Seed bank dynamics of selected vegetation types in Maputaland, South Africa

by

MILLICENT JOHANNA SUSANNA KELLERMAN

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SUMMARY

SEED BANK DYNAMICS OF SELECTED VEGETATION TYPES IN MAPUTALAND, SOUTH AFRICA

by MILLICENT JOHANNA SUSANNA KELLERMAN

for the degree Magister Scientiae

Supervisor: Prof. M.W. van Rooyen
Department of Botany
University of Pretoria

The seed bank dynamics of five selected vegetation types within the Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa, were investigated. The different vegetation types from which soil samples were randomly collected during the entire year of 2001 are (a) the very rare and unique *Licuati* forest and (b) *Licuati* thicket vegetation, (c) a bare or sparsely vegetated zone surrounding the forest edges, the forest/grassland ecotone, dominated by cat's tail grass (*Perotis patens*), (d) grassland and (e) woodland (dense savanna).

The main idea of this study was to gain a better understanding of the dynamics of some of Maputaland's most interesting and unique vegetation types. The aims were to obtain an estimate of the seed bank size, determine the species composition of the soil seed bank flora and compare the species composition with the aboveground vegetation, as well as to compare species richness between the seed bank and the standing vegetation in these selected vegetation types. Seed bank size and species composition was determined mainly by using the seedling emergence method. Soil samples were collected at three-month intervals to obtain a measure of the temporal variation in size and composition. The comparison between the seed bank flora and standing vegetation was done by means of a transect method. The depth distribution of seeds in the soil profile was investigated by collecting soil samples at six different soil depths. Soil seed densities obtained by the seedling emergence and flotation methods were also compared.

Results showed that the forest/grassland ecotone and grassland vegetation types produced the largest soil seed bank in terms of seed densities and the *Licuati* forest and thicket vegetation the smallest, in fact the latter had almost no persistent seed bank. Within each vegetation type the seed bank size showed clear seasonal variation. Seed distribution was concentrated in the upper soil layers. The flotation and physical separation method produced much larger seed numbers than the seedling emergence method. Generally, there is no or very little correspondence between the number of species recorded in the seed bank and that of the standing vegetation. It was found that the seed bank of the different vegetation types, if present, was a fairly poor predictor of the species composition of the existing vegetation, especially in terms of woody species.

CONTENTS

CHAPTER 1
INTRODUCTION

Maputaland, previously known as Tongaland, named after the Thonga Chief Mabhudu, is the coastal plain stretching from Maputo in Mozambique southwards to the St. Lucia Estuary in the northern parts of KwaZulu-Natal, South Africa. Maputaland is, after being discovered by early settlers, known for its species-rich fauna and flora, ancient geological history and rich human culture. Maputaland is recognised as a IUCN Centre of Plant Endemism, not only because of its intricate environment, but also its remarkable biodiversity and high levels of plant endemism.

Maputaland is home to extensive areas of the rare and unique *Licuati* forest and *Licuati* thicket vegetation types that are endemic to this biogeographical region. Although several phytososiological studies have been done in recent years to gain a better understanding of the species composition of Maputaland's exceptionally diverse vegetation, little is known about the vegetation dynamics and functional ecology. This is particular true for the unique *Licuati* forest and thicket vegetation types. Furthermore, the apparent inability of these vegetation types to regenerate after a major disturbance is cause for concern. This study was carried out in the Tembe Elephant Park, southern Maputaland, which conserves and protects large tracks of these unique dry forests.

The accumulation of seeds in the soil to form soil seed banks is of crucial importance to the survival of individual plant species in any plant community or vegetation type. Soil seed banks are a pool of reproductive potential and a source of genetic inheritance. Soil seed banks represent a memory of the previous floristic composition and serve as a predictor of the future vegetation. Soil seed banks also form the key to primary and secondary succession and play a very important role in the establishment and restoration of natural vegetation following disturbance. The soil seed bank also portrays the fruiting phenology and subsequent seed fall of any plant species in a specific area and gives an indication of the species' survival potential. Therefore, it is very important that the soil seed bank in a specific habitat or vegetation type is thoroughly investigated and thus fully understood, to understand the dynamics of the aboveground vegetation.

The aim of this study was to examine the most important aspects of seed bank dynamics of the soil seed bank in five selected vegetation types in the Tembe Elephant Park, Maputaland. The seed bank studies included a (a) comparative study of two commonly used seed extracting methods to determine seed density, (b) study of the depth distribution of seeds in the soil seed bank, (c) investigation of the spatial and temporal variation in seed bank size and species composition and (d) a comparative study of the species richness and species composition of the soil seed bank and standing vegetation.

CHAPTER 2
STUDY AREA

2.1 LOCATION

Maputaland, previously known as Tongaland, is located in the Indian Ocean coastal region. The area is bordered in the north by the Inkomati-Limpopo River in southern Mozambique, in the south by the St. Lucia Estuary in northern KwaZulu-Natal and in the west by the Lebombo Mountain Range (Van Wyk 1996). The Tembe Elephant Park, which is situated within the heart of Maputaland, will be the focus area of this study and is located at latitude 26º 51.56'S–27º 03.25'S and longitude 32º 24.17'E–32º 37.30'E (Figure 2.1).

Chief Mazimba Tembe allocated land in the Tembe Tribal Ward to establish a game reserve that would serve several conservation purposes. Reasons for the establishment and proclamation of such a reserve were to (a) protect the lives and property of the local people from damage and injury by elephant, (b) preserve the last naturally occurring population of the African elephant, *Loxodonta africana,* in KwaZulu-Natal, (c) protect one of the largest populations of Livingstone's suni, *Neotragus moschatus* in southern Africa, as well as other wildlife endemic to Maputaland, and (d) preserve and protect the rare and unique *Licuati* or Sand Forest vegetation type (KwaZulu/Natal Nature Conservation Services 1997).

The Tembe Elephant Park was officially proclaimed on 21 October 1983 and is 30 013 ha in extent. It is situated approximately 55 km northeast of Jozini, with Sihangwane as base camp being located at latitude 27º 02.12'S and longitude 32º 25.00'E. The Tembe Elephant Park currently forms part of the Tembe Tribal Ward and many rural communities still have their home in this ward (KwaZulu/Natal Nature Conservation Services 1997, Matthews *et al.* 2001).

The Tembe Elephant Park encloses extensive areas of pristine indigenous Sand Forest, also known as *Licuati* forest in Mozambique (Izidine *et al.* 2003), as well as other woodland, thicket, grassland and wetland vegetation types (Moll 1980, Matthews *et al.* 2001). According to Low and Rebelo (1998) the vegetation of the

Tembe Elephant Park is classified primarily as *Subhumid Lowveld Bushveld* of the Savanna Biome, with patches of Sand Forest belonging to the Forest Biome.

2.2 GEOLOGY

The formation of the modern Maputaland landscape started 140 million years ago, during the break up of Gondwanaland. During this time the resistant volcanic rhyolite lavas, that form the Lebombo Mountain Range and underlie the coastal plain, were steeply tilted eastward. At the newly formed coastline, Cretaceous marine sedimentary rock and conglomerates were laid down on the seaward sloping rhyolite base, to form the present day level coastal plain (Maud 1980). From the end of the Cretaceous, through the Tertiary and Quaternary, the coastal plain was repeatedly exposed and submerged as sea levels rose and fell due to Glacial periods and the geomorphological processes taking place on the southern African continent. Recurring marine transgressions and regressions resulted in cycles of sedimentation and erosion, with marine deposits being laid down, then eroded and redistributed by wind and water. This resulted in the formation of a series of north-south aligned dune ridges parallel to the present day coastline (Goodman 1990).

The oldest of these north-south trending sand dunes in South Africa is immediately adjacent to the Lebombo Mountains and appears to be of Plio-Pleistocene age (Davies 1976). However, the steep-sided dunes along the coast are young, and may still be forming in places (Van Wyk 1996). Incised coastal river valleys filled as sea levels rose during the late Holocene, resulting in the deposition of fertile alluvial material along drainage lines and the formation of pans, swamps and marshes where drainage lines became submerged (Goodman 1990).

2.3 TOPOGRAPHY

With the exception of the narrow Lebombo Mountain Range, which rises to an elevation of about 600 m in the west, Maputaland is topographically a nearly flat, low-level, sandy coastal plain with a maximum elevation of 150 m (Van Wyk 1996). The Tembe Elephant Park consists of linear north-south trending dunes interspersed with depressions that, if soil clay content is high, may form perennial pans. The highest sand dunes in the study area, Nhlela and Beacon Ridges, reach a height of 129 m above sea level, whereas the lowest lying areas such as the Muzi Swamp have an altitude of approximately 50 m (Van Wyk 1996, Matthews *et al.* 2001). Topographically the Nhlela and Beacon Ridges have relatively steep gradients with short hill slopes and are probably the remnants of the oldest dune systems in the study area (Van Wyk 1996).

2.4 SOILS

Most of the Maputaland Coastal Plain is covered with infertile aeolian sands deposited during the Tertiary and Quaternary geological eras. In contrast, the soils of western Maputaland are more fertile, especially along the west bank of the Pongola River. The soils of the Pongola flood plain are mainly derived from alluvium, river terraces and Cretaceous sediments and have been used for agricultural purposes for centuries (Maud 1980).

The sandy soils of the north-south directed dune ridges to which the *Licuati* or Sand Forest vegetation type is restricted, commonly exhibit well-drained profiles characterised by very deep, red or yellowish, high base status soils with less than 5% clay content. The soils supporting *Licuati* or Sand Forest in Maputaland, especially in the Tembe Elephant Park, are classified according to the South African system as Hutton or Clovelly Forms and can be grouped as entisols or inceptisols (Matthews *et al.* 2001).

Within the study area dark brown, even black sands underlie the forest vegetation itself, whereas the bare or sparsely vegetated zones around the forest edges are characterized by white sands. Woodland and grassland soils differ from forest soils, especially in terms of water permeability. Forest soils seem to be water repellent, mainly because they contain organic compounds and hydrophobic substances not present in woodland and grassland soils (Matthews *et al.* 2001, Fourie *et al.* 2002). Although there is much organic matter build-up, good drainage and excessive leaching and nutrient uptake by standing biomass lead to a low nutrient content in these forest soils (Van Wyk 1996).

The water table in the Tembe Elephant Park varies from ground level (e.g. Muzi Swamp) to depths of 60 m and more below the soil surface (Van Wyk 1996, Matthews *et al.* 2001, Izidine *et al.* 2003).

2.5 CLIMATE

Maputaland is characterised by hot, humid summers and cool, dry winters with no frost occurring in the winter season. Rain is received throughout the year, but with a definite summer period and morning mist is common during the winter months. The mean annual temperature varies from 21°C along the Lebombo Mountains to 23°C in the centre of the coastal plain, moderating slightly along the coast to 22°C (Van Wyk 1996, Van Wyk & Smith 2001).

A climatogram or so-called Walter diagram illustrates the mean temperature and rainfall data for the period 1990 to 2001 as obtained from the Sihangwane Weather Station (50 m above sea level, 27º 02.12'S; 32º 25.00'E), located in the Tembe Elephant Park (Figure 2.2). These data revealed the mean annual temperature for the Tembe Elephant Park as 23.1°C, with the highest maximum temperature being recorded as 45.0°C, and the lowest minimum temperature recorded as 4.0°C (Matthews *et al.* 2001).

The climate is described as moist tropical/subtropical along the coast becoming dry tropical/subtropical a short distance inland (Van Wyk & Smith 2001). The annual rainfall in Maputaland averages about 1 100 mm along the coast and declines progressively inland to as low as 500–600 mm on the western plains (Van Wyk 1996). Rainfall increases to over 800 mm per annum along the top of the Lebombo Mountains (Maud 1980, Watkeys *et al*. 1993). The highest monthly precipitation occurs between October and April (Watkeys *et al.* 1993). According to rainfall data obtained from Sihangwane, the mean annual rainfall for the Tembe Elephant Park is 721 mm (Matthews *et al.* 2001). During the hot summer months, high levels of humidity characterise the Tembe Elephant Park and surrounding Maputaland (KwaZulu/Natal Nature Conservation Services 1997).

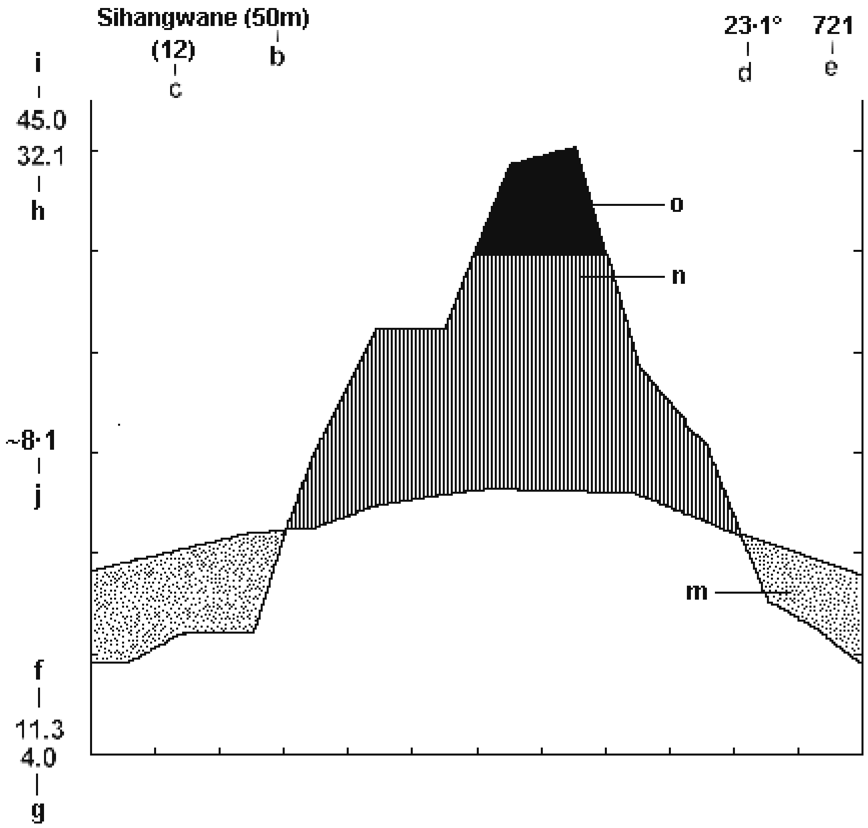

Figure 2.2. Climatogram of Sihangwane Weather Station, Tembe Elephant Park, Maputaland, northern KwaZulu-Natal, South Africa (b= height above sea level, c= duration of observations in years, d= mean annual temperature in ºC, e= mean annual precipitation in mm, f= mean daily minimum of the coldest month, g= lowest temperature recorded, h= mean daily maximum of the warmest month, i= highest temperature recorded, j= mean daily temperature variations, m= relative period of drought, n= relative humid season, o= mean monthly rain > 100 mm) following Walter (In: Cox & Moore 1994).

2.6 FLORA AND ENDEMISM

The study area falls within the Maputaland Centre of Plant Endemism, which is part of the Maputaland-Pondoland Region, a centre of high species diversity, rich in endemic plants and animals (Van Wyk & Smith 2001)(Figure 2.3).

