

## Chapter 5

### The role of canopy gaps in the regeneration of coastal dune forest

#### Abstract

*Question:* Are gap-dynamics determining the composition of coastal dune forest regenerating after strip-mining?

*Location:* Regenerating coastal dune forests, Richards Bay, KwaZulu-Natal Province, South Africa

*Methods:* The proportion of the canopy in gap-phase was estimated from 20 m wide strip-transects in three known-age regenerating coastal dune forest sites. For each gap, we measured the area, the species responsible for gap creation (gap-maker), the species most likely to reach the canopy (gap-taker) and the composition of adults, seedlings and saplings. We paired each gap with an adjacent plot of the same area that was entirely under intact canopy sampled in the same way.

*Results:* The majority of species had higher abundances under canopy gaps and in the largest canopy gaps. *Acacia karroo* was the most abundant gap-maker, but the probability of replacement was low even in the largest gaps. The most abundant gap-takers were forest pioneers with wide tolerances for light. Shade tolerant species were rare in the community.

**Conclusions:** The patterns of species composition within regenerating coastal dune forest are a response to the canopy characteristics and represent an early stage in forest succession. Gap-dynamics did not fully explain regeneration dynamics in coastal dune forest as canopy disturbance punctuated succession rather than resetting it. The future composition of the canopy should favour shade tolerant species.

**Keywords:** *Acacia karroo*, gap dynamics, habitat restoration, niche differentiation, shade tolerance, succession.

## Introduction

Whitmore (1989) proposed that forest trees could be categorised into two major groups of species, those whose seeds can germinate under intact canopy known as “climax” or more recently “shade-tolerant” species and those whose seeds cannot germinate under intact canopy, but require full sunlight, known as “pioneer” or “shade-intolerant” species. The maintenance of these two groups of species in the forest canopy is, according to gap-dynamics theory, the result of gap-phase regeneration, a small scale successional sequence that results in a new tree replacing the original canopy individual (Schnitzer & Carson 2001). This leads to a shifting mosaic of intact canopy and gaps over time as different individuals take advantage of a canopy gap, then eventually die allowing another individual to take its place in the canopy. Where small gaps in the canopy occur, shade tolerant species can recruit to the canopy from the sub-canopy (saplings) or the gap can close through lateral infilling (Rebertus & Veblen 1993; West et al. 2000). In large gaps, the change in light availability promotes the persistence of shade intolerant species allowing them to recruit to the canopy (Huston & Smith 1987).

The gap-dynamics paradigm has been questioned repeatedly, with some authors suggesting that it is irrelevant in determining composition of forest communities. In some mature tropical and sub-tropical forests, there is little niche separation and species have wide tolerances for light availability (for example, South African Plateau Forest, Midgley et al. 1995; South African Coastal Scarp Forest, Obiri & Lawes 2004; Panamanian Tropical Rainforest, Hubbell et al. 1999). In these forests, the composition of the tree community is unpredictable. The stochastic nature of canopy gap availability and recruitment limitation means that chance plays a greater role than determinism (see the review by Brokaw & Busing 2000). However, recently Chambers

et al. (2009) showed that neutral or chance processes become less important and niche processes more important in determining species composition in central Amazonian forest along a gradient of increasing gap size.

Our interest in gap-dynamics stems from our experiences in a sere of regenerating coastal dune forest undergoing restoration after strip-mining (see study site description below and van Aarde et al. 1996a, b, c; Wassenaar et al. 2005). Mature coastal dune forest is characterised mainly by shade tolerant canopy and sub-canopy, but with some shade intolerant canopy species suggesting that a number of large disturbances do occur (Everard et al. 1995). In regenerating coastal dune forests, the pioneer species, *Acacia karroo*, currently dominates the canopy. As these individuals are senescent by about 30 or 40 years of age (Gourlay et al. 1996), we increasingly observe them falling and creating gaps in the canopy. If these large gaps promote the persistence of shade-intolerant pioneer species to the detriment of shade-tolerant forest species then the end-goal of a restored coastal dune forest could take a lot longer than we have previously predicted (between 38.7 and 40.5 years; Wassenaar et al. 2005). In addition, if large gaps do promote shade intolerant pioneers then *A. karroo* may replace itself leading to a stagnation of succession. The use of the *A. karroo* successional pathway post-mining has been criticised in the past for exactly this reason (West et al. 2000).

