

**VEGETATION PATTERNS IN THE KALAHARI
AFFECTED BY *ACACIA ERIOLOBA*:
THE IMPORTANCE OF THE
REGENERATION NICHE**

Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften
(Dr. rer. nat.)

der Naturwissenschaftlichen Fakultät III
-Biologie und Vorklinische Medizin-
der Universität Regensburg

vorgelegt von
Martijn Kos
aus Amsterdam

Februar 2007

Promotionsgesuch eingereicht am: 25.1.2007

Tag der mündlichen Prüfung: 25.6.2007

Die Arbeit wurde angeleitet von: Prof. Dr. Peter Poschlod

Prüfungsausschuss: Vorsitzender: Prof. Dr. Thomas Dresselhaus
1.Gutachter: Prof. Dr. Peter Poschlod
2.Gutachter: Prof. Dr. Steven Higgins
3.Prüfer: Prof. Dr. Erhard Strohm

Contents

Chapter 1	General introduction	1
Chapter 2	Seed size and persistence as determinants of colonization potential in a guild of bird dispersed plants from the Kalahari	15
Chapter 3	Directed dispersal of fleshy fruited plants to <i>Acacia erioloba</i> trees in the Southern Kalahari	26
Chapter 4	Spatial patterns and functional ecology of the soil seed bank of the dry Nossob river valley, Southern Kalahari	40
Chapter 5	Correlates of inter-specific variation in germination response to water stress in an arid savannah	64
Chapter 6	Slow germination in annuals growing in association with <i>Acacia</i> canopies in an arid Kalahari savannah	75
Chapter 7	Seeds use temperature cues to ensure germination under nurse plant shade in xeric Kalahari savannah	89
Chapter 8	The importance of abiotic filters versus seed dispersal for species sorting: A soil sod transplanting experiment in an arid Kalahari savannah	104
Chapter 9	Conclusions and Perspectives	115
	Summary	123
	References	129
	Acknowledgements	141
	Appendices	i-v

Chapter 1

General Introduction

The woody vegetation in arid ecosystems forms an important component of structural diversity in other wise often featureless surroundings. Shrubs and trees create microhabitats contrasting with surrounding open habitat and increase the niches available for plant species. It is commonly observed that plants of a variety of life-histories and growth forms establish only or predominantly under their canopies (Went 1942; Archer *et al.* 1988; Silvertown & Wilson 1994; Pugnaire *et al.* 1996; Facelli & Brock 2000; Fensham & Butler 2004). This pattern has been termed the ‘nurse plant effect’ (Shreve 1931, 1951; Niering *et al.* 1963), or nucleation (Yarranton & Morrison 1974) and served as a classic example of facilitation (*sensu* Yarranton & Morrison 1974). Woody perennials thus contribute considerably to the structuring of plant communities and promote biodiversity in arid environments.

Although these associations have been well described the processes behind the patterns are not completely understood. Many environmental factors follow steep gradients going from the open matrix to the area under canopies, both abiotic and biotic. And accordingly a range of hypotheses has been proposed to explain such associations. These include increased dispersal of seeds to canopies, higher water availability, protection from herbivores, higher nutrient availability, reduced radiation and temperature and physical support (Flores & Jurado 2003).

Most studies on the effects of woody species on the vegetation in arid areas focus exclusively on the species that occur under the canopies of woody species. However, to understand the mechanisms that contribute to the vegetation patterns mediated by the woody vegetation comparative studies are needed. Such patterns may also be caused partially by negative effects of woody vegetation on matrix species. Species that occur under canopies need to be compared with species growing in the surrounding open matrix. Trade offs prevent species to be good at everything and as a result species will function better in some habitats than in others. It is therefore likely that species from the matrix are just as well excluded from growing under canopies as canopy species are excluded from the matrix, each having their highest competitive ability in their ‘choice’ habitats.

The species pool concept (Ricklefs 1987; Taylor *et al.* 1990; Zobel 1997) offers a useful framework for the study of mechanisms behind the observed vegetation patterns

affected by woody plants in arid regions. According to the species pool concept only a certain set of species from a specified region or landscape is able to colonize and persist in a habitat within that region or landscape. Abiotic factors (soil type, nutrient availability, micro and macro climate) and biotic interactions (competition, mycorrhizal infection, herbivory, seed predation, pollination) function as a filter (Zobel 1997). Which species are able to coexist in a community/habitat is in the first place determined by the ability of species to disperse to that habitat. But abiotic factors and biotic interactions form an environmental sieve which determines which species that arrive in the community can actually establish and thrive there.

Although there exists a large body of literature devoted to the study of facilitative effects of woody vegetation an important aspect of plant ecology, the regeneration niche, is often neglected (possibly with the exception of dispersal), or it is acknowledged but empirical studies are not undertaken. This seems to reflect a general pattern in the history of plant ecology where spatial vegetation patterns have often been explained on the basis of an incomplete set of traits, mostly those of the adult plant (Grubb 1977). In a spatially and temporally heterogeneous environment plants need to track conditions and resources favourable for growth. The fact that plants are largely immobile means that movements are restricted mainly to the seed stage. Plants can therefore track habitat mainly by seed dispersal, persistence and germination cueing. The ability of plants to disperse to preferred patches or habitat choice (Bazzaz 1991) can be spatial or temporal. An example of spatial habitat choice is the directed dispersal of seeds of the cloud forest tree *Ocotea endresiana* to perches of bellbirds which also provide the optimal conditions for establishment (Wenny & Levey 1998). Habitat choice can also be temporal. For example when desert annuals only germinate after a certain amount of rain has fallen (Guterman 1993). In a proximal sense plants, of course, do not actively choose habitat. Rather habitat choice is imposed on plants by seed dispersal and subsequently the environment (Bazzaz 1991). Regenerative traits will thus determine in the first place where a plant will grow. Establishment and further growth up to reproduction may further modify the spatial distribution of a plant population but this will take place within the template laid out by seed dispersal, seed persistence and germination. As the seed stage provides basically the only opportunity for plants to determine the conditions they experience in later life, there will be strong selection on regenerative traits to let plants disperse to and germinate and establish only in favoured habitat. When regenerative traits limit the distribution of seedlings, this is therefore very likely to have an effect on adult plant distribution. To elucidate the mechanisms that determine which species from the species pool can establish in a (micro-)habitat it is therefore essential to study the regenerative biology of

species. The importance of the regeneration niche for community assembly was also shown by Weiher & Keddy (1995) who by the experimental filtering of 20 wetland species demonstrated that the filter that prevented germination or early establishment or both was of primary importance.