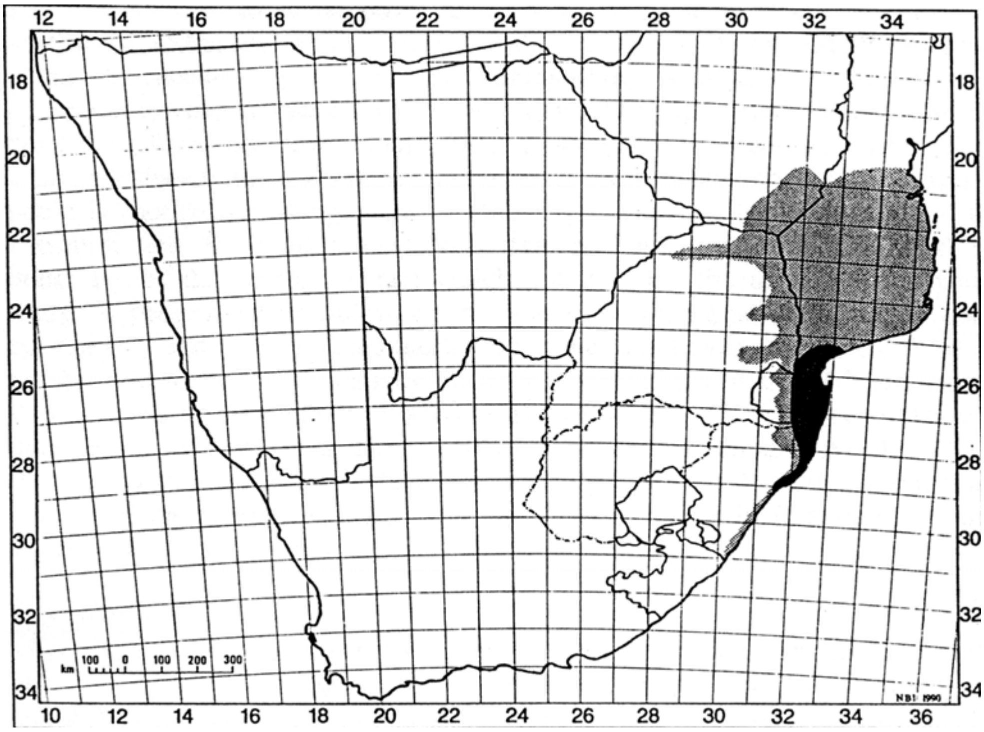

Figure 2.3. Map of southern Africa showing the location of the Maputaland Centre of Endemism (solid black) and the main area in which the distribution of certain Maputaland Centre endemics are found (shaded) (Van Wyk 1996).

The diverse landscapes as well as the complex mosaic of vegetation types, which characterise the Maputaland Coastal Plain, contribute to the high levels of diversity found in the Maputaland region. Biogeographical research showed that most of the flora and fauna is of Afrotropical origin, and those endemic taxa appear to have evolved only recently (Van Wyk 1996). The number of vascular plant species in the Maputaland Centre of Endemism is estimated at 2 500 and may even be as high as 3 000. Of these, at least 230 plant species or infraspecific taxa are endemic or near endemic (MacDevette *et al*. 1989, Van Wyk 1996, Matthews *et al.* 2001). Faunal diversity and endemism are also very high, especially in terms of bird and reptile species (Van Wyk 1996, McGeogh *et al*. 2002).

A substantial number of the floristic endemics are associated with the *Licuati* or Sand Forest, a very rare and unique vegetation type endemic to the Maputaland Centre of Endemism. The Woody Grassland is another vegetation type that is endemic and characteristic of the Maputaland Region (Van Wyk 1996).

2.7 VEGETATION

2.7.1 Introduction

The Maputaland Coastal Plain includes a wide variety of vegetation types such as forest, grassland, savanna, woodland, thicket and palm veld. The Maputaland Region is also characterised by vast areas of wetland, such as marshes, lakes and estuaries. The above mentioned vegetation types form a complex mosaic, making the vegetation of the Maputaland Region exceptionally diverse.

Fifteen major vegetation types were identified and described by Moll (1978,1980) in the northern parts of the Maputaland–Pondoland Region. Several of the vegetation types possess high levels of species richness and each vegetation type contains its own characteristic species composition. The vegetation in the Tembe Elephant Park is depicted in Figure 2.4.

Rutherford and Westfall (1994) classified the vegetation of South Africa, according to the dominant and co-dominant plant life forms and their correlation with regional climatic conditions, into seven major biomes. They defined a biome as a broad ecological unit that represents a major life zone extending over a large natural area. Elements of three of these biomes occur in the Tembe Elephant Park: (a) the Forest Biome, (b) the Grassland Biome and (c) the Savanna Biome. The vegetation in the Tembe Elephant Park will be discussed in relation to these biomes.

2.7.2 Forest Biome

Rutherford and Westfall (1994) define the Forest Biome as woody vegetation characterised by a continuous canopy cover with multi-layered vegetation underneath (Rutherford & Westfall 1994, Low & Rebelo 1998). The Forest Biome is by far the smallest biome in southern Africa and occurs mainly in the southern parts of the Western Cape Province, although many smaller forest patches can be found both in the Grassland and Savanna Biomes along the eastern escarpment and eastern shores of South Africa and southern Mozambique. Forests are patchily distributed and are mainly restricted to frost-free areas. To persist, forest vegetation requires a minimum of 500 mm of rain annually in winter rainfall areas, and a minimum of 725 mm of rain annually in summer rainfall areas. Forests occur from sea level to altitudes of over 2 100 m. Forest vegetation is fire-sensitive, but rarely burns, mainly due to the high humidity characteristic of forest habitats. Forests are also characterised by edge or ecotonal plant communities bordering the forest patches, which are able to tolerate fire (Low & Rebelo 1998, Geldenhuys 1999, Van Wyk & Smith 2001).

Three main forest types have been recognised for South Africa: (a) Afro-montane Forests, (b) Coastal Forests, and (c) Sand Forests (Low & Rebelo 1998). According to Geldenhuys (1999) Afro-montane forests occur along the Drakensberg Escarpment, the KwaZulu-Natal and Eastern Cape midlands, the south and southwestern Cape mountains and coastal plateau, whereas Coastal and Sand Forests occur on the Indian Ocean coastal dunes and lowlands. These forests are not floristically uniform, with Afro-montane Forests having much lower species diversity than Coastal and Sand Forests. Thus, species richness is higher in drier, warmer forests than wetter, cooler forests (Gerhardt & Hytteborn 1992, Low & Rebelo 1998, Geldenhuys 1999).

This study focuses on Sand Forest, which is a remarkable, and unique vegetation type endemic to Maputaland, an area confined to the tropical and subtropical coastal belt of southern Mozambique and northeastern KwaZulu-Natal. Sand Forest, also known as *Licuati* Forest (Izidine *et al*. 2003), occurs under drier conditions than other southern African forest types and is best developed on the ancient north-south trending dune cordons in the hinterland of the coastal plain (Van Wyk & Smith 2001). Growing in an environment that is unusually harsh for forest with rainfall only averaging as little as 600 mm per year, these Sand Forests are amongst the driest forests in the world (Murphy & Lugo 1986, Kirkwood 2000, Matthews *et al*. 2001). Sand Forest forms a mosaic of short and tall forest patches bordered by grassland in a matrix of open to closed woodland.

The tropical dry *Licuati* or Sand Forest is of particular interest. It occurs as isolated islands of dry, dense, semi-deciduous to deciduous forest vegetation merged into a mosaic of fire tolerant savanna and grassland vegetation. Sand Forest is often characterised by bare or sparsely vegetated zones on the edges of these forest patches (Moll 1980, Van Wyk 1996, Kirkwood & Midgley 1999, Matthews *et al.*

2001). This forest type occurs on ancient sand dunes, which are probably remnants of former shorelines (Van Wyk 1996) and is patchily distributed throughout the full range of these north-south trending inland sand dunes. Patches of short and tall forest, which cover a relatively small total surface area, are enclosed in larger areas of open and closed woodland, usually bordered by grassland vegetation (Kirkwood & Midgley 1999, Izidine *et al.* 2003).

The *Licuati* or Sand Forest vegetation is exceptionally species rich with a high number of woody endemics. Matthews *et al.* (2001) classified the *Drypetes arguta-Uvaria lucida* subsp. *virens* sand forest plant community of deep, dry sandy inland areas in the Tembe Elephant Park into two sub-communities: (a) *Cola greenwayi-Balanites maughamii* tall sand forest and (b) *Psydrax fragrantissima-Hyperacanthus microphyllus* short sand forest. In a similar way Gaugris *et al.* (submitted) classified the *Ptaeroxylon obliquum-Hymenocardia ulmoides* sand forest vegetation in the Tshanini Game Reserve south of Tembe Elephant Park into the *Rothmannia fischeri-Ptaeroxylon obliquum* low to short sand forest and the *Strychnos henningsii-Ptaeroxylon obliquum* tall sand forest. Izidine *et al.* (2003) recently proposed the terms *Licuati* forest for tall sand forest and *Licuati* thicket for short sand forest. Note that, for the remainder of this study, the short and tall sand forest types will be referred to as *Licuati* thicket and *Licuati* forest, respectively.

The *Licuati* forest canopy is consistently dominated by tree species such as *Balanites maughamii* (green thorn), *Cola greenwayi* (hairy cola), *Dialium schlechteri* (Zulu pod-berry), *Drypetes arguta* (water ironplum), *Hymenocardia ulmoides* (red-heart tree), *Pteleopsis myrtifolia* (mock bush-willow), *Uvaria lucida* subsp. *virens* (large-fruited cluster pear), *Ptaeroxylon obliquum* (sneezewood) and *Newtonia hildebrandtii* (Lebombo wattle). The extensive tracts of *Licuati* forest occurring south of Maputo in Mozambique tend to have *Afzelia quanzensis* (pod-mahogany) as a co-dominant species in the upper canopy (Kirkwood 2001). Although significant correspondence was found in the species composition of the *Licuati* forest and thicket vegetation, the *Licuati* thicket is floristically distinguished from the *Licuati* forest by short stature tree and shrub species such as *Psydrax fragrantissima* (Tonga quar), *Cleistanthus schlechteri* (false tamboti), *Croton pseudopulchellus* (small lavender fever berry), *Hyperacanthus microphyllus* (Tonga thorn-gardenia), *Grewia microthyrsa* (sand raisin), *Tricalysia junodii* (fluffy-flowered jackalcoffee), *Ochna barbosae* (sand plane) and *Combretum mkuzense* (sand forest bushwillow). Undergrowth is poorly developed with very little shrub vegetation and almost no herbaceous layer (Kirkwood 2000, Matthews *et al.* 2001, Izidine *et al.* 2003).

On a broader scale Kirkwood and Midgley (1999) recognised a taller eastern sand forest type on white to yellow sands and a shorter western type on red sands in the Maputaland Region, with associated turnover in subdominant species.

Sand Forest, also referred to as 'tropical dry forest' or 'dry, semi-deciduous forest', covers only 0.03% of South Africa's land surface of which 44.62% is conserved within nature reserves and resource parks (Low & Rebelo 1998, Kirkwood 2000). Sand Forest is considered an ancient vegetation type (Kirkwood 2000), since carbon dating recently indicated that most of the tall trees dominating the upper canopy layer of Sand Forest patches are probably several hundred years old (Kirkwood 2000). It is also speculated that some of the giant Lebombo wattles, *Newtonia hildebrandtii*, may be over a thousand years of age (W.S. Matthews, Ezemvelo KwaZulu-Natal Wildlife, Tembe Elephant Park – PO Box 356, KwaNgwanase). Van Wyk & Smith (2001) hypothesized that Sand Forests display allelopathic properties (chemically mediated inhibitory effects on surrounding vegetation) which may assist in maintaining this forest type and help to explain the sharp boundary between the forest and surrounding vegetation.

2.7.3 Grassland Biome

The Grassland Biome is found mainly on the high central plateau of South Africa, inland areas of the Natal coastal plain and mountainous areas of south Eastern Cape Province (Rutherford & Westfall 1994). Topography in this biome is characterised by flat and rolling landscapes, but includes the escarpment itself. Altitudes vary from near sea level to as high as 2 850 m where frosts are common in the cold winter months. The Grassland Biome is limited to the summer rainfall areas of South Africa. This biome is characterised by the strong dominance of hemicryptophytes of the Poaceae family (grasses). Trees are absent, except in a few localized habitats. Geophytes are often abundant, contributing to the extremely high biodiversity of the Grassland Biome. Frosts, fire and grazing maintain the grass dominance and prevent the establishment of trees (Low & Rebelo 1998).

The Grassland Biome occupies approximately 26.0% of the South African land surface (Bredenkamp 1999). This study focuses on satellite grasslands, which are local patches of grassland within the zones of other biomes. According to O'Connor and Bredenkamp (1997) these grassland patches seem to be restricted to distinctive topographic-geological complexes and specific soil conditions. In Maputaland, satellite grassland patches occur in a mosaic of surrounding forest and savanna vegetation in areas of poorly drained sandy soils with average rainfall and high humidity.

The grassland and savanna vegetation surrounding the fragmented patches of *Licuati* forest and thicket vegetation differ greatly from the forest vegetation both in structure and composition (Matthews *et al.* 2001). Grassland associated with these forest patches is characterised by a dominant herbaceous layer consisting primarily of grass and forb species. Prominent grass species characteristic to this grassland vegetation include *Andropogon schirensis* (stab grass), *Aristida stipitata* subsp. *stipitata* (long-awned grass), *Bewsia biflora* (false love grass), *Digitaria eriantha* (common finger grass), *Pogonarthia squarrosa* (herringbone grass), *Perotis patens* (cat's tail grass) and *Urelytrum agropyroides* (quinine grass). Other diagnostic species include the forbs *Tephrosia longipes* subsp. *longipes*, *Indigofera inhambanensis* and *Trachyandra cf salti*, as well as the sedge *Cyperus obtusiflorus* (Moll 1980, Van Wyk 1996, Matthews *et al.* 2001).

The above mentioned grassland type, associated with the *Licuati* forest and thicket vegetation, is believed to serve as a sharp ecotonal zone between the forest and woodland vegetation.

2.7.4 Savanna Biome

The Savanna Biome, covering approximately 46.2% of southern Africa's surface area, is characterised by vegetation composed of a herbaceous layer with an upper layer of woody plants. The canopy layer of woody plants can vary from widely spaced (open savanna) to 75.0% canopy cover (closed savanna). The latter case savanna is often referred to as woodland (Rutherford & Westfall 1994). The Savanna Biome extends from Namibia, Botswana and higher rainfall areas of the Northern Cape Province to the Orange Free State, northern Gauteng, Limpopo, Mozambique, central and eastern Swaziland, areas of KwaZulu-Natal and the Eastern Cape Province (Rutherford & Westfall 1994).

The Savanna Biome occurs mainly in the summer rainfall areas of southern Africa, which are characterised by a wide range in temperature between summer and winter, with occasional frost during the colder, dryer months. Fire is a very important factor keeping the savanna vegetation intact and the vegetation of the Savanna Biome is well adapted to fire.

