBH less than 1 cm and herbaceous species comprising the shrub plants *Trichocladus crinitus* (Thunb.) Pers. (Hamamelidaceae) and *Carissa bispinosa* (L.) Desf. ex Brenan (Apocynaceae), were evaluated using the Braun-Blanquet scale (DWAF 1995; Sutherland 1999). Five factors per species were considered when measuring the diameters of woody plants with a DBH more than 1 cm: 1) individuals were numbered from 1 to 50 using plastic tags and metallic strings, and the points of measurements were marked on each plant; 2) to simplify the monitoring process, the South African national tree numbers were used instead of plant names; 3) diameters of trees between 1 cm and 5 cm were taken using a caliper, and those larger than 5 cm by means of a diameter tape; 4) damages to trees were recorded; 5) locations of trees were mapped (Philip 1994; DWAF 1995; Coates Palgrave 2002).

iii. KOOMANSBOS FIRE GAP

In each quadrat, trees dead or alive measuring more than 5 cm in diameter were recorded, comprising the collapsed trees (Everard 1994). Crown and stem fire injuries on woody plants were characterized, as well as the way how those plants are growing after such disturbance (Everard 1994). Dead or alive individual trees having a diameter smaller than 5 cm were not

measured but their numbers were recorded, and for every quadrat each herbaceous species cover was visually rated (Everard 1994; Sutherland 1999).

During the initial gap measurements, an attempt was made at marking and measuring each individual of some woody plant species, but this proved to be too time consuming. Therefore, these woody plant species were recorded as ground flora. The same woody plant species were also included in the ground flora category for the 2003 study (Appendices 2.1-2.5).

2.2.5. Standardization of methods used in gap sizes and origins for 2003 study

As stated earlier for the 2003 study the gaps described above were resurveyed using the same methods applied in previous assessments (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996). However, the nine artificially created gaps, and the two natural ones (Plaatbos windfall and Koomansbos fire gaps) have different set of methods (Vermeulen 1995; Everard 1994; Euston-Brown & Geldenhuys 1996). In order to have a non-biased comparison between them, the methods in this study were standardasized as follows: 1) only trees with a DBH greater than 5 cm were considered as adults; the species richness and diversity were assessed for this category; 2) woody species under 5 cm DBH were listed as juveniles, and the species richness and diversity also assessed for this category; 3) the Braun-Blanquet value was taken as reference to estimate the percentage cover of ground flora species; and 4) the percentage cover, species richness and diversity were estimated per square meter for each gap (Philip 1994; Sutherland 1999; KCS 2003).

In the plots under forest canopy adjacent to each artificially created gap, few individual trees with a DBH greater than 5 cm and small percentages of ground flora species were found. The amount of data collected in these plots were not significantly large to conduct a non-biased analysis of plant community structure (e.g. could not create a valid matrix for non-metric multidimensional scaling). Therefore, these data were not considered for the 2003 study.

2.2.6. Data analysis

i. TYPES OF DATA

In order to understand the activities of plants after disturbances well, data gathered for this study were grouped into: 1) nominal data that did not need arithmetical values (e.g. presence/absence data, vegetation characteristics such as trees, shrubs, herbaceous, shade

tolerant species, pioneer and invasive plants); and 2) ordinal data that needed arithmetical values (e.g. percentage cover using Braun-Blanquet scale) (Kent & Coker 1996; Sutherland 1999). In the analysis process, the set of methods for having significant illustrations of the plant data have been grouped into three classes: 1) univariate methods; 2) distributional techniques; and 3) multivariate methods (Orloci *et al.* 1979; Warwick *et al.* 1984; Kent & Coker 1996).

ii. UNIVARIATE METHODS

In this study univariate methods comprise: 1) the transformation of species counts for a sample into a simple coefficient like a species diversity index such as Shannon; 2) the numbers of distinct species for a fixed amount of individuals (species richness); 3) the level to which the species counts are dominated by a small number of species (dominance or evenness index); and 4) the selection of particular indicator species verifying specific hypotheses about changes occurring like the fern species *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), which invaded the burnt area at Koomansbos (Everard 1994; Kent & Coker 1996; Clarke & Warwick 2001; Henderson & Seaby 2001; KCS 2003). The hypotheses mentioned here are: 1) the cover of such herbaceous species would increase in the gaps; and 2) the growth rate of trees might decrease as a consequence.

a. Shannon diversity index

The Simpson (D) index might be used for assessing biodiversity in a vegetation community, but it is a subjective indicator, and the existing objective version is only applicable with count variables (Pielou 1969; Kent & Coker 1996; Henderson & Seaby 2001). On the contrary, Shannon index (H'), which may be applied with all types of variables, implies that plants are arbitrarily collected out of a significant community, and supposes that each species has been taken into account (Pielou 1969; Kent & Coker 1996; Henderson & Seaby 2001; Onaindia *et al.* 2004). The normality of plant abundance is not considered when evaluating the Shannon index, which is not so sensitive to data ranges, and subjective simply for plant richness (Huston 1979; Magurran 1988; Kent & Coker 1996; Sutherland 1999). This index is usually chosen due to the fact that the numbers of individuals are uniformized into proportions, making it simple to understand differently to another index such as McIntosh (Kent & Coker 1996; Henderson & Seaby 2001).

The software Multi-Variate Statistical Package (MVSP) version 3.13h (KCS 2003) was used to determine diversity indices between gaps of different sizes and origins. The output consists

not only of the Shannon diversity index (H'), but also the number of species and the evenness (J), which is defined as the diversity divided by the maximum possible diversity (Krebs 1989; KCS 2003):

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

Where: 1) p_i is the proportion of individuals or the abundance of the i th species expressed as a proportion of total cover; 2) S is the number of species; 3) \ln is the logarithm base n ; in the present study, calculations have been made by using logarithm base 10 (\log_{10}); the selection of \log_{10} has been maintained when comparing biodiversity among data sets (Kent & Coker 1996), and the higher the value of H' the greater the diversity. The equitability or evenness index (J) of the Shannon diversity index (H') was calculated based on the following formula (Kent & Coker 1996):

$$J = \frac{H'}{H'_{\max}} = \frac{\sum_{i=1}^s p_i \ln p_i}{\ln s}$$

The higher the value of J , the more even the species were in their distribution within the gaps (Kent & Coker 1996).

b. Nonparametric statistics

In this study nonparametric statistics have been used for analyses because conditions for normality and homogeneity of variance were not met (Winer *et al.* 1991; Wheater & Cook 2000; StatSoft, Inc. 2003). Therefore the Kruskal-Wallis ANOVA by ranks and median test was chosen for evaluation of variables (Keller & Warrack 1997; Wheater & Cook 2000; StatSoft, Inc. 2003). This test supposes that data considered are continuous and ranked (Keller & Warrack 1997; Wheater & Cook 2000; StatSoft, Inc. 2003). The test evaluates the assumption that data were extracted out of distributions which have an equal median (Wheater & Cook 2000; StatSoft, Inc. 2003). Therefore, it is similar to the parametric one-way ANOVA with the difference that the Kruskal-Wallis considers only ranks (Keller & Warrack 1997; Wheater & Cook 2000; StatSoft, Inc. 2003). Analyses were conducted to evaluate if there were significant differences between biodiversity indices across gaps of different sizes and origins, therefore the null hypothesis tested was that there was no statistical dissimilarity (Keller & Warrack 1997; Wheater & Cook 2000). Diversity indices included: 1) Shannon (H'); 2) evenness (J); 3) species richness (S); 4) abundance (N); 5) density per square meter

for species richness and abundance; 6) DBH. The software Statistica 6 was used for these statistical analyses (StatSoft, Inc. 2003).

c. Calculations for comparison purposes

The abundance of individual tree species (N) and number of species (S) were calculated for each different size of artificially created gaps (small, medium and large) as well as for distinct origins (large artificials, fire and windfall) prior to interpretation (Kent & Coker 1996). The density (D) or abundance of individual trees as well as number of species per square meter (m²) (Philip 1994) was also calculated for each category of gap size and origin according to the following formula: $D=N/\text{Gap area (m}^2\text{)}$ or $D=S/\text{Gap area (m}^2\text{)}$. Small gap areas were averaged between them as well as medium and large gaps, and this was also done according to gap origins. Therefore, three final areas were obtained for each category of gap size and origin. Artificially created gaps, fire gap and windfall gap, have different areas. The number of individual trees in each of these categories is thus expected to be different. In order to have valid comparison between these different sites, the number of individual trees as well as species found per total area for each category was converted to square meter (m²) using the formula described above. When comparing abundance of trees and number of species between gaps of different origins, the following gaps were considered: 1) large artificial created gaps; 2) fire gap; 3) windfall gap. The average areas of each category of gap origins is considered to be large enough to have similar effects on plant species if these gaps were from the same origin (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996; Euston-Brown & Geldenhuys 1996; Van Wyk & Geldenhuys 1997) (greater than 787 m² and less than 1600 m²). The average DBH of each tree species was calculated per gap, and then the mean DBH for each gap category was assessed.

Relative frequency of species

The species percentage distributions across gaps were calculated for each category of gap size and origin. For instance, here is the method used to calculate the proportion of adult tree species which were only found in the small artificially created gaps:

$$\frac{(\text{Total number of adult tree species in the small gaps}) \times 100}{\text{Total number of adult tree species in all the gaps}} =$$

$$\frac{S(\text{small gaps}) \times 100}{S(\text{small gaps}) + S(\text{medium gaps}) + S(\text{large gaps}) + S(\text{fire gap}) + S(\text{windfall gap})} =$$

$$\frac{7 \times 100}{7 + 15 + 16 + 15 + 25} = \frac{700}{78} = 8.97\%$$

Where: 1) small, medium and large gaps are the abbreviations for small, medium and large artificially created gaps; 2) S is the total number of species recorded in the gaps specified in brackets. Species which were found in different gaps were counted once; for example, *Apodytes dimidiata* subsp. *dimidiata* E. Meyer ex Arn. was located in two different small artificially created.

The method described above was also used to estimate the percentages of other groups of species (e.g. juvenile trees and ground flora) across the same category of gap size and origin. Percentages are given in the results (section 2.3).

iii. DISTRIBUTIONAL TECHNIQUES

In this study, distributional techniques include all the graphs that illustrate plant responses to disturbances (Warwick *et al.* 1984; Kent & Coker 1996; Clarke & Gorley 2001). Graphs like dominance curves have been shown to be helpful in assessing the impacts of perturbations (Warwick *et al.* 1984; Clarke & Warwick 2001). However, in distributional methods related to community perturbation, similarities among data sets are not necessarily due to species specificities: two data sets might precisely have a similar distribution, and not having any similar species (Warwick *et al.* 1984; Clarke & Warwick 2001).

iv. MULTIVARIATE METHODS

Multivariate techniques assess usually the species similarity indices related to the numbers of individuals among several data sets (Kent & Coker 1996; Clarke & Gorley 2001). Variables are organised in similar assemblages or graphical representations where the data sets are plotted according to these indices that illustrate community structure (e.g. non-metric multi-dimensional scaling) (Bray & Curtis 1957; Kruskal & Wish 1978; Clarke & Gorley 2001; KCS 2003). In order to get indices, which are ecologically meaningful, variables require to be examined in abundance (Kent & Coker 1996; Clarke & Warwick 2001). These methods are appropriate to underline dissimilarities related to distinct study areas, especially when it comes to estimate stress intensities (Clarke & Warwick 2001).

a. Multivariate approach

Multivariate variables can be structured in a double entry table (e.g. quadrats-species) (Magurran 1988; Kent & Coker 1996), and additional entries can change data composition as well as mapping configuration (Kruskal & Wish 1978; Kent & Coker 1996). In a multivariate approach, determine association indices among plants and amongst quadrats is a recommended way for the assessment of vegetation (Kent & Coker 1996). There are three different multivariate methods estimating resemblances among floristic variables and amongst quadrats: 1) those considering presence/absence species; 2) those taking into account individual numbers; and 3) those incorporating the two previous methods (Kent & Coker 1996; Clarke & Gorley 2001; Clarke & Warwick 2001). The Bray-Curtis index of similarity, used in this study, is appropriate for assessing presence/absence species and individual numbers (Bray & Curtis 1957; Kent & Coker 1996; Clarke & Warwick 2001; Clarke & Gorley 2001).

Bray-Curtis coefficient

The software PRIMER version 5 was used for evaluating the Bray-Curtis index and assessing similarity of vegetation variables (Kent & Coker 1996; Clarke & Gorley 2001). Prior to this evaluation individual numbers were organised in a double entry table and modified using firstly the fourth root transformation and then presence/absence conversion (Van Rensburg *et al.* 1999; Clarke & Gorley 2001). This was done in order to down-weight abundant species comparatively to infrequent ones (Kent & Coker 1996; Clarke & Gorley 2001). Before that step the individual numbers were converted into proportions by standardizing vegetation variables (Clarke & Gorley 2001). The Bray-Curtis indice, which was firstly applied in environmental sciences by Bray and Curtis (1957), has been widely used ever since. The indice of resemblance among the j th and k th variables is known as S_{jk} and has two equivalents (Clarke & Gorley 2001):

$$S_{jk} = 100 \left\{ 1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p (y_{ij} + y_{ik})} \right\} = 100 \frac{\sum_{i=1}^p 2 \min(y_{ij}, y_{ik})}{\sum_{i=1}^p (y_{ij} + y_{ik})}$$

Here: 1) y_{ij} is the entry in the i th row and j th column of the data matrix, it means the number of individuals for the i th species in the j th data set ($i = 1, 2, \dots, p; j = 1, 2, \dots, n$); 2) equally, y_{ik} is the count for the i th species in the k th data set; 3) $|\dots|$ is the positive value of the difference; 4) $\min(\dots)$ is the minimum of the two counts; 5) the separate sums in the numerator and denominator are both over all rows (species) in the matrix.

The proportion of individual numbers per species is considered in the Bray-Curtis index, which has a scale from 0 to 1 (identical) (Kent & Coker 1996). This index is suitable for assessing similarities in significant ecosystems like forests because it incorporates only cases having species in the two entries of data matrices (Clarke & Gorley 2001). The Bray-Curtis index is sensitive to the individual numbers per species, infrequent plants do not significantly influence the index, and this problem is solved through data conversion that weight equally abundant species and uncommon ones (Kent & Coker 1996; Clarke & Warwick 2001).

b. Non-metric multidimensional scaling (NMDS)

Initially applied in psychology, non-metric multidimensional scaling (NMDS or MDS) is obtained by following these main two points: 1) creation of a double entry table needed to assess similarities between variables; and 2) selection of an index as well as data conversion formulas to highlight some points (Kruskal & Wish 1978; Glass & Hopkins 1996; Clarke & Warwick 2001; Clarke & Gorley 2001). Conversion formulas influence MDS because they affect similarity indices calculated among data sets (Kruskal & Wish 1978; Clarke & Gorley 2001), and therefore affecting the configuration of the map (Kruskal & Wish 1978; Orloci 1978; Orloci *et al.* 1979; Clarke & Warwick 2001). Various studies can be suitable for MDS application because: 1) not many conditions exist when analysing variables; 2) it deals effectively with missing data; 3) it has an accurate graphical representation of similarities and differences between data sets in two or three dimensions; and 4) it has been advised amongst the best classification methods (Everitt 1978; Orloci 1978; Orloci *et al.* 1979; Clarke & Gorley 2001; Clarke & Warwick 2001).

c. Steps for multivariate analysis

Using the software PRIMER 5, the main steps followed for multivariate analysis were: 1) a triangular similarity or distance matrix was drawn considering gaps as samples and selecting the Bray Curtis coefficient; 2) data were transformed and standardized using fourth root; 3) a one-way analysis of similarities (ANOSIM) was applied considering the following factors: small, medium and large artificially created gaps, as well as fire and windfall gaps; in that case the null hypothesis tested was that there were no assemblage differences between groups of gaps; 4) tests comparing pairs of those groups were performed; groups were seen to be statistically distinct only when the overall probability was less than 0.05; and 5) a non-metric multi-dimensional scaling (NMDS) was used to illustrate similarities and differences among

groups of gaps in term of community structure; in that regard the stress value was usually less than 0.2 and therefore a two dimensions' map was created in order to have the best view of the gaps (Van Rensburg *et al.* 1999; Wheater & Cook 2000; Clarke & Gorley 2001).

2.3. RESULTS

In 2003, the number of plant species per category was recorded across all gap sizes and origins (Appendices 2.1-2.5). A total of 34 tree species were identified, as were eleven shrub species, six alien species, three pioneer species, 39 herbaceous species and two shade tolerant species (Appendices 2.1-2.2). Amongst adult trees, the following species categories were mostly found: 1) alien species in medium, large and fire gaps; 2) shade tolerant species in medium, large, fire and windfall gaps; 3) shrub species in fire and windfall gaps; 4) pioneer species in the windfall gap (Appendix 2.3). Different juvenile tree species were mainly recorded as follows: 1) alien species in large and fire gaps; 2) shade tolerant species in medium, large, fire and windfall gaps; 3) shrub species in medium, large, fire and windfall gaps; 4) pioneer in medium, large, fire and windfall gaps (Appendix 2.4). Alien herbaceous species were mostly in the fire gap (Appendix 2.5). As expected from the species-area relationship, the windfall gap had more plant species than fire gap, large, medium and small artificially created gaps (Appendix 2.3-2.5).

The percentage distributions across all the gaps were calculated for each group of species (i.e. adult and juvenile trees, and herbaceous). Out of the total number of adult tree species found in all the gaps, the percentage distributions were: 8.97% (in small gaps), 19.23% (in medium gaps), 20.51% (in large gaps), 19.23% (in fire gap) and 32.05% (in windfall gap). The distributions of juvenile tree species were: 13.97% (in small gaps), 18.39% (in medium gaps), 20.69% (in large gaps), 19.54% (in fire gap) and 27.59% (in windfall gap). The herbaceous species distributions were: 17.43% (in small gaps), 16.51% (in medium gaps), 15.60% (in large gaps), 15.60% (in fire gap) and 34.86% (in windfall gap) (Appendix 2.3-2.5).

As expected, there was a higher percentage of adult and juvenile tree species in the large than medium and small gaps. There was more adult and juvenile tree species in the windfall than fire and large gaps. There was more herbaceous species in small than medium and large gaps; this suggested that as the gap area was larger, the number of herbaceous species was decreasing. There was more herbaceous species in windfall than fire and large gaps (Appendix 2.3-2.5).

2.3.1. Tree species

i. ABUNDANCE OF TREES

The abundance (N) of adult and juvenile trees across gap sizes had different trends (Fig. 2.5a; Fig. 2.7a), but not statistically significant (Table 2.3; Table 2.7). Nevertheless, the mean abundance of trees was higher in large gaps than in medium and small ones (Fig. 2.5a). The density (N/m²) of adult and juvenile trees showed that medium gaps had a greater assemblage of individuals per square meter than small and large gaps (Fig. 2.5b; Fig. 2.7b), although this difference was not statistically confirmed (Table 2.3; Table 2.7).

The abundance of adult and juvenile trees among gaps of different origins also showed diverse tendencies (Fig. 2.7a), but were not statistically significant (Table 2.4; Table 2.8). The windfall gap appeared to have more adult trees than fire gap and artificially created gaps (Fig. 2.7a). The fire gap had more juvenile trees than the windfall and artificially created gaps (Fig. 2.7a). The density of adult and juvenile trees across gap origins showed different trends (Fig. 2.6; Fig. 2.7b), although there were not statistically supported (Table 2.4; Table 2.8). The density of trees in the fire gap was higher than in windfall and artificially created gaps (Fig. 2.6).

ii. THE NUMBER OF SPECIES

The mean number of tree species (S) showed different trends across artificially created gap sizes (Fig. 2.5a), although they were not statistically significant (Table 2.3; Table 2.7). Large gaps had more tree species than medium and small ones (Fig. 2.5a). The density of tree species (S/m²) showed also different tendencies across artificially created gap sizes (Fig. 2.5b; Fig. 2.7b), but there were not statistically distinct (Table 2.3; Table 2.7). Adult tree species were more dense in medium gaps than in small and large ones (Fig. 2.5b). However, the density of juvenile tree species was higher in small gaps than in medium and large ones (Fig. 2.5b).

The mean species number across distinct gap origins appeared also to be different (Fig. 2.7a), although this was not statistically supported (Table 2.4; Table 2.8). The windfall gap had a higher species number than the fire and artificially created gaps (Fig. 2.7a). The trend of the species density across gap origins appeared also to be different (Fig. 2.6; Fig. 2.7b), but was not statistically significant (Table 2.4; Table 2.8). The windfall gap had a higher density of adult tree species than both the artificial and fire gaps (Fig. 2.6). However, the density of juvenile tree species was higher in the fire gap than in the windfall and artificially created

gaps (Fig. 2.6).

iii. SHANNON-WIENER (H') AND EVENNESS (J) DIVERSITY INDICES

The Shannon-Wiener (H') and evenness (J) diversity indices were different across artificially created gap sizes, although this was not statistically significant (Tables 2.2-2.3; Table 2.7). The mean values of the Shannon-Wiener index were higher for large gaps than for medium and small ones (Table 2.3; Table 2.7). These values suggest that large gaps are more diverse in tree species than medium and small ones. Values were in line with the fact that abundance and species number were higher in large gaps than both medium and small ones (Fig. 2.5a). When looking at the evenness values for juvenile trees, small gaps had a higher mean value than large and medium ones (Table 2.7). Those results showed that juvenile trees were more even in their distribution within the small gaps than in the large and medium ones. Those values were in line with the fact that the density of juvenile tree species was higher in the small gaps than both the medium and large ones (Fig. 2.5b). However, when considering the evenness values for adult trees, medium gaps had a greater mean value than large and small ones (Table 2.3). This illustrated that adult trees were more evenly distributed in the medium gaps than in the large and small ones. These figures confirmed the observation that medium gaps have higher densities of adult trees than both large and small ones (Fig. 2.5b).

In the case of gap origins, there were no statistical differences, although there was a trend showing that Shannon diversity was higher for the windfall gap than both fire gaps and large artificially created gaps (Table 2.4; Table 2.8). Therefore, windfall gap appeared to be more diverse than both fire and large artificially created gaps. This was in line with the fact that the windfall gap had a higher tree species number than fire gaps and large artificially created gaps, although abundance of juvenile trees was higher in fire gap (Fig. 2.7a). A different tendency was observed for the evenness values (Table 2.4; Table 2.8). Although there was not a statistical difference, there was a trend showing that the mean evenness number in large artificially created gaps was greater than in the windfall gap and fire gap (Table 2.4; Table 2.8). Therefore, tree species were more evenly distributed within the large artificially created gaps than in the windfall and fire gaps. As stated above, this result did not fit into the fact that the windfall gap had higher tree species number than both fire and artificially created gaps (Fig. 2.7a).

iv. DBH ASSESSMENT

With regard to gaps of different sizes, the mean DBH of adult trees was higher in the large gaps than in medium and small ones, although this difference was not statistically confirmed (Table 2.5; Figs 2.8a-b). The density of DBH per square meter was greater in small gaps than in medium and large ones, and this difference was statistically significant (Table 2.5; Figs 2.8c-d). The Multiple Comparisons post hoc test confirmed this result between small large gaps, but there was not a significant difference among small and medium gaps as well as amongst medium and large gaps (Table 2.5). The density observed was partially due to the size of the openings, because small gaps had smaller areas than medium and large gaps. Since small gaps had a mean DBH of adult trees that is almost the same as for medium and large gaps, the result of the following ratio was expected to be higher for small gaps: mean DBH/area.