The above discussion of the importance of the regeneration phase indicates that the regeneration phase is of crucial importance for the assemblage of plant communities under nurse plants. Below I discuss the ways in which seed dispersal, persistence and germination could determine which plant species can reach which microhabitat and can pass the biotic and abiotic filters associated with different microhabitats in arid landscapes dominated by a two phase pattern of woody vegetation and open interspaces.

Dispersal

Directed dispersal is thought to be especially important in arid ecosystems (Wenny 2001). Shrubs and trees in arid regions form an important structural element in otherwise often featureless surroundings. Consequently many animals use woody perennials for nesting, shade, foraging, perching etc. Animals that have the potential to disperse seeds can therefore be expected to play an important role in the origin and maintenance of associations of plant species with woody perennial canopies. Birds are expected to be especially important (Wenny 2001, Sekercioglu 2006) due to their mobility combined with the fact that the bird mediated seed rain concentrates under isolated trees in open landscapes (Jordano 2000 and references therein). Dispersal, especially when directed, also has the potential to direct evolution of other traits such as germination behaviour by determining the habitat plants experience.

Seed persistence, seed bank

Persistence of seeds (dispersal in time) is an important determinant of the ability to colonize and maintain a population in a habitat (Ehrlén & van Groenendaal 1998). The importance of persistence may differ between different habitats. When conditions for seedling establishment are more favourable under canopies carry-over of seeds is expected to be less than in the matrix. On the other hand canopy and matrix may differ in disturbance regime due to increased animal activity under canopies and species from habitats with a high disturbance frequency tend to have more persistent seeds than those of less disturbed habitats (Thompson *et al.* 1998). Also the built up of a seed bank may be hampered by seed predation which may also differ between (micro-) habitats. When seeds of columnar cacti depending on nurse plants were placed on leaf litter, that accumulates under trees, and sand more seeds were

removed from sand than from leaf litter (V. Sosa & A. Hernandez, unpublished data in Sosa & Fleming 2002). Aspects affecting seed survival like soil moisture, microorganisms, seed predation and burial processes may all differ between canopy and matrix. The optimal strategy in one microhabitat may therefore result in high seed losses in the other microhabitat.

Germination cueing

Germination is a high-risk event for most plants (Harper 1977) that is commonly associated with high mortality rates (Fenner 1987a). Mechanisms reducing the risks associated with germination/establishment are therefore expected to be under strong selection pressure. Risks associated with germination are habitat specific (Meyer *et al.* 1995; Meyer *et al.* 1997) but the risks encountered by germinating seedlings in a particular habitat also depend on species specific traits. Seedlings from large seeds, for example, are thought to be more resistant against environmental hazards like drought (Leishman & Westoby 1994; Leishman *et al.* 2000). Germination behaviour therefore develops in response to the habitat and species specific risks encountered by seedlings. Risk avoidance by germination cueing can be spatial (gap detection) or temporal (response to rain fall, chilling requirements). Germination responses to environmental factors can thus be very precise mechanisms of habitat choice in plants, specific environmental conditions must be present to break dormancy and additional conditions must be present to enable subsequent germination (Baskin & Baskin 1998). By being so particular about the environmental requirements for germination of seeds plants ensure that their seedlings and later life-stages experience a specific set of environmental conditions. Germination behaviour is therefore not only influenced by other traits but can itself influence the evolution of those traits (Donohue 1995; Donohue *et al.* 2005). The germination behaviour of a species may evolve in response to habitat specific risks and other traits of a species evolved in that habitat in such a way that germination will only take place in a specific (micro-) habitat.

But germination and other life stages can also be uncoupled. Especially because the spatial scales important for seeds and seedlings differ from those for adult plants (Harper 1977). There does not need to be a relationship between adult plant requirements and germination requirements which is why the distribution of plant species may not be accurately predicted from adult traits alone. An example is the effect of soil texture on plants. Soil texture can influence the risk of desiccation for seedlings: water in the seed zone of coarse soils may descend rapidly compared with fine soils. Psammophytes therefore tend to germinate at higher water potentials than non-psammophytes (Allen *et al.* 2000). On the other

hand coarse soils provide generally more favourable moisture conditions for adult plants in arid regions due to greater porosity which results in smaller run-off, deeper and more rapid penetration, smaller capillary forces resulting in less evaporation, and a lower wilting point (Leistner 1967).

In arid ecosystems, germination associated risks are most likely related to water availability. Risks can be temporal: germination after small amounts of rain increases the chance of desiccation. Risks will also differ spatially between different habitats. Water will drain quickly from the germination zone in coarse soils as opposed to fine soils. Sun exposed slopes will be more arid. Evapotranspiration will be reduced in the shade under trees and by growing in the shade plants can reduce water use. Soils under tree canopies in (semi) arid areas have been reported to be moister than soil in the surrounding matrix (Kennard & Walker 1973; Parker & Muller 1982; Joffre & Rambal 1988; Facelli & Brock 2000). Besides the effect of shade litter also has a positive effect on soil moisture (Tiedemann & Klemmedson, 1977). It should be noted that not all effects of nurse plants on water availability may be positive. Interception of rain by the canopy (Belsky *et al.* 1989; Tielbörger & Kadmon 2000) and competition for water with the nurse plant may have negative effects on water availability.

