

**The effect of the spatial scale of tree harvesting on woody
seedling establishment and tree dynamics at Ongoye Forest
Reserve**

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Abstract

Subsistence harvesting pressure in most African countries focuses on the small and mostly unproductive trees found in the understorey stratum and can have potentially insidious ecological effects. Harvest intensities at Ongoye Forest Reserve (OFR) vary significantly across the forest (range = 87 - 567 stumps ha^{-1}), with harvesting focussed exclusively on poles from tree species that grow only in the understorey. Growing evidence indicates that seedling establishment from the pool of species available beneath a closed canopy is greatly influenced by the differential ability of species to take advantage of the short burst of resources in newly-created understorey gaps. Seedling dynamics in these gaps may determine forest tree diversity and dynamics and consequently harvest gaps have the potential to significantly affect natural forest dynamics.

This study examined seedling establishment beneath intact understorey and within artificially created understorey gaps of different sizes (single stem gaps, two stem gaps, four stem gaps, eight stem gaps and control 'gap', where no stems were removed) that simulated different spatial scales of harvesting intensity of understorey trees. This experiment examined the proposition that successful seedling establishment and natural succession is strongly dependent on the scale of harvesting. Seedling abundance, species richness, irradiance (photosynthetically active radiation and the red to far-red ratio), soil nutrient composition and herbaceous layer cover was measured in each gap size in 2005 before harvesting, and again in 2007.

The mean seedling abundance was not significantly different among gap treatments, although there was a trend towards more seedlings in 2005 than 2007. Seedling abundance in all gaps was greater than at control sites beneath the intact understorey. There was a continuous increase in seedling richness in 2007. An average species richness of 4.3 was recorded in the control sites, beneath a shaded understorey. Here, seedling richness increased by 18.24% with the removal of a single understorey tree (Gap 1). Species richness increased with increasing experimental gap size increased so that the greatest mean species richness (6.2 species) was recorded where eight neighbouring trees were removed (Gap 8). Light transmission reaching the seedling stratum was greater in larger gaps and there was a trend towards more seedlings and

greater species richness in the higher light environments of such gaps. Soil nutrient levels did not influence seedling abundance and species richness in gaps. The herbaceous layer suppressed seedling establishment. In the largest gaps (115.4m²) created by harvesting, seedling composition was more deterministic than in small gaps where seedling establishment and density was random, accordingly there were more species in larger gaps from a more defined species assemblage. Current harvesting levels of pole-sized understorey trees, where only small gaps are created in the understorey, are unlikely to alter forest dynamics and species composition at OFR. This study demonstrates that harvesting eight adjacent trees crosses the harvest intensity threshold between sustainable natural tree dynamics and a potential successional shift to an alternative state. Clearly, for natural dynamics to be maintained harvesting intensities will have to be regulated.

Keywords

Seedlings, understorey gaps, species richness, pole-size trees, regeneration, gap dynamics.

Preface

The research described in this dissertation was conducted at the Centre for Environment, Agriculture and Development (CEAD) and the Forest Biodiversity Research Unit (School of Biological and Conservation Sciences) at the University of KwaZulu-Natal (UKZN) under the supervision of Dr Mark Dent (CEAD) and co-supervision of Associate Professor Mike Lawes, School for Environmental Research, Theme Leader: Wildlife and Landscapes Theme, Charles Darwin University, Australia. (formerly from UKZN).

This study was initiated by Dr S. Boudreau in 2005 under the supervision of the author, an employee of Ezemvelo KwaZulu-Natal Wildlife. The author continued with and completed the study which is the original work of the author and has not otherwise been submitted in any form for any degree or diploma to any other University. Where use has been made of the work of others, it is duly acknowledged in the text.

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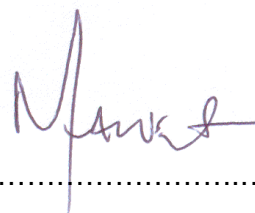
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Declaration

Ideclare that:

- i) The research reported in this thesis, except where otherwise indicated, is my original work.
- ii) This thesis has not been submitted for any degree or examination at any other university.
- iii) This thesis does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other researchers.
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Where other written sources have been quoted, then:

- a) their words have been re-written but the general information attributed to them has been referred;
- b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced.

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Date:

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Dedication

This dissertation is dedicated to my mother and late father, who through their love of the outdoors nurtured my interest in conservation and who always believed that I can achieve all I set out to do.

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List of Abbreviations and Acronyms

ANOVA	Analysis of Variance
Ca	Calcium
EKZNW	Ezemvelo KwaZulu-Natal Wildlife
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
K	Potassium
MANOVA	Multiple Analysis of Variance
MRPP	Multi Response Permutation Procedure
N	Nitrogen
OFR	Ongoye Forest Reserve
P	Phosphorus
PAR	Photosynthetically Active Radiation
PCA	Principle Components Analysis
PFD	Photon Flux Density
R:FR	Red:Far-red
SAWS	South African Weather Service

Chapter 1: Introduction

1.1 Introduction

The Ongoye Forest Reserve (OFR), like many other indigenous forests in southern Africa, is of significant value to the livelihoods of neighbouring communities. It is categorised as a specially protected forest area under the National Forest Act, 1989 (Act No. 84 of 1998) and is managed mainly for ecosystem protection and recreation. However, it is recognised that the management of the forest has to balance the resource requirements of local communities while simultaneously maintaining forest ecosystem function.

Current levels of subsistence harvesting at OFR appear to have a low impact on forest dynamics (Boudreau and Lawes, 2005), although harvesting levels have increased in recent years. The primary concern is that this harvesting targets pole-sized stems from mostly those tree species that are confined to the understorey (Boudreau *et al.*, 2005). This study is a first step towards assessing the ecological role of understorey trees and the effect of the scale of harvesting of these trees on the regeneration of woody seedlings.

The removal of understorey trees may have a significant affect on forest dynamics. High harvesting intensities could result in missing size-classes for highly preferred species, decreasing the likelihood of conspecific replacement and increasing the risk of successional collapse as unrepoductive individuals are removed (Hall and Rodgers, 1986, McKenzie, 1988). The latter possibility is particularly of concern in African forests, which unlike Neotropical and Asian forests, have numerous species that are, unique to and dominate the understorey stratum and are not represented in the canopy (LaFrankie *et al.*, 2006). Removal of these understorey species by harvesting will have as yet unknown consequences for African forests. In addition, the rapid colonisation of understorey gaps by lianas or other gap-filling species may also arrest succession. Harvesting can also alter forest physiognomy by decreasing the abundance of single-stem species, which make good poles, promoting multi-stemmed species or a multi-stemmed form, which is generally less harvested because stems are often not straight

(Hall and Rodgers, 1986). While resprouting causes multi-stemmed individuals, these are better able to sustain selective harvesting than single-stem species (Lawes *et al.*, 2004), but canopy height, physiognomy and species composition is much reduced in forests dominated by multi-stemmed species (Midgley, 1996) than those dominated by single-stemmed species.

Gap dynamics theory suggests that differences in shade tolerance influence the spatial and temporal patterns of tree species recruitment (Brokaw, 1985, Connell, 1978, Sheil and Burslem, 2003, Whitmore, 1989). The role of canopy gaps in the regeneration of pioneer shade-intolerant and light-demanding species has been demonstrated in several studies (Brokaw, 1987, Dalling *et al.*, 1998, Lawton and Putz, 1988, Popma *et al.*, 1988, Schnitzer and Carson, 2001). Shade-tolerant species establish under the forest canopy or in small gaps while light demanding species recruit into large gaps (Brown and Jennings, 1998, Denslow, 1987, Whitmore, 1989). Unlike canopy gaps, gaps in the understorey favour shade-tolerant species and the large numbers of understorey species at OFR and other African forests may indicate that the conventional notion of canopy gap dynamics may not apply. Harvesting pressure on these understorey species and the potential consequences for both the forest dynamics and subsistence livelihoods demands urgent study. Based on the philosophy that conservation and the development needs of local people cannot be addressed independently of one another, and that conservation actions that take precedence over the individual and communal concerns of local people, are likely to be unsuccessful in their application (Lawes and Obiri, 2003). Consequently, the management of OFR based purely on biodiversity and ecological principles could result in conflict between the management authority and neighbouring communities.

Forest management must be based on an understanding of the ecology of the resources and the resilience of biodiversity and ecosystem processes to development impacts. Current resource use at OFR is by subsistence harvesters, controlled largely by the Mzimela Traditional Council, who derive much of their building, fuel, forest derived foods and medicinal needs from the forest. Sustainable resource use is achievable at OFR, provided the necessary harvesting controls are in place, as increasing population growth rates and densities will continue to place pressure on natural resources.

1.2 Statement of the problem

This study stems from research questions identified by Boudreau and Lawes (2005) from their finding that small understorey gaps at OFR created by subsistence harvesters did not adversely affect the maintenance of tree diversity. In their study, Boudreau and Lawes (2005) examined only understorey gaps created by the removal of a single understorey tree. However, often harvesters removed many adjacent stems and the effect of larger understorey gaps and the influence of the spatial scale of harvesting on woody tree seedling establishment and tree dynamics was unclear. This study sets out to examine the latter to assist in developing evidence-based adaptive management of harvesting impacts.