When looking at gap origins, it appeared that the mean DBH was higher in the fire gap than in the windfall and artificially created gaps, although this difference was not statistically significant (Table 2.6; Figs 2.8a-b). The density of DBH per square meter was also higher in the fire gap than both the windfall and artificial ones, but this was not statistically confirmed (Table 2.6; Figs 2.8c-d).

2.3.2. Ground flora species

i. PERCENTAGE COVER

The mean range percentage cover of ground flora species was higher in the large gaps than in medium and small ones (Fig. 2.9b). However, it appeared that the presence of ground flora species had a negative impact on the density of tree species per square meter in those large gaps (Fig. 2.5b).

Concerning gap origins, large artificially created gaps had a higher range percentage cover of ground flora species than fire and windfall ones (Fig. 2.9c). This was explained by the fact that the windfall gap had a higher number of adult trees than the fire and large artificial gaps (Fig. 2.7a). More tree species created more shade areas within the windfall gap reducing the sunlight penetration, therefore slowing the growth and the percentage cover of herbaceous species.

ii. SPECIES RICHNESS

The mean number of species appeared to be different across gap sizes, although it was not statistically significant (Table 2.9; Fig. 2.9a). Nevertheless, large gaps contained more species number than medium and small ones (Fig. 2.9a). This was due to the size of each gap, which positively influenced the number of herbaceous species. However, when assessing the species number per square meter, the trend showed that small gaps had a higher density than medium and large ones (Fig. 2.9c). This result was statistically significant (Table 2.9). The Multiple Comparisons post hoc test confirmed the significance between small and large gaps only (Table 2.9). The density observed was explained by the fact that the number of species was not significantly different between gap sizes compared to their areas, therefore the following ratio was bigger for small gaps: mean $S/area$.

In the case of gap origins, the number of species and the related density were higher in the windfall gap than in the fire and large artificial ones, but this difference was not statistically significant (Table 2.10; Fig. 2.9c). Although the range percentage cover and the related density were higher in large artificial gaps (Fig. 2.9c), it seemed that the species number of ground flora did not increase with the percentage cover of herbaceous plants. This was because in large artificially created gaps, a single ground flora species dominated the other herbaceous plants and had a higher percentage cover, which influenced the total cover.

iii. SHANNON-WIENER (H') AND EVENNESS (J) DIVERSITY INDICES

Shannon's diversity indices were different across gap sizes and origins, but it was not statistically significant (Tables 2.9-2.10). Large artificial gaps were the most diverse as they had the highest Shannon's index compared to both medium and small ones (Table 2.9). This was in line with the fact that large gaps had the highest species richness (Fig. 2.9a). The evenness index was greater for the small gaps than for the medium and large ones, although this difference was not statistically confirmed (Table 2.9). The trend illustrated that herbaceous species were more evenly distributed in the small gaps than other growth forms, and this result was caused by the fact that the species number per square meter was higher in those small gaps (Fig. 2.9c).

Gap origins were not statistically different in term of Shannon's index (Table 2.10). Nevertheless, the windfall gap was more diverse because it had a higher Shannon's index than the fire and artificial ones. This was in line with the fact that it had the highest ground flora species number (Fig. 2.9c). Although there was not a statistical difference, there was a trend

showing that the fire gap had a greater evenness index than the windfall and large artificial ones (Table 2.10). The result was in line with the fact that the fire gap had the highest species number per square meter (Fig. 2.9c).

iv. RANK ABUNDANCE CURVES

In the case of artificial gap sizes, dominance by specific species in samples of adult trees was less marked in the large gaps than in the medium and small gaps (Fig. 2.10a). It meant that dominance of particular adult tree species was lower in the large gaps than in the medium and small gaps. This confirmed that adult tree species were more diverse in large gaps than medium and small gaps (Tables 2.2-2.3). For juvenile trees, dominance of specific species was lower in the large gaps than in the small gaps (Fig. 2.10b). This confirmed also that juvenile trees were more diverse in large gaps than medium and small gaps (Table 2.2; Table 2.7). For the ground flora species cover, dominance of particular species was lower in small gaps than in large and medium gaps (Fig. 2.10c). This was not in line with the fact that diversity of herbaceous species was higher in large gaps than in medium and small gaps (Table 2.2; Table 2.9). However, this confirmed that ground flora species were more evenly distributed in small gaps than in large and medium gaps (Table 2.2; Table 2.9).

Concerning gap origins, dominance of specific adult tree species was lower in windfall gap than in large artificial and fire gaps (Fig. 2.10a). This confirmed that adult tree species were more diverse in windfall gap than in both large artificial gaps and fire gap (Table 2.2; Table 2.4). Dominance of particular juvenile tree species was lower in the windfall gap than in large artificial gaps and fire gap (Fig. 2.10b). This confirmed also that juvenile tree species were more diverse in the windfall gap than in the large artificial gaps and fire gap (Table 2.2; Table 2.7). Dominance of specific ground flora species was lower in the windfall gap than in the fire and large artificial gaps (Fig. 2.10c). This confirmed that herbaceous species were more diverse in the windfall gap than in the fire and large artificial gaps (Table 2.2; Table 2.9).

2.3.3. Multivariate analysis

i. ARTIFICIALLY CREATED GAP SIZES

There were no statistical differences between the abundances of adult and juvenile trees, and among the ground flora covers across various sizes of artificially created gaps (Fig. 2.11b; Fig. 2.11d; Fig. 2.12b). The null hypothesis was then accepted, which meant that there were no assemblage differences between gap sizes. Therefore, artificially created gaps did not

appear to be significantly different in terms of community tree species as well as ground flora assemblages associated with gap sizes. However, while looking at the location of each set of gap size experiment, a difference can be notified between gap sizes. This does not mean that the experimental design is flawed. When setting up the original experiment, the three groups of the following gap sizes were created in relatively close proximity from each other: 1) J1AB, J1AM and J1AS; 2) 4EB, 4FM and 4ES2; 3) 4FB, 4EM and 4ES1. Those groups were not significantly different in terms of ecological properties. In the first group, the medium (J1AM) and large gaps (J1AB) were more similar in tree species community assemblages and both different from the small gap (J1AS) (Fig. 2.11b; Fig. 2.11d). In the second group, 4EB (large), 4FM (medium) and 4ES2 (small) gaps appeared generally to be different from each other. In the third group, 4FB (large) and 4EM (medium) were more similar and both different from 4ES1 (small). Concerning ground flora species, in each location of each set of gap sizes, it appeared also that there were dissimilarities between small, medium and large artificial gaps (Fig. 2.12b), although 4ES2 (small) and 4FM (large) gaps were more similar.

ii. GAP ORIGINS

There were no statistical differences between the abundances of adult and juvenile trees, and among the ground flora covers across various sizes of artificially created gaps (Fig. 2.11a; Fig. 2.11c; Fig. 2.12a). The null hypothesis was then accepted, which meant that there were no significant assemblage differences between gap origins. When looking at the position of each set of gap origins, a difference was found between the following gaps: large artificial gaps (4EB, 4FB and J1AB), the windfall gap (PLAA) and the fire gap (KOOM) appeared to be dissimilar for herbaceous and juvenile tree species especially.

2.4. DISCUSSION

2.4.1. Disturbances and indigenous forest changes

Results showed that perturbations such as fire, windfall and harvesting had different effects on the regeneration of plant species in the areas surveyed in Tsitsikamma indigenous forests (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996), although these differences were not always statistically significant. It may be expected that recruitment and growth processes of woody plants in the study areas will be slower as a result of increasing perturbation severity (e.g. large gaps) (Martin & Gower 1996; Van Wyk & Netshiluvhi 1997); species diversity might be also impacted. Plant succession in those study areas appeared to also be correlated to

species sensitivity to sunlight (Martin & Gower 1996; Euston-Brown *et al.* 1996). For instance, following higher disturbances (e.g. large gaps), alien species such as *Acacia melanoxylon* R. Br. (Fabaceae), *Albizia lophantha* (Willd.) Benth (Mimosaceae), as well as pioneer plants like *Haleria lucida* L. (Scrophulariaceae) and *Rapanea melanophloeos* (L.) Mez (Myrsinaceae) have significantly grown in the large gaps (Appendices 2.1-2.5). If further perturbations do not occur in those openings, these pioneer plants will probably be replaced by other indigenous species that will grow enough to close the gaps (Connell & Slatyer 1977; Martin & Gower 1996; Onaindia *et al.* 2004). However, alien species are predicted to reduce the indigenous plant growth because they use more resources while affecting the soil characteristics and increasing the probability of forest fires (CARA 1983; Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997; Henderson 2001). Aliens are therefore better competitors.

In addition to those changes occurring in plant community structure, other modifications were also taking place within the composition and function of these disturbed sites (Everard 1994; DWAF 1995; Martin & Gower 1996; Van Wyk & Netshiluvhi 1997). In this study, results illustrated some events occurring in the process of gap regeneration and showed how they related to the forest plant communities. As observed in the large and medium gaps, factors like die-back and plot damage due to random incident (fallen branches from gap edge trees) may affect plant succession (Connell 1978; Ishii *et al.* 2000; Midgley *et al.* 2002; Lusk *et al.* 2003; Cameron & Benton 2004). Die-back is defined as the progressive dying of a tree, caused by disease or bad conditions (OED 1989).

Results implied that plant community arrangement within the indigenous forest gaps was due to an interaction between ecological condition and vegetation characteristics (Connell & Slatyer 1977; Connell 1978; Kent & Coker 1996). Disturbance of the original plant vegetation structure (e.g. windfall, fire and harvesting) has affected the way that plants responded to ecological changes (Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997; Cameron & Benton 2004). Results produced in this study showed that gaps within the indigenous forests of Tsitsikamma had important effects for the structure of plant species community because changes in sunlight intensity have caused variations of ecological factors in those gaps (Watt 1923; Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997). Therefore, these changes have led to biological responses, which make forest gaps important sites for species regeneration and diversity (Watt 1923; Connell 1978; Huston 1979; Martin & Gower 1996; Lusk *et al.* 2003; Onaindia *et al.* 2004).

After analysing the variations in vegetation community structures between gaps of different sizes and origins, it has been shown that plant species assemblages were heterogenous within those gaps independently of their sizes and origins (Figs 2.11-2.12), while abundance and species richness were different within the same gap category (Table 2.2). The appearance of alien plants and the negative effect of herbaceous species observed on tree regeneration within those gaps implied that these indigenous forests should be less disturbed in order to avoid large gaps (Grime 1973; Van Wyk & Netshiluvhi 1997). Therefore, human induced disturbances such as harvesting should be reduced in those forests (Seydack 1991; Dyck *et al.* 1994). From the results, it appeared that the regeneration process across gaps of different sizes and origins was still at the colonisation stage (Tilman 1988; Potts *et al.* 2002). In terms of mechanisms of succession it could be said that plant species communities were still experiencing the recruiting phase (Connell & Slatyer 1977; Tilman 1988), as shown by the important level of recruitment of juvenile tree species (Figs 2.5-2.6). The openings of gaps in these indigenous forests may have caused a certain types of nutrients to be more available for particular species to grow, which could justify the observed high recruitment of some young trees (Tilman 1988; Albert & Barnes 1987; Everard 1994; Cameron & Benton 2004). However, for some other plants the results might be in line with the Tilman's concept (1988), which states that the nutrients increase with decreasing light, therefore causing higher colonisation rate for shade tolerant species (e.g. *Burchellia bubalina* (L.f.) T.R. Sim (Rubiaceae)).

Juvenile tree abundance as well as mean DBH value were higher in the fire gap compared to the windfall and artificially created gaps. This illustrated the fact that regeneration of woody species has more chance to occur in the combusted area due to an increase in soil nutrients caused by fire (Albert & Barnes 1987; Everard 1994; Rieske 2002). In general, fire is a major perturbation cause, which can control forest tree regeneration (Everard 1994; Petraitis *et al.* 1989; Rieske 2002; Onaindia *et al.* 2004) and it can also cause internal changes in plants controlling growth and competition (Rieske 2002; Midgley *et al.* 2002). At koomansbos, fire may accelerate the decline of shade tolerant plants (Hea 2002; Rieske 2002). In that gap, trees from burned sites had a better growth rate than non-burned areas (Everard 1994).

The Intermediate Disturbance Hypothesis (IDH) was verified for the tree abundance and species number densities only (Fig. 2.5b). The IDH stated that species richness was higher at an intermediate level of disturbance (e.g. medium gaps) (Grime 1973; Connell 1978; Huston 1979; Petraitis *et al.* 1989; Lenz *et al.* 2004). In general, the most resistant species are eliminated by severe perturbations while the more abundant plants are not harmed by weak

disturbances (Petraitis *et al.* 1989; Lenz *et al.* 2004). According to the IDH, in medium gap sizes pioneer species were allowed to growth and to coexist with the most abundant plants (Grime 1973; Connell 1978; Huston 1979; Petraitis *et al.* 1989; Lenz *et al.* 2004).

The percentage cover of ground flora plants appeared to be positively correlated to the area size, sunlight availability and absence of adult trees in the gaps (Fig. 2.9). However, the lack of a significant statistical difference across gap origins in term of ground flora species numbers and related densities illustrated that gaps ranging between 787 m² and 1600 m² had almost a similar effect on the growth of ground flora species and that the way how those gaps were created does not play a major role in the growth rate of ground flora species. As the percentage of those herbaceous species increased, the mortality of tree seedlings decreased (Van Wyk & Netshiluvhi 1997). This confirmed the assumption that the regeneration of woody species will be reduced in large gaps where herbaceous species occurred the most (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997).

There may be an over-inflation of species richness in some gaps compared to others as a consequence of the non-linear relationship between richness and area (Gaston & Blackburn 2000, 2003). However, this artefact appears to be minimal in this case because the plot size were the same across small, medium and large artificially created gaps; and the species density were not significantly different between large artificially created gaps and large natural gaps. For the same reason, the ages of the different gaps appear also to be minimal. Not all trees were removed in the artificially created gaps (e.g. trees less than 10 cm tall were left standing). An assumption may be that these trees might have increased the DBH substantially compared to the fire gap where all trees were probably burnt. In actual fact, the initial survey of the fire gap showed that there was a loss of roughly 86% of the young woody species, and about 82% of adult trees and seedlings combined (Everard 1994). A non-metric multidimensional scaling (NMDS) of the abundances of adult and juvenile tree species assemblages between gaps of different origins and sizes did not show a statistical difference (Figs 2.11-2.12). This highlight that the effect of these remaining trees were also minimal as illustrated in Table 6 (P<0.05).

2.4.2. Conservation implications and impact on forest management

Disturbances play a significant role in the structure of plant community and have important ecological implications for the species conservation in the indigenous forests (Geldenhuys & MacDevette 1989; Dyck *et al.* 1994; Midgley *et al.* 1997). It is suggested that representative areas of Tsitsikamma indigenous forests should be conserved and disturbance minimized

(Geldenhuys & MacDevette 1989; Midgley *et al.* 1997). Monitoring of the impact of disturbances (natural or not) on the indigenous forests should be undertaken more regularly (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Human induced disturbances in Tsitsikamma forests are expected to lead to higher perturbations of these habitats and the subsequent development of a vegetation structure, which could be different from the original (Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Quantifying these changes by ecological surveys is an essential first step in formulating conservation decisions (DWAF 1995; Euston-Brown & Geldenhuys 1996). Should surveys of plant species in the gaps be continued as a constant monitoring programme, they may provide additional indications of the extent to which indigenous forest areas will change within a particular disturbance sector (Petraitis *et al.* 1989; Hea *et al.* 2002; Potts *et al.* 2002), (DWAF 1995; Van Wyk & Netshiluvhi 1997). Such monitoring might assist with the difficult conservation decisions that surround the harvesting of the Tsitsikamma indigenous forest areas (DWAF 1995; Euston-Brown *et al.* 1996). Understanding indigenous forest gap regeneration is important when management recommendations are made (Seydack 1991; DWAF 1995). For the plants to regenerate adequately in the indigenous forest gaps, especially after harvesting (although it is selective), it is essential to know what successional stage these species occupy prior to such human induced disturbances, and what type of harvesting system will generate the desired conditions for plant succession (Martin & Gower 1996; Euston-Brown *et al.* 1996).

2.5. CONCLUSION

The aim of this study was to look at variations in plant species structures between gap sizes and amongst gap origins. Species assemblages across gap sizes and origins were not statistically significant but there were different trends observed. This implied that community structures across those gaps were variable and that gaps play a role in the structuring of plant species within natural forests (Petraitis *et al.* 1989; Martin & Gower 1996; Potts *et al.* 2002). The differences observed may be related to factors such as the sensitivity of forest plants to sunlight and progressive environmental changes occurring within the gaps (Tilman 1988; Van Wyk & Netshiluvhi 1997).

This study verified the hypothesis that gaps observed may close according to their sizes, origins and the plant species particularities. From the study results it is predicted that large gaps (artificial, fire and windfall) as well as medium gaps will take time before reaching their initial state because herbaceous species and periodic events are reducing the regeneration of

tree seedlings (DWAF 1995; Van Wyk & Netshiluvhi 1997). However, small gaps tend to be closed from adjacent trees which are leaning towards those gaps and lack of competition from herbaceous species will increase the chance of closing those gaps (Van Wyk & Netshiluvhi 1997). Unfavourable climatic or site conditions coupled with human practices not compatible with natural gap dynamics may influence the extinction of some forest plants in these gaps, especially in the medium and large ones (Geldenhuys & MacDevette 1989; Van Wyk & Netshiluvhi 1997). Extinction of those plants is likely to threaten vegetation structure in indigenous forests and would change natural plant and animal activities (Tilman 1988; Petraitis *et al.* 1989; Midgley *et al.* 1997). Global and future climate change is also likely to have important consequences within these indigenous forest gaps, and requires research and planning.

For future studies the relationship between species characteristics, distribution and resource absorption or soil composition at a local scale may be assessed (Albert & Barnes 1987; Tilman 1988; Cameron & Benton 2004). Plant species may change the composition of soil or distribute themselves according to resource available on each site. In addition, soil studies may determine if there is a trend between resource distribution and plant species characteristics. Comparison of similar studies in various geographical areas may also be conducted to observe different plant responses across distinct regions.

Table 2.1 Summary of gaps created in Tsitsikamma indigenous forests: small (J1AS, 4ES1 and 4ES2), medium (J1AM, 4EM and 4FM), large artificially created gaps (J1AB, 4EB and 4FB), fire gap (KOOM), and windfall gap (PLAA).

Gap site	Gap name	Gap size	Date of creation (subsequent surveys)	Area (m ²)	Gap creation	Context
Lottering	4ES1	Small	06/11/1995 (3, 4, 5, 6)	108	a	1, 2
Lottering	4ES2	Small	09/11/1995 (3, 4, 5, 6)	79	a	1, 2
Lottering	4EM	Medium	07/11/1995 (3, 4, 5, 6)	201	a	1, 2
Lottering	4FM	Medium	09/11/1995 (3, 4, 5, 6)	389	a	1, 2
Lottering	4EB	Large	08/11/1995 (3, 4, 5, 6)	829	a	1, 2
Lottering	4FB	Large	10/11/1995 (3, 4, 5, 6)	779	a	1, 2
Kleinbos	J1AS	Small	10/11/1995 (3, 4, 5, 6)	240	a	1, 2
Kleinbos	J1AM	Medium	10/11/1995 (3, 4, 5, 6)	363	a	1, 2
Kleinbos	J1AB	Large	10/11/1995 (3, 4, 5, 6)	755	a	1, 2
Plaatbos	PLAA	Large	31/12/1994 (3, 6)	1600	b	1, 2, 3
Koomansbos	KOOM	Large	30/08/1989 (1, 2, 6)	1000	c	1, 4

Context: (1) near to plantations, (2) next to National Road N2, (3) Nature Reserve, and (4) close to human settlements. Gap creation: (a) selective tree felling, (b) windfall, and (c) ground fire due to human activities. Subsequent surveys: (1) 1990, (2) 1992, (3) 1995, (4) 1996, (5) 1998, and (6) 2003.

Table 2.2 Diversity indices of **(a)** adult trees, **(b)** juvenile trees and **(c)** herbaceous species across gap sizes and origins in 2003: small (J1AS, 4ES1 and 4ES2), medium (J1AM, 4EM and 4FM), large artificially created gaps (J1AB, 4EB and 4FB), fire gap (KOOM) and windfall gap (PLAA) (Shannon (H'), Evenness (J), species richness (S) and abundance (N)).