Savanna plant species have developed several defence mechanisms against herbivores. Many savanna or woodland tree species have the ability to produce secondary compounds such as tannins that cause leaves to become unpalatable and indigestible. Some species such as *Euphorbia ingens* (common tree euphorbia) and *Spirostachys africana* (tamboti) are known to produce toxins or poisonous latex, which is regarded as a protective strategy against overutilisation. The development of thorns and spines on savanna plant species is a physical mechanism to protect themselves against browsers (Bredenkamp 1999). However, many savanna tree species depend on browsing animals for effective seed dispersal.

The Savanna Biome is represented by the woodland vegetation in Tembe Elephant Park. The woodland vegetation is characterised by both a woody and herbaceous layer. Dominant tree species associated with this woodland vegetation type include *Terminalia sericea* (silver clusterleaf), *Strychnos madagascariensis* (black monkey orange), *Strychnos spinosa* (spiny monkey orange), *Acacia burkei* (black monkey thorn), *Sclerocarya birrea* (marula), *Dichrostachys cinerea* (sickle bush) and *Combretum molle* (velvet bushwillow). Grass species prominent of the woodland vegetation include *Aristida stipitata* subsp. *stipitata* (long-awned grass), *Digitaria eriantha* (common finger grass), *Diheteropogon amplectens* (broad-leaved bluestem), *Panicum maximum* (guinea grass), *Perotis patens* (cat's tail grass), *Pogonarthia squarrosa* (herringbone grass) and *Themeda triandra* (red grass) (Moll 1980, Matthews *et al.* 2001).

2.7.5 Threats to the vegetation

The persistence of the slow-growing and poorly dispersed vegetation types such as the *Licuati* forest and thicket are not only threatened by agricultural activities, clearance for firewood, timber and cattle grazing, but also by disturbances caused by animals (Sabogal 1992, Izidine *et al.* 2003) and fire. Human impact, characterised by an expanding infrastructure, cash-driven economy, increasing tourism activities and growing rural populations, are also threatening the survival of this rare and precious forest type (Murphy & Lugo 1986, Kirkwood 2000). Nearly half of the original *Licuati* forest and thicket vegetation has already been destroyed in KwaZulu-Natal (KwaZulu/Natal Nature Conservation Services 1997). The remaining patches of pristine *Licuati* vegetation are situated mostly within nature reserves and are thus quite well preserved (Low & Rebelo 1998; Matthews *et al.* 1999; Matthews & Page unpublished).

Overutilization of natural resources is of great concern globally. The sustainable utilization of natural resources is essential for the conservation and protection of pristine grassland, woodland and forest vegetation in southern Africa. Such dry deciduous forests are the third major regional forest formation in the tropics and appear to be the most threatened of all major lowland tropical forest types (Sabogal 1992). Kirkwood & Midgley (1999) stated that the *Licuati* forest covers a smaller surface area than any other vegetation type in South Africa. Therefore emphasis should, however, be placed on the unique, dry, tropical *Licuati* forest and thicket vegetation types endemic to the Maputaland Region.

Although fire plays an important role in the natural disturbance regime of the Maputaland vegetation, especially in the grassland and woodland vegetation types (Swaine 1992, Kirkwood 2001), the *Licuati* forest and thicket vegetation were found to be the exception since forest and thicket rarely burn (Izidine *et al.* 2003). The forest/grassland ecotone is easily distinguished as it forms an abrupt boundary between the forest patches and the adjacent vegetation types and often appears as a bare zone (Matthews *et al.* 2001). It has been postulated that the bare zone bordering the forest margins protects the *Licuati* forest and thicket from destructive fires by acting as a kind of natural firebreak (Izidine *et al.* 2003). *Licuati* thicket appears to be more fire tolerant than *Licuati* forest and evidence exists that once a forest patch is disturbed or destroyed by fire, little or no regeneration of the forest community occurs (Matthews *et al.* 2001, Izidine *et al.* 2003).

The grasslands of southern Africa are considered to be seriously threatened by agriculture, forestry, increasing urban and industrial development, as well as mining activities, all of which are human-related. Overgrazing and bush-encroachment are two other factors that also affect the persistence and survival of natural and undisturbed grasslands (Low & Rebelo 1998, Bredenkamp 1999).

Overgrazing, bush encroachment, industries and urbanization (Rutherford & Westfall 1994) threaten the savanna vegetation.

CHAPTER 3
AN OVERVIEW OF SOIL SEED BANK ECOLOGY

3.1 INTRODUCTION

The written evidence on the hidden life of seeds below the soil surface begins with the observations of Darwin in 1859: "I took in February three table-spoonfuls of mud from three different points beneath the water on the edge of a little pond; this mud when dry weighed 6 ¾ ounces; I kept it covered up in my study for six months, pulling up and counting each plant as it grew; the plants were of many kinds, and were altogether 537 in number; and yet the viscid mud was all contained in a breakfast cup" (Roberts 1981, Bigwood & Inouye 1988, Bakker *et al.* 1996b).

In the majority of habitats worldwide plant populations are represented not only by growing individuals aboveground, but also by a number of dormant propagules forming seed reserves in the soil (Harper 1977, Thompson 1987, Bigwood & Inouye 1988, Baskin & Baskin 1998). Soil seed banks can be defined as the store of viable as well as non-viable seeds buried in the soil which is composed in part of seeds produced in the area and partly of seeds brought in from elsewhere (Harper 1977, Roberts 1981, Warr *et al.* 1993, Bakker *et al.* 1996b). Seeds incorporated into the soil under a plant community represent not only the present vegetation growing in the area, but is also a memory of the past vegetation that occurred nearby (Harper 1977, Roberts 1981, Warr *et al.* 1993, Bakker *et al*. 1996b).

The seed bank dynamics of a plant population can be described as the continuous adding of seeds to the soil by the seed rain (Harper 1977, Milberg & Persson 1994, Hutchings & Booth 1996, Moles & Drake 1999), forming a dormant seed reservoir from which seeds are lost by germination, predation and death (Thompson & Grime 1979, Roberts 1981, Brown 1992, Bakker *et al*. 1996b) (Figure 3.1). Seed banks can be highly variable in characteristics such as size, species composition, seed longevity, seed viability, germination strategies and depth distribution of seeds in the soil (Warr *et al.* 1993; Bakker *et al*. 1996b). The soil seed bank of different vegetation types differs with regard to these characteristics.

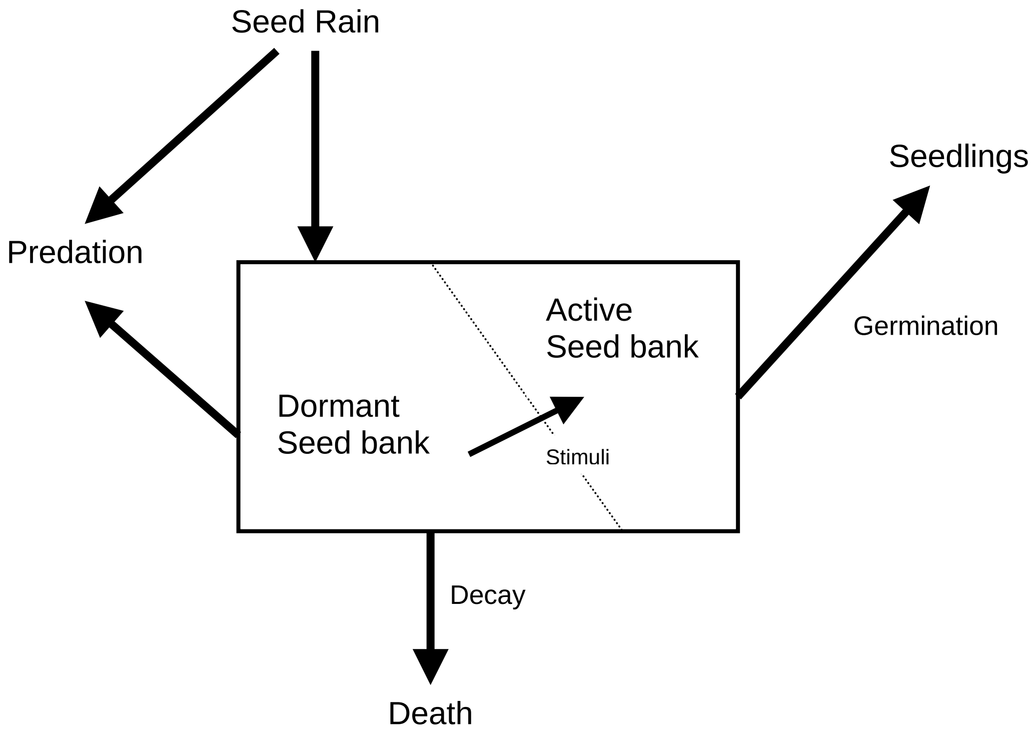

Figure 3.1. Schematic diagram showing the dynamics of a soil seed bank (after Harper 1977).

3.2 CHARACTERISTICS OF SOIL SEED BANKS

3.2.1 Seed rain

The seed bank is replenished by the seed rain, of which many seeds might have been dispersed from elsewhere (Milberg & Persson 1994, Moles & Drake 1999). Seed dispersal is of crucial importance to a plant community since the dispersal of offspring increases the fitness of the parent plant (Warr *et al.* 1993; Bakker *et al*. 1996b). Seeds that do not fall directly beneath the canopy of the parent plant, are transported to a new site of establishment by dispersal vectors such as wind, water, animals and human beings (Bakker *et al*. 1996b). The resulting spatial distribution of seeds around their maternal source is referred to as the seed shadow (Willson 1985). Successful seedling establishment after seed dispersal is influenced by the presence of natural enemies of seeds and seedlings such as pathogens, post-dispersal seed predators, parasites and herbivores; as well as sibling interactions and the probability of finding a physically suitable site for establishment (Fenner 1985, Thompson 1987).

3.2.2 Seed distribution in the seed bank

Although seeds in the soil seed bank are usually more abundant near the soil surface with numbers declining with increasing depth, each vegetation type has its own characteristic distribution of seeds in the soil profile (Poschlod & Jackel 1993, Warr *et al.* 1993, Bonis & Lepart 1994, Bakker *et al*. 1996b). Small seeds tend to be dispersed deeper into the soil than larger seeds which are more abundant in the top soil layers and litter debris on the soil surface. A number of small seeds are also buried by the activities of soil living organisms and other herbivores (Willson 1985, Warr *et al.* 1993, Bonis & Lepart 1994, Bakker *et al*. 1996b).

The depth to which seeds are distributed in the soil might have several implications for successful regeneration of a plant (Feast & Roberts 1973, Holmes & Moll 1990, Teketay & Anders 1995). Effective seed germination might be hindered due to large numbers of small seeds that are deeply buried (>50 mm) and lack the necessary resources to reach the soil surface where environmental conditions are more favourable (Harper 1977, Gross 1990). Another very important germination requirement with regard to soil depth is efficient light exposure. Light penetrates only a few millimetres into the top soil layers which means that light sensitive seeds will not germinate from greater soil depths (Brown 1992, Jankowska-Blaszczuk *et al.* 1998).

Seeds are not only vertically, but also horizontally distributed in the soil (Roberts 1981, Thompson 1986). The accumulation of seeds in depressions, which usually leads to a clustered horizontal seed distribution, is caused by animal activity, rounded seeds that might roll along the soil surface, wind and rainwater runoff (Bigwood & Inouye 1988, Matlack & Good 1990).

Knowledge about both spatial and temporal seed dispersal of a species, together with seed characteristics such as mass, size, shape, and viability, will determine the success of management in restoring and rehabilitating a target plant community (Henderson *et al.* 1988, Bakker *et al*. 1996b). Successful establishment not only depends on effective seed dispersal and available germination sites, but also on seed dispersing agents creating germination niches by disturbing vegetation structure and soil surface (Fenner 1985, Bakker *et al.* 1996b).

3.2.3 Seed bank size

According to Thompson (1987) and Warr *et al.* (1993) it is commonly assumed that the size of a seed bank is a reflection of its importance in the dynamics of the vegetation beneath which it occurs. Weeds of agricultural and horticultural lands tend to form large reserves of seeds in the soil (Thompson 1985), while tree species, especially those of advanced successional stages and stable environments, are poorly represented in the soil seed bank (Roberts 1981, 1986, Garwood 1989).

Long-lived seeds are characteristic of disturbed habitats and most are annuals and biennials. Large seeds such as those of mature tropical forest species are very short-lived, whereas smaller seeds tend to have a much greater longevity (Garwood 1989, Warr *et al.* 1993). The loss of seed viability is caused mainly by old age, fungal attack and pathogenic decomposition. Seed viability also declines as mutations and biochemical changes accumulate during the period of seed storage. Changes in the density of viable seeds present in the seed bank are influenced by changes in the environmental conditions such as temperature and water content of the soil (Harper 1977, Thompson & Grime 1979, Roberts 1981, Bakker *et al.* 1996b).

Seed longevity and seed viability are two very important factors influencing the re-establishment of natural vegetation in a specific area (Bakker *et al.* 1996b). Seed longevity is heritable and is therefore responsible for maintaining the genetic variability of soil seed banks (Simpson *et al.* 1989). Seed dormancy is also very important, because it can influence the germination rate and seedling establishment, as well as subsequent seedling survival (Baskin & Baskin 1998).

3.2.4 Species composition

Soil seed banks play a significant role in primary and secondary plant succession and to a large extent determine the composition and structure of existing vegetation. Soil seed banks are also very important in the restoration or re-establishment of native vegetation following disturbance (Van der Valk & Pederson 1989). However, it is important to note that there is extreme variation between species in the number of viable seeds that they leave in the soil. This phenomenon is responsible for the absence, in many instances, of any close relationship between the surface vegetation and the species composition of the soil seed bank (Harper 1977, Rico-Gray & García-Franco 1992, Hutchings & Booth 1996, Lunt 1997, Davies & Waite 1998, Edwards & Crawley 1999).

Soil seed banks in general are dominated by herbaceous species such as grasses, forbs and sedges. Woody species are very poorly represented in the soil seed reserve (Thompson & Grime 1979, Roberts 1981, 1986). Seed density in relation to species composition and vegetation is therefore highly variable (see section 3.4).

3.2.5 Classification of seed banks

Traditionally two types of seed bank strategies were recognized by Thompson and Grime (1979), (a) a transient seed bank where no seeds remain viable for longer than one year, and (b) a persistent seed bank where some seeds do remain viable for longer than one year. A modified version of seed bank classification was introduced by Bakker (in Bakker *et al*. 1996b) which basically defines three types: (a) transient – species with seeds which persist in the soil for less than one year; (b) short-term persistent – species with seeds which persist in the soil for more than one year, but less than five years; and (c) long-term persistent – species with seeds that persist in the soil for more than five years, also termed permanent (Roberts 1981, Bakker 1989). Seeds of pioneer and colonizing species are known to form persistent seed banks, that are usually associated with small, light, smooth and round seeds, whereas seeds of transient seed banks are characteristically large, heavy, flattened and/or elongated, with hairs or awns (Nakagoshi 1985, Thompson 1987, Bakker *et al*. 1996b).