Here we intend to investigate if the gap-dynamics paradigm is relevant to the restoration of coastal dune forest. In particular, we wish to ascertain if tree species composition and richness differs significantly between canopy gaps and intact canopy and across a gradient of gap sizes. In addition, we wish to ascertain the probability that *A. karroo* will replace itself in the canopy. See Table 5-1 for a summary of our assumptions and expectations.

## Methods

### *Study area*

The study area was located to the north of the town of Richards Bay ( $28^{\circ}43'S$ ,  $32^{\circ}12'E$ ) in the province of KwaZulu-Natal in the North-East of South Africa. Here the climate is humid and subtropical, with mean annual rainfall of  $1458.0 \pm 493.53$  mm (mean  $\pm$  SD,  $n = 34$  years between 1976 and 2009; data courtesy of Richards Bay Minerals, RBM). Rainfall peaks in February and the mean temperature was  $23.79 \pm 3.40$  °C ( $n = 3$  years between 2006 and 2009; data courtesy of RBM). The mining company RBM aims to return indigenous coastal dune vegetation to one third of its mined area. The mining process (described in full in van Aarde et al. 1996a) destroys all vegetation in front of the mine-pond. Prior to mining topsoil is removed and stockpiled. Immediately after mining, sand dunes are mechanically re-shaped and the topsoil (seeded with exotic annual plants; sunhemp and sunflowers) is replaced and then stabilised using drift-fencing. After this initial kick-start, management is limited to the removal of non-native plant species and herbivores and restoration relies on natural successional processes (van Aarde et al. 1996a, c). Sampling took place in three regenerating coastal dune forest sites aged 33, 26, and 22 years old. Sites younger than this did not have a sufficient number of canopy gaps to allow analysis.

### *Gap sampling procedure*

Strip-transects 20 m wide and separated by 50 m were walked in a North-South direction across the three regenerating coastal dune forest sites. Where we encountered a canopy gap (see

definition below) which had its central point within the 20 m strip we recorded its size and sampled vegetation within it (see below for sampling description). This gap-centre method avoids a potential sampling bias toward larger canopy gaps (Nakashizuka 1984). We calculated the fraction of the site that was under canopy gap as the sum of the areas of all gaps sampled divided by the total area of the strip transects (Runkle 1992).

### *Defining and measuring a canopy gap*

A canopy gap was defined as an opening in the canopy stratum formed by the death of a part of a tree, a single tree or a group of trees in which no trees are greater than two-thirds the height of the canopy (Runkle 1981). In each gap, we identified and measured the longest axis of the gap, and a number of equally spaced “offset” lines that bisected the longest axis. We then summed the length of the “offset” lines and multiplied this figure by the distance between the “offset” lines. Therefore, canopy gap area ( $A$ ) was calculated as:  $A = I * (C+D+E)$ , where  $I$  is the interval between offset lines and  $C, D, E$  etc are the lengths of the offset lines.

### *Sampling within canopy gaps and intact canopy plots*

We paired each gap with an adjacent plot that was entirely under intact canopy, these plots were the same area as the canopy gap and sampled in the same way. We identified and counted all tree species in each gap and intact canopy plot. In addition, we measured the height and diameter at breast height (DBH) of each individual. We recorded trees as belonging to one of three size classes; we refer to these size classes as “seedlings” (<15 cm in height), “saplings” (>15 cm and <5 cm DBH) and “adults” (>15 cm and >5 cm DBH but <2/3 canopy height). It is important to note that we used these terms nominally and made no assumptions with regard the age of individual trees, but rather their size; these two traits are not necessarily related.

### *Gap-makers & gap-takers*

The cause of a canopy gap was categorised as being either a fallen tree, a crown-collapse, or a standing dead tree. We recorded the species that had caused the gap (through its death) and the tallest seedling/sapling/adult in the gap that may replace the gap-maker (the gap-taker). An individual was only considered a gap-taker if it had the potential to reach the canopy.

### *Data Analysis*

For each gap and intact canopy plot, we calculated species richness (using rarefaction), the abundance of stems and density of stems (per m<sup>2</sup>). We used linear regression to assess the correlation between species richness, abundance and density of stems with gap area. In order to assess if the size of a canopy gap influenced species composition we first categorised the size of canopy gaps in to one of four size classes. We used the quartiles of the range of gap areas to define these gap size classes - small gaps were <94 m<sup>2</sup>, medium gaps were between 94 and 156 m<sup>2</sup>, large gaps were between 156 and 286 m<sup>2</sup> and very large gaps were >286 m<sup>2</sup>. Our data did not allow for the use of Canonical Correspondence Analysis so we followed the advice of Zuur et al. (2007) and used the Analysis of Similarities (ANOSIM). We used ANOSIM to test for differences in the species composition between four size classes, and between canopy gaps and intact canopy plots. Replacement probabilities were estimated by counting the number of gap-takers of a particular species expressed as a proportion of gap-makers replaced (Midgley et al. 1995). All analyses except linear regression were carried out in the R programme (R foundation for Statistical Computing, Vienna, Austria, URL <http://www.R-project.org>). We used Graphpad Prism (version 3.03, Graphpad Software, San Diego, California, US, URL <http://www.graphpad.com>) for the linear regression analyses.