Gap name	Gap size	H' (log 10)	J (log 10)	S	N	S/m^2	N/m^2
(a)							
J1AS	Small	0.678	0.970	5	6	0.021	0.025
4ES1	Small	0.217	0.722	2	5	0.019	0.046
4ES2	Small	0	0	1	1	0.013	0.013
J1AM	Medium	0.872	0.837	11	26	0.030	0.072
4EM	Medium	0.649	0.928	5	8	0.025	0.040
4FM	Medium	0.641	0.917	5	7	0.013	0.018
J1AB	Large	0.889	0.889	10	25	0.013	0.033
4EB	Large	0.950	0.912	11	25	0.013	0.030
4FB	Large	0.501	0.832	4	7	0.005	0.009
KOOM	Large	0.986	0.819	16	113	0.016	0.113
PLAA	Large	1.153	0.825	25	181	0.011	0.082
(b)							
J1AS	Small	0.900	0.943	9	22	0.037	0.092
4ES1	Small	0.436	0.914	3	7	0.028	0.065
4ES2	Small	0.649	0.928	5	8	0.063	0.101
J1AM	Medium	0.758	0.681	13	116	0.036	0.319
4EM	Medium	0.800	0.946	7	15	0.035	0.075
4FM	Medium	0.860	0.901	9	21	0.023	0.054
J1AB	Large	0.923	0.805	14	148	0.018	0.196
4EB	Large	0.961	0.839	14	64	0.017	0.077
4FB	Large	0.899	0.942	9	14	0.011	0.018
KOOM	Large	0.742	0.591	18	357	0.018	0.357
PLAA	Large	1.127	0.817	24	289	0.011	0.131
(c)							
J1AS	Small	0.988	0.948	11	-	0.046	-
4ES1	Small	1.017	0.942	12	-	0.111	-
4ES2	Small	0.954	1	9	-	0.114	-
J1AM	Medium	0.878	0.921	9	-	0.025	-
4EM	Medium	1.096	0.984	13	-	0.065	-
4FM	Medium	1	0.926	12	-	0.031	-
J1AB	Large	1.06	0.952	13	-	0.017	-
4EB	Large	1.001	0.962	11	-	0.013	-
4FB	Large	0.975	0.937	11	-	0.014	-
KOOM	Large	1.197	0.973	17	-	0.017	-
PLAA	Large	1.515	0.959	38	-	0.017	-

Table 2.3 Kruskal-Wallis ANOVA test for diversity indices of adult trees across gap sizes (Shannon (H'), Evenness (J), species richness (S) and abundance (N)). Mean (\pm SD)

	Small gaps	Medium gaps	Large gaps	H (2, 9)	P
H'	0.300 (0.350)	0.720 (0.130)	0.780 (0.240)	2.760	0.250
J	0.560 (0.500)	0.890 (0.050)	0.880 (0.040)	1.160	0.560
S	2.670 (2.080)	7 (3.460)	8.330 (3.790)	3.410	0.180
N	4 (2.650)	13.670 (10.690)	19 (10.390)	5.490	0.060
S/m ²	0.020(0.004)	0.020 (0.010)	0.010 (0.004)	3.950	0.140
N/m ²	0.030 (0.020)	0.040 (0.030)	0.020 (0.010)	1.160	0.560

Table 2.4 Kruskal-Wallis ANOVA test for diversity indices of adult trees across gap origins (Shannon (H'), Evenness (J), species richness (S) and abundance (N)). Mean (\pm SD)

	Large artificial gaps	Fire gap	Windfall gap	H (2, 5)	P
H'	0.780 (0.240)	0.990	1.150	3.200	0.200
J	0.880 (0.040)	0.820	0.830	3.200	0.200
S	8.330 (3.790)	16	25	3.200	0.200
N	19 (10.390)	113	181	3.370	0.190
S/m ²	0.010 (0.004)	0.010	0.020	2.250	0.330
N/m ²	0.020 (0.010)	0.110	0.080	3.200	0.200

Table 2.5 DBH (cm) per m² and per gap sizes. Kruskal-Wallis ANOVA test for adult trees across gap sizes, and probabilities for the Multiple Comparisons post hoc test (a). Mean (\pm SD). Marked (*) P values are significant at P \leq 0.050

	Small gap (1)	Medium gaps (2)	Large gaps (3)	H (2, 9)	P	(a)
DBH/m ²	0.060 (0.010)	0.020 (0.010)	0.010 (0.001)	7.200	0.030*	(1) vs. (3): 0.020* (1) vs. (2): 0.540 (2) vs. (3): 0.280
DBH/gap	7.920 (3.390)	6.540 (1.750)	7.950 (0.86)	0.620	0.730	

Table 2.6 DBH (cm) per m² and gap origins. Kruskal-Wallis ANOVA test for adult trees across gap origins. Mean (\pm SD)

	Large artificial gaps	Fire gap	Windfall gap	H (2, 5)	P
DBH/m ²	0.010 (0.001)	0.020	0.010	3.200	0.200
DBH/gap	7.950 (0.860)	17.530 (17.500)	13.590 (7.63)	3.200	0.200

Table 2.7 Kruskal-Wallis ANOVA test for diversity indices of juvenile trees across gap sizes (Shannon (H'), Evenness (J), species richness (S) and abundance (N)). Mean (\pm SD). Marked (*) P values are significant at $P \leq 0.050$

	Small gaps	Medium gaps	Large gaps	H (2, 9)	P
H'	0.660 (0.230)	0.810 (0.050)	0.930 (0.030)	4.360	0.110
J	0.930 (0.010)	0.840 (0.140)	0.860 (0.070)	1.160	0.560
S	5.670 (3.060)	9.670 (3.060)	12.330 (2.890)	4.540	0.100
N	12.330 (8.390)	50.670 (56.660)	75.330 (67.720)	2.490	0.290
S/m ²	0.040 (0.020)	0.030 (0.010)	0.020 (0.004)	5.960	0.050*
N/m ²	0.100 (0.020)	0.150 (0.150)	0.100 (0.090)	0.090	0.960

Table 2.8 Kruskal-Wallis ANOVA test for diversity indices of juvenile trees across gap origins (Shannon (H'), Evenness (J), species richness (S) and abundance (N)). Mean (\pm SD)

	Large artificial gaps	Fire gap	Windfall gap	H (2, 5)	P
H'	0.930 (0.030)	0.740	1.130	3.200	0.200
J	0.860 (0.070)	0.590	0.820	2.130	0.340
S	12.330 (2.890)	18	24	3.370	0.190
N	75.330 (67.720)	357	289	3.200	0.200
S/m ²	0.010 (0.004)	0.020	0.010	2	0.370
N/m ²	0.100 (0.090)	0.360	0.130	2.130	0.340

Table 2.9 Kruskal-Wallis ANOVA test for diversity indices of herbaceous species across gap sizes, and probabilities for the Multiple Comparisons post hoc test (a) (Shannon (H'), Evenness (J) and species richness (S)). Analysis based on the range of percentage cover estimated in each gap (Braun-Blanquet value). Mean (\pm SD). Marked (*) P values are significant at $P \leq 0.050$

	Small gaps (1)	Medium gaps (2)	Large gaps (3)	H (2, 5)	P	(a)
H'	0.990 (0.030)	0.990 (0.110)	1.010 (0.040)	0.360	0.840	
J	0.960 (0.030)	0.940 (0.040)	0.950 (0.010)	1.160	0.560	
S	10.670 (1.530)	11.330 (2.080)	11.670 (1.150)	0.640	0.730	
S/m ²	0.090 (0.040)	0.040 (0.020)	0.010 (0.0020)	6.490	0.040*	(1) vs. (3): 0.030* (1) vs. (2): 0.890 (2) vs. (3): 0.410

Table 2.10 Kruskal-Wallis ANOVA test for diversity indices of herbaceous species across gap origins (Shannon (H'), Evenness (J) and species richness (S)). Analysis based on the range of percentage cover estimated in each gap (Braun-Blanquet value). Mean (\pm SD).

	Large artificial gaps	Fire gap	Windfall gap	H (2, 5)	P
H'	1.010 (0.040)	1.200	1.520	3.200	0.200
J	0.950 (0.010)	0.970	0.960	2.130	0.340
S	11.670 (1.150)	17	38	3.370	0.190
S/m ²	0.010 (0.002)	0.020	0.020	1.670	0.430

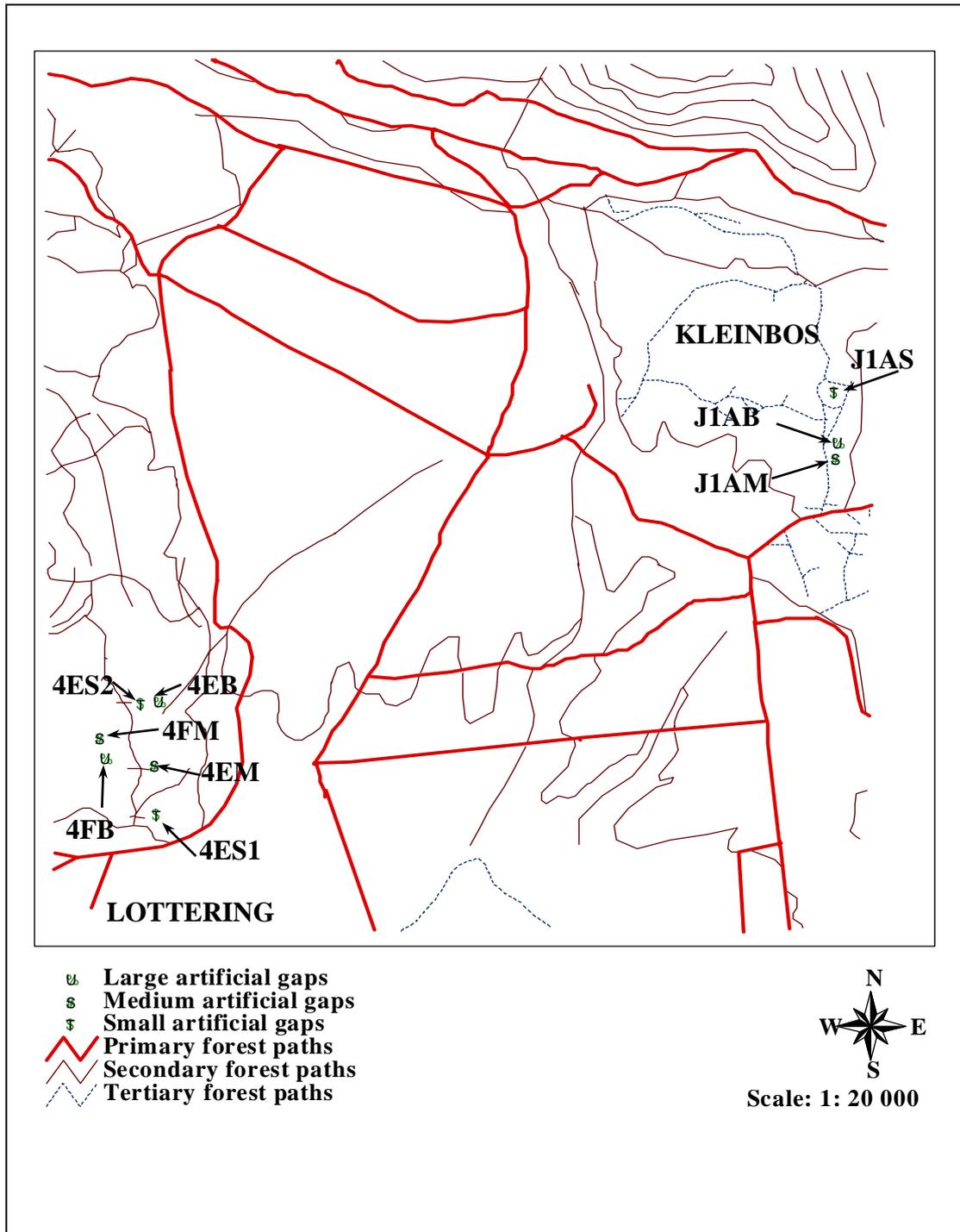


Fig. 2.1 Locations of artificially created gaps at Lottering and Kleinbos, in the Tsitsikamma indigenous forest: small (J1AS, 4ES1, 4ES2), medium (J1AM, 4FM, 4EM) and large gaps (J1AB, 4FB, 4EB).

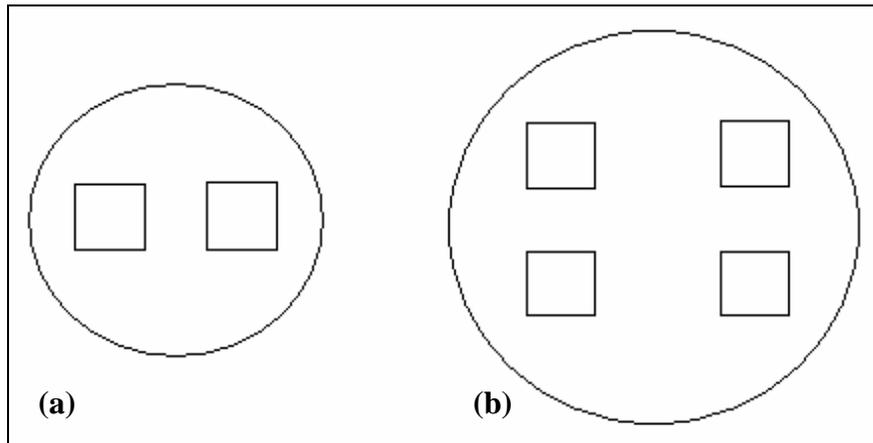


Fig. 2.2 Layout of 3m×3m plots in the (a) small and (b) medium and large artificially created gaps at Lottering and Kleinbos.

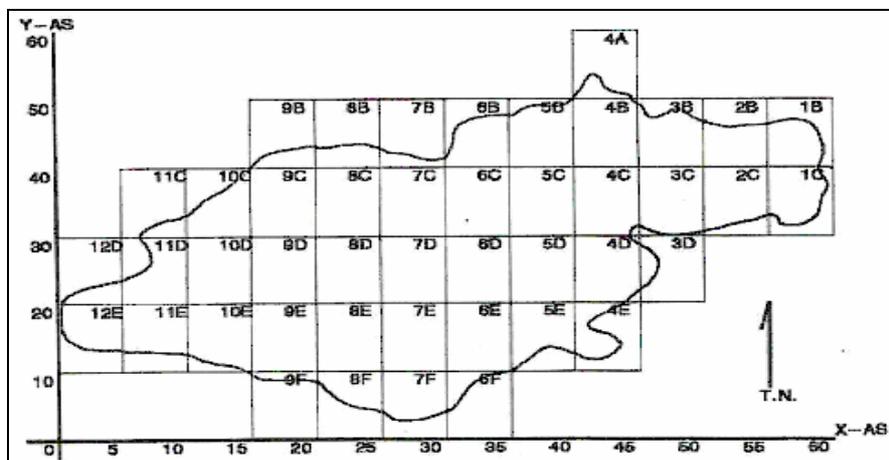


Fig. 2.3 Layout of 44 plots over the total area of the windfall created gap at Plaatbos Nature Reserve. Each plot measures 5m×10m.

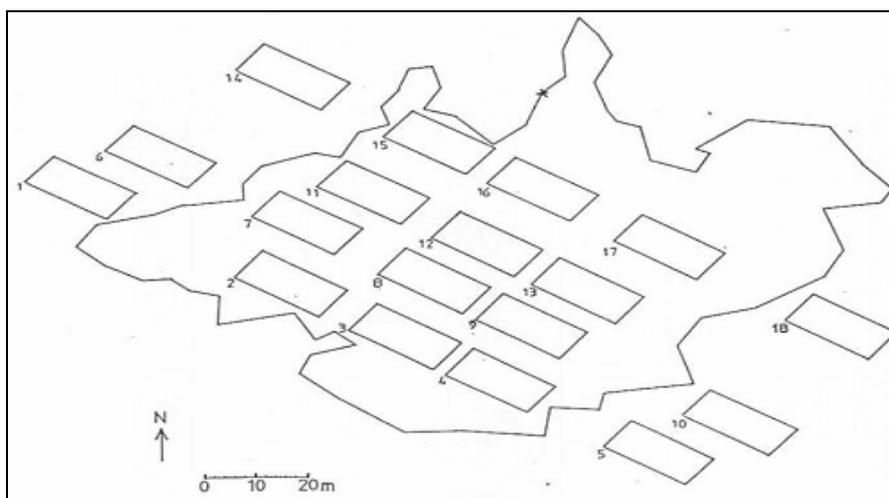


Fig. 2.4 Layout of 18 plots over the burnt area at Koomansbos. Each plot measures 10m×20m.

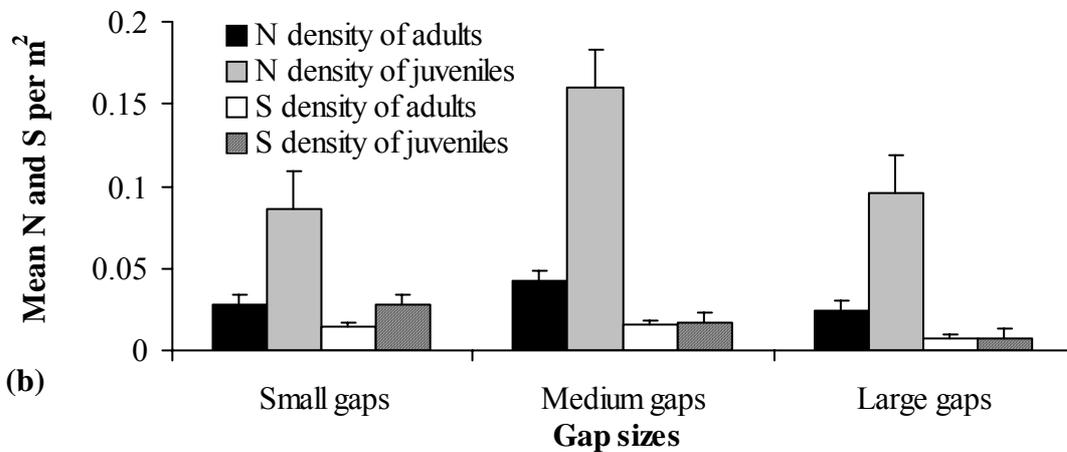
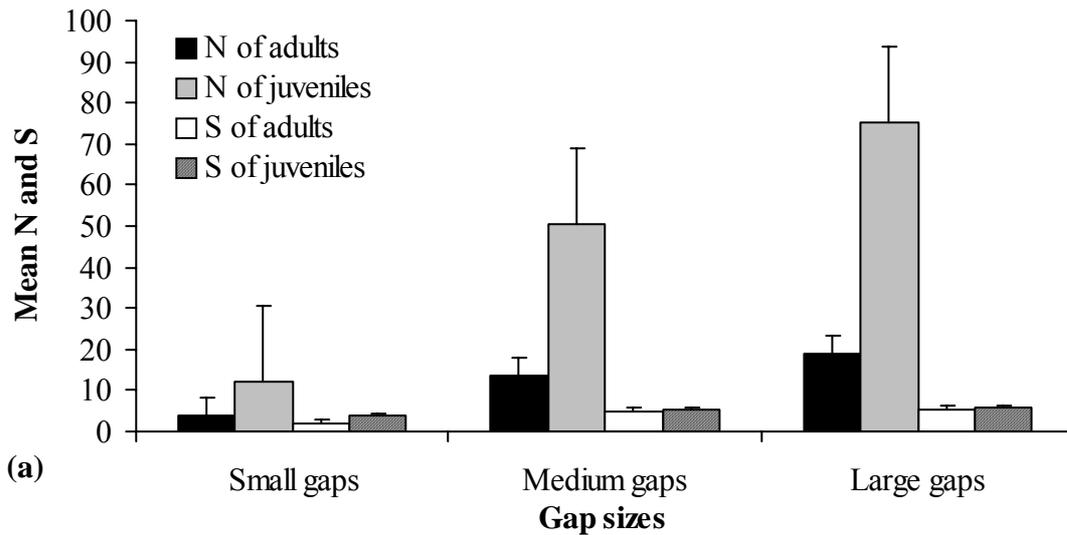


Fig. 2.5 Mean abundance (N) and species number (S) of adults and juveniles trees across artificial created gap sizes in 2003 (a) and related density (b). Bars are standard errors.

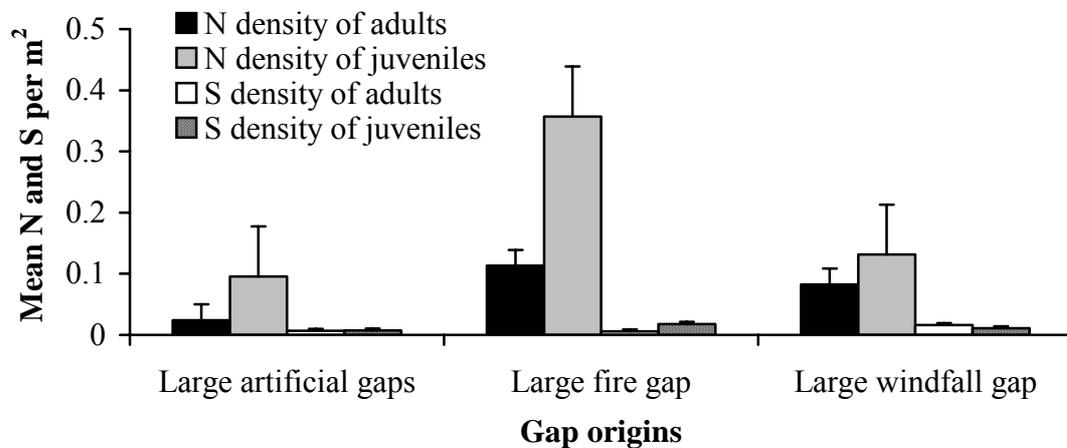


Fig. 2.6 Mean abundance (N) and species number (S) density of adults and juveniles trees across all gap origins in 2003. Bars are standard errors.

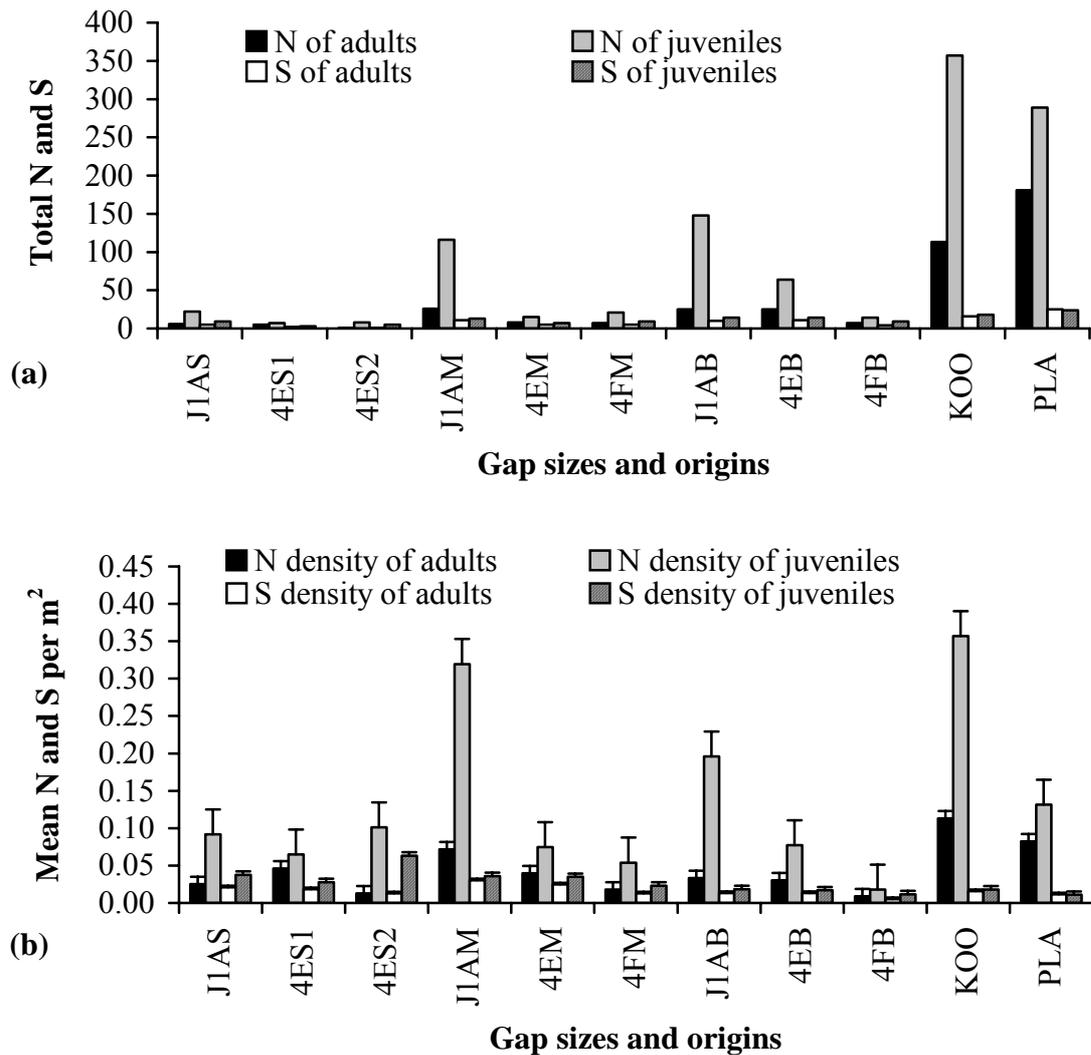


Fig. 2.7 Abundance (N) and species number (S) of adults and juveniles trees across gap sizes and origins in 2003 **(a)** and related density **(b)**. J1AS, 4ES1 and 4ES2 are small artificial created gaps. J1AM, 4EM and 4FM are medium artificial created gaps. J1AB, 4EB and 4FB are large artificial created gaps. KOO (Koomansbos) is the large fire gap. PLA (Plaatbos) is the large windfall gap. Bars are standard errors.