In spite of the considerable potential of germination cueing to govern associations with nurse plants, germination is referred to only once in a recent review on nurse-protégé interactions (Flores & Jurado 2003). Studies on the germination ecology of species associated with woody perennials in arid ecosystems are scarce (but see Steenbergh & Lowe 1977; Valiente-Banuet & Ezcurra 1991; Fulbright *et al.* 1995; Nolasco *et al.* 1997; Godínez-Alvarez & Valiente-Banuet 1998) and studies outside North-America are practically absent. However, the available information suggests, that germination cueing may be an important cause for associations with ‘nurse-plants’. Nolasco *et al.* (1997) found for example that in *Stenocereus thurberi*, a cactus species commonly associated with nurse trees, emergence of seedlings from seeds sown in full sun was nil even when ample water was available. The species did germinate in the shade and this suggests that modification of soil temperature by nurse plant canopies may be required for germination of this species.

Nurse plant life history

Understorey vegetation is affected by overstorey woody species life history and diversity is usually higher under older/larger shrubs or trees (Milton & Dean 1995; Dean *et al.* 1999; Pugnaire & Lázaro 2000; Tewksbury & Lloyd 2001). Pugnaire & Lázaro (2000) found that the seed bank composition under shrubs did not change with age but species richness of the

standing vegetation increased with shrub age. This suggests that the filter that determines which species from the species pool can establish under the shrub canopy changes with shrub age.

This is relevant also from a conservation point of view. Land use in the form of for example grazing by livestock or wood harvesting could affect the population structure of woody species for example by mainly harvesting large trees (Barnes *et al.* 1997). In this way life stages important for the completion of the life cycle of associated plant species could be reduced to very low densities or disappear altogether. Requirements for germination may only be met under shrubs or trees of a certain age or animal dispersers may only be attracted to trees and shrub individuals of a certain size. Milton & Dean (1995) and Dean *et al.* (1999) found that in the Southern Kalahari more frugivorous bird species and individuals were seen on mature than sapling or dead trees. At the same time plants with fleshy-fruits occurred under 91 % of large trees but under only 17 % of saplings and 8 % of treeless plots (Dean *et al.* 1999). This suggests that the bird mediated seed rain might be denser under large trees than under sapling trees or the surrounding matrix.

Study system: *Acacia erioloba* in the Southern Kalahari

Acacia erioloba E. Mey. (Afrikaans: kameeldoring, English: camelthorn) is the only tree to reach any great size on Kalahari sands, in areas of rainfall below 400 mm per year (Acocks 1953). It is restricted to sandy soils and its main distribution overlaps with the Kalahari sands of Southern Africa. Here it is found in the Savanna Biome in dry woodland, bush or thornveld. Over its range, rainfall varies from less than 40mm to 900mm per year (Barnes *et al.* 1997), but it is particularly common in desert and semi-desert areas where it occurs along watercourses and other situations where underground water is available. The largest specimens are found in the deep alluvial soils in riverbeds such as the Nossob, Auob, Molopo and Kuruman rivers.

Acacia erioloba is slow growing (van Rooyen *et al.* 1994; Barnes 1999) and long-lived: Radiocarbon dating of trees in the Kgalagadi Transfrontier Park revealed that the oldest sampled individual was about 250 years old (Steenkamp 2000). It develops a very long tap root and rooting depths up to 60 m have been recorded (Canadell *et al.* 1996) and its success as a large tree in arid regions probably is due to its ability to utilize deep ground water.

The camelthorn can reach a maximum height of 16m (Coates Palgrave 1983), and canopies can start to spread laterally after 17 years (Carr 1976). Mature trees have a wide spreading crown that can attain a diameter > 15 m (Fig. 1.1) and although being a deciduous species it

only loses its leaves for a very short time - during August (Smit 1999). Older trees therefore provide a large area under their canopy that is consistently buffered from temperature extremes (Fig. 1.2). Soils under large camelthorn trees are generally richer in nitrogen, phosphates and potassium than the surrounding matrix (Milton & Dean 1995; Dean *et al.* 1999, Hoffmann 2001).

Plant species richness beneath *Acacia erioloba* canopies is significantly greater than in surrounding areas (Zimmermann 2001; Seymour 2006) and a suite of species are largely restricted to the canopy of camelthorns. The species that are in their distribution more or less limited to camelthorn canopies belong mainly to two functional groups: fleshy fruited perennials and nitrophilous annuals (Milton & Dean 1995; Leistner 1996; Dean *et al.* 1999). For both groups directed dispersal is thought (but has not been demonstrated) to lead to a higher seed rain under camelthorn canopies than in the open matrix. However, the seed rain of fleshy fruited species generally tends to be concentrated under trees and shrubs that are used by birds for perching, roosting and nesting (Jordano 2000 and references therein). Nitrophilous annuals of the genera *Amaranthus* and *Chenopodium* carry their seeds among their leaves and are therefore thought to be dispersed by large herbivores (Janzen 1984; Milton & Dean 1995). The nitrophilous annual grass *Setaria verticillata* is dispersed epizoochorous on the fur of mammals (Ernst *et al.* 1992). Seed rain of these annuals is thought to be concentrated under camelthorn canopies because large herbivores are attracted to canopies that provide shade during the heat of the day and more nutritious grazing (Milton & Dean 1995; Leistner 1996).

Acacia erioloba in the Southern Kalahari thus provides a good system to study the effects of regenerative traits on the origin and maintenance of vegetation patterns affected by the woody vegetation in arid regions.