1.3 Research objectives

This research examines the proposition that successful regeneration and tree species succession in the Ongoye forest is strongly dependant on the spatial scale of harvesting on understorey trees. The regeneration response is examined in artificially created understorey gaps that simulate several spatial scales of harvesting by removal of adjacent trees. The following predictions are examined:

- i) An increase in species richness and density of understorey and canopy species with increasing size of the understorey gaps.
- ii) Light quantity and quality will increase with gap size and influence the abundance and diversity of understorey and canopy seedlings.
- iii) An increase in soil nutrients will increase the herbaceous cover thereby decreasing woody seedling abundance and diversity.

1.4 Sequence of chapters

This dissertation consists of five chapters, which are summarised here. Chapter 1 begins by outlining the issues affecting resource use at Ongoye Forest. This is followed by a literature review and the concepts pertinent to this study in Chapter 2. The location of the study area and the research methods are described in Chapter 3. The results of the experiment are presented in Chapter 4. In Chapter 5 the main findings are

discussed and conclusions and recommendations drawn from this research are provided.

Chapter 2: Literature Review

2.1 Indigenous forests and their socio-economic importance

Many indigenous forests like the Ongoye forest are located in the poorer rural areas of the country where they play an important part in the local economy, livelihoods and culture of the people. In many respects, southern Africa's forests and woodlands are regarded as the poor people's safety net, providing as much as 35% of rural households' income (Berliner, 2005, Lawes *et al.*, 2004). However, the indigenous forest resource base is the smallest, most fragmented biome in South Africa (Ashton and Hall, 1992, Becker *et al.*, 1988, Berkes, 2004, Borchert, 1999), making it arguably one of the most vulnerable.

2.1.1 Subsistence harvesting and resource use

Harvesters at OFR focussed exclusively on pole-size understorey tree species and no canopy trees were harvested (Boudreau *et al.*, 2005). Lawes and Oribi (2003) found that highly preferred species harvested from Ongoye had a fine-grained spatial scale of regeneration and consequently the density of pole-size trees was locally high. Oribi *et al.* (2002) identified similar harvesting intensities in the same forest type at Mt Thesiger in the Eastern Cape and suggested that this harvesting pressure was sufficient to have led to the extinction of fine-grained species in small forest patches (<55 ha) even though the density of pole-size trees was higher than that found at Ongoye forest (Boudreau *et al.*, 2005, Obiri *et al.*, 2002).

At Ongoye forest, harvesters focussed almost exclusively on pole-size trees from understorey species, with very few canopy species, such as *Chrysophyllum viridifolium* being harvested (Boudreau *et al.*, 2005). Boudreau *et al.* (2005) found that harvest intensity increased exponentially with the availability of the resource, as recorded for *Englerophyllum natalense*. At Hlatikhulu forest, Muir (1990) reported that species availability was the most important factor in the selection of natural resources by harvesters. Harvesting intensity plays a role in determining the species richness of residual stands (Boudreau *et al.*, 2005). However, should harvesting exceed the forests

ability to maintain woody tree seedling establishment and tree dynamics this system could collapse. Studies have demonstrated that the sustainability of harvesting is compromised where the harvesting intensity exceeds 10% of the available stems. Consequently, there are valid concerns about the sustainability of subsistence harvesting at Ongoye forest, even though it is a relatively large forest with a high density of pole-sized trees (Boudreau *et al.*, 2005, Burgess *et al.*, 2000, Hall and Rodgers, 1986, Luoga *et al.*, 2002). Often where a harvesting threshold is reached there is an accompanying shift in species preference by harvesters. For example, at the nearby Nkandla Forest Reserve a decline in the abundance of *Ocotea bullata* has caused its substitution with *Pterocelastrus rostratus* by harvesters (Scott-Shaw, *pers. comm.* 2006).

As similarly shown by Luckert and Campbell (2002), subsistence harvesters operate within a short-term decision making horizon where future benefits are ignored, to the detriment of favoured species and their long term persistence within the ecosystem. Thus, users often cannot easily be persuaded to alter harvest rates or their species preferences until it is too late and the resource base has been irreparably damaged (Boudreau *et al.*, 2005, Burgess *et al.*, 2000, Hall and Rodgers, 1986, Hardin, 1968, Sutherland and Reynolds, 1998). Ultimately, the short-term needs of harvesters and the long-term response of the forest resource base to harvesting (Boudreau *et al.*, 2005) are compromised by harvesters immediate need for natural resources for survival. The high harvesting intensities practised by local communities may result in missing size-classes in highly preferred species, decreasing the likelihood of conspecific replacement and increasing the risk of collapse of the natural successional pathway (Hall and Rodgers, 1986, McKenzie, 1988, Cooper, 1985, Muir, 1990). Therefore it is important that effective adaptive management measures be implemented where selective harvesting is occurring to avoid depleting preferred species to below sustainable levels. Continued harvesting pressure on tree species from the understorey could significantly alter forest dynamics and tree diversity (Newbery *et al.*, 1999, Obiri and Lawes, 2003). It is anticipated that this research at OFR will enable EKZNW to engage with local harvesters and the broader Mzimela community to show case the effects and potential implications that poor resource use practises will have on natural resource sustainability.

2.2 The significance of canopy and understorey gaps for forest regeneration

Growing evidence indicates that the growth environment beneath a closed canopy greatly influences what species from the available species pool can take advantage of the short burst of resources available in newly-created gaps (Connell and Lowman, 1989). For example, the growth of seedlings beneath a closed canopy was negatively influenced by the understorey layer of leaves overhanging them (Brown and Parker, 1994, Denslow *et al.*, 1991). Nichols (2005) observed that *Cnestis* plants in the understorey never flowered unless a canopy gap was created, facilitating light reaching the forest floor. Thus, understorey gaps may provide suitable conditions for the establishment of shade-tolerant species, contributing to the maintenance of forest diversity (Connell *et al.*, 1997). Whether or not low harvesting rates of understorey trees provide conditions suitable for the establishment of woody tree species is unknown and is the focus of this study.

As suggested by Grubb (1977), the spatial distribution patterns of trees may differ for each life stage of a species as a result of environmental variation. Thus, environmental heterogeneity increases the availability of potential regeneration niches. At OFR for example, the creation of varying gap sizes could influence the amounts of moisture and sunlight reaching the forest floor. In addition to this, observed bushpig disturbance to the superficial soils can alter germination conditions. A localised activity such as bushpig grubbing further supports Grubb's (1996) proposed paradigm that gaps in the litter or understorey as well as gaps in the canopy are important for regeneration. Large-seeded tree species, such as *Philenoptera sutherlandii* found at Ongoye forest, can cope with accumulated litter and make use of deeper soil, while smaller seeded species, such as *Rinorea angustifolia*, for example, have difficulty establishing in deep litter (Molofsky and Augspurger, 1992).

With varying gap sizes it is typical for pioneer shade-intolerant and light-demanding species to recruit into large gaps while shade-tolerant species establish under the forest canopy or in smaller gaps (Brown and Jennings, 1998, Denslow, 1987, Whitmore, 1989), which can result in a highly predictable succession of gap-filling species (Brokaw, 1985, Connell, 1978). Unlike the findings at OFR, West *et al.* (2000) found that in the scarp forests in Hluhluwe-iMfolozi Park, the size-class distributions

indicated a lack of regeneration which suggested a prevalence of shade-intolerant species in the canopy. Natural disturbance regimes are important drivers of forest dynamics and biodiversity (Brokaw, 1985, Carlton and Bazzaz, 1998). Forest protection which excludes any form of harvesting cannot therefore presume to restore the natural functioning of forest ecosystem processes. Researchers have thus reported a lack of regeneration of canopy dominants occurring in forests (Midgley *et al.*, 1995), where as in the case of Hluhluwe-iMfolozi Park, the natural gap-phase disturbance regime does not facilitate the regeneration of canopy species dominants.

Accumulating evidence suggests that canopy gaps play a neutral role in maintaining species richness and are thus able to promote the existing biodiversity locally present in a given forest for reasons other than the local disturbance regime, such as recruitment limitation (Boudreau and Lawes, 2005, Brokaw and Busing, 2000, Hubbell *et al.*, 1999, Obiri and Lawes, 2004, Salafsky *et al.*, 2001, Webb and Peart, 2000, Wright, 2002). A common feature in most forest types is the fact that canopy gaps are relatively rare, occupying <10% of the forest area (Boudreau and Lawes, 2005, Connell *et al.*, 1997, Midgley *et al.*, 1997, Obiri and Lawes, 2004, Parker, 1995, Uhl and Murphy, 1981). In contrast, understorey gaps created in the subcanopy stratum beneath an intact canopy, as was created at OFR for the purpose of this study are relatively common, occupying ca. 50% of a forest's area (Connell *et al.*, 1997).

Seedling recruitment within the study site at OFR comprised species locally present. However, there are exceptions where seed dispersal via mammals and birds for example could assist and facilitate a species re-establishment and or a subsequent increase in density. Thus, for successful tree recruitment, seed dispersal mechanisms both within and outside of understorey gaps are dependant on the distance of seed sources, the survivorship of seeds in the soil and the forest tree dynamics (Alvarez-Buylla and García-Barrios, 1991, Alvarez-Buylla and Martínez-Ramos, 1990). The germination of seeds within a gap is therefore largely dependant on the size of the gap as gap size is capable of influencing the rate of successful germination and establishment. Boudreau and Lawes (2005) found that newly established seedling abundance in small understorey gaps was higher for both canopy and understorey species than in the adjacent control plots under an intact understorey canopy. Boudreau and Lawes (2005) also noted advanced regeneration of understorey species

in areas where harvesting had previously taken place. However, similar trends were not evident with the regeneration of canopy species at these sites.