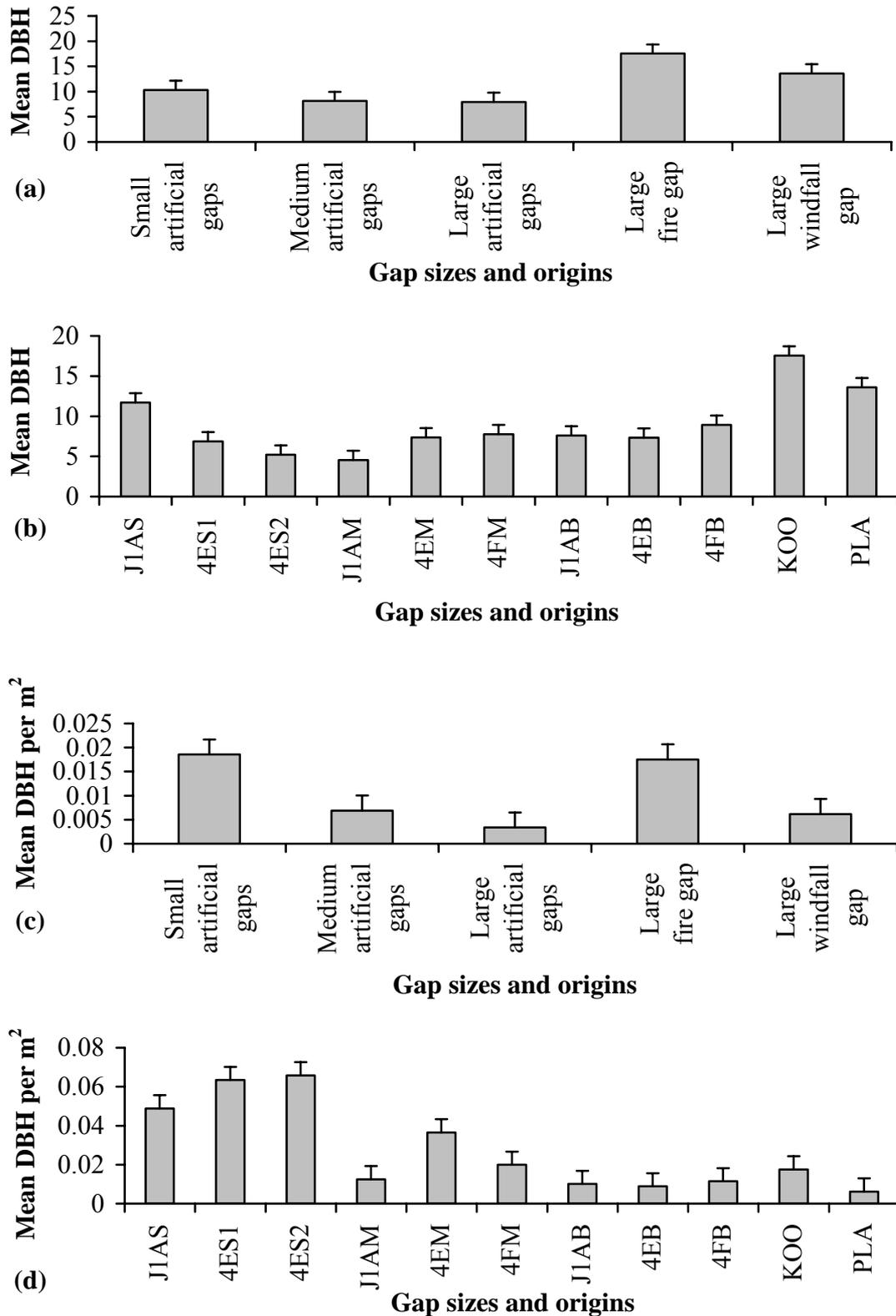


Fig. 2.8 Mean DBH (cm) of adult trees across gap sizes and origins in 2003 **(a-b)** and related density **(c-d)**. J1AS, 4ES1 and 4ES2 are small artificial created gaps. J1AM, 4EM and 4FM are medium artificial created gaps. J1AB, 4EB and 4FB are large artificial created gaps. KOO (Koomansbos) is the large fire gap. PLA (Plaatbos) is the large windfall gap. Bars are standard errors.

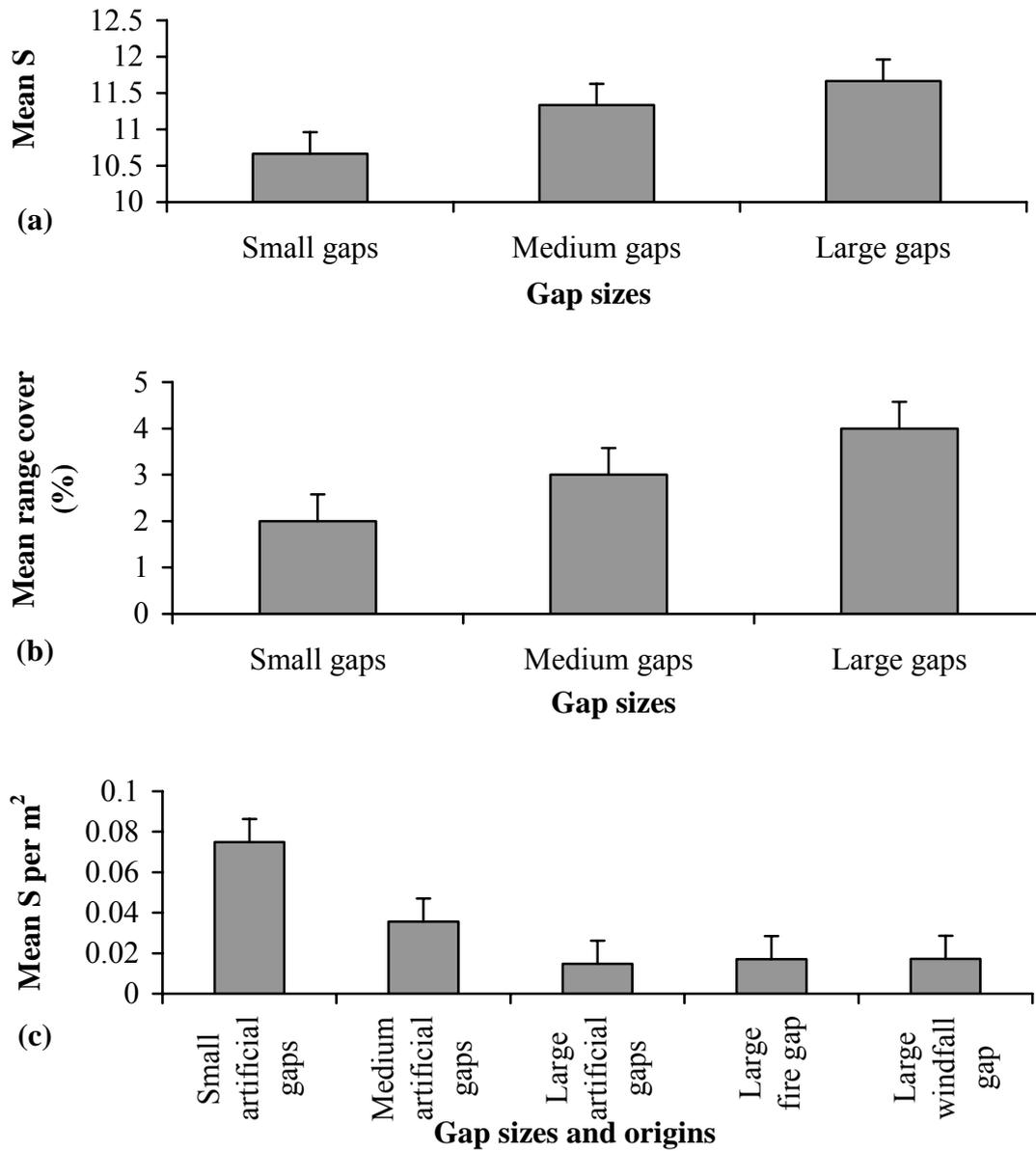


Fig. 2.9 Mean species number (S) (a) and range percentage cover (Braun-Blanquet value) (b) of herbaceous plants across gap sizes and origins in 2003, and related density (c). Bars are standard errors.

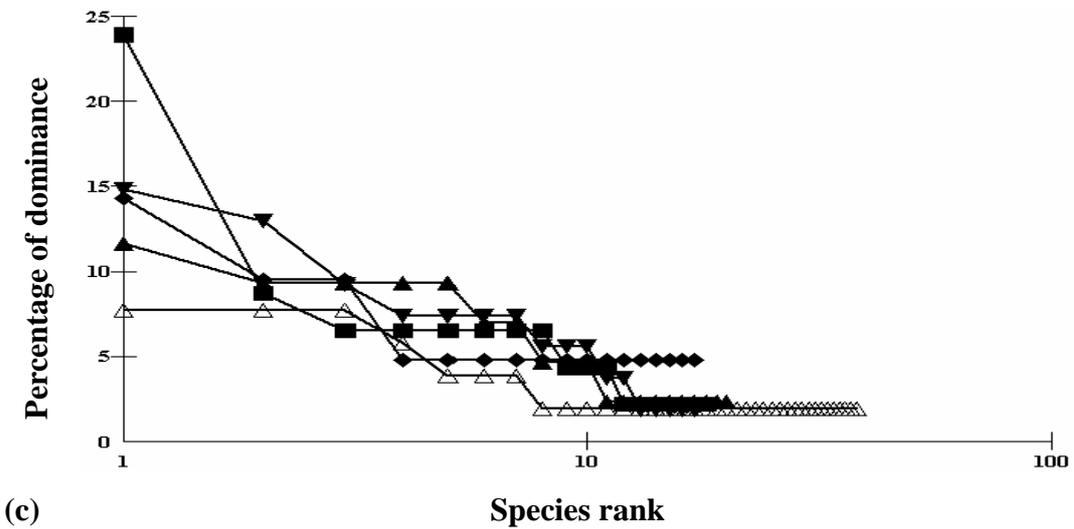
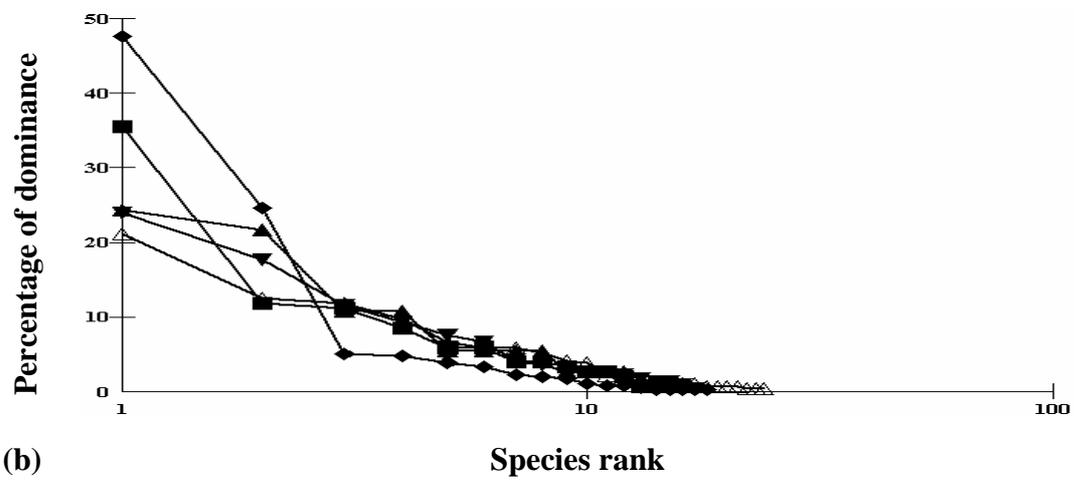
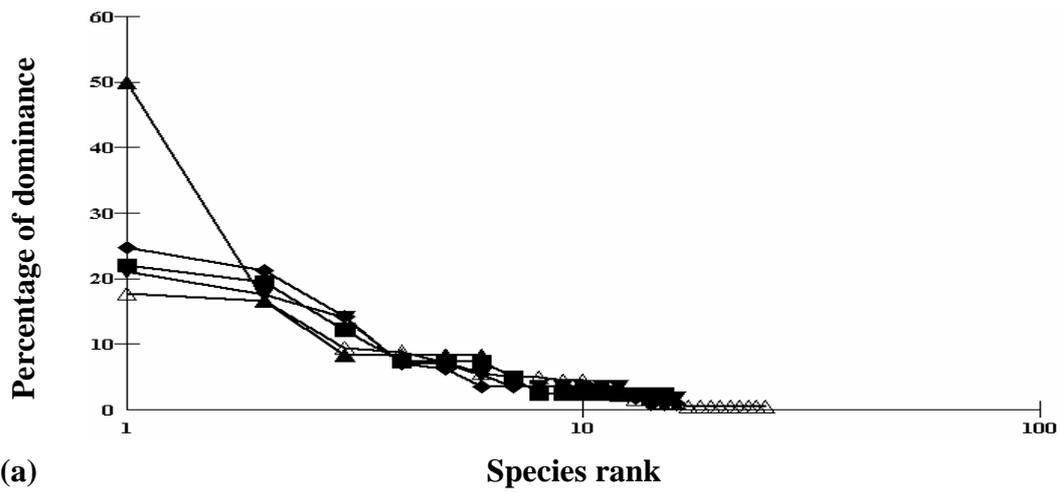


Fig. 2.10 Rank-abundance curves showing adult (a), juvenile (b) tree and herbaceous (c) species assemblage dominance between gap sizes and origins in 2003: small (\blacktriangle), medium (\blacksquare) and large (\blacktriangledown) artificial created gaps; large fire gap (\blacklozenge); large windfall gap (\triangle).

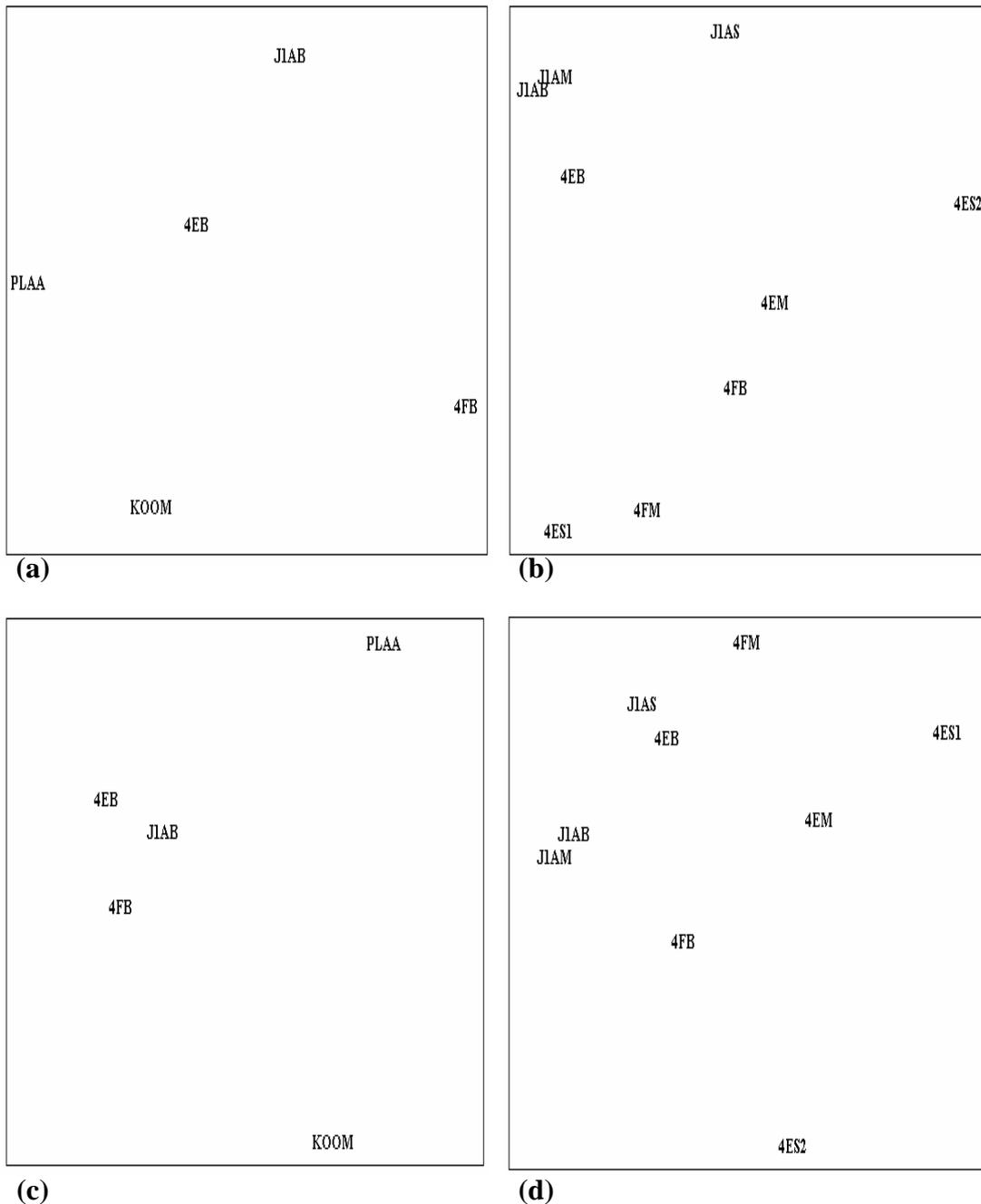
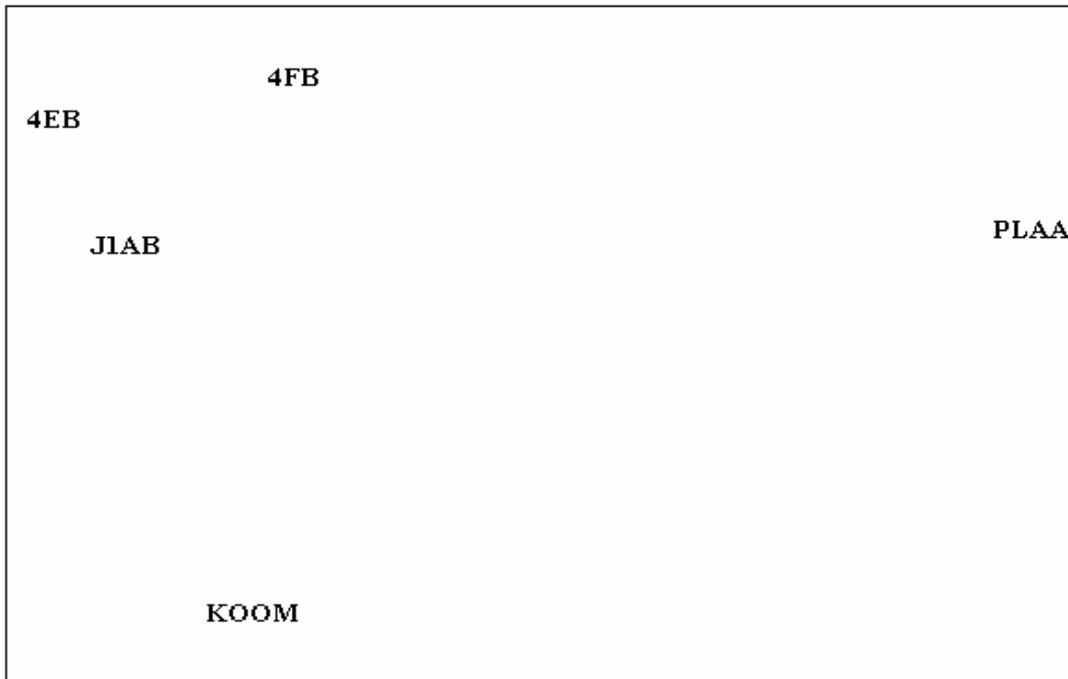
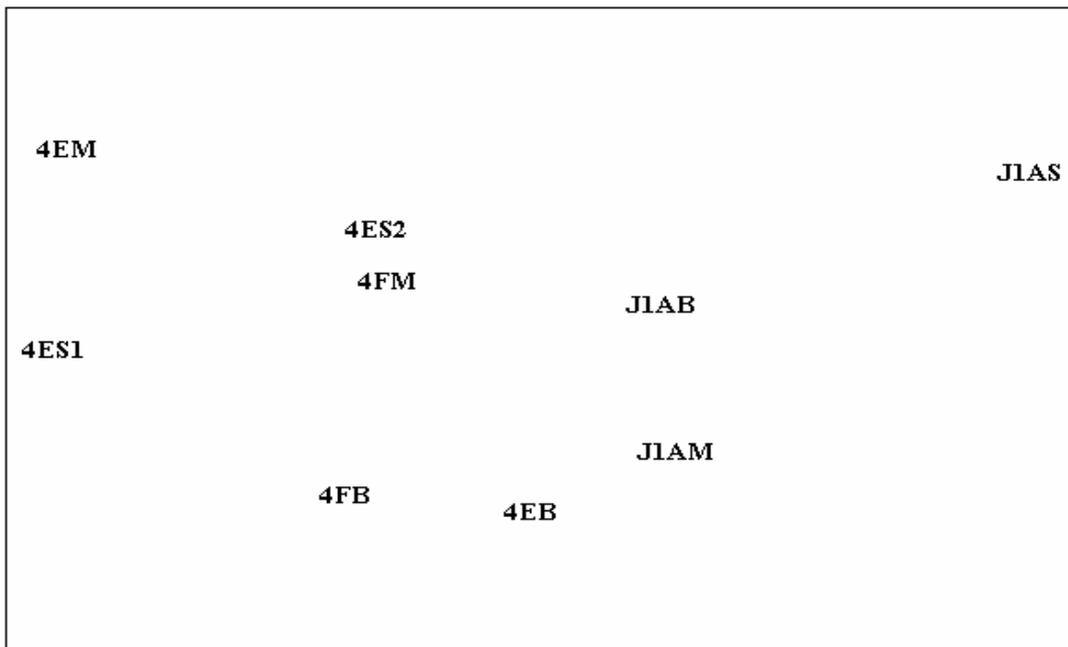


Fig. 2.11 Non-metric MDS ordination of the abundances of adult (**a-b**) and juvenile (**c-d**) tree species assemblages between gaps of different origins and sizes: small (JIAS, 4ES1 and 4ES2), medium (JIAM, 4EM and 4FM), large artificial created gaps (JLAB, 4EB and 4FB), fire gap (KOOM) and windfall gap (PLAA) (Prior to analyses, data were transformed using fourth root). **(a)** ANOSIM: Global $R=0.19$ ($P=0.17$); artificial gaps vs. fire gaps: $R=0.56$ ($P=0.50$); artificial gaps vs. windfall gap: $R=0.33$ ($P=0.50$); NMDS: Stress=0. **(b)** ANOSIM: Global $R=0.09$ ($P=0.33$); small gaps vs. medium gaps: $R=0.13$ ($P=0.50$); small gaps vs. large gaps: $R=0.09$ ($P=0.40$); medium gaps vs. large gaps: $R=-0.11$ ($P=0.70$); MDS: Stress=0.03. **(c)** ANOSIM: Global $R=1$ ($P=0.10$); artificial gaps vs. fire gap: $R=1$ ($P=0.25$); artificial gaps vs. windfall gap: $R=1$ ($P=0.25$); MDS: Stress=0.01. **(d)** ANOSIM: Global $R=0.01$ ($P=0.45$); small gaps vs. medium gaps: $R=-0.15$ ($P=0.70$); small gaps vs. large gaps: $R=0.11$ ($P=0.40$); medium gaps vs. large gaps: $R=0.07$ ($P=0.40$); MDS: Stress=0.08.