Fig. 1.1 Sapling and mature *Acacia erioloba* tree (from Barnes *et al.* 1997)

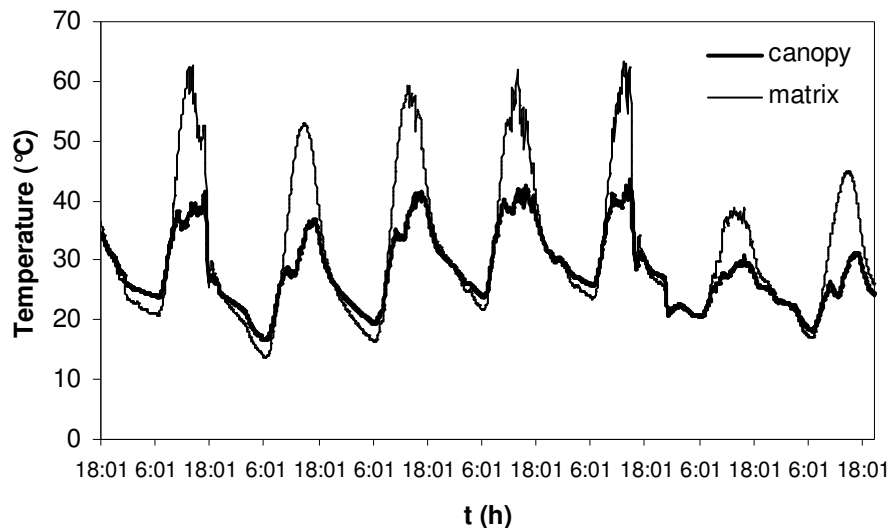


Fig. 1.2 Effect of *Acacia erioloba* on microclimate: temperature (°C) measured at random cardinal orientations under seven large tree canopies and in the adjacent matrix at 5 minute intervals for a one week period (13 February – 20 February 2003). For details on method see Chapter 7.

Study area

The sands that form the geological Kalahari System cover an area of about 2.5 million km² of the interior of southern Africa which is thought to be the largest continuous stretch of sand in the world (Leistner & Werger 1973). In a geographical sense the Kalahari is usually taken to be the portion of the Kalahari System between the Orange and Zambesi rivers. The extreme west and south-western portion of the Kalahari area where the sand forms parallel dunes is known as the Southern Kalahari (Leistner 1967). The Southern Kalahari is about 800 km long and 100-200 km wide and covers parts of Botswana, Namibia and South Africa.

The Southern Kalahari climate is extreme: in summer day temperatures can reach 45 °C while in winter nights temperatures can drop below -10 °C. Mean maximum and minimum temperatures are 37.4°C and 19.5°C in January and 22.2 °C and 1.2°C in July (van Rooyen 1984). The area receives summer rain fall (Werger 1986) and the rainy season typically lasts from about November to April, with 50 % of the total falling between January and March (Leistner 1967, see Fig. 1.3). Precipitation occurs often in the form of short but severe thunderstorms. Annual precipitation in the Kalahari increases in easterly and northerly directions (Adams *et al.* 1996). In the Southern Kalahari dune veld mean annual precipitation ranges from about 150 mm in the south-east to 300 in the north-west (Leistner 1967).

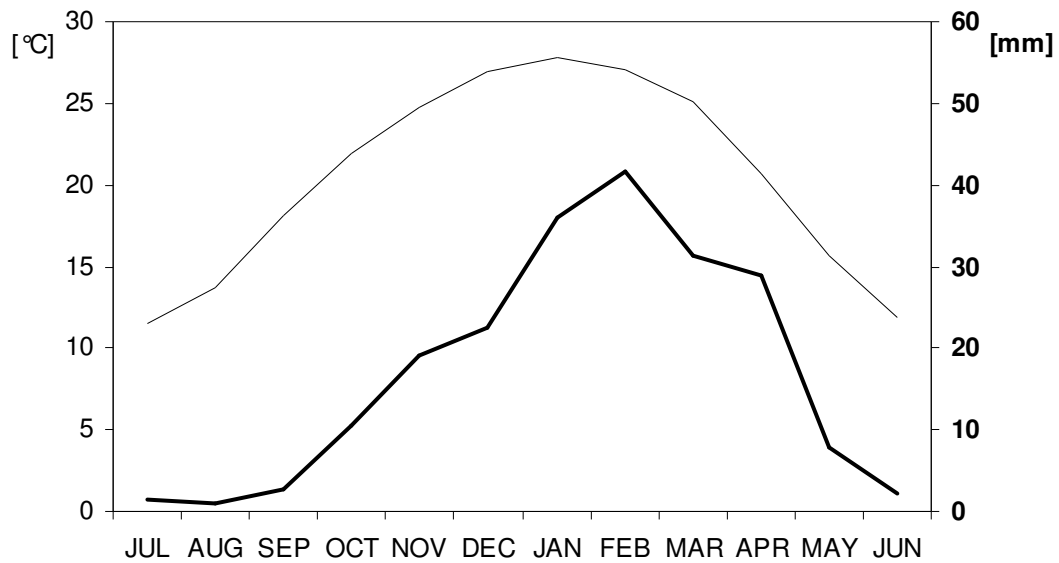


Fig. 1.3 Mean monthly temperature (thin line) and precipitation (bold line) for Twee Rivieren, R.S.A., $n = 42$ (1961-2003). Data provided by South African Weather Service.