3.3 THE ROLE OF THE SEED BANK IN RECRUITMENT AND ESTABLISHMENT

Vegetation types differ from one another in many aspects such as habitat, environmental conditions, disturbance regime, vegetation structure, species composition and reproductive strategies. Disturbance of natural vegetation by man-induced fire and animal impact or human invasion is of great concern to many conservationists and researchers in many countries, especially in those areas that are considered to be biological hotspots. Rare and endangered plant species, in particular, are in need of protection against extinction. Destruction of the vegetation by the mining and forestry industries also requires rehabilitation and restoration of plant communities after the disturbance (Van der Valk & Pederson 1989, Skoglund 1992, Warr *et al*. 1993).

For many years now it has been found that the soil seed bank of some vegetation types can be used to re-establish plant species lost from the original plant community (Harper 1977, Fenner 1985, Bakker *et al.* 1996b). The ability of seeds to remain viable in the soil seed bank for many years, enable the plant species to re-appear at the restoration site, to re-establish the previous vegetation to its original and natural state (Bakker *et al*. 1996b, Bakker & Berendse 1999). However, many vegetation types do not produce long-lived soil seed banks. In these cases restoration of the vegetation after disturbance can not be successfully accomplished from the soil contained seed bank.

Soil seed bank dynamics have to be thoroughly studied and understood, not only to interpret ecological processes, but also to assure successful management of vegetation restoration and rehabilitation.

3.4 FUNCTIONAL ECOLOGY OF SEED BANKS IN DIFFERENT VEGETATION TYPES

3.4.1 Introduction

A brief discussion of the main elements of seed banks characteristic of the three biomes occurring in the Tembe Elephant Park is presented.

3.4.2 Forest Biome

Investigations of soil seed banks beneath tropical and subtropical forests indicated that forest species, especially the dominant tree species characteristic of mature and stable forest vegetation, tend not to form large persistent seed banks (Walter 1971a, Skoglund 1992). The majority of forest seed banks are small, if present, and consist mainly of seeds of pioneer trees, shrubs and herbaceous species. The largest number of seeds is found in the litter layer and on the soil surface, with only a very small number of buried seeds forming a persistent seed bank, indicating long-term survival (Roberts 1981, Thompson 1987, Kirkwood 2000).

In contrast to most forest vegetation types where fleshy-fruited species dominate, many Sand Forest species tend to produce winged seeds, pods and exploding capsules rather than fleshy fruits (Kirkwood & Midgley 1999, Kirkwood 2000, Izidine *et al.* 2003), although Matthews *et al.* (2001) do not support this view. There are definite signs that Sand Forest has trouble regenerating due to the near absence of tree seedlings and saplings in the forest understorey and tree fall gaps (Kirkwood 2000, Matthews (Ezemvelo KwaZulu-Natal Wildlife, Tembe Elephant Park – PO Box 356, KwaNgwanase), Mucina *et al.* undated).

3.4.3 Grassland Biome

Grassland vegetation can form both transient and persistent soil seed banks. Several studies have shown that it is usually annual or biennial species that tend to form large persistent seed banks, whereas perennial grasses form smaller transient seed reserves (Roberts 1981, Thompson 1985, Warr *et al*. 1993, Kalamees & Zobel 1997, Davies & Waite 1998). Large numbers of small-seeded herbaceous species with little or no woody components (O'Connor & Pickett 1992, Milberg & Hansson 1993, Warr *et al.* 1993, Bekker *et al.* 1997, Lunt 1997, Peco *et al.* 1998) usually dominate grassland seed banks. When comparing species composition of a grassland soil seed bank and standing vegetation, seeds of most of the species that frequently occur in the standing vegetation are either absent from the seed bank, or if present, then only near the surface and in relatively small numbers (Coffin & Lauenroth 1989, Edwards & Crawley 1999, Kalamees & Zobel 2002). Thus, species richness of the seed bank flora is usually lower than the vegetation at all spatial scales (Morgan 1998).

3.4.4 Savanna Biome

Seed banks in the Savanna Biome display features of both the woody and the herbaceous component. Tree species characteristically have large seeds that tend to form transient seed banks, while the herbaceous layer species form persistent seed banks containing large numbers of small seeds (Walter 1971b, Thompson 1985, García-Núñez *et al.* 2001). Several studies have reported that many of the dominant tree species in the woodland canopy were poorly represented in the soil seed bank. Gaps in savanna or woodland vegetation caused by the fall of single trees were mostly filled by growth of surrounding trees, vegetative sprouts and germination of soil seed reserves (Roberts 1981, Thompson 1987). Seed distribution in the woodland soils is characterised by the high abundance of seeds in the litter and top soil layers.

CHAPTER 4
MATERIALS AND METHODS

4.1 SELECTION OF SAMPLE SITES

4.1.1 Spatial and temporal variation in seed bank size and species composition

Five different vegetation types were specifically selected for this study in the southwestern part of the Tembe Elephant Park, Maputaland. The selected vegetation types are the (a) *Licuati* forest, (b) *Licuati* thicket, (c) bare or sparsely vegetated zone bordering the forest edge, referred to as the forest/grassland ecotone, (d) grassland, and (e) woodland (see Chapter 2 for detailed descriptions).

The *Licuati* forest, with tree crown heights varying between 2 and 20 m, is characterised by diagnostic tree species such as *Balanites maughamii* (green thorn), *Cleistanthus schlechteri* (false tamboti), *Cola greenwayi* (hairy cola), *Dialium schlechteri* (Zulu pod-berry), *Drypetes arguta* (water ironplum), *Newtonia hildebrandtii* (Lebombo wattle) and *Ptaeroxylon obliquum* (sneezewood), with little undergrowth. Figure 4.1 illustrates typical *Licuati* forest or tall sand forest vegetation. *Licuati* thicket contains denser undergrowth, with diagnostic shrub species such as *Croton pseudopulchellus* (small lavender fever berry), *Hyperacanthus microphyllus* (Tonga thorn-gardenia), *Psydrax fragrantissima* (Tonga quar) and *Ptaeroxylon obliquum* (sneezewood) in the upper canopy layer. *Licuati* thicket is a near impenetrable short stature forest type with tree crown height not exceeding 10 m (Matthews *et al.* 2001, Izidine *et al.* 2003). Figure 4.2 illustrates a patch of *Licuati* thicket surrounded by grassland vegetation.

The ecotone between the *Licuati* vegetation and the grassland is represented by a bare or sparsely vegetated zone bordering the forest edge and is referred to as the forest/grassland ecotone. This narrow zone, illustrated in Figure 4.2, was sampled separately.

The specific grassland vegetation type that is characteristically associated with the *Licuati* forest and thicket vegetation patches was also sampled. This grassland vegetation type, illustrated in Figure 4.3, consists mainly of a herbaceous layer dominated by grass species such as *Andropogon schirensis* (stab grass), *Perotis* *patens* (cat's tail grass), *Pogonarthia squarrosa* (herringbone grass), and the forb *Tephrosia longipes* subsp. *longipes*.

The woodland that was sampled in the Tembe Elephant Park is characterised by the geoxylic-suffrutex *Salacia kraussii*, grasses such as *Aristida stipitata* subsp. *stipitata* (long-awned grass), *Themeda triandra* (red grass), *Panicum maximum* (guinea grass), and *Pogonarthia squarrosa* (herringbone grass); and the tree species *Acacia burkei* (black monkey thorn), *Afzelia quanzensis* (pod-mahogany), *Albizia adianthifolia* (flat-crown), *Garcinia livingstonei* (African mangosteen), *Strychnos madagascariensis* (black monkey orange), *Strychnos spinosa* and *Terminalia sericea* (silver clusterleaf) (Van Wyk 1996, Matthews *et al.* 2001, Izidine *et al.* 2003). The woodland vegetation is illustrated in Figure 4.4.

4.1.2 Depth distribution of seeds in the seed bank

The depth distribution of seeds in the soil was investigated in three different vegetation types within the study area. Soil samples for this experimental trial were taken from the selected sampling sites in the *Licuati* thicket, grassland and woodland vegetation types (see section 4.1.1 for description of sites).

4.1.3 Comparison of species richness between seed bank and standing vegetation

Species richness of the soil seed bank and the standing vegetation was compared along a transect of 150 m including four of the five selected vegetation types namely (a) *Licuati* thicket, (b) forest/grassland ecotone, (c) grassland and (d) woodland (see section 4.3). A site more towards the southwestern boundary of the Tembe Elephant Park was selected for the transect method, although the description of the abovementioned vegetation types still correlates with those sites selected in section 4.1.1.

4.2 SOIL SAMPLING

4.2.1 Spatial and temporal variation in seed bank size and species composition

Sixty soil samples were randomly collected at each of the five sites (5 x 60 samples) to determine the size and species composition of the soil seed bank. Soil sampling was done at three-month intervals starting January 2001 for a period of 12 months. Using a soil auger with a diameter of 57 mm, samples of the top soil layer (100 mm) were collected. The contents of the auger were emptied into a cotton soil sampling bag and the bags were neatly folded for transport to the University of Pretoria. The soil samples were stored at ambient temperatures in a dry place until needed.

Soil samples were collected in January, April, July and September 2001, which represent a summer, autumn, winter and spring soil seed bank respectively. All 60 soil samples that were collected at each site were examined by the seedling emergence method immediately after collection. The remaining soil of 15 randomly selected samples was used in the flotation studies, and the remaining soil of the other 45 of the 60 soil samples collected on one date were subjected to a re-examination in September 2001.

4.2.2 Depth distribution of seeds in the seed bank

Within each of the three vegetation types investigated, ten sampling sites were randomly selected and using the same soil auger, six separate soil samples at successive 50 mm depth intervals were taken at each site. Thus, a total depth of 300 mm per site was sampled giving 60 soil samples of different depths per vegetation type. These soil samples were all collected during July 2001 and brown paper bags were used to store the collected soil samples.

4.2.3 Comparison of species richness between seed bank and standing vegetation

Hundred and fifty soil samples were collected at 1 m intervals along the centre of the transect running from the *Licuati* thicket through the associated grassland into the woodland. Soil samples were collected and stored as described in section 4.2.1 until they were examined in September 2001 by the seedling emergence method.

4.3 TRANSECT METHOD

The comparison in terms of species composition between the soil seed bank and the standing vegetation was done along a transect which included the *Licuati* thicket, ecotone or zone surrounding the forest edge, grassland and woodland vegetation types. This transect of 150 m long and 5 m wide was sampled in July 2001. Hundred and fifty soil samples were collected at 1 m intervals along the centre of the transect (see section 4.2.3). The species composition of the standing vegetation was recorded for each 1 m interval over a width of 2.5 m at either side of the soil sample.

Comparisons between the soil seed bank and the standing vegetation were made in terms of species composition and species richness by using Sørensen's Similarity Index which reads $IS_s = [2C/(A+B)] \times 100$, where C is the number of species common to both the seed bank and standing vegetation, A is the number of species in the standing vegetation and B is the number of species in the seed bank (see Chapter 5.5) (Mueller-Dombois & Ellenberg 1974).

4.4 SEEDLING EMERGENCE METHOD

The seedling emergence method was used to determine the seed bank size and species composition of each soil sample. Small plastic pots (100 mm x 100 mm x 120 mm) were placed in a greenhouse, filled with finely ground quartz and topped with 100 cm^3 of soil from the collected sample (Figure 4.5). The remaining soil was stored again under ambient conditions for further examination. The pots were watered with tap water daily and received Arnon and Hoagland's complete nutrient solution (Hewitt 1952) fortnightly. Once a week all newly emerged seedlings were marked using toothpicks (Figure 4.6). Seedlings were identified as soon as possible and once identified removed from the pots to prevent contamination by self-seeding. Some seedlings were left to mature for later identification. Specimens were also collected for herbarium use.

Soil samples were examined immediately after collection and another 100 cm^3 of each of the remaining stored soil samples collected in January, April and July 2001 were re-examined in September 2001, when environmental conditions were thought to be most favourable for optimal seed germination. These duplicate samples were investigated in the same manner as described above. Note that the September 2001 sample collection was not duplicated.

The percentage correspondence in species composition of the five different seasonally-germinable seed banks was calculated by means of Jaccard's Similarity Index, which reads as follows: $IS_J = [C/(A+B+C)] \times 100$ where C is the number of species common to both the seed bank and standing vegetation, A is the number of species restricted to the standing vegetation, and B is the number of species restricted to the seed bank (Mueller-Dombois & Ellenberg 1974).

The H.G.W.J. Schweickerdt Herbarium (PRU), the National Herbarium (PRE), together with field guides (Bromilow 1995, Pooley 1997, Van Wyk & Malan 1997, Van Wyk & Van Wyk 1997, Pooley 1998, Van Oudtshoorn 1999, Van Wyk *et al.* 2000) and a species list compiled for the Tembe Elephant Park's vegetation (Matthews *et al*. 2001), were used to identify all emerged seedlings.

4.5 SEEDLING EMERGENCE RATE

Seedling emergence rate was determined by monitoring seedling emergence daily for six consecutive weeks during September 2000. Soil samples were taken from four selected vegetation types in the study area in the same manner as described in section 4.2. The vegetation types were (a) *Licuati* thicket, (b) forest/grassland ecotone, (c) grassland and (d) woodland. The seedling emergence method was used to obtain the daily number of emerged seedlings over a period of six weeks. Seedlings were treated in the same way as described in section 4.4.

4.6 FLOTATION

The flotation method was used to obtain a more accurate estimate of the seed bank size of the selected vegetation types. Fifteen of the 60 randomly collected soil samples at each site on each sampling date (see section 4.2.1) were selected for flotation studies. The flotation method was used especially because it is reported to give a high percentage recovery of all species present in the soil sample (Tsuyuzaki 1994), whereas the seedling emergence method usually underestimates the true size of the soil seed bank (Manders 1990). In contrast, the flotation method may overestimate the true size of the soil seed bank, because it gives an indication of viable, as well as non-viable seeds present in the soil sample (Brown 1992, Tsuyuzaki 1994). It is, however, a labour-intensive and time-consuming technique.

To separate the larger, easily visible seeds from the soil, 100 cm^3 soil from each soil sample was mechanically sieved using two different sizes of soil sieves (Endecotts Ltd, London, England); 1.4 mm and 2.0 mm. Using a Wild M3Z stereomicroscope (Heerbrugg, Switzerland) the seeds in the >1.4 mm fractions were collected and stored in glass polytops. The smaller seeds were separated from the soil particles by means of the flotation method (Chippendale & Milton 1934, Malone 1967, Janse van Rensburg 1982, Brown 1992, Tsuyuzaki 1994, Bàrberi *et al.* 1998).