(a)



(b)

Fig. 2.12 Non-metric MDS ordination of herbaceous species assemblages between gaps of different origins and sizes: small (JIAS, 4ES1 and 4ES2), medium (JIAM, 4EM and 4FM), large artificial created gaps (JIAB, 4EB and 4FB), fire gap (KOOM) and windfall gap (PLAA) (prior to analyses, data were transformed using fourth root). **(a)** ANOSIM: Global $R=1$ ($P=0.100$); artificial gaps vs. windfall gap: $R=1$ ($P=0.250$); artificial gaps vs. fire gap: $R=1$ ($P=0.250$); MDS: Stress=0. **(b)** ANOSIM: Global $R=-0.004$ ($P=0.460$); small gaps vs. medium gaps: $R=-0.150$ ($P=0.800$); small gaps vs. large gaps: $R=0.220$ ($P=0.200$); medium gaps vs. large gaps: $R=-0.110$ ($P=0.700$); MDS: Stress=0.060

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Appendix 2.1 Species known recorded as trees across all gap sizes and origins in 2003. Marked species are shrubs (S), aliens (A) or pioneers (P).

Scientific name	Family
<i>Gonioma kamassi</i> E. Meyer	Apocynaceae
<i>Ilex mitis</i> (L.) Radlk.	Aquifoliaceae
<i>Brachylaena glabra</i> (L.f.) Druce	Asteraceae
<i>Elaeodendron croceum</i> (ex <i>Cassine papillosa</i>) (Hochst.) Kuntze	Celastraceae
<i>Maytenus acuminata</i> var. <i>acuminata</i> (L.f.) Loes.	Celastraceae
<i>Maytenus peduncularis</i> (Sonder) Loes.	Celastraceae
<i>Pterocelastrus tricuspidatus</i> (Lam.) Sonder	Celastraceae
<i>Curtisia dentata</i> (N.L. Burm.) C.A. Smith	Cornaceae
<i>Platylophus trifolius</i> (L.f.) D. Don	Cunoniaceae
<i>Diospyros whyteana</i> (Hiern) F. White	Ebenaceae
^(A) <i>Acacia melanoxylon</i> R. Br.	Fabaceae
^(P) <i>Kiggelaria africana</i> L.	Flacourtiaceae
<i>Scolopia mundii</i> (Ecklon & Zeyher) Warb.	Flacourtiaceae
<i>Trimeria grandifolia</i> (Hochst.) Warb.	Flacourtiaceae
^(S) <i>Trichocladus crinitus</i> (Thunb.) Pers.	Hamamelidaceae
<i>Apodytes dimidiata</i> subsp. <i>dimidiata</i> E. Meyer ex Arn.	Icacinaceae
<i>Ocotea bullata</i> (Burch.) E. Mey.	Lauraceae
<i>Buddleja saligna</i> Willd.	Loganiaceae
<i>Nuxia floribunda</i> Benth.	Loganiaceae
<i>Ekebergia capensis</i> Sparrm.	Meliaceae
^(A) <i>Albizia lophantha</i> (Willd.) Benth	Mimosaceae
<i>Ficus burtt-davyi</i> Hutch.	Moraceae
<i>Ficus sur</i> Forssk.	Moraceae
^(P) <i>Rapanea melanophloeos</i> (L.) Mez	Myrsinaceae
<i>Ochna arborea</i> Burch. ex DC.	Ochnaceae
<i>Olea capensis</i> subsp. <i>capensis</i> L.	Oleaceae
<i>Olea capensis</i> subsp. <i>macrocarpa</i> L.	Oleaceae
<i>Olinia ventosa</i> (L.) Cufod.	Oliniaceae
<i>Podocarpus falcatus</i> (Thunb.) R. Br. ex Mirb.	Podocarpaceae
<i>Podocarpus latifolius</i> (Thunb.) R. Br. ex Mirb.	Podocarpaceae
<i>Burchellia bubalina</i> (L.f.) T.R. Sim	Rubiaceae
<i>Canthium mundianum</i> Cham. & Schlecht.	Rubiaceae
<i>Psydrax obovata</i> subsp. <i>obovata</i> (Ecklon & Zeyher) Bridson	Rubiaceae
<i>Rothmannia capensis</i> Thunb.	Rubiaceae
<i>Zanthoxylum davyi</i> (Verdoorn) Waterman	Rutaceae
^(S) <i>Halleria lucida</i> L.	Scrophulariaceae
^(S) <i>Sparrmannia africana</i> L.f.	Tiliaceae

Appendix 2.2 Species known recorded as ground flora across gap sizes and origins. Marked species are shrubs (S), aliens (A) or pioneers (P).

Scientific name	Family
<i>Isoglossa ciliata</i> (Nees) Lindau	Acanthaceae
<i>Centella eriantha</i> (Rich.) Drude	Apiaceae
^(S) <i>Carissa bispinosa</i> (L.) Desf. ex Brenan	Apocynaceae
<i>Secamone alpinii</i> Schult.	Apocynaceae
<i>Tylophora cordata</i> (Thnbg.) Druce	Apocynaceae
<i>Asplenium erectum</i> Bory	Aspleniaceae
<i>Asplenium rutifolium</i> (P.J. Bergius) Kunze	Aspleniaceae
<i>Gerbera cordata</i> (Thunb.) Less.	Asteraceae
^(S, P) <i>Chrysanthemoides monilifera</i> (L.) Norl.	Asteraceae
<i>Helichrysum cymosum</i> (L.) D.Don	Asteraceae
<i>Helichrysum petiolare</i> Hilliard & BL.Burtt.	Asteraceae
<i>Senecio deltooides</i> Less	Asteraceae
<i>Senecio</i> sp. L.	Asteraceae
<i>Blechnum attenuatum</i> (Sw.) Mett.	Blechnaceae
<i>Blechnum australe</i> L.	Blechnaceae
<i>Blechnum giganteum</i> (Kaulf.) Schldtl.	Blechnaceae
<i>Blechnum punctulatum</i> Sw.	Blechnaceae
<i>Cardamine</i> sp. Bitter-cress	Brassicaceae
^(S) <i>Cyathea capensis</i> (L.f.) Sm.	Cyatheaceae
<i>Schoenoxiphium lanceum</i> (Thunb.) Kuekenth	Cyperaceae
<i>Schoenoxiphium lehmannii</i> (Nees) Steud	Cyperaceae
<i>Pteridium aquilinum</i> (L.) Kuhn.	Dennstaedtiaceae
<i>Blotiella glabra</i> (Bory) R. M. Tryon	Dennstaedtiaceae
<i>Hypolepis sparsisora</i> (Schrud.) Kuhn	Dennstaedtiaceae
<i>Dioscorea mundii</i> L. Baker	Dioscoreaceae
<i>Polystichum pungens</i> (Kaulf.) C. Presl	Dryopteridaceae
<i>Rumohra adiantiformis</i> (G. Forst.) Ching	Dryopteridaceae
<i>Desmodium repandum</i> (Vahl) DC	Fabaceae
<i>Dumasia villosa</i> DC	Fabaceae
<i>Pyrenacantha scandens</i> Wight Planch. Ex Harv.	Icacinaceae
<i>Aristea ensifolia</i> J. Muir	Iridaceae
<i>Dietes iridioides</i> (L.) Sweet. Ex Klatt.	Iridaceae
<i>Plectranthus fruticosus</i> L'Hérit.	Lamiaceae
<i>Cissampelos torulosa</i> E. Mey. ex Harv.	Menispermaceae
<i>Oxalis</i> sp. L.	Oxalidaceae
<i>Passiflora edulis</i> (Granadilla) Sims	Passifloraceae
<i>Oplismenus hirtellus</i> (L.) P. Beauv.	Poaceae
<i>Cheilanthes</i> sp. Sw.	Pteridaceae
<i>Pteris dentata</i> Forsskal	Pteridaceae
<i>Clematis brachiata</i> Thunb.	Ranunculaceae
^(S) <i>Rubus</i> sp. L.	Rosaceae
<i>Galopina circaeoides</i> Thunb.	Rubiaceae
^(A) <i>Physalis peruviana</i> L.	Solanaceae
^(A, S) <i>Solanum mauritianum</i> Scop.	Solanaceae
^(A, S) <i>Solanum giganteum</i> Jacq.	Solanaceae
^(A, S) <i>Solanum</i> sp. L.	Solanaceae
^(S) <i>Rhoicissus</i> sp. Planch.	Vitaceae

Appendix 2.3 Presence (+) of adult tree species across gap sizes and origins in 2003: small (S1, S2 and S3), medium (M1, M2 and M3) large (L1, L2 and L3) artificial created gaps, fire gap (F) and windfall gap (W).

Species	Gaps										
	S1	S2	S3	M1	M2	M3	L1	L2	L3	F	W
<i>Acacia melanoxylon</i>				+			+	+		+	
<i>Apodytes dimidiata</i>	+		+	+	+			+	+	+	+
<i>Brachylaena glabra</i>										+	+
<i>Buddleja saligna</i>											+
<i>Burchellia bubalina</i>		+		+	+	+	+	+	+	+	+
<i>Burchellia sp.</i>				+			+				
<i>Canthium mundianum</i>	+						+				+
<i>Cassine papillosa</i>	+			+	+		+			+	+
<i>Curtisia dentata</i>								+		+	+
<i>Diospyros whyteana</i>						+	+		+		+
<i>Ekebergia capensis</i>										+	
<i>Ficus burtt-davyi</i>										+	+
<i>Gonioma kamassi</i>	+	+				+		+		+	+
<i>Halleria lucida</i>										+	+
<i>Ilex mitis</i>											+
<i>Kiggelaria africana</i>											+
<i>Maytenus acuminata</i> var. <i>acuminata</i>											+
<i>Maytenus peduncularis</i>				+	+	+		+			+
<i>Nuxia floribunda</i>											+
<i>Ochna arborea</i>											+
<i>Ocotea bullata</i>	+			+			+	+			+
<i>Olea capensis</i> subsp. <i>macrocarpa</i>	+						+	+	+	+	+
<i>Olea sp.</i>						+					
<i>Olinia ventosa</i>										+	
<i>Platylophus trifoliatus</i>								+			
<i>Podocarpus falcatus</i>								+			
<i>Podocarpus latifolius</i>				+			+	+		+	+
<i>Podocarpus sp.</i>				+							
<i>Psyrax obovata</i>							+				+
<i>Pterocelastrus tricuspidatus</i>					+					+	+
<i>Rapanea melanophloeos</i>											+
<i>Rothmannia capensis</i>											+
<i>Scolopia mundii</i>										+	
<i>Tree species unknown 1</i>				+							
<i>Tree species unknown 2</i>				+							
<i>Tree species unknown 3</i>											+

Appendix 2.4 Presence (+) of juvenile tree species across gaps sizes and origins in 2003: small (S1, S2 and S3), medium (M1, M2 and M3), large (L1, L2 and L3) artificial created gaps fire gap (F) and windfall gap (W).

Species	Gaps											
	S1	S2	S3	M1	M2	M3	L1	L2	L3	F	W	
<i>Acacia melanoxylon</i>	+			+			+	+	+	+		
<i>Albizia lophantha</i>											+	
<i>Apodytes dimidiata</i>					+			+		+	+	
<i>Brachylaena glabra</i>										+	+	
<i>Burchellia bubalina</i>	+					+	+	+		+	+	
<i>Canthium mundianum</i>							+				+	
<i>Cassine papillosa</i>			+	+	+	+	+	+			+	
<i>Curtisia dentata</i>	+			+	+	+	+	+	+	+	+	
<i>Diospyros whyteana</i>		+		+	+	+	+	+	+	+	+	
<i>Ekebergia capensis</i>											+	
<i>Ficus sur</i>											+	
<i>Gonioma kamassi</i>	+	+	+	+	+	+	+	+	+	+	+	
<i>Halleria lucida</i>				+			+			+	+	
<i>Ilex mitis</i>											+	
<i>Kiggelaria africana</i>										+	+	
<i>Maytenus peduncularis</i>				+		+	+	+			+	
<i>Nuxia floribunda</i>			+				+		+	+	+	
<i>Ochna arborea</i>										+	+	
<i>Ocotea bullata</i>	+	+	+	+	+	+	+	+	+	+	+	
<i>Ocotea sp.</i>								+				
<i>Olea capensis</i> subsp. <i>macrocarpa</i>	+			+	+		+	+	+	+	+	
<i>Olinia ventosa</i>											+	
<i>Platylophus trifoliatus</i>	+							+				
<i>Podocarpus falcatus</i>				+								
<i>Podocarpus latifolius</i>	+		+	+			+	+	+	+		
<i>Psyrdrax obovata</i>											+	
<i>Rapanea melanophloeos</i>	+			+		+	+	+	+	+		
<i>Rothmannia capensis</i>											+	
<i>Scolopia mundii</i>										+		
<i>Sparmannia africana</i>											+	
<i>Tree species unknown 3</i>				+								
<i>Tree species unknown 4</i>						+						
<i>Tree species unknown 5</i>											+	
<i>Tree species unknown 6</i>											+	
<i>Trimeria grandifolia</i>											+	
<i>Zanthoxylum davayi</i>										+		

Appendix 2.5 Presence (+) of ground flora species across gaps sizes and origins in 2003: small (S1, S2 and S3), medium (M1, M2 and M3), large (L1, L2 and L3) artificial created gaps fire gap (F) and windfall gap (W).

Species	Gaps											
	S1	S2	S3	M1	M2	M3	L1	L2	L3	F	W	
<i>Aristea ensifolia</i>												+
<i>Asplenium erectum</i>												+
<i>Asplenium rutifolium</i>	+			+			+	+	+	+		+
<i>Blechnum attenuatum</i>												+
<i>Blechnum giganteum</i>												+
<i>Blechnum punctulatum</i>												+
<i>Blechnum sp.</i>	+						+					
<i>Blotiella sp.</i>												+
<i>Carissa bispinosa</i>												+
<i>Cardamine sp</i>												+
<i>Centella eriantha</i>												+
<i>Cheilanthes sp.</i>		+			+							
<i>Chrysanthemoides monilifera</i>												+
<i>Cissampelos torulosa</i>		+	+		+	+			+			+
<i>Clematis brachiata</i>		+			+							+
<i>Cyathea capensis</i>												+
<i>Desmodium repandum</i>												+
<i>Dietes iridioides</i>	+	+	+	+	+	+	+	+	+	+		+
<i>Dioscorea mundii</i>												+
<i>Dumasia villosa</i>									+			+
<i>Fern species unknown 1</i>	+											
<i>Fern species unknown 2</i>					+							
<i>Galopina circaeoides</i>		+	+	+		+	+	+	+	+		+
<i>Gerbera cordata</i>		+			+							+
<i>Helichrysum cymosum</i>											+	
<i>Helichrysum petiolare</i>	+		+	+		+	+			+		
<i>Hypolepis sparsisora</i>	+										+	+
<i>Isoglossa ciliata</i>												+
<i>Oplismenus hirtellus</i>		+	+	+	+	+		+	+	+	+	+
<i>Oxalis sp.</i>			+		+	+	+		+	+	+	+
<i>Passiflora edulis</i>												+
<i>Physalis peruviana</i>											+	
<i>Plectranthus fruticosus</i>												+
<i>Polystichum pungens</i>												+
<i>Pteridium aquilinum</i>		+	+	+	+	+	+	+	+	+		
<i>Pteris dentata</i>												+
<i>Pyrenacantha scandens</i>	+	+		+	+	+	+	+	+			+
<i>Rhoicissus sp.</i>												+
<i>Rubus sp</i>	+	+	+	+	+	+	+	+		+		+
<i>Rumohra adiantiformis</i>	+			+			+	+				
<i>Schoenoxiphium lanceum</i>												+
<i>Schoenoxiphium sp.</i>	+	+	+		+	+	+	+	+	+		
<i>Secamone alpinii</i>					+	+	+					+
<i>Senecio deltooides</i>											+	+
<i>Senecio sp.</i>						+	+	+	+	+	+	+
<i>Solanum giganteum</i>											+	
<i>Solanum mauritianum</i>											+	
<i>Solanum sp</i>												+
<i>Tylophora cordata</i>												+
<i>Unknown species 1</i>	+											
<i>Unknown species 2</i>								+				

CHAPTER 3: PLANT GROWTH AND SOIL CHANGE IN FOREST GAPS OF DIFFERENTES SIZES

3.1. INTRODUCTION

Indices such as species diversity or percentage of plants present (before gap creation) are an indication of plant regeneration progress in the disturbed indigenous forest sites (Geldenhuys & Rathogwa 1997; Geldenhuys 1998a, 1998b, 1999a, 1999b). The monitoring of those sites is necessary in order to predict and understand how these indices may change over time (Petraitis *et al.* 1989; Majer 1989, 1990). The growth of a tree, which is an increase in its size, takes place in different parts of that tree and may be assessed by looking at indicators such as diameter and height (Philip 1994; Jayaraman 1999). The regrowth of indigenous forest plants is influenced by various factors related to the environmental properties and the species characteristics (Majer 1989, 1990; Geldenhuys 1998a, 1998b, 1999a, 1999b). As a result, differences exist between the structures of species regrowth in different forest areas and also among different species within a particular area (Majer 1989; Geldenhuys 1998a, 1998b, 1999b). For instance, in Europe, trees grow faster in spring than in winter, but in the tropics, growth may end and continue many times in a year according to the particularities of the area (Philip 1994). In some tropical regions, the growth of trees may change from one year to another because some annual periods have more rain than others (Philip 1994). In general, a plant community, which has been disturbed, tends to have a loss of species as well as an increase in abundance or dominance of a few species (Huston 1979; Petraitis *et al.* 1989; Hobbs & Huenneke 1992; Meffe & Carroll 1997).

The soil pH may vary due to normal ecological factors (Frankenberger & Johanson 1982; Niemi & Vepsalainen 2002). For instance, it has been observed that the soil pH values were mainly related to: 1) soil types; 2) vegetation diversity; 3) micro organisms; 4) soil fauna; and 5) sites characteristics (Frankenberger & Johanson 1982; Niemi & Vepsalainen 2002). The soil pH may also change as a result of human activities (Niemi & Vepsalainen 2002), which have an impact on the normal processes of mineralisation (Frankenberger & Johanson 1982; Anderson & Domsch 1993; Hackl *et al.* 2000). For example, in some boreal forests of Europe, the soil pH value may be more acidic over time as environmental factors are changing (Frankenberger & Johanson 1982; Niemi & Vepsalainen 2002). Kielland (1995) and Hackl *et al.* (2000) have compared soils from various ecosystems (e.g. tundra and forests) and the effects of vegetation types on the soil chemistry were also underlined.

The soil is made of physical, chemical and biological elements; therefore, the perturbation of the topsoil ecosystem affects all three elements (Foth 1990; SCWG 1991; Head 1992). In

various studies conducted to determine the nature and causes of soil conductivity variations, it has been found that the electrical conductivity (EC) varied over time and was mainly related to: 1) soil ionic concentration (Ca and Mg), soil moisture and soil types; 2) soil temperature, soil vegetation cover and survey period (Trudgill 1988; Wardle 1992; Singer & Munns 1996; Hartsock *et al.* 2000). Species diversity and richness are predicted to be highest under low conductivity and decrease as EC becomes higher (Robson 1989; Hartsock *et al.* 2000). Species richness is also predicted to be highest on the low and medium levels of soil pH, and lowest on the high levels (Robson 1989; Hartsock *et al.* 2000).

The objectives of this study were: 1) to assess the rate of increase of plant species by comparing diversity indices between 1995 and 2003. This was done to evaluate how the growth rate differed between gaps and a simple growth rate model was used in that evaluation; 2) to measure whether or not the subsequent growth of plant species was associated with soil quality changes inside the gaps (Philip 1994).

3.2. MATERIALS AND METHODS

3.2.1. Simple growth rate model

In this study, the growth rate was considered to be the rate at which biodiversity indices of vegetation are increasing or decreasing between the two survey periods (e.g. 1995 and 2003) (OED 1989; Petraitis *et al.* 1989; Philip 1994; Sutherland 1996; Geldenhuys 1998a, 1998b, 1999b). In the simple growth rate model, the variation in diversity index value was expressed as a proportion of this value at specific points in time, which was the start or the end of the growth period considered: $v_n = v_0 + ni$ or $i = (v_n - v_0)/n$ (Philip 1994).

Where: 1) v_n = index value in year n at the end of period between surveys (e.g. 2003); 2) v_0 = index value at the start of period between surveys (e.g. 1995); 3) n = number of years in period between surveys (e.g. 2003 – 1995 = 8); and 4) i = rate of growth (e.g. cm/year).

In the results, only the rate of growth (i) was reported (Table 3.1). When assessing diameter growth, only adult and juvenile trees that were alive and measured in 1995 and 2003 were used in the analyses. In the previous reports of surveys done in the fire and artificially created gaps, there was a lack of accurate data record on herbaceous species cover per plot (Everard 1994; Euston-Brown *et al.* 1996; Van Wyk & Netshiluvhi 1997). Thus, the growth rate of herbaceous species could not be assessed for this study and only trees as well as artificially created gaps were taken into account in this chapter.

3.2.2. Soil sample analysis

Soils were collected from inside the gaps as well as from sites adjacent to the gaps, over a two-day period to reduce variations between samples (Foth 1990; Head 1992), and all samples were collected within the top 5 cm of soil. The following total of soil cores (5 cm deep, 4.7 cm in diameter) were collected randomly in the study sites: 1) small gaps: 10 samples per gap; 2) medium gaps: 20 samples per gap; and 3) large gaps: 30 samples per gap (Rozanov 2002). Those numbers were arbitrarily chosen on the basis that: 1) large gaps were approximately three times bigger than small gaps; and 2) medium gaps were roughly two times larger than small gaps (Euston-Brown *et al.* 1996; Rozanov 2002). Samples were marked and analysed at the Soil Sciences Department, University of Stellenbosch. A total of 480 samples were collected from the field, and analyses were carried out for soil pH as well as EC (1:2.5 soil/water) (Head 1992; Sutherland 1996).

i. ELECTRICAL CONDUCTIVITY (EC)

In this study, EC, which was a measure of soil electricity, was assessed by looking at the level of salts in water containing soil samples (Rhoades *et al.* 1989; Hartsock *et al.* 2000). Salts in water generate ions conducting electricity; therefore, EC augments as the level of ions and salts augments (Rhoades *et al.* 1989; Foth 1990). Soil EC variations are due to differences such as soil type and structure, water quality, rainfall, time of measurement, soil temperature, level of organic matter and salts, exchange between ions, types and quantity of minerals (Rhoades *et al.* 1989; Hartsock *et al.* 2000).

ii. pH (H₂O)

Soil pH was measured by assessing the acidity of soil dissolved in water (Sutherland 1996). Soils having a greater hydrogen ions (H⁺) than water (pH less than 7) are acidic, and soils having a lesser hydrogen ions (H⁺) than water (pH greater than 7) are basic, which means that as the degree of hydrogen ions in the soil increases the soil pH decreases therefore become more acidic (Foth 1990; SCWG 1991; Sutherland 1996).

iii. BIOASSAY USING RADISHES

Radishes (scarlet globe) were used (i.e. biomass assessment) to get a rough estimate of the differences between soils from inside and adjacent to the gaps (Keddy *et al.* 1995; Milton 2003; Xuan *et al.* 2004a, 2004b). One of the advantages of radishes is that they grow faster than most of forest indigenous tree species such as *Podocarpus falcatus* (Podocarpaceae) (Venter & Venter 1996; Milton 2003). Radishes give reliable and rapid results for relative

availability of N, P and K in similarly collected and treated soil samples (Keddy *et al.* 1995; Milton 2003; Xuan *et al.* 2004a, 2004b). Because of the large portion of their roots that is constituted of nutrients and water extracted from the soil, the radish is an ideal plant to utilize in this experiment (Keddy *et al.* 1995; Xuan *et al.* 2004a, 2004b).