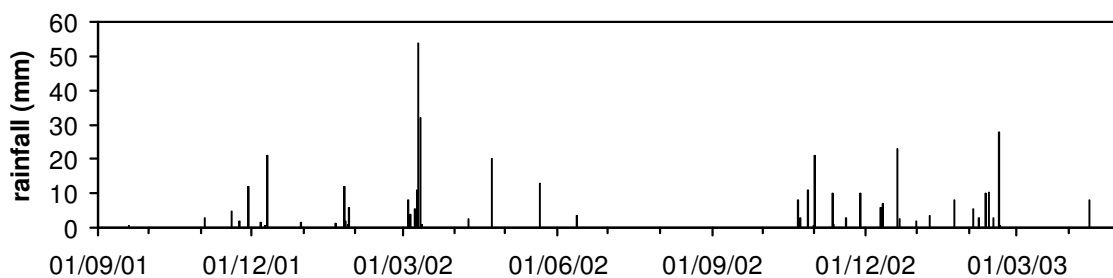


Fig. 1.4 Daily rain fall for Farm Alpha, Gordonia District, for the 2001-2002 and 2002-2003 rainy season. Data provided by Prof. A.O.E. Rasa.

Mean annual precipitation at Twee Rivieren, about 40 km North of the main study site, is 203 mm (period 1961-2003, $n = 42$, $SD = 98$). A C.V. of 48 % indicates that precipitation is highly variable among years (data provided by South African Weather Service). Data for the farm Alpha, about 5 km from the main study site also indicate this: for the 2001-2002 rainy season 224 mm was recorded but for 2002-2003 only 188 mm (data provided by Prof. Dr. A.O.E. Rasa). These data also illustrate that the within year distribution of precipitation is very variable (Fig.1.4). Rain fall is not only unpredictable in time but also in space as convectional storms are often very local (Leistner 1967).

The vegetation is part of the savannah biome (van Rooyen & Bredenkamp 1996a,b). Savannas are characterized by the co-dominance of trees and grasses. In areas that receive less than about 650 mm mean annual precipitation (MAP) maximum woody cover is constrained

by MAP, above a MAP of about 650 mm savannahs are ‘unstable’ systems where MAP is sufficient for woody canopy closure and fire and herbivores are required for the coexistence of trees and grass (Sankaran *et al.* 2005). The Southern Kalahari is an arid to semi-arid region and the savannah here is a MAP determined savannah or ‘stable’ savannah. where water constrains woody cover and permits grasses to coexist.

The vegetation of the dune area is a very open savannah that consists of a well developed grass layer with scattered shrubs of mainly Grey Camel Thorn (*Acacia haematoxylon*), and a very sparse tree layer consisting of Camel Thorn (*Acacia erioloba*) and Shepherd's Tree *Boscia albitrunca* (Leistner 1967). Most large Camel Thorns, however, grow in the river courses intersecting the dunes where therefore the field work was carried out. The rivers flow only episodically after exceptionally high rainfall. Because the river-beds are lower than the surrounding country, organic matter, fine soil particles and minerals collect in them. Soils in the dry river beds of the Southern Kalahari are generally more fine than in the surrounding dune veld with a sand content from 40 to 85 %. They have a high pH and are rich in phosphates and potassium. Most large trees grow on raised, rarely inundated alluvium which forms a transition between the seasonally inundated alluvium and the surrounding sand formations. The soils of the raised alluvium vary from sandy clayey loam to loamy sand and may be covered by a thin layer of compact calcareous sand (Leistner 1967). The vegetation of the Kalahari rivers intersecting the duneveld is an open savanna with Camel Thorn trees (*Acacia erioloba*) and fruiting shrubs scattered in a relatively bare matrix with a sparse cover of perennial grasses (*Stipagrostis* spec.) -mainly on the sandiest soils- and low shrubs (Acocks 1953, Leistner 1967, Milton & Dean 1995).

Study sites

Most of the field work was carried out in an about 2.5 km long and 100 to 250 m broad strip of dry river bed (Nossob river) between the road (R360) and the border fence to Botswana (26°48' S and 20°39' E, Northern Cape, Republic of South Africa, Fig. 1.5). The dominant shrubs at the site are *Phaeoptilum spinosum*, *Rhigozum trichotomum* (in the matrix) and *Lycium bosciifolium* (which is usually found in association with *P. spinosum* or *Acacia erioloba*). Besides *Acacia erioloba* large tree specimens of *Acacia haematoxylon* also occur and the shrubs *Acacia mellifera* and *Acacia hebeclada* are also present at low densities. The area has not been grazed by livestock to any large extent since 1974 due to the erection of a border fence for veterinary purposes. However, goats occasionally cross the fence from Botswana. Large native herbivores like Springbok (*Antidorcas marsupialis*), Gnu



Fig.1.5 View of the main study site in the Nossob river valley with large *Acacia erioloba* tree, June 2003.

(*Connochaetes taurinus*) and Gemsbok (*Oryx gazella*) are also practically excluded as they only occur in the Kalagadi Tranfrontier Park and on farms that are well fenced. The small antelopes Duiker (*Sylvicapra grimmia*) and Steenbok (*Raphicerus campestris*) do occur.

Part of the field work for Chapter 2 was carried out at a second study site on a farm near Vorstershoop in the Papanislaagte a dry tributary of the Molopo river (hereafter called the Molopo site; S 25° 50' and E 23° 02', North West Province, Republic of South Africa). The site has been farmland since 1953, and is grazed by cattle and some horses. Live stock is excluded every fourth year to enable soil and vegetation to regenerate. The farm was not grazed by livestock since 2001. This site receives more precipitation than the main study site, with 332 mm/year.

Comparative method

Treating species as independent data points when testing for trait correlations is the equivalent of pseudoreplication in a designed experiment (Harvey & Pagel 1991; Rees 1995). Statistical methods that treat species values as statistically independent points are not valid, because

closely related species will tend to share many characters through common descent rather than through independent evolution (see Harvey & Pagel, 1991). This may result in two characteristics being found together among species without there being any interesting reason: among homeothermic vertebrates, for instance, there is a very strong tendency for species with denucleated red blood cells to be covered with fur. This "strong correlation" is spurious, an artifact of the non-independence of species.

