Bothalia 37,2: 249–258 (2007)

Seasonal variation in soil seed bank size and species composition of selected habitat types in Maputaland, South Africa

M.J.S. KELLERMAN* and M.W. VAN ROOYEN*†

Keywords: *Licuati*, Maputaland, Sand Forest, seed bank dynamics, Tembe Elephant Park, temporal variation, transient seed bank

ABSTRACT

Seasonal variation in seed bank size and species composition of five selected habitat types within the Tembe Elephant Park, South Africa, was investigated. At three-month intervals, soil samples were randomly collected from five different habitat types: a, *Licuati* forest; b, *Licuati* thicket; c, a bare or sparsely vegetated zone surrounding the forest edge, referred to as the forest/grassland ecotone; d, grassland; and e, open woodland. Most species in the seed bank flora were either grasses, sedges, or forbs, with hardly any evidence of woody species. The *Licuati* forest and thicket soils produced the lowest seed densities in all seasons. *Licuati* forest and grassland seed banks showed a two-fold seasonal variation in size, those of the *Licuati* thicket and woodland a three-fold variation in size, whereas the forest/grassland ecotone maintained a relatively large seed bank all year round. The woodland seed bank had the highest species richness, whereas the *Licuati* forest and thicket soils were poor in species. Generally, it was found that the greatest correspondence in species composition was between the *Licuati* forest and thicket, as well as the forest/grassland ecotone and grassland seed bank floras.

INTRODUCTION

The Maputaland Centre of Plant Endemism (Van Wyk 1996) is known as a centre of high species diversity, rich in endemic plant and animal species (Scott-Shaw 1999; Van Wyk & Smith 2001) and is as such recognized by the International Union for the Conservation of Nature (IUCN). A rare and unique vegetation type that is endemic to the Maputaland Centre of Plant Endemism is the Sand Forest (*Licuati* forest in Mozambique—Izidine *et al.* 2003) which houses a substantial number of floristic endemics. However, the survival of many of Maputaland's endemic plant species is threatened by the rapid expansion of the human population and the associated demand for firewood, building material, medicinal plants, as well as land for agriculture and cattle grazing (Lawes *et al.* 2004; Kyle 2004). Even in formal conservation areas, elephants (*Loxodonta africana*) and fire could potentially threaten the long-term survival of many species. It is therefore of the utmost importance that these biota-rich areas be conserved and managed properly.

To provide valuable information on the species composition of Maputaland's diverse vegetation, several phytosociological studies have been done in recent years (e.g. Kirkwood & Midgley 1999; Matthews *et al.* 2001; Gaugris *et al.* 2004), but little is known about the vegetation dynamics and functional ecology. This is especially true for the Sand Forest vegetation where active management strategies are essential to ensure the long-term survival of this vegetation type. Formulating successful strategies that will maintain the integrity of the Sand Forest, can only be achieved if they are based on a sound knowledge of the vegetation dynamics and functional ecology of the system.

Seed bank dynamics are an important aspect of the functional ecology of a vegetation type. Soil seed banks represent a pool of reproductive potential and a source of genetic inheritance and play an important role in vegetation establishment after a disturbance (Warr *et al.* 1993; Bakker *et al.* 1996). The absence of a soil seed bank has important consequences for the dynamics of a species or vegetation type, because in such cases the vegetation will not be able to regenerate from a soil-stored seed bank after a disturbance. A soil seed bank, however, is not a static entity and the seed density and species composition of the soil seed bank flora constantly vary in space and time (Thompson & Grime 1979; Roberts 1986; Milberg & Hansson 1993; Crawford & Young 1998; De Villiers *et al.* 2004).

The present study is the first to investigate the soil seed banks in Maputaland. The main focus was on the Sand Forest and its associated vegetation types. The objectives of the study were to compare the seasonal changes in the soil seed bank in terms of a, seed density and b, species composition across five different habitats in the Tembe Elephant Park in northern KwaZulu-Natal.

THE STUDY AREA

The Tembe Elephant Park (26° 51.56' S–27° 03.25' S and 32° 24.17' E–32° 37.30' E) lies in the core of the Maputaland Centre of Plant Endemism, is 30 013 ha in extent and encloses extensive areas of pristine, endemic Sand Forest as well as other woodland, grassland and wetland vegetation types (Moll 1980; Matthews *et al.* 2001).

Sand Forest, also known as *Licuati* forest in Mozambique (Izidine *et al.* 2003), occurs under more arid conditions than other southern African forest types (Moll 1977; Moll & White 1980; Ward 1981; Low & Rebelo 1998; Kirkwood & Midgley 1999). It shows clear links to the tropical forest of southern Africa but has a relict character and as such is characterized by a low rate of regeneration with few seedlings and saplings (Von Maltitz *et al.* 2003). The Sand Forest can be subdivided into two related vegetation types: *Licuati* forest

* Department of Botany, University of Pretoria, 0002 Pretoria.
† Author for correspondence; e-mail: gretel.vanrooyen@up.ac.za.
MS. received: 2005-10-31.

(also often called Tall Sand Forest) and *Licuati* thicket (also referred to as Short Sand Forest). The *Licuati* forest, with canopy heights up to 20 m, is characterized by diagnostic tree species such as *Balanites maughamii, Cleistanthus schlechteri, Drypetes arguta, Newtonia hildebrandtii* and *Ptaeroxylum obliquum*, and little undergrowth is present (Matthews *et al.* 2001; Gaugris *et al.* 2004). *Licuati* thicket is a near-impenetrable, short stature forest type with canopy height less than 10 m (Matthews *et al.* 2001; Izidine *et al.* 2003; Gaugris *et al.* 2004). Diagnostic species in the thicket vegetation are *Croton pseudopulchellus, Hyperacanthus microphyllus, Psydrax fragrantissima* and *Ptaeroxylum obliquum*.

The *Licuati* vegetation often occurs as a mosaic with a very specific type of grassland which is dominated by grass species such as *Andropogon schirensis, Perotis patens, Pogonarthria squarrosa* and the forb *Tephrosia longipes* subsp. *longipes*. The transition between the *Licuati* vegetation and the grassland is abrupt and is represented by a bare or sparsely vegetated zone bordering the forest edge, dominated by *Perotis patens*. This transitional zone, which is only a few metres wide, is referred to as the forest/grassland ecotone in this study.