Soil samples were collected randomly (Rozanov 2002) but aligned to the four geographical directions, and taken approximately from the middle of each site. It means four samples inside and four others adjacent to the gaps. A total of 88 samples were collected. Each soil sample was sifted using a sieve with a mesh size of about 3mm × 3mm. This was done in order to remove coarse material and obtain a more homogenous medium. Vermiculite, an inorganic soil amendment, was then mixed with the soil because it contributes to the production of humus, and increase of soil drainage, porosity and aeration necessary for plant growth (Cheung *et al.* 2000; Cotxarrera *et al.* 2002).

Each soil sample was placed into a single plastic seedling pockets, and three radish seeds were planted into each pocket. Seedling pockets were randomly placed on a single nursery bench and watered to stimulate germination. Watering was applied through an automated watering system and seedling pockets were randomly shifted on the nursery bench on a weekly basis to ensure that variations in watering, light and airflow were randomised. However, seedlings did not grow, as well as expected, and therefore, results of the experiment were inconclusive.

The following variables can be considered amongst the reasons making the bioassay experiment inconclusive in this study: 1) the sampling time and procedure of soils; 2) soils could have been parasitised by insects or chemicals; 3) the geographical origin of soils: soils collected from the high, moist forests of the Tsitsikamma, and then used in a nursery at Stellenbosch University, could not always be as ecologically well adapted as soils collected in the neighbourhood of Stellenbosch; it would have been best to conduct an in situ experiment where radishes or indigenous plants can grow under climatic conditions (e.g. temperature and rainfall) similar to those of the study areas; soil responses would be different; 4) the limited life span of seeds; 5) the origin and source of seeds (e.g. age), more likely to be the problem; and 6) the cultivation of seeds (Venter & Venter 1996).

3.2.3. Statistical analysis

Univariate analyses were conducted as defined in Chapter 3. The differences in species biodiversity indices were compared using the non-parametric tests Kruskal-Wallis and Friedman (Siegel 1956; Keller & Warrack 1997; Siegel & Castellan 1988; Jayaraman 1999; StatSoft, Inc. 2003) across the gap sizes and within plant species categories (e.g. small,

medium and large gaps; adults and juvenile trees). The Kruskal-Wallis method was used to assess if there were significant dissimilarities between growth rates across gap size groups, which were considered as independent samples (Siegel & Castellan 1988; StatSoft, Inc. 2003). The Friedman technique was applied as the nonparametric option to repeated measures ANOVA (Keller & Warrack 1997; Siegel & Castellan 1988; Jayaraman 1999; StatSoft, Inc. 2003). This technique was used to evaluate if abundances, species richness and diameters recorded in 1995 were statistically different from those of 2003. Here, variables were considered as dependent samples (Siegel & Castellan 1988; StatSoft, Inc. 2003). Soil samples were analysed using a parametric ANOVA test (e.g. pH) and the Kruskal-Wallis method (e.g. EC) (Keller & Warrack 1997; Siegel & Castellan 1988; Jayaraman 1999; StatSoft, Inc. 2003). These analyses were conducted using the software STATISTICA 6.0 (StatSoft, Inc. 2003) and a $P \leq 0.05$ was used for significance in all tests. The program Multi-Variate Statistical Package (MVSP), version 3.13 (Kovach 2004) was used to determine different diversity indices such as Shannon-Weiner as defined in Chapter 3.

3.3. RESULTS

Between 1995 and 2003, in the adult tree category, more: 1) *Acacia melanoxylon* (exotic species) was found in medium and large gaps; 2) *Burchellia bubalina* (shade tolerant species) has been recorded in medium and large gaps (Appendix 3.1). Generally: 1) less adult tree species percentage was found in small gaps (8.52% in 1995 vs. 18.42% in 2003); 2) more adult tree species percentage was recorded in medium gaps (37.04% in 1995 vs. 39.47% in 2003); 3) less adult tree species percentage was found in large gaps (44.44% in 1995 vs. 42.11% in 2003) (Appendix 3.1).

In the category of juvenile trees, there were more *Acacia melanoxylon*, *Haleria lucida* (shrub species), *Rapanea melanophloeos* (pioneer species) and *Burchellia bubalina* (shade tolerant species) in the medium and large gaps (Appendix 3.2). Generally: 1) more juvenile tree species percentage was found in small gaps (22.73% in 1995 vs. 26.67% in 2003); 2) less juvenile tree species percentage was recorded in medium and large gaps (45.45% in 1995 vs. 35.56% in 2003; 50% in 1995 vs. 37.78% in 2003) (Appendix 3.2). As expected from the species-area relationship, the percentage of adult and juvenile tree species was higher in large than medium and small gaps (Appendices 3.1-3.2).

3.3.1. Trees species

The abundance of adult trees has increased between 1995 and 2003 across artificially created gaps of different sizes (Table 3.1a; Fig. 3.1a; Fig. 3.1c; Appendix 3.1), but the associated

growth rates were not statistically significant (Table 3.3), like for the individual number recorded in 1995 from that of 2003 (Fig. 3.1a). Nevertheless, medium gaps had higher abundance growth rates than large and small gaps (Table 3.3). Medium gaps showed to have conserved their rank as the densest sites, while the densities in the small gaps appeared to be constant for both abundances and species richness (Fig. 3.2a; Fig. 3.2c). In relation with those densities, there were no significant differences (Table 3.3; Fig. 3.2a). The species richness of adult trees showed also an increase since 1995 (Fig. 3.1a; Fig. 3.2a), although the related growth rates were not statistically distinct (Table 3.3) like for species number recorded in 1995 compared to 2003 (Fig. 3.1a). Medium gaps had again greater species growth rates than large and small ones (Table 3.3). However, the species richness densities in the large gaps appeared to be constant (Fig. 3.2a).

Differences related to species richness densities of adult trees were also not statistically significant (Table 3.3; Fig. 3.2a). The mean DBH and related densities have increased across gap sizes (Table 3.2; Figs 3.3a-d), although the associated growth rates were not statistically different (Table 3.3). However there was a significant difference between the mean of DBH values recorded in 1995 compared to 2003 (Fig. 3.3a). Medium gaps had the lowest adult tree diameter and related density growth rates (Table 3.3). Shannon diversity indices of adult trees varied between 1995 and 2003 across gaps (Table 3.1a), but the related growth rates were not statistically significant (Table 3.3). Small gaps appeared to have a higher increase in Shannon diversity index than the medium and large ones (Table 3.3). Therefore, small gaps tended to be more diverse between 1995 and 2003.

Juvenile trees showed a high increase in the mean abundances and related densities across gap sizes (Table 3.1b; Fig. 3.1b; Fig. 3.1d; Fig. 3.2b; Fig. 3.2d; Appendix 3.2). This increase was especially obvious in medium and large gaps, showing that there was a high recruitment of young tree species in those gaps. The associated growth rates were not statistically different (Table 3.4), but the mean abundance values and related densities recorded in 1995 were significantly different from those of 2003 (Fig. 3.1b; Fig. 3.2b). Although large gaps had the highest species regenerations and growth rates (Fig. 3.1b), medium gaps had the highest abundance densities in 2003, while small gaps had the greatest in 1995 (Fig. 3.2b). The mean numbers of juvenile tree species and related densities showed also that there was an increase (Fig. 3.1b; Fig. 3.2b), but associated growth rates were not statistically different (Table 3.4). However, the mean species number values recorded in 1995 were significantly different from those of 2003 (Fig. 3.2b). Small gaps had the highest species richness densities in 2003. Shannon diversity index for juvenile trees varied also across gaps between 1995 and 2003 (Table 3.1b), but related growth rates were not statistically significant (Table 3.4).

Nevertheless, small gaps had higher diversity growth rates than large and medium gaps, and large gaps had an increase of species number as well as abundance more than small and medium ones (Table 3.4).

3.3.2. Soil sample analysis

Soil sample analysis showed that there was a difference between the soil quality inside and adjacent to the gaps (Figs 3.4-3.5). This result was statistically different for soil pH (Fig. 3.5b) and almost significant for soil EC (Fig. 3.4b). Moreover, soil EC was higher inside than outside the gaps (Fig. 3.4b) and soil pH was lower inside than adjacent to the openings (Fig. 3.5b). It appeared generally that soil pH was acidic inside the gaps (Fig. 3.5a) and that there was a relationship between pH and EC as illustrated by the observation that as pH increased, EC decreased (Figs 3.4a-3.5b). The analysis of soil samples taken only from inside the gaps showed that there was a difference across those gaps (Fig. 3.4a; Fig. 3.5a), but it was not statistically significant. However, it appeared that medium gaps had a higher soil EC than small and large ones (Fig. 3.4a), and that it was the contrary in the case of soil pH (Fig. 3.5a). This result was in line with the fact that medium gaps had the highest density of species richness and abundance. Therefore, it appeared that in medium gaps there were more interactions between plant species, which affected the nutrient cycling. The figures showed that positive ions were more available inside the gaps than adjacent to them. These same observations may be made in the case of medium gaps.

3.4. DISCUSSION

The results of this study showed that plant structure in the gaps is changing and that this change is a slow process (Connell & Slatyer 1977; Midgley *et al.* 1992; Van Wyk & Geldenhuys 1997), which is defined roughly by three stages: plant colonization, vegetation establishment and species loss (Grime 1973; Connell & Slatyer 1977; Huston 1979; Hobbs & Huenneke 1992). In the plots, across the gaps, tree regeneration and mortality have caused changes, which affected vegetation composition and structure (Van Wyk & Geldenhuys 1997; Geldenhuys 1999a, 1999b). Mortality was mainly due to windfalls and trees dying standing (Van Wyk & Geldenhuys 1997; Geldenhuys 1998a). The growth rates, which were not statistically significant across gaps and not always positive, were generally small like in the case of diameter growth of adult trees. This slow increase in growth rates seemed to be usual for the Tsitsikamma indigenous forest vegetation as showed for other South African natural forests (Geldenhuys & Rathogwa 1997; Geldenhuys 1998b, 1999a, 1999b). Therefore, it is important to review the study results from different indigenous forest types in order to have

general growth rates for those forests, and to make suitable suggestions for a better sustainable management of forest vegetation (Everard 1994; Philip 1994; DWAF 1995; Euston-Brown *et al.* 1996; Midgley *et al.* 2002).

In this study, it appeared that the current regeneration in each gap was still at the colonization phase (Connell & Slatyer 1977; Tilman 1988; Majer 1990; Palmer *et al.* 1999), as illustrated by a species richness and abundance higher in 2003 than 1995. The numbers recorded in 1995 were statistically different compared to 2003 for juvenile trees. In general, plant species communities were experiencing the step termed as facilitation stage (Connell & Slatyer 1977; Tilman 1988; Majer 1989, 1990). The observed change in species distribution and composition is a result of the increasing plant population; the growth of current species depends on previous species characteristics, which may have modified the soil properties (Connell & Slatyer 1977; Tilman 1988); this is highlighted by the higher increase rate of juvenile trees in the gaps. The Intermediate Disturbance Hypothesis (IDH) was verified in 1995 and 2003 (Grime 1973; Huston 1979; Petraitis *et al.* 1989; Lenz *et al.* 2004) for mainly the density of adult tree abundance.

A suggestion may be that the earlier surveys should have been used in an ordination/NMDS. A reason might be that the surveys done in the intervening years could have added valuable information as to the direction in which the changes were occurring. However, the figures used in this study to compare results from two different surveys (i.e. 1995 and 2003), indicated clearly the position of the vegetation in the gaps relative to what it was (Figs. 3.1-3.3).

The study results supported Tilman's concept (1988) that the nutrients increased with decreasing sunlight, which resulted in a higher colonisation rate. Sunlight in the gaps decreased due to the increase of plant species cover (Grime 1973; Tilman 1988; DWAF 1995). Soil analysis based on pH and EC measurements of samples taken inside and adjacent to the gaps showed that subsequent growth was related to change in soil chemistry (Majer 1980; Tilman 1988; Robson 1989, 1990). An assessment of other soil parameters in relation to plant species recruitment inside the gaps may add to the understanding of this study (Tilman 1988; Anderson & Domsch 1993; Hackl *et al.* 2000), as different patterns observed in the gaps may be also a consequence of variation in other soil parameters (Lertzman & Fall undated; Anderson & Domsch 1993). For instance, field experiments conducted in boreal forests showed that: 1) the microbial community structure in the forest humus was influenced by changes in humus pH; 2) the adaptation of the humus bacterial community to pH change resulted partly from a change in microbial species composition; 3) the structure of the forest

humus microbial community was influenced by the natural characteristics of the forest sites (Wardle 1992; Philip 1994; Pennanen 2001).

Soil EC and pH were significantly different between areas inside and adjacent to the gaps. It means that temporal and environmental changes affected EC and pH values, and this may be due to changes in ions quantity inside the gaps (Frankenberger & Johanson 1982; Rhoades *et al.* 1989; Hartsock *et al.* 2000). In fact, ions such as Ca and Mg may explain EC variations observed across the sampled sites, it means that a higher quantity of those ions in the soil may be illustrated by highest values of EC (Foth 1990; Sutherland 1996; Hartsock *et al.* 2000). However, there was an inverse relationship between EC and pH (Figs 3.4a-3.5b): inside the gaps, as EC increased pH decreased. Although, the overall pH was acidic on all the sampled sites, the soils located inside the gaps have changed and tended to be more acidic than in locations adjacent to the gaps. This low pH value meant that there was a higher quantity of hydrogen ions within the gaps (Foth 1990; SCWG 1991; Singer & Munns 1996).

3.5. CONCLUSION

As already mentioned, the objectives of this study were to assess the growth rate of plants by comparing diversity indices between two survey periods across gaps and to measure whether or not the growth of species was associated with soil quality changes inside the gaps. In general, there was higher species diversity in 2003 than in 1995 for plants. In gaps when a negative growth rate was observed, it was primarily due to: 1) dying of leader branches of the trees; 2) falling branches from edge trees leaning towards the gaps; 3) trees inside the gaps, which were dying standing and windfall that damaged plots (DWAF 1995; Van Wyk & Geldenhuys 1997). As plants began to recolonize the gaps, they added more organic material to the soil as showed by the pH and EC values that have significantly changed inside the gaps (Connell & Slatyer 1977; Tilman 1988; Cheung *et al.* 2000), the environment in those gaps became able again to support different species, and gradually a more complex ecosystem may be developed (Bradshaw 1984; Tilman 1988; Hobbs & Huenneke 1992). The establishment and growth of vegetation in the gaps occurred probably according to seed quantity and three basic resources: water, nutrients and sunlight (Tilman 1988; Euston-Brown *et al.* 1996). The availability of these resources was possibly influenced by ecological factors such as soil characteristics, rainfall and plant competition (Trudgill 1988; Petraitis *et al.* 1989; Palmer *et al.* 1999). The results in this study confirmed the main concluding remark stated in chapter 3, which pointed out that gap regeneration patterns were not uniform across gaps, as this may be due to factors such as plant sunlight sensitivity or change in environmental conditions within the gaps (Euston-Brown *et al.* 1996; Van Wyk & Geldenhuys 1997; Tilman 1988).

Future studies may still investigate the relationship between plant characteristics, nutrient uptake and soil composition according to species distribution within the gaps. Plant species may change the composition of soil or distribute themselves according to nutrient availability on each site. Furthermore, soil studies may determine if there is a trend between nutrient distribution and species characteristics. The quantity and the composition of soil microbial biomass may be particularly sensitive to changes in the soil environment (Anderson & Domsch 1993; Hackl *et al.* 2000; Pennanen 2001). Therefore, microbial biomass parameters may be used as indicators of ecosystem stress and disturbance as this has been done in other regions (Wardle 1992; Anderson & Domsch 1993; Hackl *et al.* 2000; Pennanen 2001). Information about microbial biomass characteristics in natural ecosystems would make a good contribution for the indigenous forest management (Wardle 1992; Pennanen 2001). Other future investigations may be to look at chemical properties such as Ca and Mg to see if there are strongly related to EC, and if the average contents of both Ca and Mg are really higher within the gaps (Trudgill 1988; Robson 1989; Hartsock *et al.* 2000).

Table 3.1 Diversity indices for adult (a) and juvenile (b) trees across gap sizes in 1995 (c) and 2003 (d): small (S₁, S₂, S₃), medium (M₁, M₂, M₃), large artificially created gaps (L₁, L₂, L₃). Shannon (H'), species richness (S), abundance (N) and growth rate (i)

(a)															
Gap	H' (log10)			S			N			S/m ²			N/m ²		
	c,	d	(i)	c,	d	(i)	c,	d	(i)	c,	d	(i)	c,	d	(i)
S ₁	0.3,	0.68	(0.05)	2,	5	(0.38)	2,	6	(0.5)	0.01,	0.02	(0.002)	0.01,	0.03	(0.002)
S ₂	0.35,	0.22	(-0.02)	3,	2	(-0.13)	7,	5	(-0.25)	0.03,	0.02	(-0.001)	0.07,	0.05	(-0.002)
S ₃	-	-	-	1,	1	(0)	1,	1	(0)	0.01,	0.01	(0)	0.01,	0.01	(0)
M ₁	0.76,	0.87	(0.01)	7,	11	(0.5)	12,	26	(1.75)	0.02,	0.03	(0.001)	0.03,	0.07	(0.01)
M ₂	0.76,	0.65	(-0.01)	6,	5	(-0.13)	7,	8	(0.13)	0.03,	0.03	(-0.001)	0.04,	0.04	(0.001)
M ₃	0.58,	0.64	(0.01)	4,	5	(0.13)	5,	7	(0.25)	0.01,	0.01	(0.0004)	0.01,	0.02	(0.001)
L ₁	0.92,	0.89	(-0.004)	9,	10	(0.13)	17,	25	(1)	0.01,	0.01	(0.0001)	0.02,	0.03	(0.001)
L ₂	0.90,	0.95	(0.01)	9,	11	(0.25)	18,	25	(0.88)	0.01,	0.01	(0.0003)	0.02,	0.03	(0.001)
L ₃	0.67,	0.5	(-0.02)	5,	4	(-0.13)	7,	7	(0)	0.01,	0.01	(-0.0001)	0.01,	0.01	(0)

(b)															
Gap	H' (log10)			S			N			S/m ²			N/m ²		
	c,	d	(i)	c,	d	(i)	c,	d	(i)	c,	d	(i)	c,	d	(i)
S ₁	0.66,	0.9	(0.03)	5,	9	(0.5)	9,	22	(1.63)	0.02,	0.04	(0.002)	0.01,	0.09	(0.01)
S ₂	0,	0.44	(0.06)	1,	3	(0.25)	4,	7	(0.38)	0.01,	0.03	(0.002)	0.02,	0.07	(0.01)
S ₃	0.3,	0.65	(0.04)	2,	5	(0.38)	2,	8	(0.75)	0.025,	0.063	(0.01)	0.03,	0.1	(0.01)
M ₁	0.71,	0.76	(0.01)	7,	13	(0.75)	20,	116	(12)	0.02,	0.04	(0.002)	0.01,	0.32	(0.04)
M ₂	0.81,	0.8	(-0.002)	7,	7	(0)	14,	15	(0.13)	0.04,	0.04	(0)	0.01,	0.08	(0.01)
M ₃	0.73,	0.86	(0.02)	6,	9	(0.38)	9,	21	(1.5)	0.02,	0.02	(0.001)	0.01,	0.05	(0.01)
L ₁	0.78,	0.92	(0.02)	7,	14	(0.88)	15,	148	(16.63)	0.01,	0.02	(0.001)	0.004,	0.2	(0.02)
L ₂	0.89,	0.96	(0.01)	10,	14	(0.5)	27,	64	(4.63)	0.01,	0.02	(0.001)	0.003,	0.08	(0.01)
L ₃	0.69,	0.9	(0.03)	6,	9	(0.38)	11,	14	(0.38)	0.01,	0.01	(0.0004)	0.004,	0.02	(0.002)

Table 3.2 Diameter at Breast Height (DBH) (cm) and growth rate (i) for adult trees across gap sizes in 1995 (a) and 2003 (b): small (S₁, S₂, S₃), medium (M₁, M₂, M₃), large artificially created gaps (L₁, L₂, L₃)

Gap	DBH (cm)			DBH/m ²		
	a,	b	(i)	a,	b	(i)
S ₁	7.7,	11.72	(0.50)	0.03,	0.05	(0.002)
S ₂	6.5,	6.85	(0.04)	0.06,	0.06	(0.0004)
S ₃	5,	5.2	(0.03)	0.06,	0.07	(0.0003)
M ₁	6.96,	4.54	(-0.30)	0.02,	0.01	(-0.001)
M ₂	6.08,	7.35	(0.16)	0.03,	0.04	(0.001)
M ₃	5.53,	7.75	(0.28)	0.01,	0.02	(0.001)
L ₁	6.33,	7.59	(0.16)	0.01,	0.01	(0.0002)
L ₂	6.82,	7.32	(0.06)	0.01,	0.019	(0.0001)
L ₃	6.22,	8.93	(0.34)	0.01,	0.01	(0.0004)

Table 3.3 Growth rates of diversity indices and Diameter at Breast Height (DBH) (cm) across gap sizes between 1995 and 2003. Kruskal-Wallis ANOVA test for adult trees (Shannon (H'), species richness (S), abundance (N)). Mean (\pm SD)

	Small gaps	Medium gaps	Large gaps	H (2, 9)	<i>P</i>
H'	0.01 (0.04)	0.003 (0.01)	-0.005 (0.02)	0.49	0.78
S	0.08 (0.27)	0.17 (0.32)	0.08 (0.19)	0.16	0.92
N	0.08 (0.38)	0.71 (0.9)	0.63 (0.55)	2.04	0.36
DBH (cm)	0.19 (0.27)	0.04 (0.31)	0.19 (0.14)	0.62	0.73
S/m^2	0.0003 (0.002)	0.0001 (0.001)	0.0001 (0.0002)	0.16	0.92
N/m^2	0 (0.002)	0.004 (0.005)	0.001 (0.001)	1.93	0.38
DBH/m^2	0.001 (0.001)	0.0002 (0.001)	0.0002 (0.0002)	1.16	0.56

Table 3.4 Growth rates of diversity indices across gap sizes between 1995 and 2003. Kruskal-Wallis ANOVA test for juvenile trees (Shannon (H'), species richness (S), abundance (N)). Mean (\pm SD)