## Results

### *Gap characteristics and causes*

Gap characteristics for each site are described in Table 5-2. Median gap size differed significantly between the three sites (Kruskal-Wallis test;  $P < 0.001$ ). The post-hoc test showed that gaps in the 33 year old site were significantly larger than in the other two sites, but gap size in the 26 and 22 year old sites were similar. The percentage of the site canopy composed of gaps increased with increasing regeneration age. The largest gaps were found in the 33 and 22 year old sites. The 26 year old site did not have any gaps larger than 450 m<sup>2</sup> (Figure 5-1).

Five species were responsible for the creation of canopy gaps; *A. karroo*, *Allophylus natalensis*, *Apodytes dimidiata*, *Brachylaena discolor*, and *Casuarina equisetifolia*. However, *A. karroo* was by far the most abundant gap-maker composing 99.00 % of all gap-makers ( $n = 402$ ). The mean number of gap-makers per gap was 2.83 trees. There was no significant difference between the number of gap-makers in each site (Kruskal-Wallis test;  $P > 0.05$ ). The median gap-makers in all sites were 2 trees per gap. The number of gap-makers per gap increased with increased gap area (linear regression;  $P < 0.05$ ). There was at least one fallen tree in each canopy gap, and fallen trees made up 89.80 % of all gap-makers ( $n = 402$ ). Crown-collapse made up 8.45 % of gap-makers and the remainder (1.74 %) were standing dead.

Only 11 species made up the 165 gap-takers recorded, these were as follows; *A. karroo*, *Albizia adianthifolia*, *A. natalensis*, *A. dimidiata*, *Bridelia micrantha*, *Celtis africana*, *Clerodendrum glabrum*, *Ekebergia capensis*, *Mimusops caffra*, *Psydrax obovata* and *Trichilia*



*emetica*. The most abundant gap-takers were *M. caffra* (25.45 %), *C. africana* (21.21 %) and *E. capensis* (12.12 %). The probability that the gap-taker would be the same species as the gap-maker was zero in the smallest and medium sized canopy gaps (<94 m<sup>2</sup> and between 94 and 156 m<sup>2</sup> respectively). In large (156 to 286 m<sup>2</sup>) and very large (>286 m<sup>2</sup>) canopy gaps the probability was 0.10 and 0.16 respectively. The probability that *C. africana* being the gap-taker decreased with increased gap size (0.33, 0.31, 0.23, and 0.13 in order from the smallest to very large gap sizes). The probability of *M. caffra* being the gap-taker increased with increasing gap size, but was lower in the very large gaps (0.17, 0.28, 0.33, and 0.21 respectively). Finally, the probability of *E. capensis* being the gap-taker increased with increased gap size (0.0, 0.03, 0.13, and 0.19 respectively).

#### *Tree species richness, abundance, and density*

In total, we recorded 53 species, 38 of these were present in both canopy gaps and under intact canopy. Five species (*Diospyros natalensis*, *Dovyalis caffra*, *Maytenus sp.*, *Turraea floribunda*, *Xylothea kraussiana*) were found uniquely in canopy gaps and nine (*Antidesma venosum*, *Diospyros rotundifolia*, *Drypetes gerrardii*, *Dovyalis zeyheri*, *Acacia sp.*, *Harpephyllum caffrum*, *Margaritaria discoidea*, *Memecylon natalensis*, *Pavetta revoluta*) uniquely under intact canopy. However, all these species were relatively rare (<10 individuals recorded).

For both adults and saplings in canopy gaps and under intact canopy, species richness (per stem), abundance and density significantly increased with gap size (linear regression,  $P < 0.05$ ). Seedlings however, showed no significant relationship between sample area and richness, abundance, or density (linear regression,  $P > 0.05$ ).