Several woodland types have been described for the Tembe Elephant Park ranging from sparse woodland, through open woodland to closed woodland. The open woodland, that was sampled for the seed bank study, is characterized by the geoxylic suffrutex *Salacia kraussii*, grasses such as *Aristida stipitata* subsp. *stipitata, Panicum maximum, Pogonarthria squarrosa,* and *Themeda triandra* and the tree species *Acacia burkei, Afzelia quanzensis, Albizia adianthifolia, Garcinia livingstonei, Strychnos madagascariensis, S. spinosa* and *Terminalia sericea* (Matthews *et al.* 2001; Gaugris *et al.* 2004).

The climate of Maputaland is characterized by hot, humid summers and cool, frost-free winters. According to weather data from the Sihangwane Weather Station in Tembe Elephant Park, the mean annual rainfall is 721 mm with a clear peak from October to April. The mean annual temperature for Tembe Elephant Park is 23.1°C, with absolute maximum and minimum temperatures of 45.0°C and 4.0°C (Gaugris *et al.* 2004).

METHODS

For the seed bank study, five different habitat types were selected in the southwestern part of the Tembe Elephant Park: a, *Licuati* forest; b, *Licuati* thicket; c, the forest/grassland ecotone; d, grassland; and e, woodland.

Sixty soil samples were collected within each of the five habitat types (5 × 60 samples) to determine the size and species composition of the soil seed bank. Soil sampling was carried out at three-month intervals for a period of 12 months. The top 100 mm of soil was collected with a soil auger with a diameter of 57 mm because an investigation into the depth distribution of seed in the seed bank revealed that most seeds were found in this layer (Kellerman 2004). The contents of the auger were emptied into a cotton soil-sampling bag and transported to the University of Pretoria. Soil samples which were used for the re-examination were stored in a dry, dark place at ambient temperatures until needed.

Samples were collected in January, April, July and September 2001, representing the summer, autumn, winter and spring soil seed bank, respectively. All soil samples were examined by the seedling emergence method immediately after collection. The results of this examination will be referred to as the seasonally germinable seed bank. The remaining soil of 15 randomly selected samples per habitat type was used in flotation studies (Kellerman 2004), and the remaining soil of the other 45 soil samples collected on one date per habitat type were subjected to a re-examination in September 2001. The rationale for the re-examination was, that if newly shed seeds had an after-ripening requirement, they would not germinate immediately after collection and would therefore not be detected by the seedling emergence method. By allowing an after-ripening period of a few months and re-examining duplicate samples in September, when temperatures were thought to be optimal for seed germination, the problem of an after-ripening requirement could be overcome. The results of this re-examination will be referred to as the persistent fraction of the soil seed bank. In arid regions where dormancy mechanisms are common for many species, such a re-examination indicates the size of the potentially-germinable seed bank (De Villiers *et al.* 2004).

The seedling emergence method was used to determine the seed bank size and species composition of each soil sample. Plastic pots (100 × 100 × 120 mm) were filled with finely ground quartz and topped with 100 cm^3 of soil from a sample. The pots (n = 60 per site per examination time) were placed in an uncontrolled greenhouse and watered daily with tap water and fortnightly with Arnon and Hoagland's complete nutrient solution (Hewitt 1952). Once a week, for a period of three months, all newly emerged seedlings were marked using toothpicks. Duplicate samples to determine the persistent seed bank fraction were investigated in the same manner in September 2001. Seedlings were identified as soon as possible and, once identified, removed from the pots to prevent contamination by self-seeding. Unidentified seedlings were left to mature for later identification. Voucher specimens are housed in the H.G.W.J. Schweickerdt Herbarium and nomenclature follows Germishuizen & Meyer (2003).

The percentage correspondence in species composition between the different habitat types and between the seasonally germinable and persistent fractions of the seed bank was calculated by means of Jaccard's Similarity Index (IS_J) which reads as follows:

$$IS_J = [c / (a + b + c)] \times 100$$

where c is the number of species common to both habitats or examination dates, a is the number of species restricted to one habitat or examination date, and b is the number of species restricted to the other habitat or examination date (Mueller-Dombois & Ellenberg 1974).

Data were analysed by using a one-way analysis of variance and Tukey's *post-hoc* test in the Statistica 7 computer program (Statsoft Inc., Tulsa, Oklohoma, USA).

RESULTS

Seed bank size

In general, the *Licuati* forest (Figure 1A) and *Licuati* thicket (Figure 1B) soils contained the smallest number of germinable seeds. Mean seed densities for the *Licuati* forest ranged from a low of 1 067 seeds m^{-2} in April to a high of 1 950 seeds m^{-2} in January and the *Licuati* thicket from 1 050 seeds m^{-2} in April to 3 200 seeds m^{-2} in January. In both cases the seasonal variation in seed bank size was statistically significant ($p = 0.013$ for *Licuati* forest; $p < 0.001$ for *Licuati* thicket). The *Licuati* forest and thicket 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 the highest seed densities in spring or summer. The *Licuati* thicket produced a significantly larger ($p < 0.001$) seed bank in summer than the *Licuati* forest, but seed bank size was similar in other seasons ($p > 0.05$ in all cases). When the *Licuati* forest soil samples were re-examined in spring, seed bank size was within 10% of that of the seasonally germinable seed bank. In the case of the *Licuati* thicket it was found that the autumn and winter seasonally germinable seed banks produced significantly larger seed numbers than the re-examination in spring ($p = 0.006$ for autumn comparison; 0.0008 for winter comparison), whereas the difference was not significant for the summer seed bank ($p < 0.001$).

In the forest/grassland ecotone, changes in the size of the seasonally germinable seed bank were damped ($p = 0.597$ over four seasons) (Figure 1C) and seed density ranged from 4 034 seeds m^{-2} in July to 4 667 seeds m^{-2} in September. When summer and winter collected soil samples were re-examined in spring, higher seed densities were encountered; however, these differences were not significant. The re-examined autumn soil samples yielded significantly less seeds ($p = 0.004$).