	Small gaps	Medium gaps	Large gaps	H (2, 9)	<i>P</i>
H'	0.04 (0.02)	0.01 (0.01)	0.02 (0.01)	5.63	0.06
S	0.38 (0.13)	0.38 (0.38)	0.59 (0.26)	1.41	0.49
N	0.92 (0.64)	4.54 (6.49)	7.21 (8.43)	0.87	0.65
S/m^2	0.005 (0.005)	0.001 (0.001)	0.001 (0.0003)	4.67	0.1
N/m^2	0.01	0.02 (0.02)	0.01 (0.01)	0.85	0.65

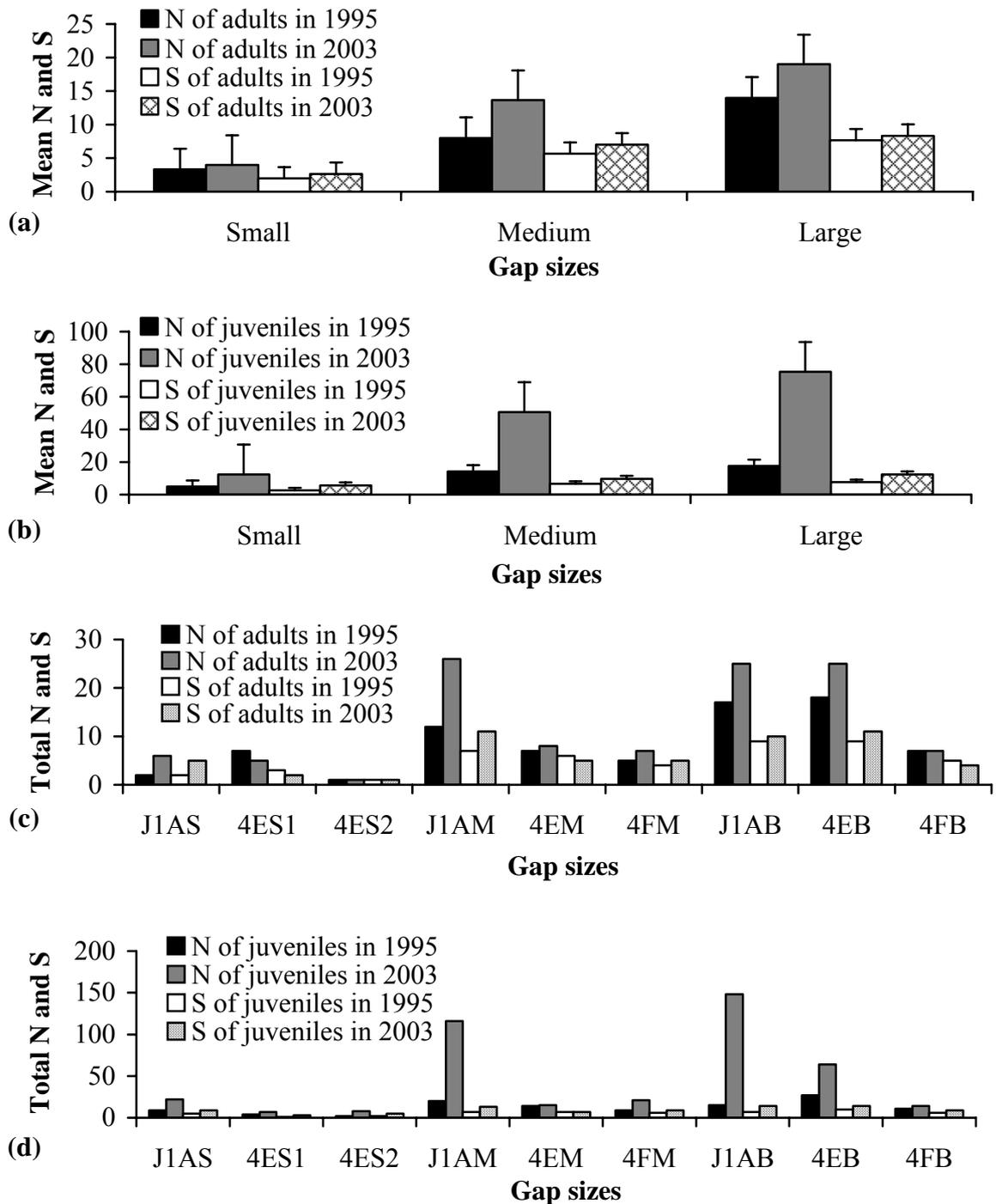


Fig. 3.1 Abundance (N) and species number (S) of adult (a, c) and juvenile trees (b, d) across gap sizes in 1995 and 2003: small (J1AS, 4ES1, 4ES2), medium (J1AM, 4EM, 4FM) and large gaps (J1AB, 4EB, 4FB). Bars are standard errors. Friedman ANOVA (n=9, df=1), 1995 vs. 2003: (a) N: $X^2=3.57$, $P=0.05$; S: $X^2=0.5$, $P=0.48$; (b) N: $X^2=9$, $P=0.003^*$; S: $X^2=8$, $P=0.005^*$. Marked (*) P values are significant at $P \leq 0.050$

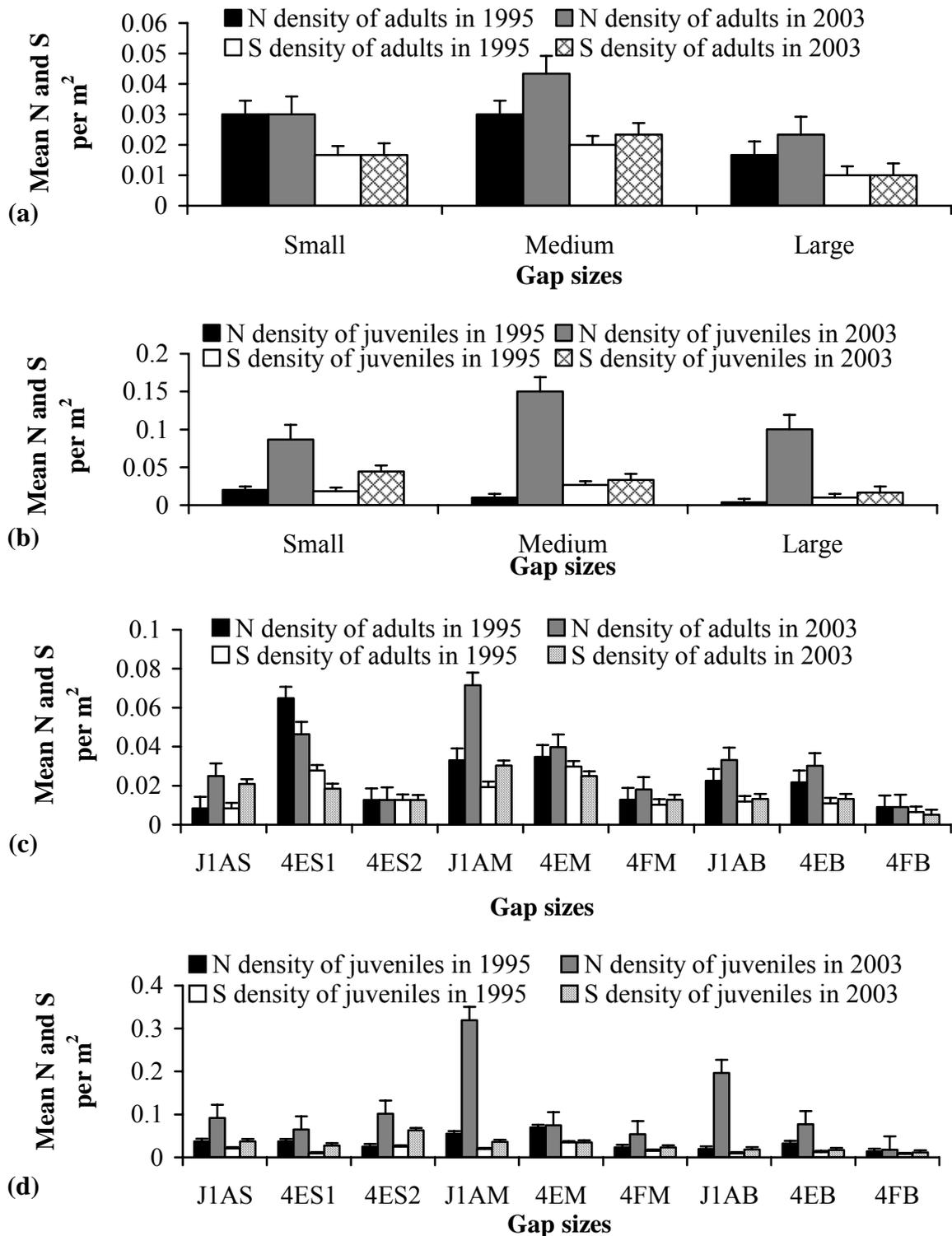


Fig. 3.2 Mean abundance (N) and species number (S) densities of adult (**a, c**) and juvenile trees (**b, d**) across gap sizes in 1995 and 2003: small (J1AS, 4ES1, 4ES2), medium (J1AM, 4EM, 4FM) and large gaps (J1AB, 4EB, 4FB). Bars are standard errors. Friedman ANOVA ($n=9$, $df=1$), 1995 vs. 2003: (**a**) N/m^2 : $X^2=2.66$, $P=0.1$; S/m^2 : $X^2=0.33$, $P=0.56$; (**b**) N/m^2 : $X^2=9$, $P=0.003^*$; S/m^2 : $X^2=6$, $P=0.01^*$. Marked (*) P values are significant at $P \leq 0.050$

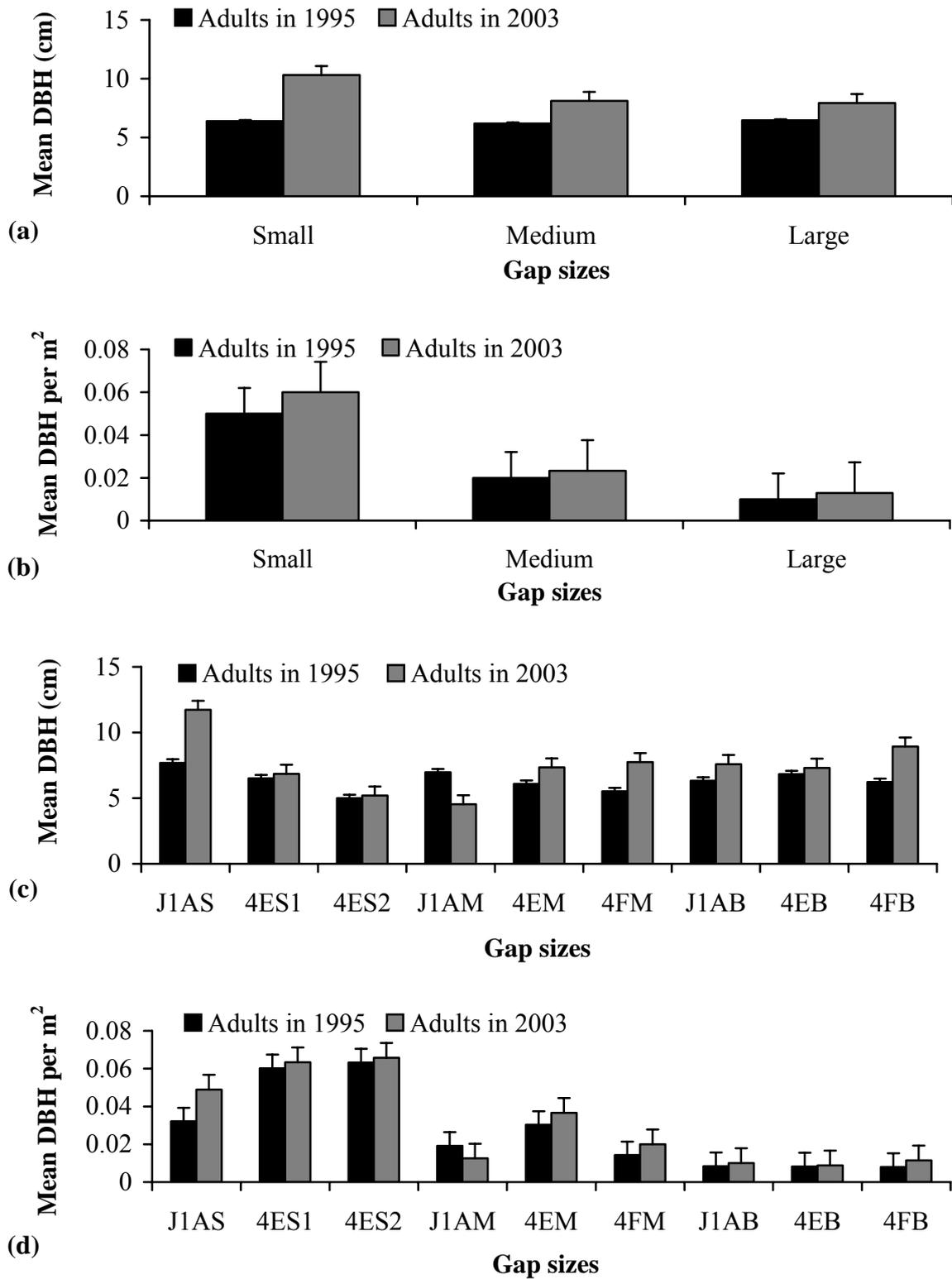


Fig. 3.3 Mean DBH (a, c) (cm) and densities (b, d) of adult trees across gap sizes in 1995 and 2003: small (J1AS, 4ES1, 4ES2), medium (J1AM, 4EM, 4FM) and large gaps (J1AB, 4EB, 4FB). Bars are standard errors. Friedman ANOVA ($n=9$, $df=1$), 1995 vs. 2003: (a) DBH: $X^2=5.44$, $P=0.02^*$; (b) DBH/m²: $X^2=2.67$, $P=0.1$. Marked (*) P values are significant at $P \leq 0.050$

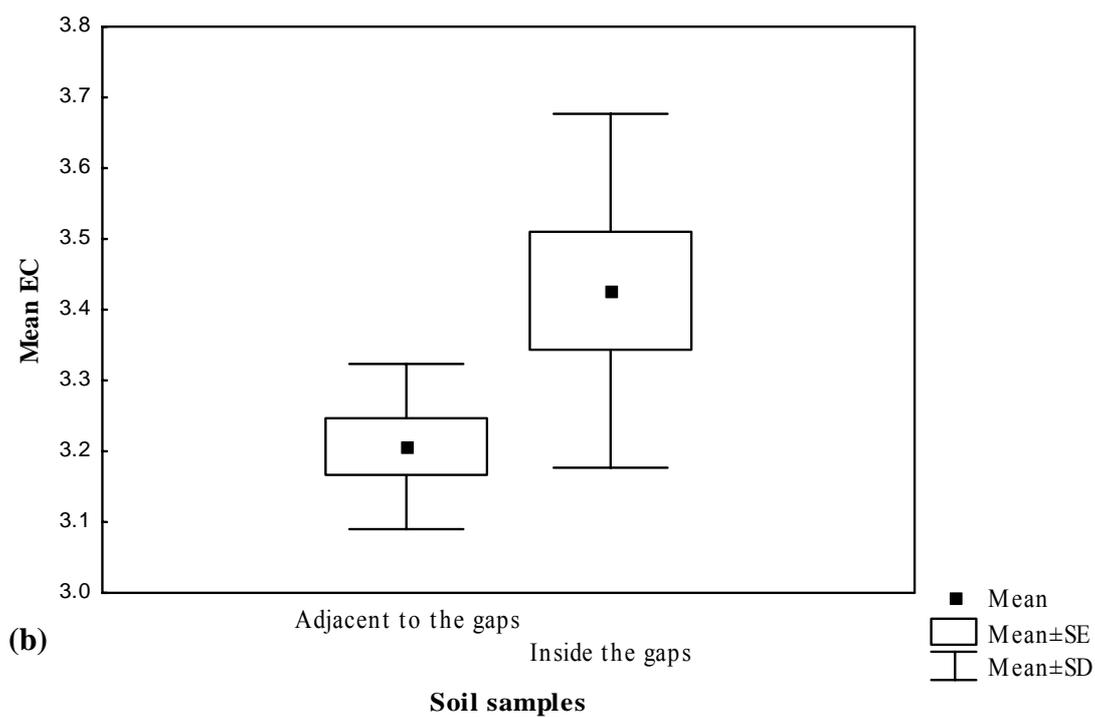
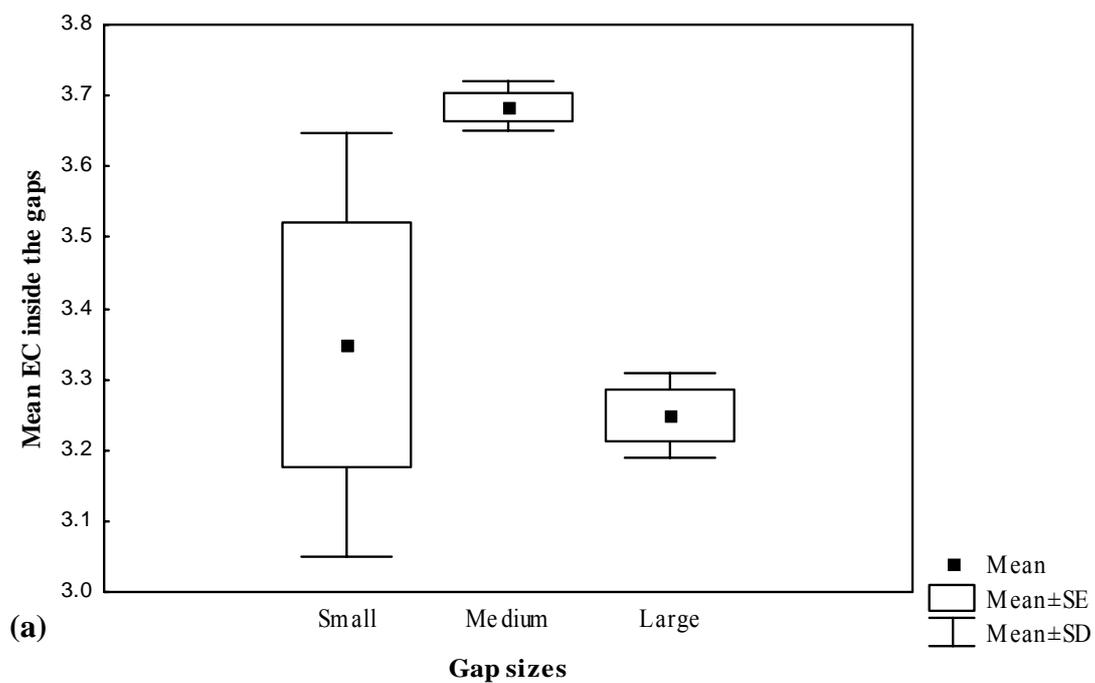


Fig. 3.4 Electrical Conductivity (EC) (μS) of soil samples collected inside and adjacent to the gaps. Kruskal-Wallis test: **(a)** $H(2, 9) = 3.92, P = 0.14$; **(b)** $H(2, 9) = 3.61, P = 0.05^*$. Marked (*) P values are significant at $P \leq 0.050$

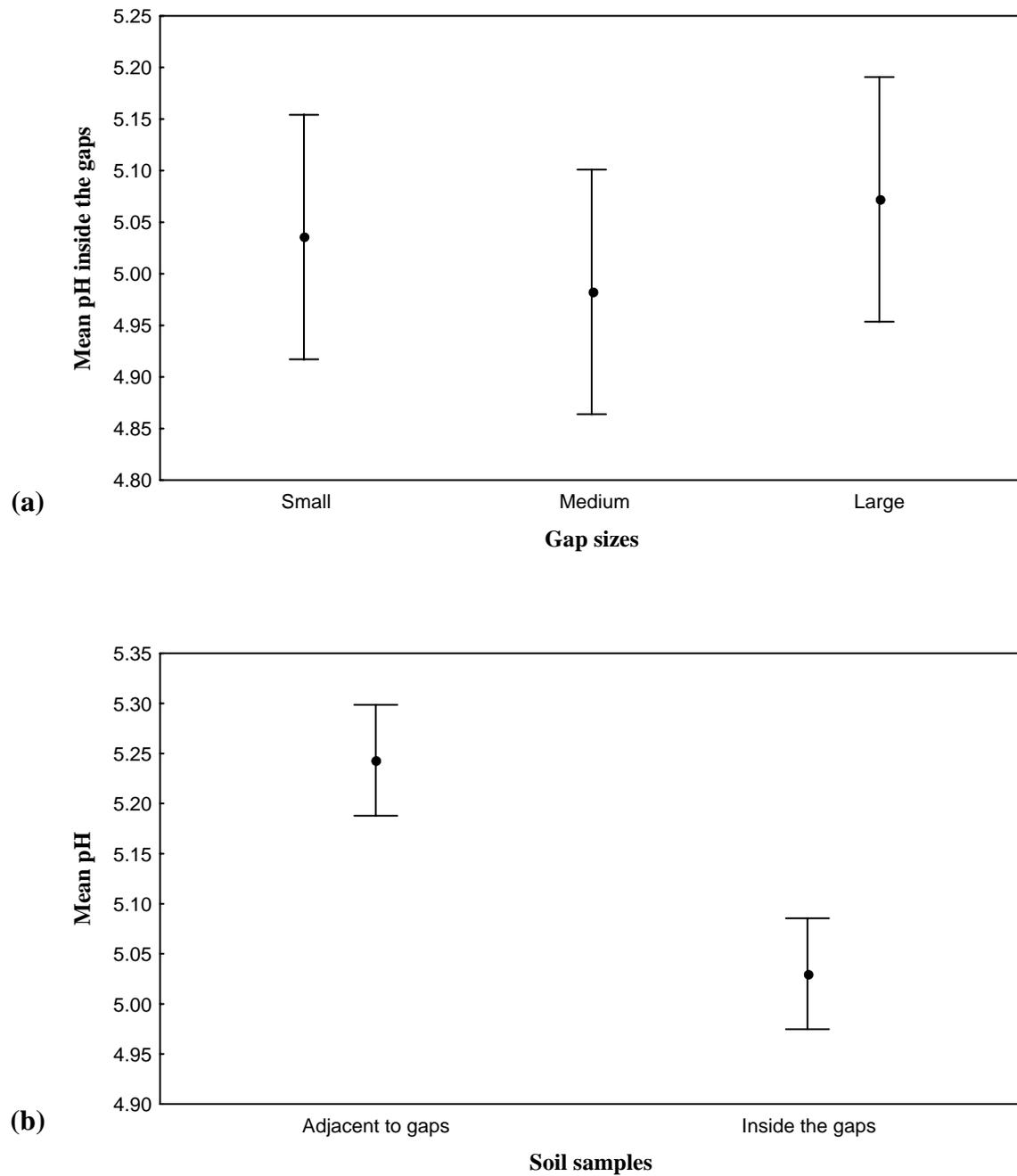


Fig. 3.5 pH of soil samples collected inside and adjacent to the gaps. One-way ANOVA test: **(a)** $F(2, 6) = 0.87, P = 0.47$; **(b)** $F(1, 16) = 33.3, P < 0.05^*$. Marked (*) P values are significant at $P \leq 0.050$

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Appendix 3.1 Presence of adult tree species across gap sizes in 1995 (*) and 2003 (+): small (S₁, S₂, S₃), medium (M₁, M₂, M₃), large artificially created gaps (L₁, L₂, L₃). Marked species are aliens (A), invasives (I) or shade tolerant (T).