Plant ecologists often argue that phylogeny does not matter if they are not asking an evolutionary question (Silvertown & Dodd 1997; see Westoby *et al.* 1995a, b, 1996 for a defence of this argument). Westoby *et al.* (1995a), for example, state: *'There is good reason to believe that differences in vegetation between soils are the result of differential colonization, persistence or extinction by species populations sifted from the regional species pool. If this is true each species' presence in a vegetation type represents an independent item for colonization and persistence on that soil by a population possessing a particular set of attributes.'* In fact following this reasoning each individual represents such an independent item. However, as Harvey *et al.* (1995) argued, we don't use individuals instead of species because we recognize that they are not independent items of information for the evaluation of a hypothesis. But similarly species do also not provide statistically independent information.

One way to obtain statistically independent data for hypothesis testing is to use congeneric species pairs. Species within the same genus share a more recent common ancestor than species in different genera, differences (contrasts) in traits therefore developed independently of differences in other genera. Each contrast is therefore independent of the others and can be used as a data point in statistical tests.

A problem with this method is related to phylogenetic niche conservatism (PNG). Lack of change in a trait can occur because because a lineage possesses a suite of traits that fit it very well to the particular ecological niche it occupies and in which it can speciate, as a result it produces many species with the same trait combination (Silvertown & Charlesworth 2001). A relevant example for this study is the presence of fleshy fruits. The behaviour of birds universally leads to the concentration of bird dispersed seeds under isolated perches (McDonnell & Stiles 1983; Tester *et al.* 1987; Hoppes 1988; Izhaki *et al.* 1991; Guevara & Laborde 1993; Debussche & Isenmann 1994; Holl 1998). In habitats characterised by a two phase pattern of woody vegetation and open interspaces most fleshy fruited species will therefore be found under woody species and in the Southern Kalahari almost all perennial species under canopies have fleshy fruits. Because of PNG species in the same genus (or even whole families like the Cactaceae in North America) will usually all have fleshy fruits. This

makes it impossible to use the method of congeneric species pairs of matrix and canopy specialists to answer our questions about trait distribution between canopy and open interspaces.

A method that also uses information at higher nodes in the phylogeny is therefore needed. Phylogenetically independent contrasts do not need to be confined to congeneric comparisons. If one uses an evolutionary model to estimate the values of traits at nodes the contrast between the nodes is also phylogenetically independent (Felsenstein 1985). When a phylogeny is fully resolved n species results in $n-1$ contrasts that can be used for hypothesis testing. Thus with a full independent contrast analysis also more degrees of freedom are available for statistical tests than when using congeneric species pairs.

It is important to realize that phylogenetically independent contrasts do not solve the problem of confounding variables. Correlation between traits does not necessarily imply a causal relationship. However, phylogenetically controlled comparative analyses help to discard correlations based on pseudoreplication, and assure that hypotheses are tested at the appropriate degrees of freedom (Harvey 1996).

Thesis outline

This study seeks to determine the effect of regenerative traits on the origin and maintenance of vegetation patterns affected by the woody vegetation in arid regions. Different components of the regeneration niche are studied to evaluate their contribution to the vegetation pattern affected by *Acacia erioloba* canopies in the dry river beds of the Southern Kalahari. The study was carried out within the BIOTA Africa project which is funded by the German Federal Ministry of Education and Research (BMBF Förderkennzeichen 01 LC 0024 FuE “Trockensavanne”).

Chapter 2 describes the colonization pattern of *Acacia erioloba* canopies by fleshy fruited species in relation to tree age and rain fall and the relationship between colonization efficiency and seed persistence and seed size

Chapter 3. To evaluate the contribution of seed dispersal to the association of fleshy fruited species with *Acacia erioloba* canopies, and the effect of *Acacia erioloba* life history on dispersal processes, the seed rain is determined under mature acacia trees and saplings and in the surrounding open matrix. In addition seed removal rates in different microhabitats are determined as this could modify the distribution of dispersed seeds.

In Chapter 4 the seed bank under acacia canopies is compared with the seed bank in the surrounding matrix. Depth distribution is determined and correlated with seed shape and mass to determine if these traits can predict seed persistence. Depth distribution of seeds and vegetation data are used to determine seed persistence type (transient, short-term persistent, long-term persistent) which is then correlated with microhabitat association.

The relationship between germination cueing and microhabitat association are treated in Chapters 5, 6 and 7. The germination response to a gradient of decreasing water potentials is determined in chapter 6 and PICs are used in a multiple regression models to evaluate effects of life history traits (seed mass, dormancy) and habitat (soil type, canopy association) on this response. In Chapter 7 germination speed e.g. the time of wetting needed for seeds to germinate is measured and the data are analyzed in the same way as in chapter 6. In chapter 8 soil temperatures are measured at different cardinal positions under mature and sapling trees and in the surrounding matrix. The germination response to temperatures characteristic of open spaces and canopies is determined and possible correlations with canopy association and seed mass are explored using PICs.

Soil sod transplants are conducted to determine if dispersal is responsible for the two-phase pattern in the vegetation observed or if this (also) reflects differences in the ability of species to germinate and emerge in a microhabitat (Chapter 8).

Chapter 2

Seed size and persistence as determinants of colonization potential in a guild of bird dispersed plants from the Kalahari

Abstract

It is thought that seed mass is a major determinant of colonization potential because small seeded species produce higher numbers of seeds that are more persistent in the soil. The strength of the correlation between seed mass and colonization potential is expected to increase with increasing aridity due to the increased importance of seed persistence. All fleshy-fruited species found under individual *Acacia erioloba* trees were recorded at two sites with different annual precipitation and seed mass was determined for each species. Seed persistence of two selected species was studied by burying seeds for one year in the soil and one and three years dry storage in the lab. Species number increased twice as fast with stem circumference at the high rain fall site, demonstrating the increased establishment opportunities there. Tree occupancy was significantly correlated with seed size only at the low rain fall site. Of the three most common species shared between the two sites tree occupancy decreased most with decreasing rain fall in species with the least persistent seeds even though the species with the most persistent seeds had larger seeds than the second most persistent species. Under more arid conditions the relevance of seed persistence for colonization potential increases. This might explain the absence of a correlation between seed size and tree occupancy under more humid conditions but more studies about persistence and its relation to seed size in (semi-) arid regions are needed.