The seasonally germinable seed density of the grassland vegetation remained fairly constant from summer through autumn to winter, but showed a marked decline in spring ($p = 0.002$ over four seasons) (Figure 1D). The number of germinable seeds in the grassland soil almost halved from a high of 5 567 seeds m^{-2} in January to a low of 2 734 seeds m^{-2} in September. The seasonally germinable summer and autumn seed banks from the grassland soil produced significantly more seedlings than the duplicate analysis in spring ($p < 0.001$ for summer comparison; $p < 0.001$ for autumn comparison). This persistent fraction of the seed bank of the grassland soil remained relatively constant ($p = 0.897$) throughout the year.

Seasonal variation in seed densities in the woodland soils varied significantly ($p < 0.001$) and ranged from 2 167 seeds m^{-2} in September to 6 467 seeds m^{-2} in July. In contrast to the other vegetation types, the largest seasonally germinable seed bank in the woodland soils was present during winter (Figure 1E). The re-examination in spring produced significantly less seedlings than the seasonally germinable seed banks of all seasons ($p < 0.001$ for summer comparison; $p <0.001$ for autumn comparison; $p = 0.039$ for winter comparison).

Species composition

In total, 52 genera and 83 taxa were identified in the soil samples, together with a few unidentified specimens (Appendices 1–5). Many seedlings died while still in the cotyledon stage before they could be positively identified. These unidentified seedlings are indicated in the tables as mortalities. In general, the *Licuati* forest and thicket seed banks had the lowest species richness per sampling time.

The largest number of taxa consistently emerged from the woodland seed bank. The highest number of taxa at a single sampling time was 35, recorded from the spring woodland soil seed bank. The re-examination of soil samples of the summer, autumn and winter collections in spring generally produced species richness counts either the same or less than the examination immediately after collection. However, the decrease in richness could be the result of the re-examination being based on 45 soil samples as opposed to 60 for the initial examination immediately after collection.

The seed bank flora of the *Licuati* forest and thicket differed vastly from those of the other three habitat types. Thirty-three taxa comprising nine grass, four sedge, 18 herbaceous and two woody species were identified in the *Licuati* forest seed bank (Appendix 1). The *Licuati* thicket soils produced 25 identified taxa including nine grass, four sedge and 12 other herbaceous species (Appendix 2). Diagnostic species of the *Licuati* forest and thicket seed banks included *Crassula* cf. *expansa, Cyperus dubius, Eragrostis* cf. *moggii, Leptochloa* cf. *uniflora* and *Panicum laticonum*. Only two woody species were encountered in the seed banks of the *Licuati* vegetation types. The seed bank flora was often dominated by a single species and seed densities in the *Licuati* forest seed bank ranged from 17 to 1 222 seeds m^{-2} for individual species at a particular sampling time and for the *Licuati* thicket from 17 to 2 822 seeds m^{-2}.

Floristic composition of the ecotone soil seed bank consisted of 45 taxa including 15 grass, six sedge, 23 herbaceous and one woody species (Appendix 3). The seed bank flora of the ecotone was dominated by the grass species *Perotis patens*, constituting 58.4% of the total number of seedlings. Other prominent species included *Bulbostylis burchellii, B. hispidula, Cyperus chersinus, Kohautia virgata, Phyllanthus* cf. *parvulus* and *Setaria sphacelata* var. *sphacelata*.

Thirty-six taxa comprising 14 grass, five sedge and 17 herbaceous species were recorded from the grassland soils (Appendix 4). Prominent species included *Bulbostylis burchellii, B. hispidula, Conostomium natalense, Digitaria eriantha, Eragrostis ciliaris, Kohautia virgata, Perotis patens, Pogonarthria squarrosa* and *Setaria sphacelata* var. *sphacelata*.

In the woodland soil seed bank the emergence of 61 species including 20 grass, seven sedge, 33 herbaceous and one woody species was recorded (Appendix 5). Prominent grass species obtained from the soil samples were *Aristida stipitata* var. *stipitata, Brachiaria chusque-*