The herb layer was mostly absent in the control sites located beneath an intact understorey canopy. It is therefore evident that that understorey gaps make a significant contribution to forest biodiversity. Boudreau and Lawes (2005) found that the species richness of understorey species was higher in gaps than under intact understorey. This suggests that understorey gaps could potentially contribute to the maintenance of tree diversity through increased seedling establishment. However, such understorey gaps may play a neutral role in maintaining species richness and could promote a diversity and mix of understorey tree species locally present (Burslem and Whitmore, 1999, Hubbell *et al.*, 1999). Furthermore, with respect to the diversity of canopy species, understorey gaps appear to have no effect. Accordingly, Boudreau *et al.* (2005) concluded that current harvesting levels at OFR were unlikely to alter the forest species composition as understorey gaps favoured species commonly targeted by harvesters and these species occur in high densities at OFR. In larger gaps, such as those created by felling eight adjacent understorey trees, light availability increases. In larger understorey gaps shade-tolerant species such as *Englerophytum natalense*, *Tabernaemontana ventricosa*, *Oxyanthus speciosus* and *Rinorea angustifolia* dominate. However, *Philenoptera sutherlandii*, a dominant canopy species at Ongoye, and a variety of lianas such as *Salacia gerrardii*, *Rhoicissus tomentosa* and *Adenia gummiifera* can take advantage of increased light availability in these large understorey gaps. Thus, gaps of different sizes and stages of re-growth are an important source of heterogeneity in the composition and dynamics (Brokaw, 1985) of coastal scarp forests, such as Ongoye.

2.2.1 Herbaceous understorey

The endemism found in scarp forests in South Africa is of significant biodiversity value, particularly in the genera *Plectranthus* and *Streptocarpus* (Mucina and Geldenhuys, 2004). *Streptocarpus wendlandii* is endemic to Ongoye forest and several *Plectranthus* species grow in abundance. The herb layer is dominated by *Asystasia gangetica*, *Microsorium colopendria*, *Zamioculcas zamifolia* and *Oplismenus hirtellus*; while vines and climbers such as *Monanthes caffra*, *Rhoicissus tomentosa* and *Scutia myrtina*

are important structural determinants in these forests (Mucina and Geldenhuys, 2004). During this study at OFR, it was evident that by creating an understorey gap which allowed more light to reach the forest floor, increased herb layer establishment occurred. Annuals and herbs are generally small, short-lived plants that place most of their energy into reproductive effort. It is known that these life forms have a high reproductive output and short generation periods with either highly dispersive or long-lived propagules (Muir, 1990). The understorey gaps created at Ongoye were very often colonised by a variety of herb and grass species, with grass species dominating areas with the highest light levels. The prostrate perennial and sometimes climbing *O. hirtellus* was quick to colonise under larger understorey gaps.

Prophytochloa prehensilis, a perennial, is ideally suited to climbing and was regularly recorded within the study area. This species, together with the more robust *Flagellaria guineensis*, is quick to establish in the large understorey gaps, very often to the detriment of woody seedling recruitment. The rapid colonisation of understorey gaps by lianas or other woody species may thus arrest the successional process.

2.2.2 Soil nutrients

Forested regions experience considerable spatial and temporal variation in the availability of soil water, which is known to control the timing and growth rates of plants in seasonal forests (Baker *et al.*, 2003). Thus, differences in soil moisture could influence the availability and concentrations of important nutrients (N, P and K) for plant growth. Nutrient availability may increase in gaps due to increased decomposition of organic matter. Pickett and White (1985) suggested that this increased nutrient release may in turn increase mass flow of nutrients to herbs, thereby accounting for the seemingly higher herbaceous cover in larger gaps. The interaction between nutrient supply and water availability could be important in determining differences in the spatial pattern of tree growth (Baker *et al.*, 2003). Identifying soil nutrients that may limit vegetative growth responses could assist in understanding the intricacies associated with forest regeneration. However, variation in irradiance, nutrients and water availability can have complex interacting effects on woody tree establishment and growth. For example, Peace and Grubb (1982) found that the response of plant growth to nutrient availability increases at higher flux densities of irradiance because faster

growth resulted in an increased demand for nutrients. This finding could have far-reaching implications; should harvesting levels be unsustainable, this could result in reduced tree densities and ultimately alter existing forest dynamics at OFR. Thus, the effect of spatial scale of harvesting on woody tree seedling establishment and tree dynamics at OFR can be appropriately managed by better understanding the diverse ecosystem processes at work.

2.2.3 Irradiance levels

Irradiance plays an important role in regulating plant productivity. Light quantity is largely responsible for controlling plant productivity, while light quality, measured by the red to far-red ratio (R:FR), guides physiological processes such as stem and leaf growth, seed germination and rates of photosynthesis (Endler, 1993). Studies have indicated that on average only 2% of photosynthetically active radiation (PAR) is available beneath the canopies of most forests (Cansham *et al.*, 1990, Griffiths *et al.*, 2007). The variation in understorey gap sizes and distribution interacts with shade tolerance to influence species abundance and the structure of the forest mosaic (Brokaw and Scheiner, 1989). Therefore, the alteration of the natural spatio-temporal frequency of understorey gaps, for instance by subsistence harvesting as in the case of creating understorey gaps at Ongoye (Burgess *et al.*, 2000, Cawe and McKenzie, 1989, Luoga *et al.*, 2002, Muir, 1990, Obiri *et al.*, 2002), has the potential to influence the regeneration dynamics and composition of woody species.

Increased light availability has been shown to positively affect seedling growth and survival under an intact canopy (Montgomery and Chazdon, 2002). However, Boudreau and Lawes (2005) found that in the first year or two after gap creation, the beneficial effects to new recruits was counterbalanced by an increase in regeneration density in the lower stratum, resulting in similar light intensity at the forest floor in both older gaps and under an intact understorey. In larger understorey gaps such as those created by felling four and eight understorey trees, increased irradiance is known to stimulate the growth of existing and newly established shrubs, lianas and herbs, rapidly reducing light availability on the forest floor (Denslow *et al.*, 1998). Thus, light quantity, as many studies have shown, is responsible for the regeneration of light demanding species in larger gaps (Boudreau and Lawes, 2005, Brokaw, 1987, Dalling *et al.*, 1998,

Lawton and Putz, 1988, Popma *et al.*, 1988, Schnitzer and Carson, 2001). Increased irradiance levels within the understorey gaps created at OFR should promote the establishment of both understorey and canopy species.

Chapter 3: Study Area and Methods

3.1 Location

Ongoye Forest Reserve is situated on State Land in the Ongoye range of hills in KwaZulu-Natal, South Africa (altitude: 299 – 500m a.s.l., 28° 50' S, 31° 42' E). The reserve is 3903 hectares in extent and is situated due west of Mtunzini, approximately 12 kilometres inland from the coast. The protected area comprises a species-rich coastal scarp forest (2940ha) set in a mosaic of coastal grassland and rocky granite outcrops (963ha) (Fig. 1). Ongoye Forest Reserve is of national conservation significance, a protected area containing one of the best known examples of coastal scarp forest in a single continuous block in South Africa (Boudreau *et al.*, 2005, Cooper, 1985, Eeley *et al.*, 1999, Huntley, 1965, Lawes *et al.*, 2004).

3.2 Climate

Mean annual rainfall for the ten years 1999 to 2008 at the coastal Mtunzini station was 1341mm (South African Weather Service, 2009). The Ongoye forest receives on average 300mm less annual rainfall than the coastal village of Mtunzini (Phadima, 2005), thus approximately 1 000mm per annum.

Ongoye Forest Reserve experiences temperate subtropical climatic conditions. Strong coastal winds are prevalent between August and September with prevailing winds associated with dry, warm conditions predominantly from the north-east. South-westerly winds are often rain-bearing and despite the reserve's distance from the sea, the shearing of trees and shrubs by salt spray laden south-east winds is common on exposed sea facing slopes (Huntley, 1965). Mist is a common occurrence in the summer months.