The flotation method was used to separate the organic material in a soil sample from the inorganic soil particles by means of a saturated aqueous potassium carbonate (K_2CO_3) solution. After sieving, the <1.4 mm soil fractions from each sample was suspended in 200 ml of the saturated aqueous K_2CO_3 solution by vigorously stirring for one minute. Using a glass column that is 200 mm in length with a diameter of 30 mm (Figure 4.7), the soil suspension was left to stand vertically for approximately 10 minutes. The pellet, which consists mainly of soil particles, was drained into a conical flask through a small rubber tube attached to the bottom of the glass column. The organic remains were separated from the K_2CO_3 solution using a Buchner funnel and Whatman nr.1 filter paper. The residue on the filter paper was rinsed with distilled water and left in a petri dish at room temperature (27ºC) to dry. The samples were studied under a Wild M3Z stereomicroscope (Heerbrugg, Switzerland) and the seeds were separated from the organic fraction with a pinset. The total number of seeds was determined for each sample. Seed viability was assessed by applying mechanical pressure onto the seeds using a pinset. Seeds that resisted the mechanical pressure were regarded all viable (De Villiers *et al.* 1994).

The flotation method also has some shortcomings. First, seed viability might be affected by the chemical solution used in the flotation process. This is important if the viability or germinability of the recovered seeds is to be examined subsequently. Secondly, there is a possibility that seeds might remain in the soil pellet, which is eventually discarded. However, Janse van Rensburg (1982) is of the opinion that the probability of seed loss due to this cause is minimised if the experimental procedure is accurately performed. Thirdly, small and cryptically shaped or coloured seeds are not always easily distinguished from soil or organic particles (Manders 1990, Tsuyuzaki 1994, Ter Heerdt *et al.* 1996).

4.7 STATISTICAL ANALYSIS

The analysis of variance (ANOVA) in the Statistica computer package (Statistica v6, Statsoft, Tulsa) was used where appropriate results were analysed. Significant difference between means were determined by *post hoc* tests using Fischer's Least Significant Difference test at ∞=0.05 (Statistica v6, Statsoft, Tulsa).

CHAPTER 5
RESULTS AND DISCUSSION

5.1 INTRODUCTION

Five different vegetation types were selected in the Tembe Elephant Park, Maputaland to examine the soil seed bank in terms of size and species composition. This study focused on some important aspects of soil seed bank dynamics to obtain a better understanding of the functional ecology of the vegetation and to what extent the soil seed bank correlates with the aboveground vegetation. Seed bank studies included a (a) comparative study of two commonly used seed extracting techniques to determine seed density, (b) depth distribution of seeds in the soil seed bank, (c) spatial and temporal variation in seed bank size and species composition and (d) comparative study of the species richness of the soil seed bank and standing vegetation. The soil seed bank was investigated during 2001.

5.2 COMPARISON BETWEEN THE SEEDLING EMERGENCE METHOD AND FLOTATION METHOD

5.2.1 Introduction

The fate of seeds in the soil is very important since at least 95.0% of all potential plants die during the seed stage or as new seedlings (Simpson *et al.* 1989). Quantifying the soil seed bank of a specific vegetation type requires the employment of simple, but effective techniques that provide accurate and reliable estimates of seed densities, species composition and seed viability (Manders 1990, Brown 1992, Ter Heerdt *et al.* 1996). Such methods should have a high percentage recovery for seeds of all species, without injury, from a large volume of soil (Tsuyuzaki 1994).

This section presents a direct comparison of two commonly used techniques in estimating the size of the seed bank (number of seeds/m²) contained in the soils of five different vegetation types within the study area. The methods employed are the seedling emergence method (see section 4.4) and a physical separation method by means of sieving and flotation (see section 4.5). A detailed analysis of the spatial and temporal patterns in seed bank size obtained by the emergence method can be found in section 5.4. In this section the focus will be on the results obtained with the flotation method and how these trends differ from those of the emergence method.

5.2.2 Results

It is important to note that all the results obtained in this study are based on the assumption of one seed equals one seedling. A comparison of seed bank size, as was determined by both the seedling emergence and flotation methods, revealed that the flotation method detected significantly higher seed density than was obtained by the seedling emergence method ($p<0.001$; One-way ANOVA) (Figure 5.1a-e). The lowest seed density obtained by the seedling emergence method was an estimated number of 930 seeds/m² found in the *Licuati* thicket soils during July (Table 5.1). The *Licuati* forest seed bank produced the lowest seed numbers by means of flotation, an estimated 3 130 seeds/m² in September. The highest seed density estimated at 5 730 seeds/m² using the emergence method was obtained from the grassland seed bank in January. An estimated number of 39 530 seeds/m² was found to be the highest number of seeds obtained by the flotation method and was recorded in the woodland soils during July.

A main effects ANOVA (Statistica v6, Statsoft, Tulsa) done on the flotation method data indicated that vegetation type did not significantly ($p > 0.05$) affect the size of the seed bank, but that sampling time did have a significant effect ($p = 0.036$). In contrast, vegetation type significantly ($p = 0.002$) affected seed bank size in the emergence method, whereas sampling time was not significant ($p > 0.05$) for this method.

The sizes of the seed banks vary depending on sampling time (season) as well as method employed within each vegetation type (Figure 5.1a-e). For the flotation method the highest number of seeds/m² was found in soil samples collected during July in four of the five different vegetation types, namely the *Licuati* forest, forest/grassland ecotone, grassland and woodland vegetation (Figure 5.1a, c-e). The *Licuati* thicket seed bank, however, shows a gradual decline in size from January to September with the highest number of seeds/m² found in January (Figure 5.1b). The *Licuati* forest seed bank produced a very low seed density (≤ 5 000 seeds/m²) in January, April and September, but a very high number of seeds, exceeding 31 260 seeds/m², in July (Table 5.1, Figure 5.1a). The seed bank of the *Licuati* thicket vegetation produced fairly high seed densities (> 22 000 seeds/m²) in January, April and July, but in September seed numbers of only 8 000 seeds/m² were recorded (Figure 5.1b). Compared to the *Licuati* forest, the thicket vegetation yielded seed densities that were five to six-fold denser in April and January. However, the July seed bank of the forest vegetation was larger than that of the thicket vegetation.

The forest/grassland ecotone seed bank, however, varies from the *Licuati* thicket vegetation in that its soils contain the lowest number of seeds/m² in April (Figure 5.1c) and seed densities of > 22 000 seeds/m² were recorded in January, July and September. Seed densities of the grassland and woodland seed banks follow a similar pattern as the *Licuati* forest seed bank showing a gradual increase in seed numbers over time with seed density peaking in July. Seed densities then abruptly decline from July to September (Figure 5.1d & e).

Seed density obtained by the seedling emergence was calculated as a percentage of the density obtained by the flotation method to compare the methods employed (Table 5.1). The biggest difference in seed numbers was obtained from the *Licuati* forest seed bank in July, and the *Licuati* thicket soils in April and July. The highest percentage correspondence in seed numbers was found in the grassland soils in January and the *Licuati* forest seed bank in September, 78% and 68% respectively. In general, the largest discrepancy between the two methods was found for the *Licuati* thicket seed bank (8%) and the largest correspondence for the grassland seed bank (37%). On a sampling date basis, July sampling produced the largest differences between the density estimates by the two methods and January sampling the smallest difference.

5.2.3 Discussion

By comparing physical separation with the seedling emergence method, it was found that seed extraction by sieving and flotation generally produced higher seed densities than seedling emergence (Table 5.1). Several studies found that total estimates derived by physical separation are higher, as the seed bank includes viable as well as non-viable and predated seeds (Gross 1990, Manders 1990, Warr *et al.* 1993). Densities estimated by sieving and flotation may be overestimated, because distinction between viable and non-viable seeds is impossible without appropriate viability tests (Brown 1992, Ter Heerdt *et al.* 1996).

The seedling emergence method is found to be the more frequently used technique since it is simple, inexpensive and, in general, highly efficient (Malone 1967, Brown 1992, Warr *et al.* 1993, Ter Heerdt *et al.* 1996). This method, however, usually underestimates the true seed bank size as it gives an indication of only the viable and thus germinable fraction of the soil seed bank (Brown 1992). Although less labour-intensive than the flotation method, results are not obtained quickly because the soil samples should be kept under greenhouse conditions for a considerable time (Feast & Roberts 1973, Gross 1990). Furthermore, seeds differ greatly in germination requirements such as light, temperature, humidity and soil moisture, therefore is it not possible to provide optimal conditions for all species present in the soil seed bank. The emergence method thus requires continuous maintenance of proper greenhouse and soil conditions to insure maximum seed germination.

Consequently, an unknown number of viable seeds do not germinate because proper germination requirements have not been met, introducing error into the estimates of seed density. Other errors associated with seed dormancy and seedling mortality also arise from improper growth conditions in the greenhouse (Malone 1967, Brown 1992).

Researchers disagree about the adequate duration period of a germination treatment when using the emergence method, but Ter Heerdt *et al.* (1996) found that ninety-five per cent of all seedlings emerged within six weeks. Several other studies found that incubation periods of six weeks to three months were sufficient to detect the majority of seeds present in the soil (Thompson & Grime 1979, Roberts 1981). In general, there is little to be gained by keeping the samples for longer than six months. Warr *et al.* (1993) and Ter Heerdt *et al.* (1996) also suggested that seedlings should be removed as soon as they can be identified, because emerged seedlings can reduce germination due to shading.

Another advantage of the emergence method is that the identification of seedlings up to species level is much easier than to identify seeds (Manders 1990, Warr *et al.* 1993). These authors suggested that the seedling emergence method provides a more accurate estimate of the species composition of the soil seed bank, while more reliable estimates of the seed density (number of seeds/m^2) in the soil is obtained by physical separation. Seedling emergence enables the examination of large volumes of soil at once, but can be restricted by the availability of long-term usage of greenhouse space (Gross 1990, Brown 1992).

In contrast to the seedling emergence method, the flotation method is not as time-dependent, but more work-intensive. Data are obtained immediately after examination, although the experimental period depends on the amount of soil subjected to investigation (Manders 1990). The flotation method also allows only small amounts of soil to be examined at a time. The use of chemical solutions in the flotation method can be detrimental to the viability of seeds of some species making viability tests inaccurate (Malone 1967, Tsuyuzaki 1994). Final separation of seeds from the residue, that still contains soil particles and organic materials, is required by means of hand sorting under a binocular microscope (Ter Heerdt *et al.* 1996). A major drawback of the flotation method is the ability to recover large numbers of small seeds that cannot easily be identified (Bàrberi *et al.* 1998) and an extensive seed library is necessary if accuracy is required at the species level (Brown 1992). In general, physical separation techniques are much more sufficient in detecting large seeded species (Fay & Olson 1978, Warr *et al.* 1993).

Studies by Gross (1990), Warr *et al.* (1993) and Bàrberi (1998) showed that selecting appropriate sampling times is of great importance to interpreting seasonal variation in a soil seed bank. In this study the flotation method indicated that the optimum sampling time for seed bank studies is during the winter period (July), except for the *Licuati* thicket vegetation where the optimum sampling time was summer (January) (Figure 5.1a-e). Sampling time did not significantly affect the seed density estimates obtained by the seedling emergence method indicating that there was no season that clearly favoured optimal seed germination in all vegetation types. Favourable environmental conditions for seed germination of both *Licuati* forest and thicket seed bank species apparently occurred in spring (September) and summer (January). Seeds contained in the grassland and woodland soils, however, germinated fairly readily in autumn (April) and winter (July) (Table 5.1). Considerably lower seed densities were detected during September in these two vegetation types using the seedling emergence method. This observation is ascribed to the possibility that the sampling time of these soils in the field was after the first seasonal rainfall (Rainfall data for September 2001 – 22 mm, Sihangwane Weather Station, Tembe Elephant Park). Because optimal conditions for germination occur in mid spring, the seed bank would have lost many seeds to germination after the early rainfall. Similar observations were made by Warr *et al.* (1993).

Roberts (1981) and Warr *et al.* (1993) found that forest species tend to produce large seeds that form transient seed banks that are usually present only in the surface soil. Large numbers of seeds were recovered from the forest soils by means of mechanical sieving and the flotation method, whereas very small seed densities were detected by seedling emergence (Table 5.1). These findings agree with studies done by Manders (1990), who found that large, hard-coated seeds, normally produced by woody species, achieved low percentage germination, while the emergence method revealed the presence of small seeds, which might have escaped detection in the flotation method. In contrast to the *Licuati* thicket where high seed densities were recorded from January to July, the *Licuati* forest soils produced a large seed bank size only in July. These results suggest that seed shed in the thicket vegetation already commences late spring to early summer, whereas seed shed in the forest vegetation is restricted to late autumn and early winter. The concentration of a large seed density to a single sampling date for the *Licuati* forest vegetation highlights the transient nature of the seed bank and the short period for which seeds remain viable.

Species of grassland vegetation are known to produce large numbers of small seeds that form persistent seed banks rather than large seeds forming transient seed banks (Roberts 1981, Thompson 1987). This explains the fairly constant seed bank size of the grassland and forest/grassland ecotone with an increase in seed density during winter following seed fall in autumn (Figure 5.1c & d). The woodland seed bank corresponds with the latter two vegetation types in showing the same trend towards seed densities present in the soil over time, except that the woodland soil produced a much larger number of seeds/m² than the grassland and ecotone soils (Figure 5.1e).

For the entire data set, the seedling emergence method detected only 18% of the number of seeds found by the flotation method. The lowest correspondence between the two methods, regarding sampling time, was found for the July sampling (12%) (Table 5.1). This can probably be ascribed to the fact that conditions in July are highly unfavourable for the germination of most seeds. The sampling time yielding the highest correspondence between the methods was January (26%).

The vegetation type yielding the highest correspondence between the two methods was the grassland (37%) (Table 5.1), supporting Manders's (1990) findings that the emergence method is more successful with small seeds than with large seeds. The *Licuati* thicket produced the lowest correspondence between the two methods (8%), followed by the *Licuati* forest seed bank producing the second lowest correspondence (15%). The forest/grassland ecotone and woodland seed banks produced 21% and 18% correspondence respectively between the two methods.

5.2.4 Conclusion

This study was restricted to the estimation of seed bank size (number of seeds/m²) due to the great chance of error that can occur in determining species composition employing the flotation method. Possible errors associated with the flotation method are the lack of complete recovery of small seeded species and inaccurate seed identification. Thus, seeds were not identified and proper viability tests were not performed, because of the large numbers of seeds involved and the wide diversity of seed types.

Useful comparative data was obtained in this study by sampling the soils once every season during 2001. Variation in sampling time and seed bank size was found in all vegetation types involved, using both the seedling emergence and flotation methods. However, the effect of vegetation type on the size of the seed bank was significant only for the seedling emergence method and sampling time was significant only for the flotation method. In general, it was found that seed extraction by sieving and flotation generally produced higher seed densities than seedling emergence

Although each technique possesses its own relative advantages and disadvantages, both methods have the ability to detect differences, and thus neither one can be stated as being better than the other. The seedling emergence method, which gives an indication of the seasonally-germinable seed bank, will probably remain the favourite amongst researchers due to its lower labour requirements and relative ease of species identification. However, the flotation method opposed to seedling emergence determines the potentially germinable seed bank size. A combination of methods as used in this study, can draw on the strengths of both methods and improves the interpretation of the results and allows for a better understanding of the seed bank dynamics.

Brown (1992) stated that the selection of the appropriate method should be based on the available expertise, facilities, and the goal of the research project. Determining only the soil seed bank densities of selected vegetation types in the study area leaves ample opportunity for further investigation of species composition.