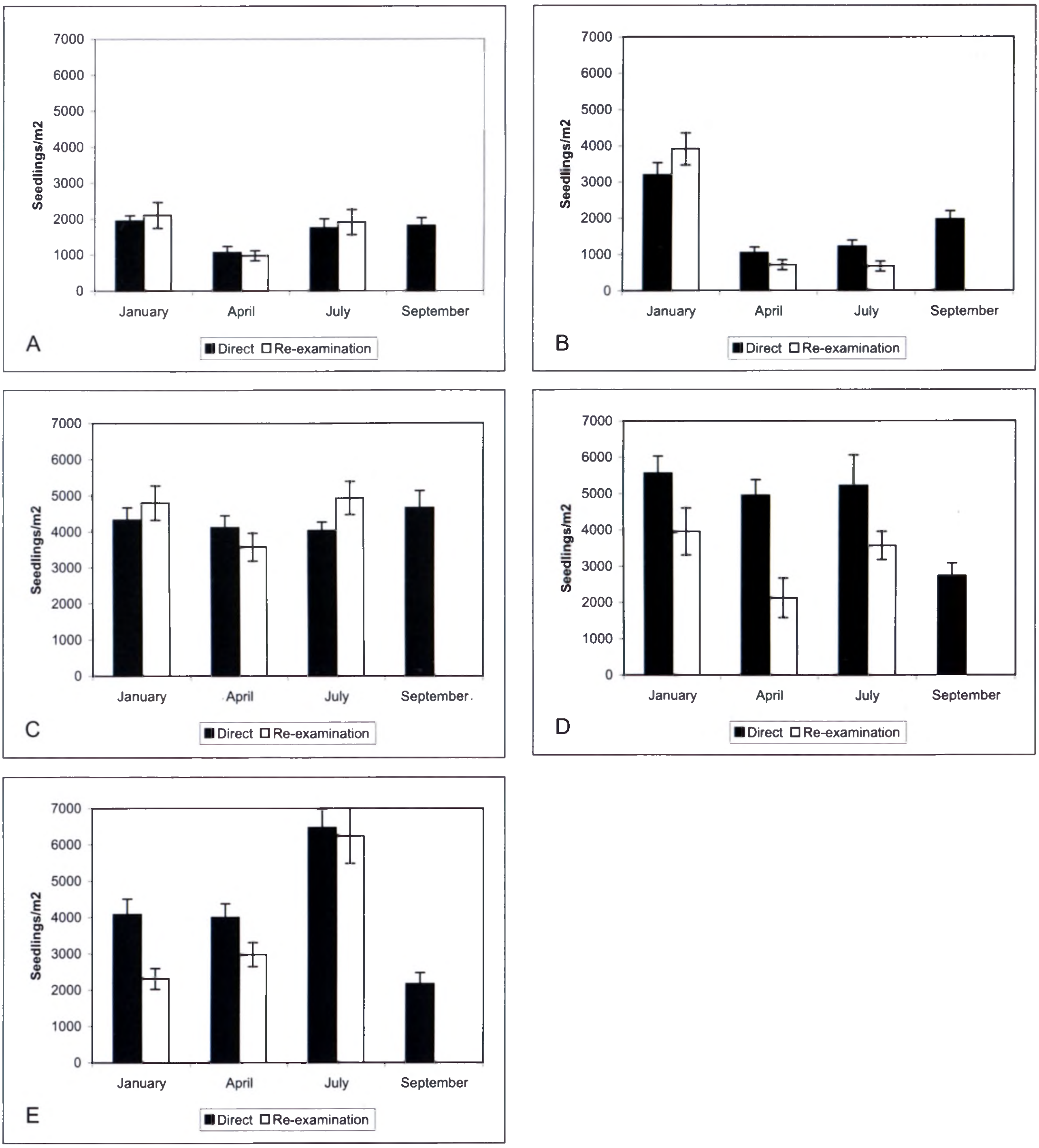

FIGURE 1.—Seed bank size (mean number of seeds m^{-2}) as obtained from soils collected in five selected habitat types in Tembe Elephant Park, when examined directly after collection, and re-examined in September. A, *Licuati* forest; B; *Licuati* thicket; C, forest/grassland ecotone; D, grassland; and E, woodland.

oides, Digitaria eriantha, Eragrostis ciliaris, Panicum maximum, Perotis patens, Pogonarthria squarrosa and *Setaria verticillata.* Other prominent herbaceous species recorded from the woodland seed bank soils were *Achyranthes aspera, Bulbostylis hispidula, Cyperus chersinus, Justicia flava, Kohautia virgata, Persicaria* cf. *decipiens* and *Phyllanthus parvulus.*

Species such as *Conyza albida, Gamochaeta pennsylvanica, Hypochaeris radicata, Oxalis* cf. *semiloba, Pseudognaphalium luteo-album* and *Sonchus asper* occurred in relatively large densities in the seed banks of all the investigated habitat types.

Jaccard's Similarity Index indicated a 62% correspondence in species composition between the *Licuati* forest and thicket seed banks (Appendix 6). The species composition of the forest/grassland ecotone and grassland seed banks also showed a high degree of similarity (58%, Appendix 6). There was a low correspondence of 29% between the *Licuati* forest and the forest/grassland ecotone in spite of their close spatial association. The woodland seed bank was more closely related to the grassland seed bank in composition than to the *Licuati* vegetation types. In general there was a low correspondence in species composition between the seasonally germinable seed bank and the re-examination in spring (Appendix 7).

DISCUSSION

Seed bank size

Several studies have indicated that forest seed banks are relatively small to almost nonexistent in both size and species richness (Warr *et al.* 1993; Crawford & Young 1998). Mature, dry, tropical forests generally produce very low seed bank densities and should there be higher seed numbers present in soils underlying dry forest vegetation, it could be ascribed to the abundant seed rain 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). Data from *Licuati* forest and thicket soils collected in the present study agreed well with these findings in that they produced the lowest seed densities of all the examined habitat types. Examples of mean seed densities obtained in other forest seed bank studies by the seedling emergence method include 265 to 2 910 seeds m^{-2} (Matlack & Good 1990), 203 to 5 613 seeds m^{-2} (Brown 1992), 330 to 3 437 seeds m^{-2} (Jankowska-Blaszczuk & Grubb 1997), 156 to 4 148 seeds m^{-2} (Falińska 1998), 610 to 7 009 seeds m^{-2} (Halpern *et al.* 1999) and 137 to 6 920 seeds m^{-2} (Olano *et al.* 2002). Seed densities reported for the *Licuati* vegetation types (1 050 to 3 200 seeds m^{-2}) are in the same order of magnitude as those mentioned above for the other forest types. However, Kellerman (2004) warned that these values, obtained with the seedling emergence method, could have greatly underestimated the true size of the seed bank. The most noteworthy difference in the seed bank size between the *Licuati* forest and thicket vegetation types was that the *Licuati* thicket produced a significantly larger soil seed bank than the *Licuati* forest in summer. This could reflect differences in the floristic composition, reproductive strategies, timing of seed fall, seed germination requirements and seed dispersal efficiency between these two vegetation types.

Compared with the forest and woodland soils, the forest/grassland ecotone soil produced a large seed bank almost year round, implying that seasonal variation was of lesser significance. The same trend in temporal variation was observed in grasslands studied by Coffin & Lauenroth (1989), Milberg & Hansson (1993) and Kalamees & Zobel (1997). The grassland seed bank sampled in the Tembe Elephant Park only partly followed this trend being relatively constant for the largest part of the year, but showing a marked decline in spring. The persistent fraction of the seed bank of the grassland soil remained remarkably constant throughout the year. Mean seed density varied from 4 034 to 4 667 seeds m^{-2} in the forest/grassland ecotone and from 2 734 to 5 567 seeds m^{-2} in the grassland, which compares well with reported grassland seed densities of 122 to 2 748 seeds m^{-2} (Coffin & Lauenroth 1989), 2 580 to 10 060 seeds m^{-2} (Milberg & Hansson 1993) and 1 421 to 2 567 seeds m^{-2} (Kalamees & Zobel 1997). Seed bank studies of South African grasslands by O'Connor & Pickett (1992) and Adams (1996) found mean seed densities varying between 300 and 10 000 seeds m^{-2}.

The woodland seed bank differed from the forest/grassland ecotone and grassland seed banks in that it produced distinctly more germinable seeds in winter with greatly reduced seed densities observed in spring. Mean seed density varied from 1 734 to 6 467 seeds m^{-2}. Dougall & Dodd (1997) and García-Núñez *et al.* (2001) reported similar seed densities in their studies of neotropical savanna vegetation with mean seed densities of 897 to 9 100 seeds m^{-2}. The relatively smaller seed densities recorded from both the grassland and woodland soils in spring might have been the consequence of germination induced by early rainfall in September before the soil collection. Rainfall data for the Sihangwane Weather Station in Tembe Elephant Park for September 2001 was 22 mm, which would have been sufficient to trigger the germination of many seeds.