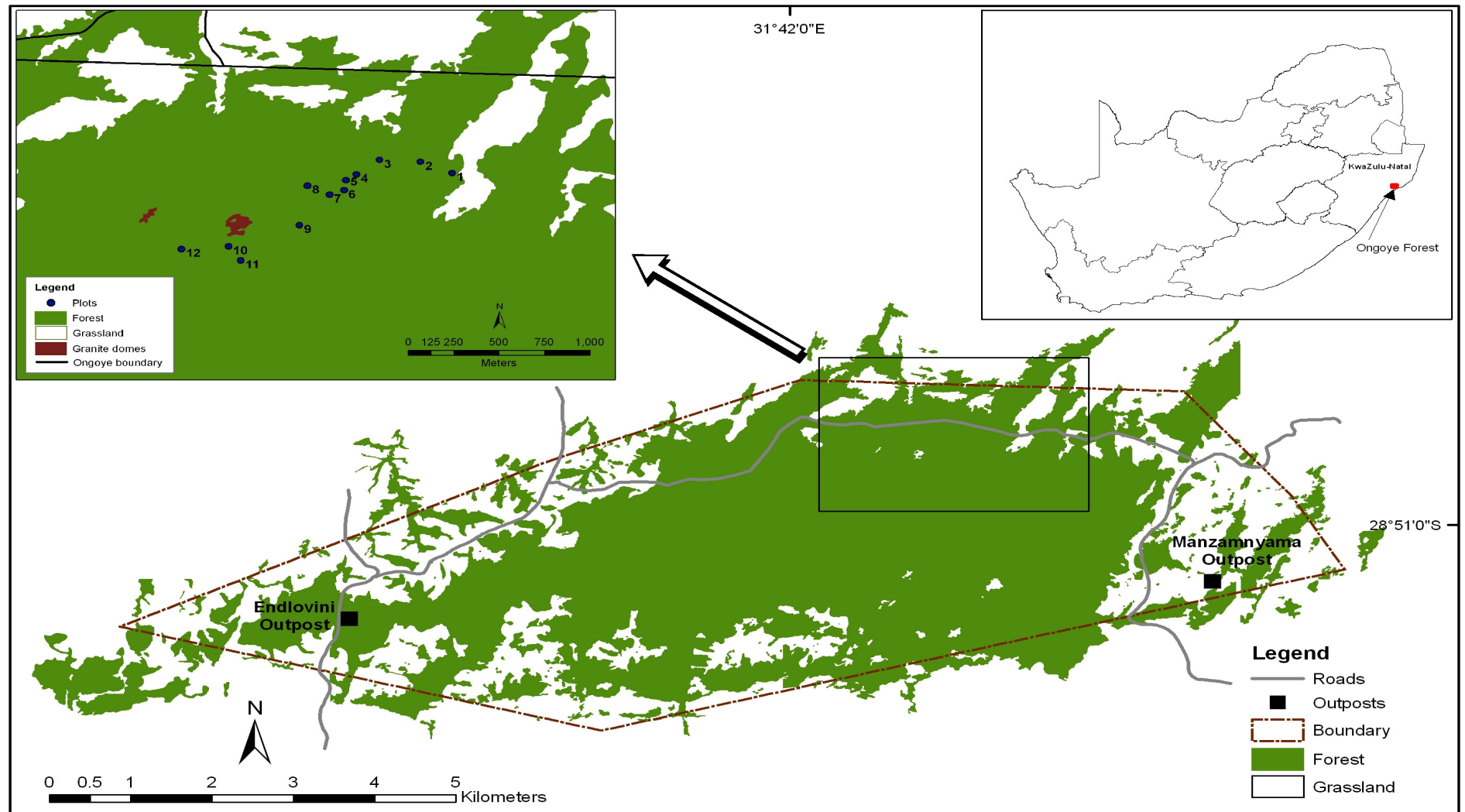


Figure 1. Ongoye Forest Reserve, KwaZulu-Natal, South Africa.

3.3 Forest classification

Recent classification of forest vegetation types (Mucina *et al.*, 2007) places OFR within the Eastern Scarp Forests and more specifically forest subtype D, *Philenoptera sutherlandii-Macaranga capensis* Community. These scarp forests are described as having a poorly developed herb layer, a well developed seedling and sapling stratum, an open understorey and a medium to high canopy (15-25m) (Von Maltitz *et al.*, 2003).

3.4 Sample site selection and creation of artificial gaps

Twelve stands within intact scarp forest dominated by *Englerophytum natalense* and showing similar forest physiognomy, aspect and slope, were selected. The sites were located more than 100m apart. At each of the twelve sites, understorey gaps of varying sizes were created by removing neighbouring understorey trees, regardless of species, to simulate different spatial scales of harvesting. Gap sizes and the spatial scale of harvesting was defined by the number of adjacent trees (all trees with 5cm < DBH < 15cm) removed: Gap 1 - one tree removed; Gap 2 - two trees removed; Gap 4 - four trees removed; Gap 8 - eight trees removed, and Control - no trees removed. The highest harvest intensity (Gap 8) is similar to the maximum local harvest intensity previously recorded at OFR (Boudreau and Lawes, 2005).

Understorey gaps were created without affecting canopy trees. Control plots were established under the intact understorey at each treatment site. The gap perimeter was defined as a line joining the stems of live understorey trees at the edges of the gap. Gap area was calculated as $\pi LW/4$, where L = gap length, the largest distance between gap edges and W = gap width, the longest distance perpendicular to the length (Runkle, 1981). Canopy and understorey heights were estimated against a 2.5m rod at each site.

3.5 Seedling establishment

Square quadrats (1m²) were placed randomly in each understorey gap and at least 2-3m apart. The number of quadrats per gap differed among the gap sizes. In the

Controls and in Gaps 1 and 2, two 1m² quadrats were established and in Gaps 4 and 8, four 1m² quadrats were established. Quadrats were permanently marked and were measured in 2005 and 2007. Height of seedlings in each quadrat was measured from ground level to the terminal growth bud. Seedling stem diameter was measured at ground level. Seedling abundance and richness data were analysed using a randomised block design ANOVA with sample sites as blocks. To avoid pseudoreplication and because quadrats within each gap are non-independent subsamples of experimental units (gaps) the seedling data was combined and mean values used in analysis.

A multi-response permutation procedure (MRPP) (McCune and Grace, 2002), a non-parametric procedure for testing the hypothesis of no difference between groups, was used to test whether the seedling species composition of small gaps (Gap 1 and Gap 2) differed from the composition of large gaps (Gap 4 and Gap 8). The Sorensen (Bray & Curtis) distance measure was used and the distance matrix was rank transformed to adjust for the loss of sensitivity to the distance measure, which occurs with increased community heterogeneity. The test statistic (T) for MRPP describes the separation between groups with more negative values reflecting stronger separation.

Indicator species analysis (IndVal) (Dufrene and Legendre, 1997) was used to identify species characteristic of the small and large gaps. IndVal combines information on the concentration of species abundance and the faithfulness of occurrence (or fidelity) of a species in a particular group. Indicator values were tested for statistical significance using a Monte Carlo technique based on 1000 randomisations. Both the MRPP and IndVal analyses were performed using PC ORD Version 4.34 (McCune and Grace, 2002)

A generalised linear mixed model (GLMM) in which sample site was included as a random effect was used to determine what environmental factors affect seedling abundance and richness. A Poisson error distribution and log-link function were used in the model. The variables in the model were grass cover, herb cover, gap size, the red to far-red ratio, and % PAR. Because most of these variables were measured in 2007 their relationships in this year were examined only. Competing hypotheses or models comprising different combinations of variables were compared and the best model selected using Akaike's information criterion (AIC_c) for small sample sizes. The AIC_c

was estimated for all possible model combinations, however only those models with $\Delta AIC_c < 4$ were evaluated. The best fit model has the lowest ΔAIC_c and the fewest parameters (Burnham and Anderson, 2002). Models with a $\Delta AIC_c < 2$ are not statistically different in terms of their explanatory power, thus the rules of parsimony are applied to select the model with the lowest ΔAIC_c and fewest parameters.

3.6 Herbaceous layer

The percentage aerial cover of grasses and herbs was estimated in each quadrat in 2007 to assess the influence of ground cover vegetation on seedling establishment in the different understorey gaps

3.7 Soil nutrients

Soil samples were collected at two depths: 0 - 5cm and 5 - 15cm in the soil profile using a Beater soil auger with a diameter of 25mm. Litter debris was initially cleared and the auger used to remove the first 0 - 5cm soil. The auger was re-inserted into the hole and the deeper subsoil (5 - 15cm) removed. To control for small-scale soil heterogeneity within the gaps, fifteen random soil samples were collected from each gap at a site. All the subsamples from the same depth interval in a gap were combined. The soil samples were analysed within a few days of collection by the KwaZulu-Natal Department of Agriculture and Environmental Affairs: Soil Fertility and Analytical Services at Cedara Agricultural College. The following fertility parameters were estimated: soil density (g/mL), phosphorus (P, mg/L), potassium (K, mg/L), calcium (K, mg/L), magnesium (Mg, mg/L), exchangeable acidity (cmol_e/L), total cations (cmol_e/L), humic acid saturation (%), pH (KCl) zinc (Zn, mg/L), manganese (Mn, mg/L), copper (Cu, mg/L) and clay content.

PC Ord. Version 4.34 software was used to run a Principal Components Analysis (PCA) to identify standardised soil variables to account for different measurement scales and associated differences in variance (Total % nitrogen, Ca, clay and soil density) that most described the variation in soil fertility parameters among gaps. To avoid Type I errors induced by testing the same null hypothesis many times, I simultaneously tested for differences between the gap sizes in the dependent soil

variables identified by PCA using MANOVA (James and McCulloch, 1990). GenStat 7th Edition (VSN International Limited) software was used to conduct the MANOVA. The test statistic Wilks' lambda (λ), which varies between 0 and 1, measures how much of the total variance is due to the residual, with smaller values indicating larger group differences. Should λ be significant, univariate F-tests are then consulted to determine which of the response variables contributes most to the group differences.