The richness (species per stem), abundance and density of adults did not differ significantly between canopy gaps and under intact canopy (Wilcoxon rank – sum test,  $P > 0.05$ ). In contrast, sapling richness, abundance and density were all significantly greater in canopy gaps than under intact canopy (Wilcoxon rank – sum test,  $P < 0.05$ ). For the seedlings, species richness was greater in canopy gaps than under intact canopy (Wilcoxon rank – sum test,  $P < 0.05$ ), however abundance and density were not significantly different (Wilcoxon rank – sum test,  $P > 0.05$ ).

#### *Species composition – gap area*

We considered species with abundances of less than 10 individuals as rare and these were excluded from subsequent analysis. The composition of both adults and saplings differed significantly between gap size categories (ANOSIM,  $P < 0.05$ ). Of the nine adult species recorded, five species were equally abundant in all canopy-gap size classes (Kruskal-Wallis test,  $P > 0.05$ ). These included *Canthium inerme*, *C. africana*, *Grewia occidentalis*, *Teclea gerrardii* and *Trema orientalis* (see Table 5-3). The remaining four were all significantly more abundant in large or very large gaps (Kruskal-Wallis test,  $P < 0.05$ ). These included *B. discolour*, *A. natalensis*, *M. caffra* and the non-native *Cestrum laevigatum* (Table 5-3). Only one individual adult *A. karroo* was recorded in a canopy gap. Most (17 out of 23) of the saplings species recorded in canopy gaps were recorded in all gap sizes, and half (12 out of 23) showed significant differences in the mean number of stems (per 100 m) across the gradient of gap sizes (Kruskal-Wallis test,  $P < 0.05$ ). Five species were not recorded in the smallest gap size category ( $< 94 \text{ m}^2$ ), these were *A. karroo*, *E. capensis*, *C. laevigatum*, *Peddia africana*, and *Psychotria capensis*. Seedling composition showed no significant difference between gap size categories (ANOSIM,  $P > 0.05$ ).

Seedlings were not found in the smallest gap size category (<94 m<sup>2</sup>) and we did not find seedlings in the 22 year old site.

The composition of adults differed significantly between canopy gaps and intact canopy plots in the 33 year old site only (ANOSIM,  $P < 0.05$ ). Of the 9 adult species, 6 had significantly greater abundances in plots in canopy gaps (Wilcoxon rank – sum test,  $P < 0.05$ ). These were *C. inerme*, *B. discolour*, *A. natalensis*, *M. caffra*, *C. laevigatum* and *G. occidentalis* (Table 5-3). The 33 and the 22 year old site showed significant difference in the composition of saplings in canopy gaps compared to intact canopy plots (ANOSIM,  $P < 0.05$ ). There was no significant difference in composition in the 26 year old site (ANOSIM,  $P > 0.05$ ). Ten of the 23 sapling species were equally abundant in canopy gaps and in intact canopy plots. The remaining 13 species were more abundant in canopy gaps than under intact canopy.

There was no significant difference in the seedling composition between canopy gaps and under intact canopy in all sites (ANOSIM,  $P > 0.05$ ). However, only one species (*Zanthoxylum capense*) had seedlings in both canopy gaps and under intact canopy.

## Discussion

In regenerating coastal dune forest, the canopy consists almost exclusively of a single species, *A. karroo*, and the death of these trees effects the species composition of dune forest and may shape the future success of restoration. The majority of species (15 out of 23) showed niche-differentiation mostly having higher abundance in canopy gaps, particularly large or very large gaps. Shade intolerant species dominate the regenerating sites. This may be considered alarming in the context of a restoration project that aims to restore coastal dune forest, especially considering that mature coastal dune forest is characterised by shade tolerant species in its canopy and sub-canopy layers. Shade intolerant species are rare in mature coastal dune forest, relying on infrequent large scale disturbances to reach the canopy (Everard et al. 1995). However, as we shall show here this predominance of shade intolerant species appears to be a primary stage in the succession of coastal dune forest.

An individual *A. karroo* rarely dies alone and the resultant large multi tree-fall gaps promote the persistence of shade intolerant species (Everard et al. 1995). The majority of canopy gaps in regenerating coastal dune forest formed through tree-fall. Fallen trees cause a larger disturbance in the canopy than standing dead trees or branch-fall due to the physical action of the tree falling, which can damage understorey vegetation. In addition, a fallen tree will no longer intercept light. The short lifespan of *A. karroo* may mean that gaps and multi-tree gaps open more readily in regenerating coastal dune forest than in mature forests. The proportion of canopy under gap and the mean gap area were both relatively large when compared to other forests (see Table 5-4), with the exception of boreal forests. Boreal forests are similar to regenerating coastal dune forest in that they have few canopy dominant species and are characterised by large scale

disturbance such as fire, timber extraction, and insect outbreaks (see Table 5-4). These characteristics of the canopy of regenerating coastal dune forest may explain the predominance of shade intolerant trees.