Species composition

Each habitat's seed bank was characterized by its own species composition although the *Licuati* forest and thicket seed banks showed a large degree of similarity, as did the forest/grassland ecotone and the grassland seed banks (62% and 58% respectively). The relatively low (29%) similarity between the *Licuati* forest and the forest/grassland ecotone stresses the abrupt transition in species composition from the forest to the surrounding edge. Species composition showed large seasonal variation within a specific habitat type. Thompson & Grime (1979), Roberts (1986) and Morgan (1998) drew similar conclusions. The largest similarity in species composition was found between the summer and autumn seed banks.

Dry, tropical forest types, such as the *Licuati* forest and thicket, are generally characterized by high species richness in the standing vegetation (Murphy & Lugo 1986; Swaine 1992; Matthews *et al.* 2001, Gaugris *et al.* 2004). However, tropical forest seed banks are usually very small or almost nonexistent and a large portion of the viable seeds that do occur in forest soils, belong to pioneer species (Roberts 1981; Thompson 1985; Rico-Gray & García-Franco 1992; Skoglund 1992; Bigwood & Inouye 1998; Jankowska-Blaszczuk *et al.* 1998). The similarity in species composition between the seed bank and the aboveground flora in the *Licuati* forest was reported to be only 7.8% (Kellerman 2004). An analysis of the floristic composition of both the *Licuati* forest and thicket soils showed that the soil seed bank was composed primarily of grasses, sedges, annuals and short-lived perennial species, supporting the evidence from other studies that dry, tropical forest climax species do not produce persistent seed banks.

It is generally believed that the Sand Forest is unable to regenerate after a major disturbance and this has led to many concerns about the long-term survival of this vegetation type. The lack of seeds of forest or thicket canopy species in the soil seed pool of these vegetation types could be one of the contributing factors why the *Licuati* vegetation does not regenerate readily after major disturbances. In the present study the seeds of the prominent canopy species were absent at all examination times, indicating that the seed bank of these species is either very short-lived or that the germination requirements of the seeds were not met by the seedling emergence method applied. If the seed banks of canopy species are transient, as most studies on forest seed banks seem to indicate, regeneration would have to depend on seed dispersal from undisturbed sites.

The re-examination of the forest and thicket soils revealed a few important trends. The summer seasonally germinable seed bank was dominated by weedy annual species such as species of *Conyza*, *Sonchus* cf. *asper*, *Gamochaeta pennsylvanica* and *Pseudognaphalium luteo-album*. These species apparently do not persist well in the seed bank, because their numbers were greatly reduced in the re-examination of duplicate samples in spring. In contrast, the re-examined samples were dominated by other species e.g. *Leptochloa* cf. *uniflora* (*Licuati* forest) and *Panicum laticonum (Licuati* thicket). These grass species dominating in the spring re-examination apparently require some after-ripening to break seed dormancy.

The seasonally germinable seed bank of the forest/grassland ecotone was dominated by the grass species *Perotis patens* and sorrel *Oxalis* cf. *semiloba*. In the grassland seed bank, the relative contributions of the species differed among seasons. The most important species in the seasonally germinable seed bank were *Bulbostylis hispidula, Conyza albida, Oxalis* cf. *semiloba* and *Sonchus* cf. *asper*. The re-examination in spring of both the ecotone and grassland soils showed an increase in the seed density of *Perotis patens*, indicating that the seeds of this species require some after-ripening for optimal germination. A study to investigate the similarity between the seed bank and aboveground flora found a 44.4% similarity for the grassland (Kellerman 2004). This value is substantially higher than that of the *Licuati* thicket.

The woodland vegetation in the Tembe Elephant Park is composed of an upper tree layer and a prominent herbaceous or grass layer. The woodland soils examined in this study produced the highest number of species. Interesting though, was that the woodland soils produced the highest richness from the smallest seed density as was observed from the spring seed bank data. Despite the large number of species, only one woody species was recorded from the woodland soil seed bank.

In conclusion, with the exception of the forest/grassland ecotone, the seed banks of all habitat types investigated in this study, showed pronounced seasonal variation. The *Licuati* forest and *Licuati* thicket seed banks had the lowest seed densities and also the lowest species richness. In general, grass and sedge species comprised more than 40% of the seed bank flora that emerged from the soil samples. The remaining species were mostly annual and perennial forbs, with hardly any evidence of woody species.

ACKNOWLEDGEMENTS

The authors thank Ezemvelo KwaZulu-Natal Wildlife (EKZNW) for the opportunity to do this study in the Tembe Elephant Park and Wayne Matthews of EKZNW for his assistance and valuable advice. The material is based on research supported by the National Research Foundation (GUN 2053522).

REFERENCES

ADAMS, K.M. 1996. Influence of sward defoliation and soil disturbance on seedling emergence and survival in the Southern Tall Grassland. *African Journal of Range and Forage Science* 13: 131–136.

ALVAREZ-BUYLLA, E.R. & GARCÍA-BARRIOS, R.G. 1991. Seed and forest dynamics: a theoretical framework and an example from the neotropics. *The American Naturalist* 137: 133–154.

ARÉVALO, J.R. & FERNÁNDEZ-PALACIOS, J.M. 2000. Seed bank analysis of tree species in two stands of the Tenerife laurel forest (Canary Islands). *Forest Ecology and Management* 130: 177–185.

BAKKER, J.P., POSCHLOD, P., STRYKSTRA, R.J., BEKKER, R.M. & THOMPSON, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45: 461–490.

BIGWOOD, D.W. & INOUYE, D.W. 1988. Spatial pattern analysis of seed banks: an improved method and optimised sampling. *Ecology* 69: 497–507.

BROWN, D. 1992. Estimating the composition of a forest seed bank: a comparison of the seed extraction and seedling emergence methods. *Canadian Journal of Botany* 70: 1603–1612.

COFFIN, D.P. & LAUENROTH, W.K. 1989. Spatial and temporal variation in the seed bank of a sem-arid grassland. *American Journal of Botany* 76: 53–58.

CRAWFORD, E.R. & YOUNG, D.R. 1998. Spatial/temporal variations in shrub thicket soil seed banks on an Atlantic Coast Barrier Island. *American Journal of Botany* 85: 1739–1744.