3.8 Irradiance levels

Light quantity controls plant productivity while light quality, estimated indirectly by the red to far-red ratio (R:FR), influences physiological processes such as stem and leaf growth, seed germination, and photosynthesis rates (Endler, 1993). Light quantity is estimated as the photosynthetically active radiation (photon flux density, PFD; $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) in the portion of the spectrum used by plants (400-700nm) received in a given area over a set time period.

Photosynthetically active radiation (PAR) and R:FR at ground level in experimental gaps were measured using Apogee quantum sensors. All light measurements were recorded under diffuse light during overcast conditions between 10h00 and 15h00. Percent light transmittance (%T) provides an estimate of diffuse light quality expressed as a percentage of photon flux density in the understory to that in the open (Capers and Chazdon, 2004). We used one-way ANOVA to test for habitat differences in light measurements.

Chapter 4: Results

4.1 Soil nutrients

Based on a PCA biplot graph the important soil variables were identified and appear to differ between the sample depths (Fig. 2). The soil variables with the highest weights were selected for further analysis; these were Total % N, Ca, Clay, and soil density.

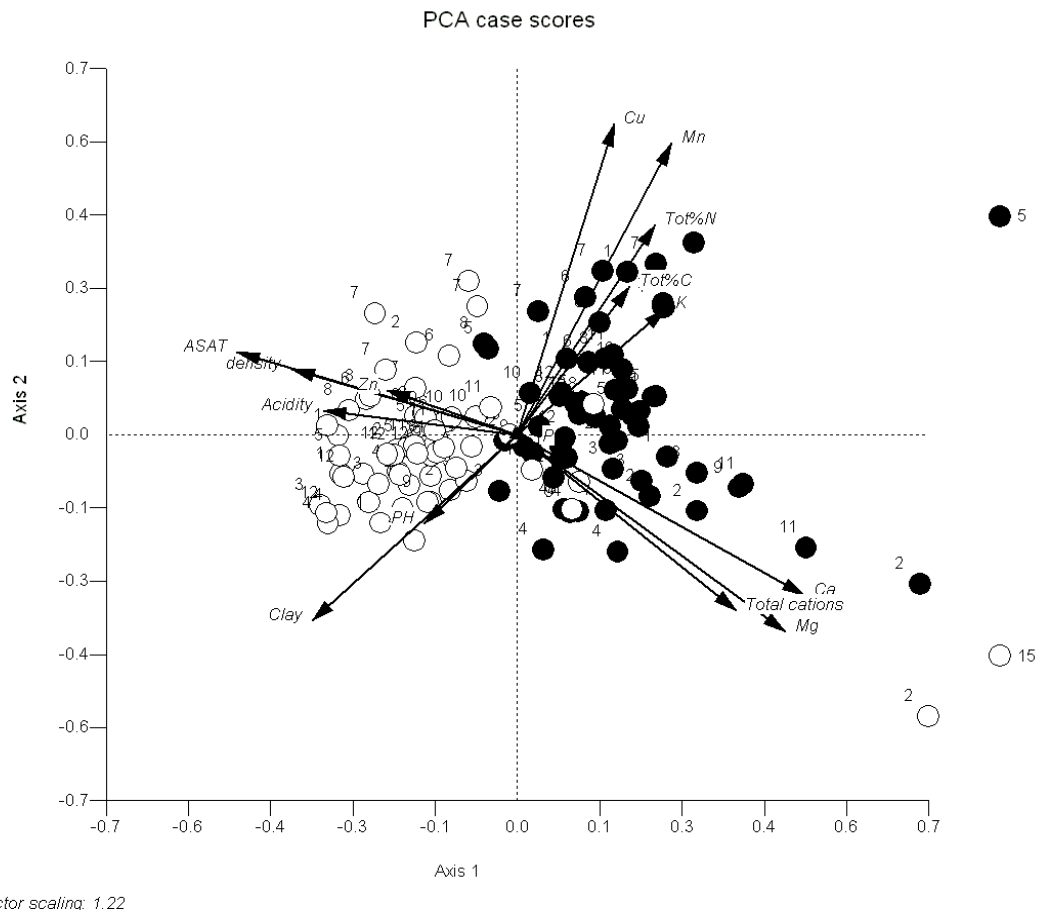


Figure 2. Biplot based on Principal Components Analysis (PCA) of soil variables from two sample depths. Note that solid circles denote samples at 5cm depth and clear circles at 15cm depth

4.1.1 Soil variables

There was a significant difference in the important soil variables identified using the PCA between the two soil depths (5cm - 10cm) (MANOVA; Wilks' $\lambda = 0.34$, $P < 0.0001$, Table 1).

Table 1. Univariate F-statistics and summary statistics (mean \pm SE) for differences in soil nutrients at two depths.

Soil depth	5 cm		15 cm		$F_{1,108}$	P
	Mean	SE	Mean	SE		
Ca	380.9	18.4	193.0	20.3	53.79	<0.001
Clay	19.1	0.9	25.3	0.8	49.32	<0.001
Total % N	0.61	0.02	0.42	0.01	57.26	<0.001
Density	0.82	0.01	0.92	0.01	61.8	<0.001

However, there was no significant difference among gap treatments in the soil variables (MANOVA; Wilks' $\lambda = 0.847$, $P < 0.362$, Table 2), indicating that any differences among gaps in seedling establishment or diversity is not due to soil characteristics.

Table 2. Univariate F-statistics and summary statistics (mean \pm SE) for differences in soil nutrients among gap treatments.

Soil variable	Mean	SE	$F_{4,105}$	P
Ca	288.0	49.3	1.06	0.382
Clay	22.24	1.64	0.12	0.976
Total % N	0.51	0.05	0.64	0.637
Density	0.87	0.02	0.48	0.753

4.2 Light environment

Average transmission of total incoming PAR varied significantly between gap treatments ($F_{4,45}=4.31$, $P<0.01$, Fig. 3). The percentage transmittance was highest in

the larger forest gaps (Gap 4 and Gap 8 treatments), intermediate in the smaller forest gaps (Gap 2 and Gap 1 treatments) and lowest beneath the closed canopy. R:FR also varied among forest environments ($F_{4,45}=5.77$, $P<0.001$) and showed some agreement with light transmission readings. PAR reaching the forest floor under intact understorey strata was very low with daily values averaging less than $3 \mu\text{mol.m}^{-2}.\text{s}^{-1}$ and 99% of PAR was intercepted by forest foliage (Table 3).

Table 3. Summary statistics (mean \pm SE) for gap size, percentage transmittance of PAR and the R:FR for experimental treatment sites.

Treatment	Gap 1	Gap 2	Gap 4	Gap 8
Average area m^2	22.5 ± 2.4	33.0 ± 2.8	55.5 ± 8.7	115.4 ± 9.0
% T	5.2 ± 6.3	5.0 ± 5.3	5.2 ± 3.8	7.5 ± 5.4
R:FR	0.8 ± 0.0	0.8 ± 0.1	0.8 ± 0.1	0.9 ± 0.1

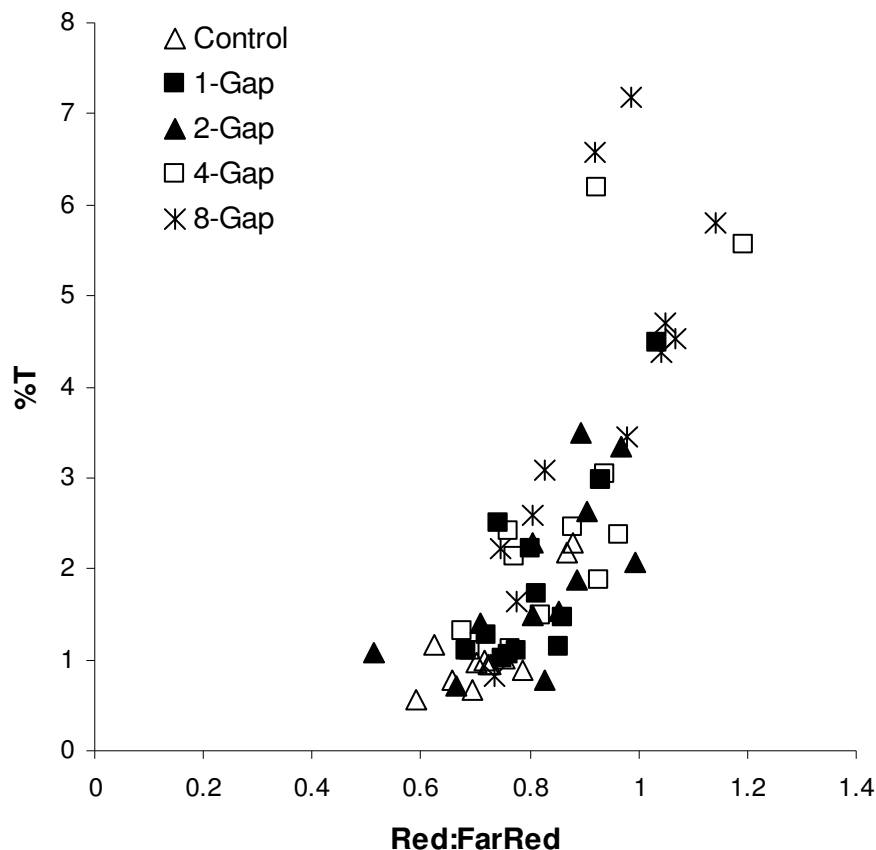


Figure 3. The relationship between percent transmittance of PAR and the red to far-red ratio of the light in the different gap sizes showing that light quantity and quality increased with increasing gap size.