In the 26 and 22 year old regenerating sites, the adult size class did not differ significantly between intact canopy and canopy gaps. This suggests that the adult size class is the same as the sub-canopy prior to the creation of the canopy gap. However, in the 33 year old regenerating site, the adult size class differed significantly between intact canopy and canopy gaps. Despite ensuring that an intact gap-maker was present in each recorded gap it appears that in the oldest site, gaps are old enough to have influenced the adult tree composition. Gap expansion may explain this phenomenon. The original gap maker may have decomposed, and subsequent trees fallen in to the gap. This cascading disturbance is characteristic of some forests where the probability of mortality is greater at the edge of a canopy gap when compared to those in intact canopy (Vepakomma et al. 2010). The greater mean gap size in the oldest site may also be a result of this gap expansion.

Sapling composition differed significantly between intact canopy and canopy gaps for both the 33 and 22 year old sites. This difference fits with the gap-dynamics paradigm. Most species were present in both intact canopy and under canopy gaps, but abundances between the two canopy types differed significantly. Very few species were more abundant under intact canopy at any size class. This finding agrees with Ruger et al. (2009) who showed that in tropical rainforest the majority of the tree community regenerate better in higher light. Very few species (20 %) regenerated under light conditions lower than the typical tropical forest understorey conditions. Species in regenerating coastal dune forest appear to have wide tolerances for light

conditions but regenerate with greater abundance under increased light conditions, as is indicated by the higher abundances in larger canopy gaps for the majority of species.

Interestingly, the 26 year old site did not show any difference between canopy gaps and intact canopy. One plausible explanation for this may stem from the frequency distribution of gap sizes in this site compared to the other two sites. The 26 year old site had fewer large gaps and no gaps greater than 425 m<sup>2</sup>. Recently, Chambers et al. (2009) suggested that in small gaps (typical of most forest types) neutral or stochastic processes (e.g. recruitment limitation) determine species composition. In large gaps however (defined as >1000m<sup>2</sup> by Chambers et al. 2009), pioneer species have a competitive advantage over other species. In our regenerating sites, the smaller gaps may have had similar light conditions to intact canopy where species tended to have similar abundances in both gap and intact canopy suggesting that conditions were similar and tolerances wide. However, in the largest gaps situated in the 22 and 33 year old sites, there was a greater differentiation and more pioneer species (such as *A. karroo*, *C. inerme*, and *C. laevigatum*).

In regenerating coastal dune forest seedlings were most abundant in canopy gaps. They were absent from small gaps, and with the exception of *P. africana* and *Z. capense*, were absent from intact canopy. This again suggests that the majority of species in the regenerating coastal dune forest tree community are shade intolerant and very few can tolerate low light levels.

This apparent lack of shade tolerant species is indicative of the characteristics of the current canopy. This canopy, dominated by *A. karroo*, will not replace itself after its senescence. *Acacia karroo* is a typical pioneer species as it has small and numerous wind dispersed seeds (Coates-Palgrave 2003). This species had low abundance of seedlings, saplings, and adults under

intact canopy, confirming its pioneer status. The probability of *A. Karroo* replacing itself was zero in small and medium sized canopy gaps. In large and very large canopy gaps, the probability increased but was still very low (0.10 to 0.16). Therefore, there is only a small probability that this pioneer species will replace itself within the canopy. Unless gaps become increasingly larger *A. karroo* will not replace itself and therefore will not remain the dominant tree species, countering previous criticisms of RBM's rehabilitation process (West et al. 2000).

Contrary to our expectations, there were no shade intolerant gap-takers. The most abundant gap-taker was *M. caffra*. This species has a wide tolerance for environmental conditions; it can survive and grow within the salt-spray zone but is also a dominant canopy species within mature coastal dune forest (Coates-Palgrave 2003). The second most abundant gap-taker was *C. africana*, which is often described as a forest pioneer species (Midgley et al. 1995b; Coates-Palgrave 2003). In our study, *C. africana* seedlings were more abundant in canopy gaps than under intact canopy, and were only found in the largest canopy gaps. However, at the sapling size class, *C. africana* were more abundant in small and medium sized gaps. This suggests once again that this species has wide tolerances for light. It appears that the changes in the canopy of regenerating coastal dune forest are deterministic with the longer living pioneer species with wide environmental tolerances replacing the short-lived *A. karroo*. In the future *M. caffra* and *C. africana* may fundamentally alter the light penetration in to regenerating coastal dune forest. Both *M. caffra* and *C. africana* are broadleaved species whilst *A. karroo* has small compound leaves that are smaller in surface area. These may provide more suitable conditions for shade-tolerant species typical of forest than under the present *A. karroo* canopy.