Introduction

Seed mass influences two important aspects of plant life history. First seed mass of a plant is negatively correlated with the number of seeds it can produce (Shipley & Dion 1992; Greene & Johnson 1994; Turnbull *et al.* 1999; Jakobsson & Eriksson 2000). Species with small seed are therefore considered to have superior colonizing abilities compared with large seeded species (Coomes & Grubb 2003). Second, seed mass is positively correlated with the resistance of seedlings against environmental hazards such as drought, herbivory or lack of resources such as light or nutrients (Leishman *et al.* 2000).

That smaller-seeded species are superior colonizers is reflected in the fact that they tend to dominate in the early stages of succession (Salisbury 1942; Baker 1972; Fenner 1987b; Rydin & Borgegård 1991; Kahmen & Poschlod 2004). Part of the high colonizing ability of small seeds is due to the fact that besides dispersal in space dispersal in time tends to be higher in smaller-seeded species: It has been shown for many floras around the world that species with persistent seeds have usually smaller seeds than species with transient seeds (Leck 1989; Thompson *et al.* 1993; Bekker *et al.* 1998; Funes *et al.* 1999; Moles *et al.* 2000; Thompson *et al.* 2001). However, it should be noted that such a relationship was not found for arid Australia (Moles *et al.* 2003) and South African fynbos (Holmes & Newton 2004).

In a landscape where a group of species is confined to a habitat that is distributed patchily (e.g. forest fragments, trees in a savanna) it is therefore expected that small seeded species occupy more habitat patches than large seeded species. Ehrlén & Eriksson (2000) found seed size to be negatively correlated with forest patch occupancy in forest herbs. Tackenberg (2001) found that the number of populations of species confined to isolated rocky outcrops in a matrix of agricultural land increased with dispersal potential and that including seed production in the dispersal potential strongly improved the relationship: higher seed production (smaller seeds) means higher seed dispersal potential (Poschlod *et al.* 2005). However, Jacquemyn *et al.* (2003) found a positive relationship between seed size and number of forest patches occupied. The discrepancy might be explained by the fact that Jacquemyn *et al.* (2003) included all forest species in their analysis and attributed the relationship to that the most common species were large seeded and bird dispersed shrubs. Tackenberg (2001), therefore, used species that did not differ in their essential functional traits except dispersal potential. Focusing on seed-size variation within a functional group therefore gives better interpretable results because functional traits other than seed size are less likely to vary.

Under different rain fall scenarios changes in the relationship between seed size and colonization potential are expected when seed persistence is correlated with seed size. The presence of a seed bank clearly has a higher advantage in more arid environments compared with more moist environments. For example the most extreme form of non-persistence, desiccation sensitive or recalcitrant seeds, is rare in arid and semi-arid ecosystems (Tweddle *et al.* 2003). If rainfall is more erratic seeds have to survive longer periods in the soil. Therefore we assume that the colonization potential of all species will increase under higher rain fall but the difference in colonization ability between species with a long time persistent seed bank and species with a transient or short time persistent seed bank will be larger under

more arid conditions. Provided that there is a correlation between seed size and persistence an increase in the advantage of persistent seeds will strengthen the correlation between patch occupancy and seed size.

We tested these hypotheses in the semi-arid savanna of the Kalahari river beds where a guild of fleshy fruited plant species typically occurs under the canopy of *Acacia erioloba* trees growing in a matrix of grass and low shrubs (Acocks 1953; Milton & Dean 1995; Dean *et al.* 1999). As the Kalahari is characterised by a gradient of precipitation with rain fall increasing in easterly direction this provides an opportunity to compare areas with a relatively similar species pool but differing in rain fall.

In summary we address the following questions:

1. Does species number in a tree occupied patch increase with time?
2. Does time of arrival and tree occupancy correlate with seed size?
3. Do species arrive faster and occupy more trees when rain fall increases?
4. Does colonization success decrease more in large seeded species than small seeded species when rainfall decreases?
5. Does the order in which species arrive change with rainfall and is this related to seed persistence?

To test the hypotheses 1.) presence for each fleshy fruited species was recorded under trees from a range of sizes in two areas with contrasting rainfall, 2.) seed size was determined and 3.) seed persistence in the soil of selected species was estimated by burying seeds for one year in the field and monitoring viability under dry storage.

Methods

Study area and survey

The study was carried out in the dry river beds intersecting the South African part of the Kalahari which forms a part of the savanna biome. The vegetation of these river beds can be described as an open savanna with camelthorn trees (*Acacia erioloba*) and fruiting shrubs scattered in a matrix of grass and low shrubs (Acocks 1953; Milton & Dean 1995). The rainy season typically lasts from about November to April, with 50 % of the total falling between January and March (Leistner 1967; Meyer 2004). Annual precipitation in the Kalahari increases in easterly and northerly directions with the driest southwestern areas receiving

about 150 mm and the northern parts up to 800 mm (Adams *et al.* 1996). Two sites with contrasting rain fall were selected for the purpose of this study:

The low rain fall site was situated in the dry Nossob river valley, appr. 40 km south of Twee Rivieren (hereafter called the Nossob site, 26°48' S and 20°39' E, Northern Cape, Republic of South Africa) and the vegetation is classified as Shrubby Kalahari Dune Bushveld (van Rooyen & Bredenkamp 1996b). It has not been grazed by livestock since 1974. Rainfall is about 200 mm/year and temperature varies between -10 and 45 ° C, average 20 °C.