4.3 Herb and grass cover

Light quality was highest in larger gaps (Table 3), particularly within Gap 4 and Gap 8 treatments, probably accounting for more grass and herbaceous cover within these treatments, and the lowest cover in the Control treatments under an intact canopy.

Table 4. Summary statistics (mean \pm SE) for percentage herbaceous cover for experimental treatment sites in 2007.

Treatment	Control	Gap 1	Gap 2	Gap 4	Gap 8
Average % cover	1.1 \pm 0.2	8.4 \pm 4.3	17.4 \pm 5.9	12.5 \pm 5.8	16.3 \pm 4.6

Herb and grass cover varied significantly across the gap treatments (Table 4). The mean cover in the controls in 2007 was 1.1%, while mean cover increased in Gap 2 (17.4%) and in Gap 8 treatments (16.3%).

4.4 Seedling abundance

There was no difference among gaps in seedling abundance. There was a significant difference between years ($F_{1,99} = 3.95$, $P < 0.05$, Fig. 4) in the number of seedlings.

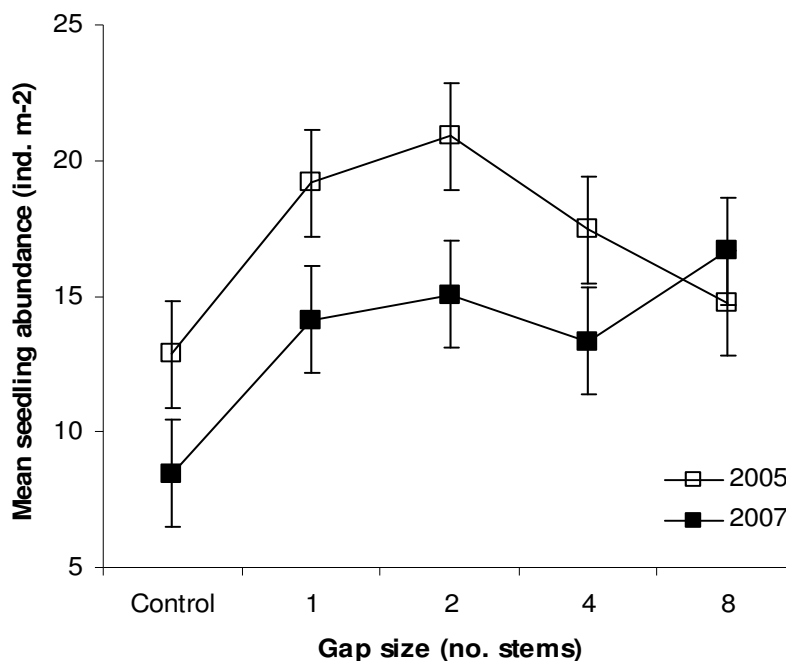


Figure 4. Seedling abundance (mean \pm SE) in gaps between years 2005 -2007.

Overall there were fewer seedlings in 2007 than in 2005 and because the control also reflects this difference, this apparent reduction in seedling abundance is not caused by the gap treatment (gap creation) but is a general forest wide trend, probably related to changes in climate between times.

4.5 Seedling species richness

Although seedling richness differed significantly among gaps ($F_{4,99}=4.77$, $P<0.001$, Fig. 5) there was no difference between 2005 and 2007.

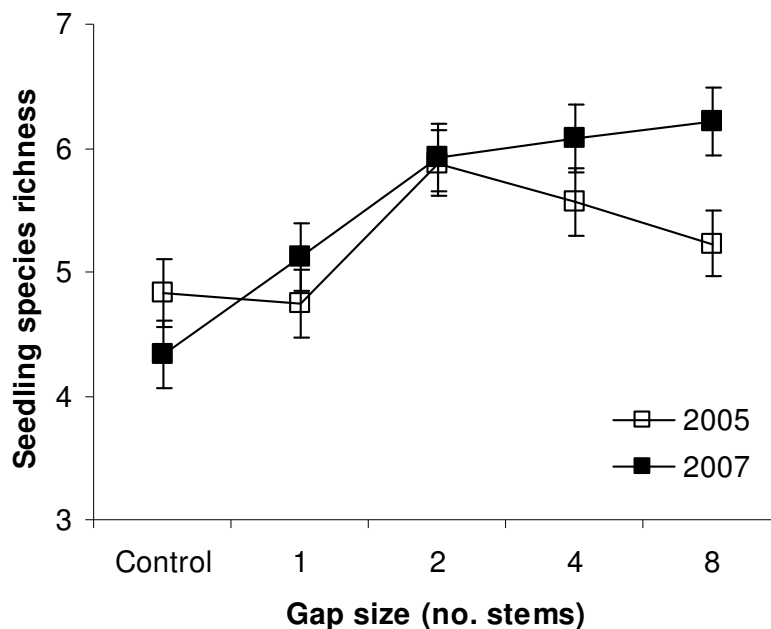


Figure 5. Seedling species richness (mean \pm SE) among gaps, 2005 - 2007.

4.6 Seedling species composition

The MRPP based on seedling abundance identified significant differences in seedling species composition between small and large gaps (MRPP, $T = -2.546$, $P = <0.05$). Indicator species analysis identified seven species characteristic of large gaps (Table 5). There were no species characteristic of small gaps.

Table 5. Indicator Value (IV) of indicator species characteristic of large gaps (Gaps 4 and 8) and small gaps (Gaps 1 and 2) in 2007.

Species	Seedling density (m ²) Large gaps	Seedling density (m ²) Small gaps	IV	P*
<i>Salacia gerrardii</i>	9.6 (±0.57)	0.5 ±(0.11)	79	0.001
<i>Tabernaemontana ventricosa</i>	5.6 (±1.52)	5.2 (±0.88)	68.2	0.015
<i>Secamone filiformis</i>	1.4 (±0.54)	0.6 (±0.26)	58	0.003
<i>Drypetes gerrardii</i>	0.9 (±0.19)	0.5 (±0.17)	54.2	0.033
<i>Garcinia gerrardii</i>	0.4 (±0.13)	0.3 (±0.13)	49.6	0.009
<i>Ochna holstii</i>	0.2 (±0.08)	0.1 (±0.07)	35.6	0.039
<i>Atalaya natalensis</i>	0.2 (±0.13)	0	20.8	0.05

The indicator species comprise understorey trees and two lianas, all of which are able to establish and grow in relatively low light conditions. Five of the seven species are dispersed as fruit and *S. filiformis* and *A. natalensis* are wind dispersed. All these species have the ability to germinate in varying intensities of light and even in shade. However, higher light levels in larger gaps encourage relatively fast height growth and long etiolated plants were frequently observed in such understorey gaps.

4.7 Modelling the predictors of the gap environment using Generalised Linear Mixed Models (GLMM)

The effects of the gap environment on seedling abundance in gaps were modelled using GLMM (Table 6). The best model included gap size and grass cover and supports the trend of larger gaps having more seedlings per unit area. However the juxtaposition of the Gap 1 and Gap 8 trends means that this is not a significant trend. Counter-intuitively the abundance of woody seedlings increases with increasing grass cover (Fig. 6). This may be related to light quality and indeed the next most parsimonious model (with a ΔAIC_c of 0.14) included the red to far-red ratio, which is generally considered an indicator of light quality (Capers and Chazdon, 2004). Thus, understorey gaps improve light quality at the forest floor and conditions for woody seedling establishment (Fig. 7) but also encourage grass growth, which may suppress woody seedlings (Boudreau and Lawes 2005).

Table 6. Summary of all seedling abundance AIC_c model combinations, with the rules of parsimony applied, the best fit model is represented by the model with the lowest ΔAIC_c and the fewest parameters.

Model	ΔAIC_c	AIC_c	w_i	Explained deviance %
Null	53.64	489.6		
Gap+Grass	0.00	436.0	0.32	13.11
Gap+RFR+Grass	0.14	436.1	0.30	13.51
Gap+%PAR+RFR+Grass	1.86	437.9	0.13	13.60
Gap+Grass+Herb	1.96	438.0	0.12	13.14
Gap+%PAR+Grass	2.02	438.0	0.12	13.13
Gap+RFR+Grass+Herb	2.29	438.3	0.10	13.51
RFR+Grass	3.21	439.2	0.07	11.17
Gap+%PAR+RFR+Grass+Herb	4.04	440.0	0.04	13.59
Gap+%PAR+Grass+Herb	4.08	440.1	0.04	13.14