The unit of coastal dune forest regeneration and replacement patterns in this early stage of succession is larger than that generally described by gap-phase dynamics (Yavitt et al. 1995). Gap-phase dynamics may give way to patch dynamics at this scale. However, in reality this is purely semantics. Both paradigms suggest that disturbances lead to a resetting of the successional process. We have shown here that the dominant early pioneer of regenerating coastal dune forest, *A. karroo*, is replaced by other shade intolerant (but with wider tolerances) species. The probability of self-replacement was low even in the largest gaps. Canopy gaps in regenerating coastal dune forest punctuates succession but does not reset it.

Our previous work has predicted that the composition of regenerating coastal dune forest will be similar to an undisturbed coastal dune forest within 40 years (Wassenaar et al. 2005). However, we have shown here that even if predicted changes in composition do occur the structure of the forest may take a longer time to mimic an undisturbed coastal dune forest. Regenerating coastal dune forest is currently undergoing the first phase of succession with forest pioneers with wide environmental tolerances replacing the dominant canopy species. The nature of these forest pioneer species (broadleaved) and stochastic generation of canopy gaps should lead to greater heterogeneity in light conditions allowing greater niche space available for shade tolerant species to establish in regenerating sites and lead to the successful regeneration of dune forest.



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Table 5-1. A summary of our assumptions and expectations

Variable		Assumptions	Expectations		Analysis
			Shade intolerant trees	Shade tolerant trees	
Tree species composition, richness and abundance	In gaps of various sizes	Tree species exhibit niche differentiation in terms of shade-tolerance	Shade intolerant species will proliferate in large gaps as there is greater available sunlight	Shade tolerant species will be fewer in larger gaps because they are out-competed by shade intolerants	Linear regression (for richness, abundance, and density) ANOSIM
	Between gaps and paired non-gaps (under closed canopy)	Gaps and intact canopy differ in the available light that reaches trees under the canopy	Shade intolerant trees will be more abundant (with greater species richness) in gaps because of high light availability	Shade tolerant trees will be more abundant and with greater species richness under canopy (non-gap)	ANOSIM
Replacement probabilities – the probability that a gap-maker is replaced by an individual of the same species	In gaps of various size	The tallest individual of a canopy species will be the first to take over the canopy position of the gap-maker	The probability that a shade intolerant tree will be replaced by an individual of its own species will increase with increased gap size	The probability that a shade tolerant will replace a shade intolerant will decrease with increased gap size	Calculation of probability

Table 5-2. Gap characteristics in three regenerating coastal dune forest sites

	33 year old site	26 year old site	22 year old site
Number of gaps measured	46	40	53
Area of smallest gap (m <sup>2</sup> )	98	28	16
Area of largest gap (m <sup>2</sup> )	732	405.5	778
Mean gap size (m <sup>2</sup> ± standard deviation)	352 ± 211	149 ± 81	150 ± 149
Percentage of site canopy composed by gaps (%)	27	17	13



Table 5-3. Differences in the abundance of each species in canopy gaps and intact canopy, as well as in each canopy gap size class (Small, Medium, Large or Very Large) for the three size classes (Adult, Sapling and Seedlings). A significant difference is indicated in the table by the labels “Canopy gap” or “Intact Canopy” indicating where the abundance of each species was significantly greater. The size classes where species had significantly greater abundance are labelled. The label “ns” indicates a non-significant difference.