5.3 DEPTH DISTRIBUTION OF SEEDS IN SOILS OF SELECTED VEGETATION TYPES

5.3.1 Introduction

The dispersal of seeds is usually seen as an area phenomenon, but there is also a depth and a time dimension to dispersal. Seeds that land on a soil surface may either stay on the surface or are distributed down a soil profile (Harper 1977, Warr *et al.* 1993, Bakker *et al.* 1996a). Accumulation of seeds in soils to form a soil seed bank not only occurs vertically, but also horizontally forming clustered distributions in some locations (Thompson 1986, Bigwood & Inouye 1988). See Section 3.2.2 for a detailed description of seed distribution in soil seed banks.

The depth distribution of seeds in the soil seed bank of three selected vegetation types within the study area was determined. Soil samples at different depths from ten different sample sites were collected from the *Licuati* thicket, grassland and woodland vegetation types respectively. The size and species composition of the soil seed bank was determined using the seedling emergence method by counting and identifying the number of seedlings that emerged from each of the six levels of soil depth sampled at each site (see section 4.4).

5.3.2 Results

a) *Licuati Thicket*

In the *Licuati* thicket soils the greatest densities of seeds were found at depths of >50–100 mm and >100–150 mm, thereafter numbers declined with increasing depth (Figure 5.2a). Only approximately half of the number of seedlings that emerged from soil in the >50–100 mm and >100–150 mm depth zones were present in the topsoil layer (0–50 mm). A mean of 250 seedlings/m² emerged from this topsoil layer. Soil samples collected at a depth of >250–300 mm produced no seedlings. The total number of seedlings contained in the *Licuati* thicket seed bank up to a depth of 300 mm was 1 550 seedlings/m² (Table 5.2).

Ten plant taxa were identified in the *Licuati* thicket soil seed bank. Seedlings emerged included four grass species, two sedge species, fern species and three herbaceous species (Table 5.3). Only 12.5% of the total number of taxa that were found in the soil seed bank of all three investigated vegetation types was exclusive to the *Licuati* thicket vegetation (Table 5.2). However, these species, which are diagnostic to the Licuati thicket vegetation, represented 40% of the species recorded from this soil seed bank alone. The other species recorded from the *Licuati* thicket soil samples were also detected in the grassland and woodland seed banks. It was found that some species were more abundant near the soil surface and only a few reached deeper soil levels. Within the 0–50 mm soil layer of the *Licuati* thicket seed bank three species were found, whereas five species were recorded at depths of >50–100 mm and >100–150 mm respectively (Table 5.4).

b) *Grassland*

In the grassland soils it was clear that the highest density of seeds was found in the top 50 mm (Figure 5.2b). A mean number of 3 000 seedlings/m² emerged from soil samples collected up to a depth of 50 mm from the soil surface. Seedling numbers generally declined with increasing depth in the grassland soils. A total number of 7 950 seedlings/m² emerged from the grassland seed bank up to a depth of 300 mm (Table 5.2). Seedlings emerged from all depths sampled (Table 5.5).

Thirteen taxa in total were recorded from different soil depths in the grassland seed bank (Table 5.2). These included two grass species, three sedge species, six herbaceous species, pteridophytes and one woody species (Table 5.5). Two species, *Bulbostylis burchellii* and *Kohautia virgata*, were distributed across the entire sampling depth, with declining numbers with increasing depth.

It was found that 18.8% of the total number of species recorded in all three vegetation types occurred only in the grassland seed bank and were not detected in either the *Licuati* thicket or the woodland soils (Table 5.2). In contrast, 46.2% of species recorded from the grassland soils were diagnostic to this seed bank. The topsoil layer (0–50 mm) produced eight different species, while nine species were recorded at a depth of >50–100 mm. In contrast to the *Licuati* thicket seed bank, where no species were detected in the >250–300 mm depth zone, six species were recorded from this soil layer in the grassland seed bank (Table 5.4).

c) *Woodland*

The largest number of seedlings in woodland soils emerged from soils sampled from >50–100 mm, with a slightly smaller seed density in the top 50 mm soil layer (Figure 5.2c). Seed densities generally declined with increasing depth below 100 mm. Seeds germinated from all six levels of soil depth. A total number of 5 450 seedlings/m² emerged from the woodland soil seed bank (Table 5.2).

The highest species diversity was found in the woodland vegetation type with 21 different species recorded from the soil samples examined (Table 5.2). The species composition of the woodland seed bank included six grass species, two sedge species and thirteen herbaceous species (Table 5.6). No seedlings of tree or shrub species were recorded. A high percentage (43.8%) of the total number of species recorded from all three vegetation types were exclusive to the woodland seed bank and 66.7% of species recorded from the woodland soils were found to be diagnostic to this vegetation type (Table 5.2). It was also found that the number of species was more evenly distributed to a greater depth than was the case for the other vegetation types. Depths of 0 mm to 250 mm produced nine, fifteen, eleven, ten and ten species per soil layer respectively. Only three species were detected in the >250–300 mm depth zone (Table 5.4).

5.3.3 Discussion

a) *Licuati Thicket*

Forests, especially tropical and subtropical forests, tend to have no persistent soil seed bank, but are rather characterised by banks of persistent seedlings (Walter 1971a, Roberts 1981, Rico-Gray & García-Franco 1992, Baskin & Baskin 1998). The near absence of soil seed banks containing large densities of small, long-lived seeds underneath forest vegetation can be attributed to the fact that most of the shade-tolerant true forest species do not produce seeds that easily enter the buried seed bank (Harper 1977, Thompson 1985, Teketay & Anders 1995). Mature tropical forest species produce large, short-lived seeds that usually form a transient seed bank, where no seeds remain viable in the soil for longer than one year (Thompson & Grime 1979, Halpern *et al.* 1999, Guariguata 2000).

Most of the seeds present in the *Licuati* thicket soil samples were those of grass and other herbaceous species. Viable seeds of the dominant tree species in the forest canopy were absent from the soil seed bank (compare section 5.3.2a). Studies done by Roberts (1981), Rico-Gray & García-Franco (1992), Warr *et al*. (1993), Teketay & Anders (1995) and Crawford & Young (1998) in other forest vegetation confirm these trends. They proposed that the near absence of seeds of tree species in the forest soils is attributable to low seed inputs and rapid loss from the surface seed bank by seed predation and decomposition. A number of the species recorded from the forest seed bank were not represented in the standing vegetation and Roberts (1981) found that it might indicate long-term survival of seeds of some species of previous successional stages. In the *Licuati* thicket seed bank differences in species composition were found within the soil profile (Table 5.3). These differences reflect variation among species in seed rain, rates of incorporation and/or seed longevity (Garwood 1989, Warr *et al.* 1993).

Roberts (1981), Teketay & Anders (1995) and Olano *et al.* (2002) observed that in forest soils the highest seed numbers were found in the topsoil and the litter layer on the soil surface. Milberg (1995) proposed at least two possible factors that could be responsible for the seed abundance in the topsoil layers of forest seed banks. Firstly, forest species tend to produce seeds that are short-lived in the soil and might not have had time to reach greater soil depths and secondly, germination conditions such as light and temperature are likely to be more favourable near the soil surface.

In this study a smaller number of seeds germinated from the litter/topsoil layer (0–50 mm) than from the >50–100 mm and >100–150 mm depth zones (Figure 5.2a). Seed germination, seed predation and seed decay could be responsible for the low seedling density near the soil surface. The relatively higher seed density in the >50–100 mm and >100–150 mm depth zones can be ascribed to the incorporation of smaller seeds, produced by herbaceous species, into the loose-textured thicket soils by percolating rainwater and burrowing animals. The small seeds of pioneer tree and shrub species can also be transported deeper into the soil profile by the caching activities of birds and rodents (Bigwood & Inouye 1988, Garwood 1989). Seed densities in the *Licuati* thicket soils declined with increasing depth below 150 mm.

Roberts (1981) and Teketay & Anders (1995) observed the same trend in the topsoil layers of other tropical forest vegetation.

The probability of germination often decreases with depth, because germination requirements such as light, moisture and temperature are likely to be better near the soil surface than deeper down the soil profile (Brown 1992, Jankowska-Blaszczuk 1998). Baskin & Baskin (1998) found that small, light-sensitive seeds tend to be dispersed deeper into the soil profile. These seeds need efficient light exposure to germinate successfully and being buried to greater depths, where no light penetration occurs, consequently decrease their germination potential. Some seeds, however, can germinate in total darkness, but if they do not have the necessary resources to reach the soil surface, seedling emergence is negatively influenced.

Depth distribution of forest seeds depends not only on the age, size and shape of seeds, but also on the extent to which topsoil is mixed with deeper soil layers, together with the species' germination requirements and the effect of dormancy (Milberg 1995, Baskin & Baskin 1998). In general, a very small number of seeds germinate from forest soils, because seeds that are buried deeper down the soil profile need to be brought to the soil surface by dispersing factors such as burrowing animals and falling trees. Disturbances by these elements do not occur that often in natural forests, and if so, only a fragment of the entire population is brought from various depths to the soil surface. Thus, most of the soil seed bank dies and decays *in situ* (Harper 1977, Roberts 1981, Garwood 1989, Milberg 1995).

The small number of species recorded is an indication of a very low species diversity of the thicket soil seed bank. The relatively small number of seedlings that emerged from the soil samples also indicates a fairly small soil seed bank in terms of seed densities. It was also found that the majority of seedlings emerged from the upper soil layers. These findings support Warr *et al.* (1993) who concluded that seed bank density and species richness decrease with successional maturity.

b) *Grassland*

Grassland vegetation is mainly characterised by grasses, forbs and species of rushes and sedges (Roberts 1981, Thompson 1985). Grassland species are both annual and perennial in their reproduction strategies and can produce persistent and transient seed banks (Harper 1977, Hutchings & Booth 1996). In general, annual or biennial species produce large numbers of small seeds forming persistent seed banks, whereas perennial species produce smaller numbers of seeds that remain viable in the grassland soil seed bank for shorter periods (Thompson & Grime 1979, Henderson *et al.* 1988, Kalamees & Zobel 2002).

Grasses, mostly annual species make the greatest contribution to the soil seed bank of grassland vegetation, and most of them occur near the soil surface (Thompson 1985). Seeds of most grassland species are short-lived in the soil and more abundant near the soil surface, but some species are distributed over larger sampled depths (Simpson *et al.* 1989, Warr *et al.* 1993). The large number of seedlings that emerged from the topsoil layers (0–50 mm) and the gradual decline with increasing depth in this study supports the observations of Roberts (1981), Holmes & Moll (1990) and Bonis & Lepart (1994). Seedlings emerged from all depths sampled indicating the presence of seeds in the soil profile as deep as 300 mm.

In this study it was found that grassland produced the largest seed bank in terms of seed density, although the species diversity was relatively low. Roberts (1981) suggested that the species composition of mature grassland seed banks should be of greater significance than the total number of seeds present in the soil profile. According to Harper (1977) areas dominated by perennial grasses tend to have quite small seed banks (280–2 450 seeds/m^2), which might lead us to the conclusion that the grassland vegetation we sampled in our study could be either dominated by annual and/or biennial species or composed of species that were introduced to this grassland from adjacent plant communities by several dispersal agents (Figure 5.2b). This is possible due to the presence of species in the grassland seed bank that are not represented in the vegetation (Edwards & Crawley 1999, Kalamees & Zobel 2002) (compare section 5.3.2b).

Harper (1977), Roberts (1981), Warr *et al*. (1993), Kalamees & Zobel (1997) and Jankowska-Blaszczuk *et al.* (1998) observed the degree of correlation between the species composition of the seed bank and that of the associated vegetation type. They found that there is generally very little correspondence between the species present in the soil seed bank and the standing vegetation (see section 5.5 for further comparisons).

c) *Woodland*

Woodland soils, as the *Licuati* thicket soils, are also characterised by the accumulation of a litter layer on the soil surface in which a large number of seeds can be found (Roberts 1981, O'Connor & Pickett 1992). This litter layer did, however, not contain the highest seed density in this study. The largest number of seeds was found in the >50–100 mm topsoil layer (Figure 5.2c). Seeds were found to all depths sampled and, in general, seed density declined with increasing depth below 100 mm.

The woodland seed bank showed the highest species diversity compared with the other two vegetation types, although the seed bank size, in terms of number of seedlings emerged, was smaller than the grassland seed bank. Woodland vegetation tends to have few species that produce long-term persistent seed banks since the majority of species are woody (Thompson 1985). The size of the woodland seed bank is therefore intermediate between that of the *Licuati* thicket and grassland vegetation. It was also found that the seeds of herbaceous species, especially weedy species, dominated the woodland seed bank. Roberts (1981), Thompson (1985) and Warr *et al.* (1993) observed a similar trend in various other woodland seed banks. They found that the greatest numbers of seeds present in the soil beneath woodland vegetation were those of species characteristic of more open habitats subjected to frequent disturbances. This implies that the seeds that germinated from the woodland soils in this study might be either those of species introduced to the woodland vegetation by wind or animal dispersal or represent species derived from vegetation present in the area in previous years.

An almost uniform distribution of species with depth in the woodland seed bank could be an indication of exposure to disturbances more frequently than is the case with *Licuati* thicket and grassland soils. Garwood (1989) and Warr *et al.* (1993) also observed this distribution pattern of species in woodland soils.

5.3.4 Conclusion

The grassland seed bank yielded the highest numbers of seedlings, thus representing the largest seed bank and the *Licuati* thicket vegetation the smallest. In general, the largest number of species in the soil seed bank was found at a depth of >50–100 mm. Five, nine and fifteen species were recorded from this depth zone in the soil profile of the *Licuati* thicket, grassland and woodland vegetation types respectively.

The size of the seed bank is correlated with the vegetation structure of these three vegetation types. *Licuati* thicket vegetation is characterised mainly by trees with very little undergrowth and the tree species generally have relatively small seed banks. Grassland vegetation consists mainly of herbaceous species, which produce large numbers of small dormant seeds to build up a large seed bank. Woodland vegetation is composed in both a tree or shrub layer and a herbaceous layer (Rutherford & Westfall 1994), therefore the intermediate seed bank size.

In this study it was found that seeds were more concentrated in the upper soil layers than at deeper soil depths in all three vegetation types, although to a lesser extent in *Licuati* thicket than in grassland or woodland. Seed predation, decomposition, unfavourable germination conditions and the possible effect of dormancy could be responsible for the smaller species richness in the *Licuati* thicket seed bank. Seeds, however, were distributed down the soil profile in larger numbers in the grassland and woodland vegetation than was the case in the *Licuati* thicket vegetation.

5.4 SPATIAL AND TEMPORAL VARIATION IN SIZE AND SPECIES COMPOSITION OF THE SOIL SEED BANK OF SELECTED VEGETATION TYPES

5.4.1 Introduction

Soil seed banks are portrayed as the collection of viable and non-viable seeds in the soil primarily produced by the vegetation under which it occurs (Harper 1977, Roberts 1981, Bigwood & Inouye 1988). Thus, a soil seed bank in a defined area represents a vast pool of regenerative potential, serves as an indicator of primary and secondary plant succession and plays a very important role in restoration ecology and vegetation establishment after disturbance (Warr *et al*. 1993, Bakker *et al.* 1996b)

A soil seed bank is not a stationary entity because of continuous exposure to biological and environmental changes (see Chapter 3 for detailed description). Investigations of soil seed bank dynamics revealed that seed density in the soil and species composition of the seed bank flora constantly vary in space and time (Thompson & Grime 1979, Roberts 1986, Milberg & Hansson 1993, Crawford & Young 1998).