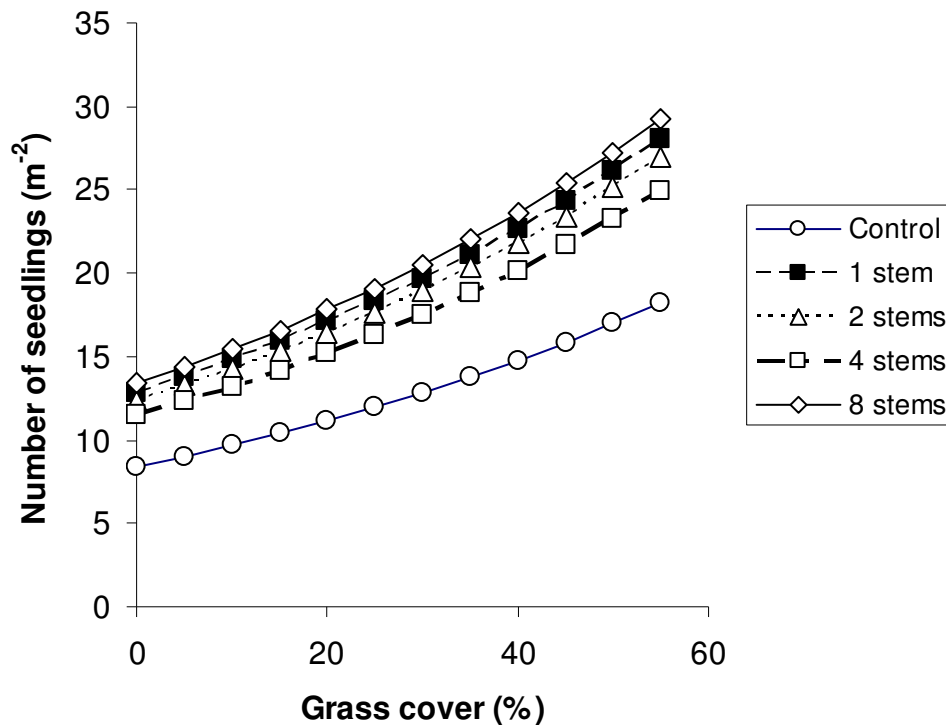


Figure 6. Fitted relationship between grass cover and numbers of seedlings within gap treatments at Ongoye Forest Reserve.

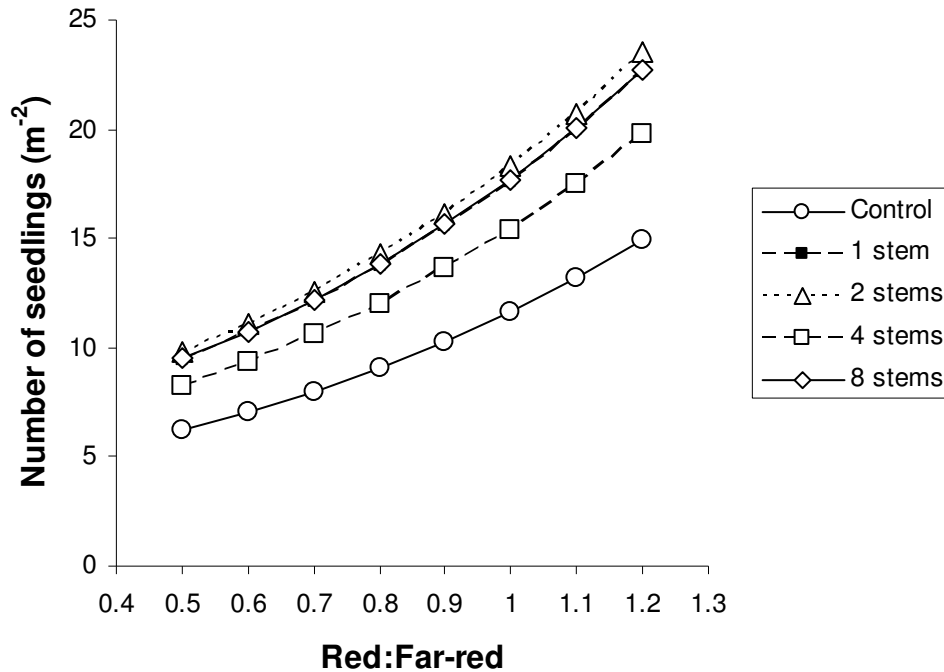


Figure 7. The fitted effects of light quality on seedling abundance within gap treatments at Ongoye Forest Reserve.

Seedling richness model results were similar to those for seedling abundance (Table 6). Gap “size” was implicated as was light (% PAR) but not grass cover, this is expected because while grass cover is a proximate correlate of seedling abundance it does not necessarily influence what species establish; in contrast light quality strongly affects abundance and this in turn is correlated with species richness (Fig. 7). Gap size did not have a significant affect on seedling species richness (Fig. 8).

Table 7. Summary of all seedling richness AIC_c model combinations, with the rules of parsimony applied, the best fit model is represented by the model with the lowest ΔAIC_c and the fewest parameters.

Model	ΔAIC_c	AIC_c	w_i	Explained deviance %
Null	12.33	227.1		
%PAR	0.00	214.7	0.16	6.38
Gap+%PAR	0.01	214.8	0.16	10.05

%PAR+RFR	1.02	215.8	0.09	6.84
%PAR+Grass	1.04	215.8	0.09	6.83
%PAR+Grass+Herb	1.68	216.4	0.07	7.46
Gap+%PAR+RFR+	1.84	216.6	0.06	10.18
Gap+%PAR+Grass	1.86	216.6	0.06	10.17
RFR	2.15	216.9	0.05	5.42
%PAR+RFR+Grass	2.16	216.9	0.05	7.25
Gap+RFR	2.21	217.0	0.05	9.08
RFR+Grass	2.35	217.1	0.05	6.25
%PAR+RFR+Grass+Herb	3.09	217.8	0.03	7.75
RFR+Grass+Herb	3.24	218.0	0.03	6.77
Gap+RFR+Grass	3.39	218.1	0.03	9.49
Gap+%PAR+Grass+Herb	3.61	218.4	0.03	10.34
Gap+%PAR+RFR+Grass	3.67	218.4	0.02	10.31
Gap+%PAR+RFR+Herb	3.79	218.5	0.02	10.26
Gap+RFR+Herb	3.86	218.6	0.02	9.28
Gap+Grass	4.91	219.7	0.01	7.88

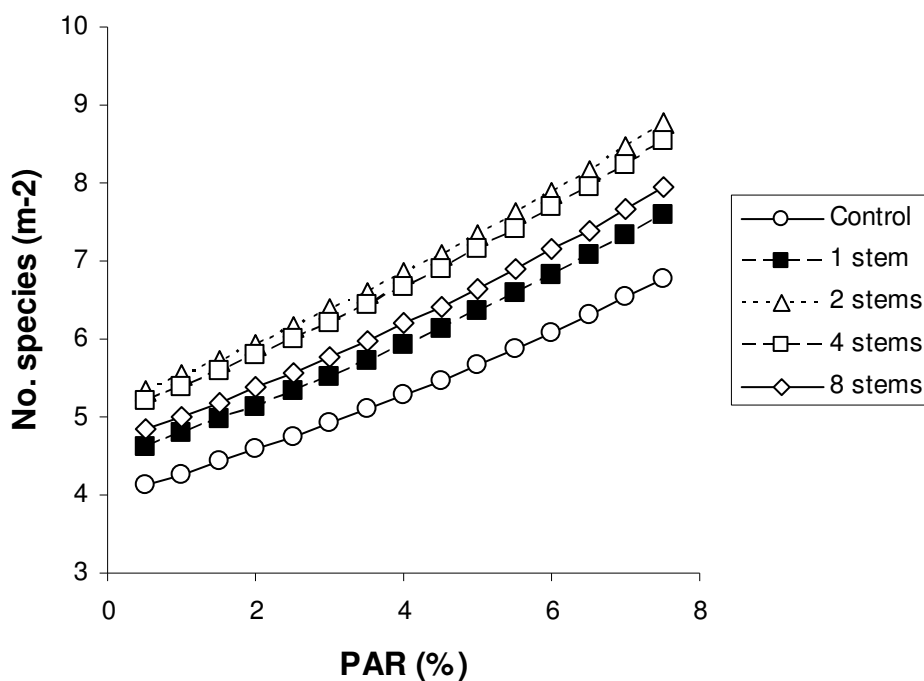


Figure 8. The effects of increased light on species richness within gap treatments at Ongoye Forest Reserve.

Chapter 5: Discussion and Conclusions

5.1 Environmental conditions that favour seedling establishment and species richness in understorey gaps

The maintenance of tree diversity has long been attributed to the creation of understorey gaps largely due to the rarity of canopy gaps (Connell *et al.*, 1997, Midgley *et al.*, 1995, Obiri and Lawes, 2004, Uhl and Murphy, 1981). The germination of seedlings and woody sapling recruitment determines the future species composition of a forest. Most of these species spend their entire lives in the subcanopy or understorey gaps beneath an intact canopy (Connell *et al.*, 1997). Thus, the creation of understorey gaps, either through natural processes or through subsistence harvesting of pole-sized trees (Burgess *et al.*, 2000, Cawe and McKenzie, 1989, Luoga *et al.*, 2002, Muir, 1990, Obiri *et al.*, 2002), could potentially affect successional processes underpinning regeneration dynamics and woody species composition at OFR.

Trends in seedling abundance did not differ among gaps, this could be attributed to the limits of seedling density being achieved in all gaps and are thus not recruitment limited. However, the diversity of seedlings was greater in larger gaps than in the control, suggesting an effect of the gap treatment. The creation of artificial understorey gaps of varying size at OFR did not alter environmental conditions in gaps except for light parameters (PAR and R:FR). Solar radiation levels are important in the understorey as plant productivity is controlled by light quantity while light quality, measured by the red to far-red ratio, drives physiological processes such as stem and leaf growth, seed germination, and photosynthesis rates (Endler, 1993). The main effect of increased light in large gaps was to allow herbs and grasses to dominate and possibly suppress woody seedling establishment in all but the largest artificial gaps. Therefore, counter to expectation the larger understorey gaps actually increased species diversity although seedling abundance did not increase in spite of improved light quality at the forest floor, possibly because of competition for space with increased grass and herb cover.