Species	Size class					
	Adult		Sapling		Seedling	
	Canopy gap vs. Intact canopy	Gap size	Canopy gap vs. Intact canopy	Gap size	Canopy gap vs. Intact canopy	Gap size
Acacia karroo			Canopy gap	Large/Very Large	Canopy gap	Large/Very Large <sup>1</sup>
Allophylus natalensis	Canopy gap	Large/Very Large	Canopy gap	Small/Medium	Canopy gap	Very Large <sup>1</sup>
Apodytes dimidiata			ns	ns		
Brachylaena discolor	Canopy gap	Medium/Large/Very Large	Canopy gap	ns		
Bridelia micrantha			ns	ns		
Canthium inerme	Canopy gap	Ns	Canopy gap	ns		
Celtis africana	ns	Ns	ns	Small/Medium	Canopy gap	Very Large <sup>1</sup>
Cestrum laevigatum	Canopy gap	Very Large	Canopy gap	Large/Very Large		
Ekebergia capensis			ns	Large/Very Large		
Grewia occidentalis	Canopy gap	Ns	ns	ns		
Kraussia floribunda			Canopy gap	Medium/Large/Very Large		
Mimusops caffra	Canopy gap	Very Large	ns	ns		

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Peddia africana			ns	Medium/Large	Intact Canopy	Not in gaps <sup>2</sup>
Psychotria capensis			Canopy gap	ns		
Psydrax obovata			ns	Small		
Rhus natalensis			Canopy gap	Very Large		
Rhus nebulosa			Canopy gap	Very Large		
Scutia myrtina			Canopy gap	ns	Canopy gap	Medium/Large/Very Large
Teclea gerrardii	ns	Ns	ns	ns		
Trema orientalis	ns	Ns	ns	ns		
Tricalysia sonderiana			ns	Small/Very Large		
Trichilia emetic			ns	Large/Very Large		
Zanthoxylum capense			ns	ns	Intact Canopy	Large <sup>3</sup>

<sup>1</sup> *A. karroo* seedlings were only found in large and very large canopy gaps, there was no significant difference in abundance between these two gap size classes (Mann-Whitney test,  $P > 0.05$ ). *A. natalensis* and *C. africana* seedlings were only found in very large gaps and therefore we could not assess significant differences between size classes.

<sup>2</sup> *P. africana* seedlings were not found in canopy gaps.

<sup>3</sup> Most *Z. capense* seedlings were found under intact canopy.

Table 5-4. Reported gap proportion and gap area from a variety of forest types, “N/A” indicates where information was not available.

Forest type	Location	Gap proportion (%)	Gap area (m <sup>2</sup> )	Reference
Laurel Forests	Anga National Park, Tenerife	0.4 – 0.6 <sup>1</sup>	77.62 ± 37.22 <sup>2</sup>	Arévalo & Fernández-Palacios 1998
Plateau Forest	Knysna Forest, South Africa	2 – 10	124.1 ± 72.0 72.1 ± 46.3	Midgley et al. 1995
Coastal Scarp Forest	Mount Thesiger Reserve, South Africa	7.8	87.8 ± 7.4	Oribi & Lawes 2004
Red oak mixed hardwood Forest	Pennsylvania, USA	0.16	N/A	Pedersen & Howard 2004
Mangrove	Kosrae, Micronesia	2.3	64.4 ± 79.5	Pinzón et al. 2003
Mangrove	Los Haitizes National Park, Dominican Republic	1.9	724	Sherman et al. 2000
Neo-tropical Forest	Barro Colorado Island, Panama	4.3	79	Yavitt et al. 1995
Boreal Forest	Lake Duparquet Training and Research Forest, Canada	38 <sup>3</sup> (1998) 32 <sup>4</sup> (2003)	156.4 <sup>3</sup> (1998) 202.3 <sup>4</sup> (2003)	Vepakomma et al. 2010
Boreal Forest	Gaspé Peninsula, Canada	N/A	40	Reyes et al. 2010
Subalpine Forest	Yatsugatake Mountains, Japan	11.2 11.3	84.3 ± 78.6 64.7 ± 84.4	Narukawa & Yamamoto 2001
Boreal Forest	Lake Duparquet Training and Research Forest, Canada	7.1 <sup>5</sup> 40.4 <sup>6</sup>	N/A	Kneeshaw & Bergeron 1998
Juniperus-Laurus Forest	Terceira Island, Portugal	N/A	25.1 ± 4.8	Elias & Dias 2009
Tropical Wet Evergreen Forest	Namdapha National Park, India	N/A	59.90 ± 38.64	Deb & Sundriyal 2007
Boreal Forest	Gaspé Peninsula, Canada	42	70	De Römer et al. 2007
Atlantic Montane Rain Forest	Carlos Botelho State	N/A	88.28 ± 11.38 <sup>2</sup>	de Lima & de Moura 2008