DE VILLIERS, A.J., VAN ROOYEN, M.W. & THERON, G.K. 2004. The restoration of Strandveld Succulent Karoo degraded by mining: an enumeration of topsoil seed banks. *South African Journal of Botany* 70: 717–725.

DOUGALL, T.A.G. & DODD, J.C. 1997. A study of species richness and diversity in seed banks and its use for the environmental mitigation of a proposed holiday village development in a coniferized woodland in south-east England. *Biodiversity and Conservation* 6: 1413–1428.

FALIŇSKA, K. 1998. Long-term changes in size and composition of seed bank during succession: from meadow to forest. *Acta Societatis Botanicorum Poloniae* 67: 301–311.

GARCÍA-NÚÑEZ, C., AZÓCAR, A. & SILVA, J.F. 2001. Seed production and soil seed bank in three evergreen woody species from a neotropical savanna. *Journal of Tropical Ecology* 17: 563–576.

GAUGRIS, Y.J., MATTHEWS, W.S., VAN ROOYEN, M.W. & BOTHMA, J. DU P. 2004. The vegetation of the Tshanini Game Reserve and a comparison with equivalent units in the Tembe Elephant Park in Maputaland, South Africa. *Koedoe* 47: 9–29.

GERMISHUIZEN, G. & MEYER, N.L. (eds). 2003. Plants of southern Africa: an annotated checklist. *Strelitzia* 14. National Botanical Institute, Pretoria.

GUARIGUATA, M.R. 2000. Seed and seedling ecology of tree species in neotropical secondary forests: management implications. *Ecological Applications* 10: 145–154.

HALPERN, C.B., EVANS, S.A. & NIELSON, S. 1999. Soil seed banks in young, closed-canopy forests of the Olympic Peninsula, Washington: potential contributions to understory re-initiation. *Canadian Journal of Botany* 77: 922–935.

HEWITT, E.J. 1952. *Sand and water culture methods used in the study of plant nutrition*. Commonwealth Agricultural Bureau, Farnham Royal, Bucks.

IZIDINE, S., SIEBERT, S. & VAN WYK, B. 2003. Maputaland's *Licuati* Forest and Thicket. *Veld & Flora* 89: 56–61.

JANKOWSKA-BLASZCZUK, M. & GRUBB, P.J. 1997. Soil seed banks in primary and secondary deciduous forest in Białowieża, Poland. *Seed Science Research* 7: 281–292.

JANKOWSKA-BLASZCZUK, M., KWIATKOWSKA, A.J., PANUFNIK, D. & TANNER, E. 1998. The size and diversity of the soil seed banks and the light requirements of the species in sunny and shady natural communities of the Białowieża Primeval Forest. *Plant Ecology* 136: 105–118.

KALAMEES, R. & ZOBEL, M. 1997. The seed bank in an Estonian calcareous grassland: comparison of different successional stages. *Folia Geobotanica & Phytotaxonomica* 32: 1–14.

KELLERMAN, M.J.S. 2004. *Seed bank dynamics of selected vegetation types in Maputaland, South Africa.* M.Sc. dissertation, University of Pretoria.

KIRKWOOD, D. & MIDGLEY, J.J. 1999. The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. *Bothalia* 29: 293–304.

KYLE, R. 2004. Resource use in the indigenous forests of Maputaland: are conservation strategies working? In M.J. Lawes, H.A.C. Eeley, C.M. Shackleton & B.G.S. Geach, *Indigenous forests and woodlands in South Africa: policy, people and practice*: 713–736. University of KwaZulu-Natal Press, Pietermaritzburg.

LAWES, M.J., OBIRI, J.A.F. & EELEY, H.A.C. 2004. The uses and values of indigenous forest resources in South Africa. In M.J. Lawes, H.A.C. Eeley, C.M. Shackleton & B.G.S. Geach, *Indigenous forests and woodlands in South Africa: policy, people and practice:* 227–276. University of KwaZulu-Natal Press, Pietermaritzburg.

LOW, A.B. & REBELO, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.

MATLACK, G.R. & GOOD, R.E. 1990. Spatial heterogeneity in the soil seed bank of a mature Coastal Plain forest. *Bulletin of the Torrey Botanical Club* 117: 143–152.

MATTHEWS, W.S., VAN WYK, A.E., VAN ROOYEN, N. & BOTHA, G.A. 2001. Vegetation of the Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany* 67: 573–594.

MILBERG, P. & HANSSON, M.L. 1993. Soil seed bank and species turnover in a limestone grassland. *Journal of Vegetation Science* 4: 35–42.

MOLL, E.J. 1977. The vegetation of Maputaland—a preliminary report of the plant communities and their future conservation status. *Trees in South Africa* 29: 31–58.

MOLL, E.J. 1980. Terrestrial plant ecology. In M.N. Bruton & K.H. Cooper, *Studies on the ecology of Maputaland*: 52–68. Rhodes University & Wildlife Society of South Africa, Grahamstown.

MOLL, E.J. & WHITE, F. 1980. The Indian Coastal Belt. In M.N. Bruton, & K.H. Cooper, *Studies on the ecology of Maputaland*: 575–598. Rhodes University & Wildlife Society of South Africa, Grahamstown.

MORGAN, J.W. 1998. Composition and seasonal flux of the soil seed bank of species-rich *Themeda triandra* grasslands in relation to burning history. *Journal of Vegetation Science* 9: 145–156.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology*. Wiley, New York.

MURPHY, P.G. & LUGO, A.E. 1986. Ecology of tropical forest. *Annual Review of Ecology and Systematics* 17: 67–88.

O'CONNOR, T.G. & PICKETT, G.A. 1992. The influence of grazing on seed production and seed banks of some African savanna grasslands. *Journal of Applied Ecology* 29: 247–260.

OLANO, J.M., CABALLERO, I., LASKURAIN, N.A., LOIDI, J. & ESCUDERO, A. 2002. Seed bank spatial pattern in a temperate secondary forest. *Journal of Vegetation Science*: 775–784.

RICO-GRAY, V. & GARCÍA-FRANCO, J.G. 1992. Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science* 3: 617–624.

ROBERTS, H.A. 1981. Seed banks in soil. *Advances in Applied Biology* 6: 1–55.

ROBERTS, H.A. 1986. Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology* 23: 639–656.