Presented here are the results of a study carried out during the entire year of 2001, within five different vegetation types selected in the Tembe Elephant Park, Maputaland. An analysis of the variation in seed bank size over a 12-month period and a general description of the corresponding species composition of each individual seed bank is provided. Seedling emergence rates were also investigated. The complete methodology regarding this study is discussed in Chapter 4.

5.4.2 Results

(a) Seed bank size

The seedling emergence method was used to provide an indication of the viable seed numbers present in the respective soil seed banks. A total of 6 067 seedlings emerged from the soil samples during the entire germination trial period. Seed density (mean number of seeds/m²) per sampling date for each vegetation type was determined by using the following calculation: (total number of seedlings emerged)/(number of samples) x 1000. The quantitative analysis of the seed bank size showed great seasonal variation among the different vegetation types (Figures 5.3a-e). The figures show the mean seed densities as obtained from soils collected in each of the five vegetation types examined directly after collection once every season, as well as the mean seed numbers for the summer (January), autumn (April) and winter (July) seed banks when re-examined in spring (September). Values obtained when samples were examined directly after collection are referred to as the seasonally-germinable seed bank, whereas those obtained with the re-examination in spring are referred to as the short term persistent seed bank.

On average the *Licuati* forest and thicket soils clearly produced the smallest seed banks (Figures 5.3a–b) when compared to the other three vegetation types, namely forest/grassland ecotone, grassland and woodland (Figures 5.3c–e). Mean seed densities for the *Licuati* vegetation ranged from 500 to 3 200 seeds/m². Both the *Licuati* forest and thicket soil seed banks showed a similar trend in seasonal variation in that they had the smallest seed numbers present in the soil during autumn, gradually increasing towards spring and reaching optimal seed densities in spring or summer. Even when the summer, autumn and winter seed bank sizes were examined in spring, which would theoretically implicate more favourable environmental conditions for optimal seed germination, the same trend in seasonal variation was observed. It was, however, found that direct examination of seed densities of the summer, autumn and winter seed banks generally produced larger seed numbers than the duplicate analysis in spring. Another interesting observation regarding the soils underneath the *Licuati* vegetation is that the *Licuati* thicket produced a larger seed bank in summer than the *Licuati* forest.

Temporal variation in soil seed bank size (mean number of seeds/m²) was also found in the ecotone, grassland and woodland vegetation types (Figures 5.3c–e). Quantitative analysis of the spatial variation across vegetation types in soil seed densities showed that the ecotone and grassland soils on average tend to produce larger seed numbers than the woodland soils. Mean seed densities for these three vegetation types ranged from 1 733 to 6 467 seeds/m². Seasonal variation was clearly observed in all three these vegetation types, although to a lesser extent in the ecotone vegetation. The seasonally-germinable ecotone seed bank size was generally found to be quite similar throughout the year producing its largest seed reserves in spring. The largest number of seeds recorded from the seasonally-germinable grassland soil was found in summer, producing the smallest seed densities in spring. In contrast to the previous two observations, the largest seasonally-germinable seed bank in the woodland soils was present during the winter season. As with the grassland seed bank, the smallest seed densities in the woodland soils were also found in spring.

As was observed in the *Licuati* forest and thicket seed banks, it was found that the direct examination of seed densities of the summer, autumn and winter seed banks from the ecotone, grassland and woodland soils, generally produced larger seed numbers than the duplicate analysis in spring. The persistent fraction of the seed bank of grassland soils remained remarkably constant throughout the year.

(b) Species composition

Both spatial and temporal variation in the species composition of the soil seed bank occurred in the Tembe Elephant Park (Table 5.7–5.11). Fifty-two genera and 83 taxa were identified in the soil samples, together with some unknown species. Seed density (mean number of seeds/m²) was determined using the equation: (total number of seedlings emerged per species)/(total number of samples) x 1000. Note that these calculations were done on species level and not for the entire vegetation type as was the case in 5.4.2. Species frequency or percentage abundance per species was calculated as follows: (number of seedlings emerged per species)/(total number of seedlings emerged from entire sample) x 100.

The seed bank flora of the *Licuati* forest and thicket vegetation types differed greatly from those of the forest/grassland ecotone, grassland and woodland seed banks both in species composition and species richness. Thirty-four taxa comprising of nine grass, four sedge, and 21 herb and forb species were recorded from the *Licuati* forest seed bank (Table 5.7). The *Licuati* thicket soils produced 26 species including nine grass, four sedge and 13 other herbaceous species (Table 5.8). Diagnostic species of the *Licuati* forest and thicket seed banks were *Crassula cf expansa, Cyperus dubius, Eragrostis cf moggii, Leptochloa cf uniflora* and *Panicum laticonum*.

Seed densities in the *Licuati* forest and thicket seed banks ranged from 16.7 to 2 116.7 seeds/m² for individual species at a particular sampling time.

Floristic composition of the ecotone soil seed bank consisted of 46 species including fifteen grass, six sedge and 25 herb and forb species (Table 5.9). The seed bank flora of the ecotone vegetation type was found to be dominated by the grass species *Perotis patens* (cat's tail grass) constituting 58.4% of the total number of seedlings. Other prominent species included *Bulbostylis burchellii, Bulbostylis cf hispidula, Cyperus chersinus, Kohautia virgata, Phyllanthus cf parvulus* and *Setaria sphacelata* var*. sphacelata*. Seed densities in the ecotone seed banks ranged from 16.7 to 2 033.3 seeds/m² among individual species over the experimental period.

Thirty-eight taxa comprising of fourteen grass, five sedge and 19 herb and forb species were recorded from the grassland soils (Table 5.10). Grasses primarily dominated the herbaceous layer, which characterises the floristic structure of the grassland vegetation type. Prominent species included *Bulbostylis burchellii, Bulbostylis cf hispidula, Conostomium natalense, Digitaria eriantha, Eragrostis ciliaris, Kohautia virgata, Perotis patens, Pogonarthia squarrosa* and *Setaria sphacelata* var. *sphacelata.* Seed densities in the grassland seed banks ranged from 16.7 to 2 033.3 seeds/m² among individual species over the experimental period.

In the woodland soil seed bank the emergence of 61 species including 20 grass, seven sedge and 34 herbaceous species was recorded (Table 5.11). Prominent grasses obtained from the soil samples were *Aristida stipitata* var. *stipitata, Brachiaria chusqueoides, Digitaria eriantha, Eragrostis ciliaris, Panicum maximum, Perotis patens, Pogonarthia squarrosa* and *Setaria verticillata.* Other prominent herbaceous species recorded from the woodland seed bank soils were *Achyranthus aspera, Bulbostylis cf hispidula, Cyperus chersinus, Justicia flava, Kohautia virgata, Persicaria cf serrulata* and *Phyllanthus cf parvulus.* Seed densities in the woodland seed banks ranged from 16.7 to 1 683.3 seeds/m² among individual species over the experimental period.

Similarities in species composition of the soil seed banks were also observed since the distribution patterns of some exotic therophytes extended throughout all the selected vegetation types. Species such as *Conyza albida, Gnaphalium pensylvanicum, Hypochaeris radicata, Oxalis cf semiloba, Pseudognaphalium luteo-album* and *Sonchus cf asper* were found to occur in relatively large densities in all the selected seed banks.

A comparative analysis of the seasonal variation in species richness between the soil seed banks of the respective vegetation types revealed variability throughout the entire examination period. Generally the *Licuati* forest and thicket seed banks were observed to produce the smallest species richness (number of species) per sampling time, especially when collected in winter and examined in spring, with only eight and seven species emerging from the soil samples respectively (Table 5.12). It was found that the largest numbers of species consistently emerged from the woodland seed bank. With 35 species recorded from the spring soil seed bank, woodland soils were found to contain the highest species richness in comparison to the forest, ecotone and grassland soils. Furthermore, the re-examination of soil samples of the summer, autumn and winter collections in spring produced species numbers either the same or less than the direct examinations.

The percentage correspondence in species composition of the seasonally-germinable seed banks of the five vegetation types was calculated by means of Jaccard's Similarity Index ($IS_J = [C/(A+B+C)] \times 100$) (see section 4.4). Generally, it was found that the largest percentage correspondence in species composition occurred between the summer and autumn seed banks (Table 5.13 a–e). Both the *Licuati* thicket and woodland vegetation types showed the largest percentage correspondence in species composition between the summer and autumn seed banks with 67% and 61% respectively (Table 5.13b & e). The lowest percentages correspondence in the species composition of the seasonally-germinable seed banks were found in the *Licuati* forest vegetation (Table 5.13a). Although species richness does not differ much in terms of seasonal variation and examination time, the correspondence in species composition is fairly low.

Spatial variation occurred in the species composition of the different soil seed banks when the selected vegetation types were compared to one another (Table 5.14). The *Licuati* forest and thicket, as well as the forest/grassland ecotone and grassland seed bank floras were found highly correlated, especially with regards to percentage correspondence in species composition (62% and 58% respectively). There was a relatively low 29% correspondence between the *Licuati* forest and the forest/grassland ecotone (Table 5.14).

(c) Seedling emergence rate

Seedling emergence rate was recorded in four selected vegetation types within the study area (Figure 5.4). Seedling emergence rate was observed over a period of six weeks after starting to water the soil samples (see section 4.5). The largest number of seedlings emerged from the forest/grassland ecotone, grassland and woodland soils within the first three weeks of examination. Very little seed germination was found to occur in the *Licuati* thicket soils during the first three weeks.

Seed germination rate in the woodland soils increased dramatically during the first two weeks, then gradually decreased from the third week on until the end of the examination period. Seedling emergence from the forest/grassland ecotone soils initially showed a more constant rate and dropped slowly from the third week onwards. In grassland soils seedling emergence remained relatively high until the fourth week. A slight increase in seedling numbers emerging from the grassland soils was observed from about day 14 to day 21, with an abrupt decrease in the seedling emergence rate during the last two weeks of examination.

Seed germination and thus seedling emergence from the *Licuati* thicket soils only started after three weeks of examining the collected soil samples. In contrast to the germination dynamics observed in the other vegetation types, seedling emergence from the *Licuati* thicket soils continued to increase gradually until the sixth week.

5.4.3 Discussion

(a) Seed bank size

Several studies confirmed that forest seed banks are relatively small to almost non-existent in both its size (number of seeds/m²) and species composition (Warr *et al*. 1993, Crawford & Young 1998). Mature dry tropical forest flora was found to produce very low seed densities and should there be higher seed numbers present in soils underlying dry forest vegetation, it could be ascribed to the abundant seed rain typical of pioneer species characteristic of early successional stages (Matlack & Good 1990, Alvarez-Buylla & García-Barrios 1991, Rico-Gray & García-Franco 1992, Falińska 1998, Jankowska-Blaszczuk *et al*. 1998, Arévalo & Fernández-Palacios 2000, Guariguata 2000). Examples of mean seed densities obtained in other forest seed banks studies by the seedling emergence method included 265–2 910 seeds/m² (Matlack & Good 1990), 203–5 613 seeds/m² (Brown 1992), 330–3 437 seeds/m² (Jankowska-Blaszczuk & Grubb 1997), 156–4 148 seeds/m² (Falińska 1998), 610–7 009 seeds/m² (Halpern *et al.* 1999) and 137–6 920 seeds/m² (Olano *et al*. 2002).

Data obtained from *Licuati* forest and thicket soils collected in the study area correlated well with these findings in that they produced the smallest seed banks in terms of seed density (500 to 3 200 seeds/m²). It should, however, be noted that these values obtained with the seedling emergence method may have greatly underestimated the true size of the seed bank. The observation that *Licuati* thicket vegetation produced a larger soil seed bank than the *Licuati* forest in summer, could be explained by possible differences in the floristic composition, reproduction strategies, timing of seed fall, seed germination requirements and seed dispersal efficiency between these two vegetation types.

The forest/grassland ecotone and grassland soils were found to produce the largest seed banks almost all year around in comparison to the forest and woodland soils, implicating that seasonal variation was of lesser significance. Mean seed density varied between 2 667 to 5 5667 seeds/m². The same trend in temporal variation was observed in grasslands studied by Coffin & Lauenroth (1989), Milberg & Hansson (1993) and Kalamees & Zobel (1997) who found seed densities of 122–2 748 seeds/m², 2 580–10 060 seeds/m² and 1 421–2 568 seeds/m², respectively. Seed bank studies of South African grasslands by O'Connor & Pickett (1992) and Adams (1996) found mean seed densities varying between 300 to 10 000 seeds/m².

The woodland seed bank differed from the forest/grassland ecotone and grassland seed banks in that they produced distinctly larger seed numbers in winter with dramatically reduced seed densities observed in spring. Mean seed density varied between 1 734 to 6 467 seeds/m². Dougall & Dodd (1997) and García-Núñez *et al.*

(2001) found similar results in their studies of neotropical savanna vegetation with mean seed densities of 897–9 100 seeds/m². The relatively smaller seed densities recorded from both the grassland and woodland soils in spring might be the consequence of increased seed losses from the winter seed bank through predation and germination induced due to early rainfall in September (rainfall data for September 2001 – 22 mm, Sihangwane Weather Station, Tembe Elephant Park) (Thompson & Grime 1979).

To conclude, when analysing soil samples to determine estimated seed bank size, both spatial and temporal variation in seed densities was observed.

(b) Species composition

Both spatial and temporal variability in species composition of the selected soil seed banks was observed. Each soil seed bank showed a tendency towards a characteristic species composition, especially the *Licuati* forest and thicket seed banks. Dry tropical forest types, such as the *Licuati* forest and *Licuati* thicket, are generally characterised by high species richness in the standing vegetation (Walter 1971a, Murphy & Lugo 1986, Swaine 1992). However, Roberts (1981), Thompson (1985) and Skoglund (1992) found tropical forest seed banks to be very small and almost non-existent. They also found that a large portion of the viable seeds that do occur in forest soils, are mostly pioneer species typical of early successional stages. Similar studies done by Bigwood & Inouye (1988), Rico-Gray & García-Franco (1992) and Jankowska-Blaszczuk *et al.* (1998) confirmed these findings. Analysis of the floristic composition of the *Licuati* forest and thicket soils found that the soil seed bank was composed primarily of herbaceous annuals and short-lived perennial species supporting the evidence from other studies of dry tropical forests.

Dry tropical woodland or savanna is characterised by the coexistence of two contrasting life forms, namely trees and grasses (Walter 1971b, García-Núñez *et al.* 2001). Woodland vegetation in the Tembe Elephant Park is also characterised by an upper tree layer and a prominent herbaceous or grass layer (Matthews *et al.* 2001). The woodland soils examined in this study clearly produced the highest number of species making the woodland seed bank flora exceptionally species rich. Interesting though was to find that the woodland soils produced the highest species richness from the smallest seed densities as was observed from the spring seed bank data. Despite the high level of species richness, very few woody species were recorded from the soil seed bank. In general, seasonal variation in species composition of soil seed banks was found to be of more significance to the dynamics of the seed bank than the spatial variability. Comparative seed bank studies by Thompson & Grime (1979), Roberts (1986) and Coffin & Lauenroth (1989) positively confirmed the latter findings.