Species	Gaps								
	S ₁	S ₂	S ₃	M ₁	M ₂	M ₃	L ₁	L ₂	L ₃
^(A, I) <i>Acacia melanoxylon</i>				+			+	*+	
<i>Apodytes dimidiata</i>	+		+	+	+			*+	+
^(T) <i>Burchellia bubalina</i>	*	+		*+	*+	+	*+	*+	*+
^(T) <i>Burchellia sp.</i>				+			*+		
<i>Canthium mundianum</i>	+						+		*
<i>Cassine papillosa</i>	+			*+	*+	*	*+	*	*
<i>Curtisia dentata</i>					*			*+	
<i>Diospyros whyteana</i>				*	*	*+	*+	*	*+
<i>Diospyros sp.</i>				*					
<i>Gonioma kamassi</i>	*+	+	*		*	*+	*	*+	
<i>Maytenus peduncularis</i>				*+	+	+		+	
<i>Ocotea bullata</i>	*+	*		*+	*	*	*+	*+	*
<i>Olea capensis subsp. macrocarpa</i>	*+				*	*	*+	*+	*+
<i>Olea sp.</i>						+			
<i>Platylophus trifoliatus</i>								+	
<i>Podocarpus falcatus</i>								+	
<i>Podocarpus latifolius</i>	*		*	*+		*	*+	*+	
<i>Podocarpus sp.</i>				+					
<i>Psyrax obovata</i>							+		
<i>Pterocelastrus tricuspidatus</i>					+				
<i>Tree species unknown 1</i>				+					
<i>Tree species unknown 2</i>				+					

Appendix 3.2 Presence of juvenile tree species across gap sizes in 1995 (*) and 2003 (+): small (S₁, S₂, S₃), medium (M₁, M₂, M₃), large artificially created gaps (L₁, L₂, L₃). Marked species are aliens (A), shrubs (S), invasives (I), pioneers (P) or shade tolerant (T).

Species	Gaps								
	S ₁	S ₂	S ₃	M ₁	M ₂	M ₃	L ₁	L ₂	L ₃
^(A,I) <i>Acacia melanoxylon</i>	+			+			+	*+	+
<i>Apodytes dimidiata</i>					+			*+	
^(T) <i>Burchellia bubalina</i>	*+			*	*	+	*+	*+	*
<i>Canthium mundianum</i>							+		*
<i>Cassine papillosa</i>			+	*+	*+	*+	*+	*+	*
<i>Curtisia dentata</i>	+			+	*+	+	+	*+	+
<i>Diospyros whyteana</i>		+		*+	*+	*+	*+	*+	*+
<i>Diospyros sp.</i>				*					
<i>Gonioma kamassie</i>	*+	+	*+	+	*+	*+	*+	*+	+
^(S) <i>Halleria lucida</i>				+	+		+		
<i>Maytenus peduncularis</i>				*+		+	+	+	
<i>Nuxia floribunda</i>			+				+		+
<i>Ocotea bullata</i>	*+	*+	+	*+	*+	*+	*+	*+	*+
<i>Ocotea sp.</i>								+	
<i>Olea capensis subsp. macrocarpa</i>	*+			+	*+	*	*+	*+	*+
<i>Platylophus trifoliatus</i>	+							+	
<i>Podocarpus falcatus</i>				+					
<i>Podocarpus latifolius</i>	*+		*+	*+		*	*+	*+	+
^(P) <i>Rapanea melanophloeos</i>	+			+		+	+	+	+
<i>Tree species number 3</i>				+					
<i>Tree species number 4</i>						+			

CHAPTER 4: GENERAL DISCUSSION AND RECOMMENDATIONS

4.1. GENERAL DISCUSSION

4.1.1. Visual observations of artificially created gaps of different sizes in 2003

i. SMALL GAPS

As expected from the species-area relationship, observations in 2003 showed that small gaps had fewer plant species than medium and large ones. Edge trees appeared to have a negative impact on the regeneration of small gaps (Euston-Brown & Geldenhuys 1996; Euston-Brown *et al.* 1996). For instance, at Lottering (small gap J1AS), an edge tree has collapsed, closing the main entrance to this gap and creating another opening, while causing some other trees to fall. It appeared that edge trees were likely to fall into the gaps for two reasons: 1) when they were tall and thin: the centre of gravity of short trees being close to the ground, therefore they were more likely to resist the wind than taller plants; 2) when they were growing isolated from other edge trees: plants surrounded by other woody species were moving less, losing few leaves and branches than others (Kimmins 1997; Lassig & Mocalov 2000; OED 2004). In some plots, it appeared that *Trichocladus crinitus* were growing in abundance under the shade of fern species, besides the fact that various individuals were losing their leaves. This suggested that the growth of that shrub species might benefit from the shade of fern plants. In 2003, more exotic woody plants and herbaceous species were recorded, however many indigenous seedlings were growing curved due to the presence of ferns. The monitoring of ground flora plants showed that more *Schoenoxiphium sp.* than *Dietes iridioides* were present, and various parts of the former species were degenerating due to possibly an over exposure to sunlight. This suggested that *Schoenoxiphium sp.* was probably a ground flora species less sunlight tolerant than other herbaceous plants like *Hypolepis sparsisora*. However, *Schoenoxiphium sp.* appeared to grow well in areas having fewer woody species including *Trichocladus crinitus*. Seedlings of *Acacia melanoxylon* and *Rapanea melanophloeos* were found in abundance, confirming that these species were pioneer plants. Fern species seemed to degenerate when growing close to the gap edges where less sunlight was available and more canopy cover occurred.

ii. MEDIUM GAPS

At Lottering (medium gap J1A), it was noticed that *Halleria lucida* and the shrub plant *Rubus sp.* seemed to degenerate under the shade of other woody species. This confirmed that those

species were pioneer species and sunlight tolerant. Fallen branches from edge trees were noticed to impact negatively on the growth of various gap plant species. Edge trees also caused other openings, therefore creating more sunlight penetration in the gap cited above. Species such as *Halleria lucida*, *Acacia melanoxylon* and *Rapanea melanophloeos* were abundant as adults, juveniles and seedlings. It is predicted that the number of those species will increase. Those species were growing mainly in the center of medium gaps and in areas having few ferns and trees. During the 2003 survey, more herbaceous cover and pioneer species were found in medium gaps. In some plots, seedlings of species like *Burchellia bubalina* were abundant and have been mainly growing under the shade of a dense fern population such as *Pteridium aquilinum*. This suggested that those species were mostly shade tolerant. Thus, it is expected that the population of *Burchellia bubalina* is going to increase if the percentage cover of *Pteridium aquilinum* augments.

However, a considerable number of other juvenile woody species measured in previous surveys were found dead or missing, while those alive were degenerating. It appeared that these juvenile plants had a high mortality rate due to a great percentage cover of herbaceous species (DWAF 1995; Euston-Brown *et al.* 1996). Surprisingly, some *Podocarpus latifolius* have been found healthy under a dense population of fern species. In other plots, a succession of several generations of fern species seemed to have occurred, while having also a negative effect on the growth of shrub species like *Halleria lucida* and *Trichocladus crinitus*. In addition, few herbaceous species and *Halleria lucida* were found in plots having a high abundance of woody species mainly shade tolerant (e.g. *Burchellia bubalina*, *Trichocladus crinitus* and *Podocarpus latifolius*). These plots were amongst the shadiest ones.

In plots where *Trichocladus crinitus* were found to be lower, other woody species were abundant. This illustrated the positive and negative interactions between plants. In general, medium gaps had more ground flora species than the small ones. In plots where more healthy plants were found, more debris was also present. This illustrated the fact that woody species debris highly contributed to the regeneration of medium gaps as dead trees are a source of nutrient and energy needed by other plants to grow better (Meffe & Carroll 1997; Spence 2001).

In some plots with more ground flora species, seedlings of woody species were dominated by pioneer plant species such as *Acacia melanoxylon* and *Rapanea melanophloeos* (Euston-Brown *et al.* 1996; Coates 2002). Besides having a high proportion of debris, few species number for both pioneer and herbaceous plants was noticed in other plots. It is possible to expect that some gaps would have more ground flora species than others due to past

occasional events, which have caused the characteristics of those gaps to change (Euston-Brown *et al.* 1996; Lassig & Macalov 2000; Ackerly 2003a, 2003b). It appeared that herbaceous species such as *Dietes iridioides* and *Schoenoxiphium sp.* that are shorter than ferns were growing closer to the gap boundaries where it was shadier than in the middle of the gaps. Therefore, it is suggested that those herbaceous species are more shade tolerant than the ferns.

iii. LARGE GAPS

As for medium gaps, edge trees have collapsed and damaged some plots. The survey of those plots was unnecessary because a significant amount of plants measured previously was destroyed by these edge trees; if such destructions of plots continue, it is likely that less and less data will be collected in future monitorings. Various suggestions stated for medium gaps apply as well in the case of large ones: 1) herbaceous species that were abundant and had a negative impacts on the development of particular seedlings; 2) species such as *Burchellia bubalina* that was increasing in the shadiest areas; 3) plants like *Acacia melanoxylon*, *Rapanea melanophloeos* and *Halleria lucida* that are pioneers, have been recorded amongst the main three abundant woody species (particularly in the medium and large gaps located at Kleinbos) and were growing mostly in areas with less other trees. Surprisingly, a rare presence of *Pinus radiata* – an exotic species that has been possibly transported through wind from one of the closest forest plantations - was recorded. Many other seedlings were recorded growing close to the biggest tree species where they appeared to have more space, sunlight and oxygen than under the shade of herbaceous plants. Species diversity and richness appeared to be different between plots of the same gaps, which were created in similar conditions. This illustrated again the impact that unpredictable events might have on plant composition within gaps (Euston-Brown *et al.* 1996; Lassig & Macalov 2000; Ackerly 2003a, 2003b). In areas where a species such as *Pteridium aquilinum* was not abundant, other herbaceous plants like *Dietes iridioides* were numerous. This suggested that *Pteridium aquilinum* had also a negative effect on other herbaceous species (Euston-Brown *et al.* 1996; Rook 2002).

4.1.2. Visual observations of natural gaps in 2003

In the fire gap at Koomansbos, the growth of juvenile trees appeared to be positive (Everard 1994). Like in the case of artificially created gaps, woody species were growing mainly where

herbaceous species was less dense. *Halleria lucida* appeared to be the most abundant amongst adult trees species and *Acacia melanoxylon* being the more considerable of juvenile woody plants. It is expected that *Halleria lucida* might increase significantly in the future. In some plots, there was little presence of pioneer species, but invaders and exotic plants were present, coupled with a high percentage of herbaceous such as *Pteridium aquilinum* and *Helichrysum petiolare* that were abundant. It is predicted that some plots will be invaded by herbaceous species such as *Helichrysum petiolare*. In other plots, most of the juvenile woody plants were in the non-burnt area. Species such as *Halleria lucida* and *Pteridium aquilinum* were mainly in the burnt area. The open areas at Plaatbos windfall gap were dominated by a high percentage of fern species, especially *Hypolepis sparsisora*. The regeneration of woody plants was slow in these areas as a result (DWAF 1995).

4.1.3. Visual observations of soil in the gaps in 2003

Soils appeared to be more humid under the shade of fern species than elsewhere in the gaps. It was probably more humid under those species. Soils near to the edge appeared to have less moisture and were dryer than under the shade of fern plants. It is suspected that the amount of moisture was higher amongst fern species due to less sunlight penetration, which allowed the soil to be dryer. Also a lot of organic matter may exist amongst these ferns, especially the remaining of previous generations that were dead. The fact that there was a high percentage of those herbaceous species growing on top of the previous generation illustrated the hypothesis that the previous generations of fern species were used as a source of energy by the current one. To confirm that, it will be interesting to investigate the effect of removing the previous generations of herbaceous species on the growth rate of the current one. Future studies may look at how species such as *Hypolepis sparsisora* are changing the soil quality and influencing negatively the growth rates of surrounding tree species. Another experience may see if at one moment those herbaceous species are positive for the growth of tree species. It is known that a fern species such as *Pteridium aquilinum*, which is a shade intolerant pioneer plant, grows on various soils and may transform phosphorus from inorganic sources into an available form for plant use (Fenn *et al.* 1996; Rook 2002). Like most fern species, it contributes to potassium cycling on sites and is associated with high levels of potassium (Haywood 1998; Rook 2002). *Pteridium aquilinum* is a fire-adapted species, particularly, because fire removes competition and creates the soil conditions suitable for its establishment (Fenn *et al.* 1996; Haywood 1998; Rook 2002).

4.1.4. General limits to species richness in the gaps

A number of theories have been proposed to describe plant structures in general and the understanding of gap regeneration process in indigenous forests of Tsitsikamma may be explained by some of these hypotheses: 1) the *productivity-stability* theory, which states that the quantity of energy available among individuals and species is positively associated with primary production; 2) the *structural* theory, which argues that species richness is linked with plant community structure; 3) the *competition/predation* theory, which states that richness can be reduced by competition and exclusion of some species, but competition can also increase richness by favouring more habitat separation among species; 4) the *productivity-disturbance* theory, which combines elements of the previous hypotheses, assumes that disturbances either eliminate competition or reduce it; if the disturbance rate is very low (small gaps), species richness is low because of competitive exclusion; if the disturbance rate is very high (large gaps), species richness is also low because populations of many species are unable to recover before the next perturbation arrives; maximum species richness is predicted to occur when a balance exists between rates of population growth and rates of disturbance (intermediate level or medium gaps) (MacArthur *et al.* 1966; Pianka 1966; Connell 1975; Wiens 1977; Tilman 1982, 1985; Gentry 1992; Cowling *et al.* 1992; Huston 1994; Clinebell *at al.* 1995; Rosenzweig 1995; Meffe & Carroll 1997).

4.2. RECOMMENDATIONS

In some artificially created gaps, especially medium and large ones, *Halleria lucida* and *Acacia melanoxylon* plants were abundant. As individuals of such woody species are becoming numerous, it will be less time consuming to take only the frequency of their height in future monitoring. For data accuracy, the measurement process of trees should be clearly described in the initial report; for instance when taking the height of a leaning tree (e.g. the length or the highest growing point should be indicated)

It appeared that in some gaps, especially those located at Lottering (4FM and 4FB), more herbaceous species can be expected. It is probably due to the fact that more sunlight is available in these gaps due to unpredictable events (Euston-Brown *et al.* 1996; Ackerly 2003a). It will be interesting to look at the relationship between the weather patterns and gap regeneration. How does the weather affect gap regeneration?

The number of plots should be increased to avoid lack of data due to unforeseen events such branches falling from gap edge trees, which damage the plots. Future studies should look at

the frequency of trees falling into the gaps. Identify and record the tree species and see which one is more likely to fall. Define from that investigation, a guideline of trees with the high probability of falling in the gaps. It is suspected that those trees will be the same as those likely to have more seeds dropped in the gaps.

Plot location should be clearly done as the retrieval of those plots was not always easy, especially after gaps have been invaded by a dense herbaceous species such *Pteridium aquilinum* (Everard 1994; Van Wyk & Netshiluvhi 1997). The demarcation of plots should be done by using tall wooden sticks (at least 1.5 m) and painted with a bright colour.

The effects of animals on the regeneration of plant species may be investigated (Venter & Venter 1996; Van Wyk & Netshiluvhi 1997). Defining clearly the interactions between animals and forest plants will contribute highly to the understanding of gap regeneration; animal movements were noticed in the gaps in 2003.

In order to assess how far the regeneration process is from the initial state, it means before gap creation, the mean diameter and height of trees, which were measured and cut down when creating gaps should be compared to those of trees currently growing in the same gaps. How different the mean diameter and height are will help to predict how long the regeneration could take. Using a model (Philip 1994; Kimmins 1997), the growth rate per year may be assessed for each gap and a comparison should be done to see how long it will take for this gap to reach the original forest state.

Various issues, that might be possible subjects for future studies, were raised from the results of the 2003 survey: 1) the influence of altitude on gap regeneration: how significant is the differences in plant regrowth within gaps located in diverse geographical areas? 2) the influence of edge trees on gap restoration: as trees surrounding the openings are leaning towards the gaps, it is suspected that they are dropping their seeds within those open areas; this may as well contribute to the recolonisation process of these gaps. To verify this last assumption, here are few steps of an experiment that could be conducted: 1) when a gap has been created, record the number of seedlings in the gap that are similar species than edge trees and monitor their increase over time; 2) record as well the growth rate of other plant species; it is suspected that due to competition their increase would be lower than the first seedlings' category.

Other concerns include the investigation of wind impacts on plant composition and looking at species interactions within the gaps. When a new gap is created, a complete protocol should be clearly defined as guidelines to guarantee unbiased future surveys, and this procedure must include: 1) gap descriptions, geographical coordinates and initial images (including aerial

pictures); 2) plot locations and sampling protocol such as an accurate description of measurements (height, diameter, percentage cover or Braun-Blanquet value, plant species categories); 3) soils should be sampled as soon as possible (within the first days of gap creation) to avoid leaching due to weather and unpredictable events (e.g. wind, rainfall, sunlight); therefore, a full analysis of soil properties must be conducted (e.g. pH, EC, C, N) and results should be recorded to serve as initial controls for future sampling; 4) bioassay should be conducted in situ to avoid soil disturbance that may happen during transportation; nevertheless, another experiment must be carried out in the nursery during the same period; radishes as well as selected indigenous trees (e.g. *Rapanea melanophloeos*, *Podocarpus falcatus*) from Tsitsikamma forests should be planted on the soils taken from the gaps; soil organisms monitoring should also be investigated (Philip 1994; Euston-Brown & Geldenhuys 1996; FAO 1998; Sutherland 1999; Jayaraman 1999).

Sustainable forest management requires a good understanding of forest biodiversity, which is collected through various steps such as accurate vegetation surveys following perturbations (Dasmann 1960; Gentry 1992; FAO 1998; Spence 2001; Geldenhuys 2002; Schelhaas *et al.* 2003). Optimal forest management may be reached through the improvement and implementation of diverse practices such as protection against fire, disease and invasive species (Dasmann 1960; Kimmins 1997; Schelhaas *et al.* 2003). The indigenous forests of Tsitsikamma would gain further as more scientific findings are integrated into management practices (DWAF 1995; Euston-Brown *et al.* 1996; Kimmins 1997). For instance, more indigenous tree species may be artificially grown and transplanted into the gaps to accelerate the regeneration process, but species interactions on targeted indigenous plants should be carefully studied in nursery (Campbell 1996; Kimmins 1997). Mixed indigenous species should be planted as similar as possible to the original forests prior to disturbances (Dasmann 1960; Kimmins 1997; Schelhaas *et al.* 2003). The increase of indigenous woody species will contribute to the decrease of alien and herbaceous species which have a negative impact on tree regeneration (Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997). However, a balance should be found between valuable fern species and worthy tree species in order to comply more with conservation requirements (Campbell 1996; Kimmins 1997).

Harvesting in the Tsitsikamma indigenous forests should be reduced to decrease related disturbances that affect negatively vegetation regrowth (Campbell 1996; Kimmins 1997; FAO 1998). Although the selective cutting intends to have as little damage as possible for the remaining vegetation (DWAF 1995; Euston-Brown *et al.* 1996), soil compaction is not always considered when removing trees (Dyck *et al.* 1994; Kimmins 1997; FAO 1998). Therefore,

selective cutting as practiced in these forests may add damage to soil and still contribute to a negative change in species composition over time (Dyck *et al.* 1994; Kimmins 1997; FAO 1998). Even if gaps created during harvesting practices are said to be smaller than gaps opened by natural tree fall in those forests (DWAF 1995; Euston-Brown *et al.* 1996). As stated by the productivity-disturbance theory, if a perturbation is little (e.g. small gaps), species richness is low due to competition (Huston 1994; Kimmins 1997; Meffe & Carroll 1997). Therefore, selective harvesting in the indigenous forests of Tsitsikamma does not promote forest biodiversity (Huston 1994; Kimmins 1997; Meffe & Carroll 1997).

4.3. GENERAL CONCLUSION

As already mentioned, the general aim of this study was to verify the assumption that gaps might close in a process that is defined by their size, their origin and the plant species characteristics and that this closure may be associated with soil quality change inside of these openings. The specific goals were: 1) to investigate if gap regeneration patterns were uniform across gaps; and 2) to predict future community structure of plant species inside of these gaps. From this study results, a difference has been noticed in the vegetation composition of plant species between gaps of diverse sizes and origins, but this dissimilarity was largely not statistically significant especially amongst medium and large artificially created gaps. Only gaps of different sizes and trees were used for a comparative study between 2003 and 1995 due to a lack of precise and quantitative data gathered previously in the artificially created gaps (i.e. herbaceous) and Komansbos fire opening (i.e. herbaceous and trees) (Everard 1994; Euston-Brown *et al.* 1996). From this comparison it has been found that species diversity and richness in the artificially created gaps in 2003 were higher than recorded before for the same openings, although not often statistically considerable. The same applies to the growth rate between these gaps. As stated in reports about previous vegetation surveys done in these openings (Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997), it is as well predicted from this study that plant regeneration in some gaps (i.e. medium and large) will be slow if invasive species and ground flora cover increase as well as tree mortality rate and unpredicted events (e.g. falling of gap edge trees). It means also that species diversity will be maintained in gaps characterized by small soil perturbations, but will decline if disturbances become large (Kimmins 1997; Meffe & Carroll 1997), since gaps' closure appeared to be associated with soil quality change inside of these openings (Tilman 1982). It appeared that: 1) a significant period of time is needed for the plant composition in the gaps to approach that of the original vegetation; and 2) gaps of similar age, origin and disturbance level will tend to become

colonised by a similar range of species (Brenner & Kelly 1981; Majer 1990; Everard 1994; DWAF 1995; Van Wyk & Netshiluvhi 1997). Generally, context and stochastic events were largely more important in determining gap diversity and regeneration than gap size and origin. Various studies on gap dynamics in the indigenous forests of Tsitsikamma are important in order to have relevant information for predicting impacts of change occurring due to specific disturbances (Everard 1994; DWAF 1995; Euston-Brown *et al.* 1996; Kimmins 1997; Schelhaas *et al.* 2003). Management strategies could influence the normal process of indigenous forest regrowth (Euston-Brown *et al.* 1996; Schelhaas *et al.* 2003) and it might be possible, through scientific findings, to manage positively the regeneration procedure in the gaps. For instance, it may be necessary to manage a forest gap for the entire community rather than for specific populations (e.g. selective harvesting targets particular species) (Euston-Brown *et al.* 1996; Kimmins 1997; Meffe & Carroll 1997). In some gaps (e.g. medium and large) it may be valuable to wait for the areas to pass through a cycle of regrowths before to make accurate predictions and to know how similar the final community will be in terms of species composition to that of the original population (Majer 1990; Kimmins 1997). During those regrowths, it would be helpful to determine which species have not yet started to grow in the gaps and determine the reasons why they have not (Majer 1990; Kimmins 1997). Although, gap creation may be judged by their negative impacts, they might also provide various opportunities (Euston-Brown *et al.* 1996; Lassig & Macalov 2000; Ackerly 2003a, 2003b). Therefore, more concerns should be to understand how ecosystems respond to various types of forest gaps and how those responses are influenced by unpredicted events (Kimmins 1997; Meffe & Carroll 1997). Any useful method for forest biodiversity assessment in the gaps located at Tsitsikamma should include different species groups such as insects, fungi and lichens (Cody 1986; Spence 2001).

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