SCOTT-SHAW, C.R. 1999. *Rare and threatened plants of KwaZulu-Natal and neighbouring regions*. KwaZulu-Natal Nature Conservation Services, Pietermaritzburg.

SKOGLUND, J. 1992. The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science* 3: 357–360.

SWAINE, M.D. 1992. Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* 3: 365–374.

THOMPSON, K. 1985. The functional ecology of seed banks. In M. Fenner, *Seed ecology*: 231–258. Chapman & Hall, London.

THOMPSON, K. & GRIME, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67: 893–921.

VAN WYK, A.E. 1996. Biodiversity of the Maputaland Centre. In L.J.G. Van der Maesen, X.M. van der Burgt & J.M. van Medenbach de Rooy, The biodiversity of African savannas: 198–207. *Proceedings of the 14th AETFAT Congress, International Conference Centre, Waginingen.* Kluwer Academic Publishers, The Netherlands.

VAN WYK, A.E. & SMITH, G.F. 2001. *Regions of floristic endemism in southern Africa. A review with emphasis on succulents.* Umdaus Press, Pretoria.

VON MALTITZ, G.P., MUCINA, L., GELDENHUYS, C., LAWES, M., EELEY, H., ADIE, H., VINK, D., FLEMING, G. & BAILEY, C. 2003. *Classification system for South African indigenous forests: an objective classification for the department of Water Affairs and Forestry*. Unpublished report ENV–P–C 2003–017. Environmentek, CSIR, Pretoria.

WARD, M.C. 1981. *A preliminary investigation into the ecology of Sand Forest, Maputaland,* Unpublished B.Sc.(Hons) Project. University of Natal, Durban.

WARR, S.J., THOMPSON, K. & KENT, M. 1993. Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography* 17: 329–347.

APPENDIX 1.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in *Licuati* forest seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Ancylobotrys petersiana	17						
Aristida stipitata subsp. *graciliflora*	17						
Brachiaria chusqueoides				22			
Clerodendrum glabrum var. *glabrum*		67					
Conostomium natalense					17		
Conyza albida	667	178	167	67			100
C. canadensis	33		83		17		
Crassula cf. *expansa*		67			17		
Cyperus austro-africanus	17						
C. dubius		22		44	17	22	
C. macrocarpus				22			
C. zollingeri	33			44	300	533	17

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Digitaria eriantha						22	
Eragrostis cf. *moggii*	33						
Euphorbia inaequilatera	17				17	67	
Gamochaeta pennsylvanica	183	67	117	89	17	22	17
Gisekia pharnacioides var. *pharnacioides*		22					100
Helichrysum acutatum			50				
H. cf. *silvaticum*		67					
Hypochaeris radicata	17	22	17				
Leptochloa cf. *uniflora*	183	1222	33	400	567	1067	750
Nidorella cf. *resedifolia*		17			17		
Oxalis cf. *semiloba*	83	200	33	178	450	44	517

APPENDIX 1.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in *Licuati* forest seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September (cont.)

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Panicum deustum			17				
P. laticonum			317	22		111	33
Perotis patens		22			33		
Persicaria cf. *decipiens*							17
Phyllanthus cf. *parvulus*					17		17
Pseudognaphalium luteo-album	150		17		33		33
Pteridophytes		22					
Setaria verticillata				22			50
Solanum macrocarpon				22			
Sonchus cf. *asper*	117	44	133				17
Unknown species					17		
Mortalities	383	67	83	44	217	22	150
Total	1950	2106	1067	978	1750	1911	1817

APPENDIX 2.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in *Licuati* thicket seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Brachiaria chusqueoides				22			200
Conyza albida	583	111	183	44	17		83
Conyza canadensis	317						
Crassula cf. *expansa*		22				22	
Cyperus chersinus							17
C. dubius		67					
C. macrocarpus		44					17
C. zollingeri	17	89	17	44	33		133
Digitaria eriantha		22					
Eragrostis cf. *moggii*	33		17			22	
Euphorbia inaequilatera					50	67	
Gamochaeta pennsylvanica	17		133	22	117		117
Hypochaeris radicata	100		100	22			
Leptochloa cf. *uniflora*	117	356	33	67	383	178	
Nidorella cf. *resedifolia*					17		
Oxalis cf. *semiloba*		200	100	311	217	44	483
Panicum deustum			17				
P laticonum	1350	2822	33	111	67	133	583
Perotis patens		22		22		111	50
Pseudognaphalium luteo-album	83				200		
Pteridophytes		22					
Setaria sphacelata var. *sphacelata*				22			
S. verticillata							17
Sida cordifolia							17
Sonchus cf. *asper*	117	22	283				17
Unknown species					17		
Mortalities	467	111	133	22	100	89	233
Total	3200	3912	1050	712	1217	667	1967

APPENDIX 3.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in forest/grassland ecotone seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Aristida stipitata subsp. *graciliflora*	17		67				33
Brachychloa schiemanniana					17	67	
Bulbostylis burchellii	167	378	67	200	200	644	367
B. hispidula	200		167		50		317
B. parvinux		600		133		289	
Conostomium natalense		44					
Conyza albida	633	22	183	89	33	22	167
C. canadensis			50				
Cyperus chersinus	100	156		133	50		67
C. indecorus var. *inflatus*		22	150		33		50
C. zollingeri		22		22		22	
Digitaria didactyla					17		
D. eriantha					33		
Eragrostis cf. *chloromelas*					17	44	
E. ciliaris	133			22			
Euphorbia inaequilatera					83		
Gamochaeta pennsylvanica	217	22	67	67	117		433
Helichrysopsis septentrionale					17		
Helichrysum acutatum					33		
H. cf. *silvaticum*						22	
H. kraussii	17						
H. sp.							17
Hypochaeris radicata	150		83				50
Kohautia virgata	33	178	133	378	67	178	100
Kyphocarpa angustifolia					17		
Leptochloa cf. *uniflora*		22					
Nidorella cf. *resedifolia*						22	
Oxalis cf. *semiloba*		200	983	89	1400	133	250
Panicum cf. *repens*							17
P. maximum						22	
Perotis patens	783	2533	633	2089	1467	2711	2033
Persicaria cf. *decipiens*		22		44	17		
Phyllanthus cf. *parvulus*	33	44	17	44		22	50
Poa annua	17						17
Pogonarthria squarrosa						133	
Pseudognaphalium luteo-album	300	44	17				
Senna cf. *petersiana*						22	
Setaria sphacelata var. *sphacelata*		422		178	17		183
S. verticillata				44		22	
Sida cordifolia					17		17
Solanum macrocarpon	17						
Sonchus cf. *asper*	333		750		150		
Tamarix species							17
Tephrosia multijuga							17
Trachypogon spicatus					17		
Unknown species					67		
Mortalities	1183	67	750	44	100	556	467
Total	4333	4800	4117	3578	4034	4934	4667