Park, Brazil				
Quercus Forest	Dobbs Natural Area, USA	34	295	Cowell et al. 2010
Mangrove	Cape York Peninsula	N/A	756	Clarke & Kerrigan 2000
	and Hinchinbrook Island, Australia		253	
Old-growth Subalpine Forest	Baldwin Basin		15 <sup>7</sup>	Battles & Fahey 2000
			48 <sup>8</sup>	
			161 <sup>7</sup>	
Subalpine Forest	Bowl Research Natural Area		222 <sup>8</sup>	
			41 <sup>7</sup>	
			106 <sup>7</sup>	
			23 <sup>8</sup>	
Boreal Forest	Whiteface Mountain, USA	15	N/A	Battles et al. 1995
Sub-Boreal Forest	British Columbia, Canada	50.4	92	Bartemucci et al. 2001
Subalpine Forest		57.4	173	
Northern Temperate Forest		73.2	196	
		32.2	148	

<sup>1</sup> The lower figure excludes gaps less than 10m<sup>2</sup>,

<sup>2</sup> Expanded gap area

<sup>3</sup> Surveyed in the year 1998

<sup>4</sup> Surveyed in the year 2003

<sup>5</sup> Aspen dominated site

<sup>6</sup> Fir dominated site

<sup>7</sup> Spruce – Fir zone

<sup>8</sup> Transition zone

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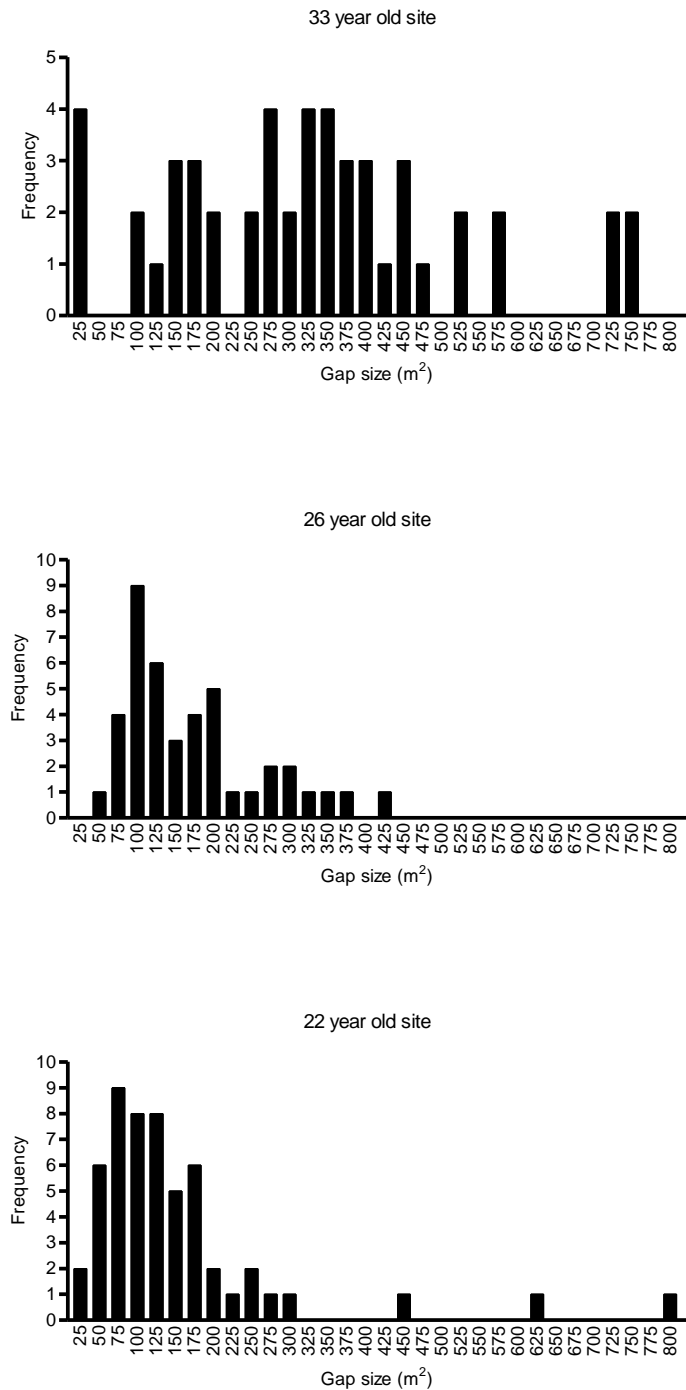


Figure 5-1. The gap size frequency distribution for the three regenerating coastal dune forests sites.