Seedling abundance did not differ among gaps although there was a trend toward more species in larger gaps. Seedlings of understorey and canopy species were more

abundant or richer in larger gaps. Although this study recorded no difference in the number of seedlings between the gap treatments in 2005 and again in 2007, the seedling densities in the treatments were however significantly greater than in the control plots. Thus, understorey gaps positively influence seedling establishment, with increased radiance within these gaps further facilitating this development. While the seedling abundance in the controls declined between years, species abundance in the treatment gaps increased, suggesting that the gaps do create opportunities for increased seedling establishment and higher species richness. Thus, even larger gaps, such as those created by Gap 4 and Gap 8 or at least gaps at a scale and size similar to those created by the more intensive harvesting (Boudreau and Lawes, 2005) of understorey trees, do not suppress regeneration. However, should harvest intensities increase, there is a predictable shift in species composition in the larger understorey gaps, where certain species capitalise on the higher light environment and are thus capable of influencing the existing species richness.

Even though the number of seedlings within the gap treatments decreased from 2005 to 2007 in all the gaps except Gap 8, because the decrease occurred in the controls too it was clearly not a response to gap creation but a general response to environmental conditions in the forest. Larger gaps appear to offer opportunities for a magnitude of species composition to prevail, although quite what mechanism accounts for this is unclear. The spatial structure of plant populations is directly influenced by seed dispersal which sets the template on which recruitment occurs. Seed dispersal is thus capable of determining which species are able to establish and coexist (Levey *et al.*, 2008). However, seedling densities did not differ among gaps, which suggests that gaps are saturated with seedlings or that all available space is occupied and seedlings do not appear to be dispersal (Levey *et al.*, 2008) or recruitment limited (*sensu* Hubbell *et al.* 1999). It is possible that the difference in seedling diversity between large and small gaps may be related to solar radiation differences and their ability to compete with grasses and herbs among woody seedlings, so that some species are advantaged in larger gaps with more grass and herb cover.

Seedling species composition differed between small and large gaps. The species involved were all understorey species capable of establishing in low to medium light levels. The seven plant species identified by the indicator species analysis were characteristic of large gaps where higher levels of diffuse light transmittance were

recorded. Gap formation is capable of increasing light transmittance which positively influences plant growth responses irrespective of plant growth forms (Chazdon *et al.*, 1996). The differences in species composition between gap treatments could have implications for selective harvesting, which could result in species with lower densities becoming locally extinct. The potential for a canopy species such as *Chrysophyllum viridifolium* for example, which establishes in small gaps and shaded microsites and is targeted at a sapling stage for poles, could potentially become locally extinct at OFR..

5.2 Conservation implications

Species composition in the gap treatments was more variable than under an intact understorey. The diversity of understorey species was greater in understorey gaps than in the controls. This study suggests that understorey gaps have the potential to contribute to the maintenance of tree diversity in the forest understorey. However, for the latter to be accepted it is important that the mechanisms that maintain diversity are understood. The grass-herb and seedling interaction appears to be important here. Larger gaps appear to create new opportunities and different microsite conditions that favour a suite of species not typical of shaded understorey environments. By creating heterogeneous recruitment microsites, diversity is maintained in the same way that canopy gap dynamics operates (Boudreau and Lawes, 2005, Connell, 1989). The creation of understorey gaps appears to promote whatever diversity and mix of understorey tree species are locally present and potentially plays a neutral role (Hubbell *et al.*, 1999) in maintaining species richness when gaps are small. However, there is a threshold intensity of harvesting of understorey poles beyond which the understorey will become dominated by species common to large gaps and diversity is predicted to decline and become dominated by a deterministic suite of species. The study clearly shows that for the larger gaps there is a species shift and the seedling assemblage has a much more predictable composition in these larger gaps than in small gaps. Thus, if the forest understorey was harvested intensively these results would suggest that there would be a predictable shift from light intolerant species to species which have a greater light tolerance. This would depart from the currently neutral regeneration dynamic and would cause tree diversity to be diminished over time. Thus, to maintain tree diversity intermediate intensities of disturbance are appropriate (*sensu* intermediate disturbance hypothesis, Burslem and Whitmore, 1999,

Connell, 1978, Hubbell *et al.*, 1999, Obiri and Lawes, 2004) and the difficulty is setting levels of harvesting and managing these levels. Currently, harvesters have removed about 10% of available stems per unit area over a 3-4 year period. This equates to harvesting intensities of 2-3% of available pole-sized stems per unit area per annum. Under current levels of subsistence harvesting of understorey species at OFR species composition is unlikely to be significantly altered, especially since regeneration in understorey gaps favours the species that are commonly harvested and that occur in high numbers (Boudreau *et al.*, 2005). This study has shown that intensive harvesting of four to eight adjacent stems or more has the potential to alter regeneration dynamics with consequences for forest composition and diversity.

5.3 Conclusions

The subsistence harvesting of timbers, which promotes the opening up of understorey gaps is beneficial for woody tree seedling establishment and tree dynamics, provided gaps are not too large. In large gaps a more deterministic pattern of species establishment prevails and this could cause tree diversity to decrease over time. Thus, harvesting of understorey trees that is concentrated in specific areas and which opens up extensive gaps has the potential to significantly alter forest dynamics. Woody tree seedling establishment could be largely dependant on gap size. The increase in available light enhances the establishment of understorey species, which is subsequently followed by rapid growth. The magnitude of species diversity among gaps, coupled with understorey gap formation, indicates that understorey gaps of different sizes and stages of re-growth are an important source of heterogeneity in the composition and dynamics of coastal scarp forests.

Species richness and seedling diversity was greatest in the larger gap treatments. Similarly, light measurements were higher in the larger gap treatments. Differences in light quantity and quality (which were correlated) across the gap sizes was associated with greater establishment of understorey and canopy species. The soil nutrient levels within gaps did not influence seedling establishment. Seedling species composition was greatest in the larger gap treatments. Similarly, in the larger gap treatments, the herbaceous layer suppressed seedling establishment. Based on these findings, even larger gaps in the understorey created by harvesting up to four and eight adjacent

stems or more has the potential to alter regeneration dynamics with consequences for forest composition and diversity. There is a trend towards a more deterministic shift in species composition with higher light tolerance characteristics among seedlings in the larger gaps that may become significant in time. This suggests that, current subsistence harvesting levels may not affect the establishment of woody tree seedlings and tree dynamics at OFR. This study shows that subsistence harvesting levels which exceed levels greater than the felling of four to eight adjacent stems would have a significant effect on the dynamics within the forest understorey at OFR. It is important for forest managers to understand the dynamics and complexities of coastal forest ecosystems. In this way potential threats will be identified timeously and allow for the implementation of an adaptive management approach. Protected areas such as OFR need to be managed with the objective of maintaining and restoring ecological functions as a means to conserve biodiversity while providing appropriate opportunities for the sustainable use of natural resources.

This study has shown that the effects of the current spatial scale of tree harvesting on woody seedling establishment and tree dynamics at OFR, has not altered forest dynamics. However, seedling dynamics within the larger gaps suggests that forest tree diversity and dynamics and harvest gaps, have the potential to significantly affect the natural forest dynamics at OFR.

5.4 Recommendations for implementation (management) and future research

This study has demonstrated that harvesting of pole-sized stems, if managed correctly, can be sustainable and also help maintain tree diversity. Natural resource use can thus be mutually beneficial to forest management and local communities. This information has to be communicated to both EKZNW management and the neighbouring Mzimela community at Ongoye. The locality of the Manzamnyama and Endlovini Field Ranger outposts, which are situated on either end of the protected area, make patrolling the central forest areas difficult. Security along the protected area boundary is equally challenging as community members have free, uncontrolled access with limited management control. There are many other resource limitations that will continue to present challenges for protected area managers. It is for this reason that alternative

management systems and processes need to be identified in order to achieve the biodiversity conservation targets set for scarp forests within KwaZulu-Natal to which OFR contributes.

Under current levels of subsistence harvesting of understorey species at OFR, species composition is unlikely to be significantly altered. However, there are two issues here that need to be considered before this conclusion can be drawn: (1) only two years passed between sampling and it would be interesting to look at the trends reflected in the 2007 data; and (2) our data does not reflect any increase in harvesting intensity since 2005 and so our findings are relevant to a situation described in 2005 only. Current levels of harvesting, creating mostly small gaps are unlikely to affect seedling abundance and diversity and in turn are predicted to have little impact on forest dynamics. However, to ensure that harvesting does not become unsustainable it will have to be closely regulated.

This study has shown that there is a shift in species composition, from light intolerant species establishment in the small gaps to species which have a greater tolerance to higher light intensities in the larger gaps. Future research into the regeneration dynamics of gap size, where the possibility exists for species to become locally extinct may provide useful information which could inform managers of the potential risks associated with a larger scale of harvesting at OFR.

This study specifically addressed seedling establishment within the varying gap treatments. Future research could investigate the survival and subsequent transition of emerging seedlings into the tree population at OFR.

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