APPENDIX 4.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in grassland seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Andropogon gayanus							17
Aristida stipitata subsp. *graciliflora*		89		22	17		33
Brachychloa schiemanniana		22				22	
Bulbostylis burchellii	117	600		511	300	733	300
B. hispidula	617		433		450		300
B. parvinux		244		289		133	17
Chloris virgata	67					44	
Conostomium natalense		178	50	22	17		
Conyza albida	783		167	22	50	89	17
C. canadensis	17		17				
Cyperus chersinus					17		
C. indecorus var. *inflatus*			17			22	33
Digitaria didactyla			17		17		
D. eriantha	100				67		
Eragrostis cf. *chloromelas*					17		
E. ciliaris	50						33
E. inamoena							17
Euphorbia inaequilatera					17	89	17
Gamochaeta pensylvanicum	167	67	17	156	317		17
Helichrysum cf. *silvaticum*		22					33
Hypochaeris radicata	500		400		33	67	17
Justicia flava	17						17
Kohautia virgata	617	1133	117	1400	1117	644	850
Nidorella cf. *resedifolia*					17	22	
Oxalis cf. *semiloba*	17	333	1283	156	2033	89	17
Perotis patens	233	978	267	822	467	1378	783
Persicaria cf. *decipiens*			17				
Phyllanthus cf. *parvulus*				22			
Poa annua							17
Pogonarthria squarrosa	17		17	44	17	311	
Pseudognaphalium luteo-album	250						
Setaria sphacelata var. *sphacelata*		222				22	33
S. verticillata				22			
Solanum sp. nov.							17
Sonchus cf. *asper*	283		950	22			
S. cf. *oleraceus*	150						
Unknown species					33		
Mortalities	1567	67	1183	44	200	67	150
Total	5567	3956	4950	3556	5217	3734	2734

APPENDIX 5.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in woodland seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Achyranthes aspera					100	111	183
Aristida stipitata subsp. *graciliflora*	117	133	167			133	
Becium filamentosum				933			17
Brachiaria chusqueoides						44	83
Brachychloa schiemanniana		22		22			
Bulbostylis burchellii		67	17			44	
B. hispidula	33		33		33		17
B. parvinux				44		22	
Clerodendrum glabrum var. *glabrum*				22			
Commelina benghalensis						44	50
Conyza albida	600	22	217	22	17	22	17
C. bonariensis		22					
C. canadensis	17		50				50
Crassula cf. *expansa*							17
C. cf. *obovata*							17
C. sp.		22	17				
Cucumis metuliferus	17						
Cyperus austro-africanus		22			17		83
C. chersinus	67	111	133	222	133	111	17
C. dubius		67		22			
C. zollingeri			33				83
Digitaria didactyla					17		
D. eriantha		156	50	89	17	467	33
Eclipta prostrata							33
Eragrostis cf. *chloromelas*							67
E. cf. *curvula*					17		
E. cf. *gummiflua*					17		
E. ciliaris	67	200	17				433
E. inamoena						22	
Euphorbia cf. *helioscopia*							17
Gamochaeta pennsylvanica	250	222	150	378	717	111	67
Helichrysum cf. *silvaticum*		44			17		
H. kraussii			17		133	133	
Hypochaeris radicata	67		117				17
Justicia flava	33		17	22	117	156	17
Kohautia virgata	350	578	250	378	667	1333	67
Momordica balsamina	17		17				17
Nidorella cf. *resedifolia*		44		44	350	67	33
Oxalis cf. *obtusa*							17
O. cf. *semiloba*	17	44	1167		1150	378	33
Panicum deustum					33		
P. cf. *repens*	183		217				
P. laticonum				22			
P. maximum	17		17	67	450		83
Perotis patens			267	22	17	89	
Persicaria cf. *decipiens*	17	22	33	22		22	

APPENDIX 5.—Seasonal variation in seed density (mean number of seeds m^{-2}) of species in woodland seed bank when examined directly (Dir.) after collection and re-examined (Re.) in September (cont.)

Species	Jan.		Apr.		Jul.		Sep.
	Dir.	Re.	Dir.	Re.	Dir.	Re.	Dir.
Phyllanthus cf. *parvulus*	250	133	83	67	83	111	117
P sp. nov.	50	67	33	22			
Pogonarthria squarrosa	67			422	67	378	
Pseudognaphalium luteo-album	367	22	33				
Setaria sphacelata var. *sphacelata*		22		111	1533	2244	50
S. verticillata	50	133			67	44	33
Sida cordifolia	33			22			
Sonchus cf. *asper*	233		400				17
S. cf. *oleraceus*	17						
Sporobolus panicoides							33
Tephrosia multijuga							17
Tragus berteronianus	17						
Wahlenbergia cf. *undulata*							33
Xanthium strumarium							50
Unknown species							83
Mortalities	1133	133	450		700	156	167
Total	4084	2312	4000	2979	6467	6244	2167

APPENDIX 6.—Jaccard's Similarity Index (%) in total species composition of soil seed banks of vegetation types in Tembe Elephant Park

	LF	LT	F/G	G	W
Licuati Forest	100	62	29	33	32
Licuati Thicket		100	33	31	32
Forest/Grassland Ecotone			100	58	45
Grassland				100	43
Woodland					100

LF, *Licuati* Forest; LT, *Licuati* Thicket; F/G, Forest/Grassland Ecotone; G, Grassland; W, Woodland.

APPENDIX 7.—Jaccard's Similarity Index calculated between direct examination of soil samples and their re-examination in spring

	Similarity (%)		
	Jan.	April	July
Licuati Forest	27	29	38
Licuati Thicket	29	54	31
Forest/Grassland Ecotone	33	33	22
Grassland	22	42	38
Woodland	25	31	50