Correspondence in species composition with regard to the temporal component of this study revealed that the largest percentage correspondence was found to exist between the summer and autumn seed banks (Table 5.13). It was thus found that species composition within a specific vegetation type varied greatly from season to season. Thompson & Grime (1979), Roberts (1986) and Morgan (1998) drew similar conclusions.

The *Licuati* forest and thicket, as well as the forest/grassland ecotone and grassland seed bank floras were found highly correlated, especially with regards to percentage correspondence in species composition (62% and 58% respectively) (Table 5.14). The relatively low 29% correspondence that occurred between the *Licuati* forest and the forest/grassland ecotone stresses the abrupt difference in species composition when comparing the edge surrounding vegetation with that of the forest patches.

To conclude, grasses (Family Poaceae) and sedges (Family Cyperaceae) were found to comprise more than 40% of the seed bank flora that emerged from the soil samples. The remaining species consisted mostly of annual and perennial herbs or forbs, with hardly any evidence of woody species. *Licuati* forest and thicket seed banks, when compared to that of the forest/grassland ecotone, grassland and woodland vegetation types, were found to have the lowest species richness. The seed bank floras differed greatly from one another in terms of sampling time.

(c) Seedling emergence rate

Several factors, either biologically or environmentally, can influence the rate of germination and seedling emergence from the soil seed bank. Seedling emergence rate is affected by seed density and distribution, seed viability, seed longevity and seed dormancy (Harper 1977, Roberts 1981, Jankowska-Blaszczuk & Grubb 1997, Baskin & Baskin 1998). An incubation period of six weeks was decided upon since Thompson & Grime (1979) and Ter Heerdt *et al.* (1996) reported that six weeks might be sufficient to detect the majority of species present in the soil. Longer germination periods of four months (Brown 1992) and two years (Roberts 1981) have also been suggested.

The striking and most important observation of this experiment appeared to be the exceptionally slow germination rate obtained from the *Licuati* thicket soils. Seed dormancy and species-specific germination requirements might be an obvious explanation for this inhibitory effect on the seedling emergence rate from the *Licuati* thicket seed bank, but another interesting phenomenon could possibly unravel the mystery. The soil conditions and hydraulic characteristics of the aeolian sands that underlie the *Licuati* forest and thicket vegetation types have recently been investigated (Fourie *et al.* 2002). The soil characteristics of these soils could possibly influence the vegetation and especially the germination rate of the seed bank flora. Unidentified organic, water repellent substances were found to exist in these sandy soils. These substances were found to be present in small quantities in the forest/grassland ecotone, but absent from both the grassland and woodland vegetation types. The high content of the water repellent substances in the forest soils prevent the seeds in the forest soils from imbibing water and germination is inhibited. The water repellent substances are apparently degraded with time and after approximately three weeks the water repellent nature of the soils is lost and germination can commence.

To conclude, the results obtained from this study suggest that the initial inhibition of seedling emergence, which was observed in the *Licuati* thicket soils, was apparently caused by these organic, water repellent substances rather than seed dormancy or species-specific germination requirements.

5.5 COMPARISON OF SPECIES COMPOSITION AND SPECIES RICHNESS BETWEEN THE SOIL SEED BANK AND STANDING VEGETATION

5.5.1 Introduction

To understand the dynamics of the standing vegetation in any given area, one should include the analysis of the buried soil seed bank (Arévalo & Fernández-Palacios 2000). Several studies found that soil seed banks might contain more species of previous successional stages than the current vegetation, since the seed bank contains species not only present in the aboveground flora, but also several not found in the immediate and nearby surroundings (Roberts 1981, Thompson 1987, Brown 1992).

The importance of soil seed banks as a source of regenerative potential and its significant role in restoring disturbed species-rich vegetation (Teketay & Anderson 1995, Halpern *et al*. 1999) and maintaining floristic diversity (Lunt 1997), are some of the reasons that have motivated researchers to compare the composition of the surface vegetation with seed reserves hidden in the soil (Kalamees & Zobel 1997, Peco *et al*. 1998).

In this study the species richness of the soil seed bank was compared to that of the standing vegetation by recording the number of species present in the seed bank and aboveground flora in a transect from the *Licuati* thicket, through grassland to woodland (see section 4.3).

5.5.2 Results and Discussion

A total number of 83 taxa from different plant life forms were recorded along the transect. Sixty species, mostly woody, were recorded in the aboveground vegetation (Table 5.15), whereas 28 species germinated from the soil seed bank (Table 5.16). Only five species, all herbaceous, were found in both the seed bank and standing vegetation. Large numbers of widespread herb, grass and sedge species, of which most are weedy therophytes, dominated the floristic composition of the soil seed bank. Perennial native species were almost entirely absent from the seed bank soils and no evidence of tree species was found. These findings correlate with similar studies done by Roberts (1981), Kalamees & Zobel (1997), Lunt (1997), Davies &

Waite (1998) and Morgan (1998). Many studies have also indicated that the floristic composition of soil seed banks is usually dominated by herbaceous species typical of early successional and disturbed habitats, and which are generally absent from the mature aboveground vegetation (Roberts 1981, Thompson 1987, Matlack & Good 1990, Brown 1992). Kalamees & Zobel (2002) stated that it is usually species producing smaller seeds that were present in significantly greater numbers in the seed bank than in the standing vegetation. The most abundant species obtained from the seed bank soils along the transect in this study were the grass species *Perotis patens*, the forb *Kohautia virgata*, and the sedges *Bulbostylis burchellii* and *Cyperus chersinus*.

The species richness of the standing vegetation was found to be significantly higher than that of the seed bank, with 55 species restricted to the aboveground flora. The canopy cover is characterised by the highly abundant tree species *Brachylaena huillensis, Pteleopsis myrtyfolia, Drypetes arguta, Terminalia sericea* and *Strychnos madagascariensis*; the shrub *Croton pseudopulchellus* and the climbers *Landolphia kirkii* and *Uvaria caffra*. The herbaceous layer of the aboveground flora is characterised by dominant grass species such as *Aristida stipitata* spp. g*raciliflora, Heteropogon contortus, Hyperthelia dissoluta, Panicum maximum* and *Perotis patens*. Several species that were recorded in the standing vegetation were completely absent from the soil seed bank. Similar results were found by Lunt (1997) and Arévalo & Fernández-Palacios (2000). Morgan (1998) also observed this phenomenon. The absence of climax species in the seed bank flora could be ascribed to the possible lack of seed sources, failure of effective seed dispersal, physiological inability to form dormant seeds or seed losses due to pre- or post-dispersal predation (Harper 1977, Rico-Gray & García-Franco 1992, Morgan 1998).

Four diagnostic groups were identified by arranging the aboveground species according to species presence and abundance along the transect (Figure 5.5). Group 1 represented species that are diagnostic of the *Licuati* thicket; Group 2 included species diagnostic of the grassland vegetation type and Group 3 represented species that were found only in the woodland vegetation. Group 4 represented species that were characteristic of both grassland and woodland vegetation. The highest species richness was found in the *Licuati* thicket, with 44 species recorded in the standing vegetation (Figure 5.5). Group 2 to 4 all showed a very low level of species richness compared with Group 1.

Five diagnostic groups were identified by arranging the seed bank species according to species presence and abundance along the transect (Figure 5.5). The same group descriptions were used as with the aboveground vegetation, with the addition of Group 5 that represented species that were commonly found in all three major vegetation types. A very low level of species richness was found in the soil seed bank throughout the entire transect.

The species composition was compared between the standing vegetation and the seed bank along the transect by means of a similarity index. In this study the Sørenson's Similarity Index (Mueller-Dombois & Ellenberg 1974) was used to calculate the similarity and is formulated in short as $IS_s = [2C/(A+B)] \times 100$, where C is the number of species common to both the seed bank and standing vegetation, A is the number of species in the standing vegetation, and B is the number of species in the seed bank. Frequency of similarity in species composition between the seed bank and the aboveground flora was found to be 7.84% in the *Licuati* thicket, 44.44% in the grassland and 16.00% in the woodland vegetation. Although the *Licuati* thicket produced the highest species richness (55 species), the grassland vegetation showed the highest percentage similarity between seed bank and standing vegetation in terms of its species composition. Roberts (1981), O'Connor & Pickett 1992, Milberg & Hansson (1993), Lunt (1997) and Peco *et al*. (1998) reported a similar lack of correspondence in species composition between aboveground vegetation and soil seed bank.

5.5.3 Conclusion

There was little correlation to be found in species composition between the standing vegetation and the seed bank along the transect, since the seed bank represents a floristically distinct and less variable component of the vegetation when compared with the standing flora. Generally, most of the species recorded in the aboveground vegetation were not found in the seed bank flora and *vice versa*. Only about six percent of the total number of species recorded along the transect were present in both the seed bank and standing vegetation.

Comparative calculations also produced relatively small percentages of similarity or correspondence in species composition between the standing vegetation and seed bank flora, except for the grassland vegetation. This suggests that the soil seed bank, especially in the *Licuati* thicket and woodland vegetation, is in fact a very poor predictor of the standing vegetation, and that the seed bank cannot be used successfully to restore degraded or disturbed *Licuati* or woodland vegetation. The grassland seed bank, however, appears to be a fairly good predictor of the standing vegetation indicating that the grassland seed bank can be used to restore former grassland after disturbance. A very important observation of the entire seed bank composition in this study is that the majority of species obtained from the soil samples were herbaceous and appeared to be weedy therophytes. Another conclusion is that most of the seed bank flora recorded were small-seeded species, which tend to form large, persistent seed reserves.

Soil-sampling time is highly important when establishing the similarity between seed bank and standing vegetation, given the annual variation in the floristic composition of seed banks. Also, the possibility exists that the total number of species present in the soil seed bank could be underestimated after six months of greenhouse germination due to the existence of still-ungerminated dormant seeds in the soil samples. For those species that are represented in the soil seed bank, the seed bank can buffer plant populations against intermittent episodes of catastrophic mortality of established plants, and extended periods of unfavourable habitat conditions.

CHAPTER 6
CONCLUDING REMARKS

The investigation of the soil seed bank of five different vegetation types within the Tembe Elephant Park, Maputaland, during 2001 revealed results that correlate well with similar studies done in other dry tropical forest, grassland and woodland vegetation.

Comparative analysis of the two seed extracting methods investigated in this study found that by comparing physical separation with the seedling emergence method, seed extraction by sieving and flotation generally produced higher seed densities than seedling emergence. For the entire data set, the seedling emergence method detected only 18% of the number of seeds found by the flotation method. The lowest correspondence between the two methods, regarding sampling time, was found for the July sampling (12%). The sampling time yielding the highest correspondence between the methods was January (26%). The vegetation type yielding the highest correspondence between the two methods was the grassland (37%). The *Licuati* thicket produced the lowest correspondence between the two methods (8%), followed by the *Licuati* forest seed bank producing the second lowest correspondence (15%). The forest/grassland ecotone and woodland seed banks produced 21% and 18% correspondence respectively between the two methods.

The results of the comparison between the two methods have important implications for future seed bank studies in the area. The large discrepancies between the two methods indicate that reliable seed density estimates, of especially *Licuati* and woodland seed banks, cannot be obtained solely by the use of the emergence method. To get a measure of the full range of seasonal variation in seed bank size of a particular vegetation type, the flotation method seems essential.

An investigation of the depth distribution of seeds in the soil profile showed that, in general, the largest number of species in the soil seed bank was found at a depth of >50–100 mm. In this study it was found that seeds were more concentrated in the upper soil layers than at deeper soil depths in all three vegetation types, although to a lesser extent in *Licuati* thicket than in grassland or woodland. Seeds, however, were distributed down the soil profile in larger numbers and to a greater depth in the grassland and woodland vegetation than was the case in the *Licuati* thicket vegetation. In many seed bank studies reported in the literature only the top 50 mm of soil was collected, based on the belief that few seeds were buried below that depth. This investigation of the depth distribution of seeds in the soil profile clearly demonstrated the need to sample to greater depths.

Spatial and temporal variation in the size and species composition of the selected seed banks were investigated and it was found that, in general, the forest/grassland ecotone and grassland soils produced the largest seed densities (number of seeds/m^2), whereas the *Licuati* vegetation types have the smallest seed banks. The size of the seed bank is correlated with the vegetation structure of these vegetation types. *Licuati* thicket vegetation is characterised mainly by trees with very little undergrowth and the tree species generally have relatively small seed banks. Grassland vegetation consists mainly of herbaceous species, which produce large numbers of small dormant seeds to build up a large seed bank. Woodland vegetation is composed in both a tree or shrub layer and a herbaceous layer, therefore the intermediate seed bank size.

The winter seed bank appeared to have the largest soil seed reserves with the lowest seed densities present during autumn. The woodland seed bank produced the largest number of species, while the *Licuati* forest and thicket soils showed a very low level of species richness. Generally, it was found that the largest percentage correspondence in species composition occurred between the summer and autumn seed banks. Also, the largest percentage correspondence in species composition was found to exist between the *Licuati* forest and thicket, as well as the forest/grassland ecotone and grassland seed bank floras, respectively. Furthermore, the seed bank flora as was obtained from these different vegetation types revealed that the majority of species were either grasses or sedges, and the remaining species composition consisted mostly of annual and perennial herbs or forbs, with hardly any evidence of woody species.

Seedling emergence rate was monitored over a period of six consecutive weeks and the results obtained from this study suggested that the initial inhibition of seedling emergence, which was observed in the *Licuati* thicket soils, was apparently caused by organic, water repellent substances present in these soils rather than seed dormancy or species-specific germination requirements. The other vegetation types investigated, in contrast to the *Licuati* soils, all showed an initial increase in seedling emergence rate during the first three weeks after which it gradually decreased from week 3 to week 6.

Finally, the species composition of the standing vegetation was compared to that of the soil seed bank. The species richness of the standing vegetation was found to be significantly higher than that of the seed bank, with many species restricted to the aboveground flora. Thus, several species that were recorded in the standing vegetation were completely absent from the soil seed bank. The largest percentage similarity in species composition was found in the grassland vegetation type and the smallest in the *Licuati* vegetation. Generally, percentage similarity or correspondence in species composition between the standing vegetation and seed bank flora was found to be relatively small. This suggests that the soil seed bank, especially in the *Licuati* thicket and woodland vegetation, is in fact a very poor predictor of the standing vegetation, and that the seed bank cannot be used successfully to restore degraded or disturbed *Licuati* or woodland vegetation. The grassland seed bank, however, appears to be a fairly good predictor of the standing vegetation indicating that the grassland seed bank can be used to restore former grassland after disturbance.

The results obtained from this study serves as a preliminary investigation of the rare and unique *Licuati* vegetation and its interaction with the surrounding vegetation, with emphasis on the soil seed bank dynamics, and leaves ample opportunity for further research on vegetation dynamics.

CHAPTER 7
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