The high rain fall area was a farm near Vorstershoop in the Papanislaagte a dry tributary of the Molopo river (hereafter called the Molopo site; S 25° 50' and E 23° 02', North West Province, Republic of South Africa) the vegetation is Kalahari Plains Thorn Bushveld (van Rooyen & Bredenkamp 1996a). The site has been farmland since 1953, and was grazed by cattle and a few horses. Live stock is excluded every fourth year to enable soil and vegetation to regenerate. The farm was not grazed by livestock since 2001. Rainfall is 332 mm/year temperature varies between -9 to 42 ° C, average 18 ° C.

In the Nossob river bed 134 *Acacia erioloba* trees were surveyed, 64 in Molopo. Both in austral summer and autumn of 2003. All fleshy fruited plant species growing within the patch formed by the vertical projection of the canopy were determined. Tree size was determined by measuring the girth of the stem at about 30 cm above ground level. Circumference at breast height could not be used as many trees branched at a very low level.

Seed mass and persistence

Seeds used to determine mass were collected at the Nossob site in the austral summer and autumn of 2001-2003. Seeds of *Ehretia rigida*, *Grewia retinervis* and *Rhus tenuinervis* were purchased from commercial seed suppliers. Seed mass was weighed for 20 seeds individually (if available, indicated in Table 2.1 if less) according to the protocol in Westoby (1998).

Seeds of *Pollichia campestris* and *Solanum capense* were collected at the end of the rainy season 2002 and dry stored for one and three years in the lab or buried in July 2002 in nylon mesh bags 3 cm deep under trees and in open spaces at the Nossob site. Per microhabitat 8 replications of 25 seeds per bag were used. Each canopy bag was buried under a different large *Acacia erioloba* tree, at a random cardinal orientation halfway between

stem and canopy dripline. Each matrix bag was buried at a random cardinal orientation, 12.5 m from the canopy dripline. After digging up seeds in May 2003 viability of seeds was determined with a tetrazolium test (International Seed Testing Association 1999). This

Table 2.1 Study species with family, seed weight (for $n = 20$, indicated if less), and presence (x) or absence (-) for the respective study sites. The last column indicates the species that were found in soil samples (+) from the Nossob site for which the seed bank was determined by the emergence method in the greenhouse (unpubl.).

Species	Family	Seed weight	Nossob, low rain	Molopo, high rain	Seed bank
<i>Asparagus africanus</i>	Asparagaceae	15.0 ± 2.6	×	? ¹	
<i>Asparagus pearsonii</i>	Asparagaceae	13.7 ± 1.9	×	? ¹	
<i>Asparagus</i> spec.	Asparagaceae	33.4 ± 2.7	×	? ¹	
<i>Corallocarpus bainesii</i>	Cucurbitaceae	16.9 ± 0.9	×	-	
<i>Cucumis africanus</i>	Cucurbitaceae	5.5 ± 1.1	×	-	
Cucurbitaceae spec.	Cucurbitaceae	-	-	×	
<i>Momordica balsamina</i> ²	Cucurbitaceae	104.2	-	×	
<i>Lycium bosciifolium</i>	Solanaceae	1.3 ± 0.3	×	-	+
<i>Lycium hirsutum</i>	Solanaceae	1.3 ± 0.3	? ³	? ³	
<i>Lycium</i> spec.	Solanaceae	-	-	×	
<i>Lycium villosum</i>	Solanaceae	1.9 (n = 1)	? ³	? ³	
<i>Solanum capense</i>	Solanaceae	3.3 ± 0.5	×	×	
<i>Solanum supinum</i>	Solanaceae	3.9 ± 0.2	-	×	+
<i>Boscia albitrunca</i>	Capperaceae	62.4 ± 14.4	×	×	
<i>Ehretia rigida</i>	Boraginaceae	5.5 ± 1.1	×	×	
<i>Grewia flava</i>	Tilliaceae	31.7 ± 8.4	×	×	
<i>Grewia retinervis</i>	Tilliaceae	42.9 ± 17.9 (n = 12)	-	×	
<i>Pollichia campestris</i>	Illecebraceae	0.4 ± 0.1	×	×	+
<i>Rhus tenuinervis</i>	Anacardiaceae	10.0 ± 1.9	×	-	

¹ the *Asparagus* species in this area could not be identified, for calculations the average seed mass of all three species was used

² seed mass taken from Flynn *et al.* (2004).

³ *Lycium hirsutum* and *Lycium villosum* are indistinguishable in the vegetative state and were therefore pooled for the analysis. Seed weight of *L. hirsutum* was used as it has the same size as *L. villosum* (A. M. Venter, unpubl.) and only one seed was found in one *L. villosum* fruit and it was therefore thought to be larger and unrepresentative.

method was also used for the three years dry stored seeds. For the '1 year dry storage' treatment, viability was determined by germinating the seeds for 8 weeks (26/19°C for *Solanum*, 22/22°C for *Pollichia*, with a 12 hour day/night regime) and then pressing the remaining seeds with tweezers. Firm, intact and germinated seeds were recorded as viable (Baskin & Baskin 1998). Dry storage in the lab was at 5° C.

Statistics

The relationship between seed size and tree patch occupation and time of arrival was analyzed with simple linear correlation. Prior to analysis seed size was log transformed. The relationship between species number and tree circumference was analysed by means of linear regression. We tested for a difference in the regression coefficients as described in Zar (1999).

The proportion of viable seeds for the storage treatments was arcsine transformed prior to analysis. The homogeneity of variances between treatments was determined by means of an F_{\max} test. Differences between seed storage treatments were then tested for by one-way ANOVA followed by a Tukey-test.

Results

The number of species increased with stem circumference in both the Nossob ($y = 0.022x - 0.207$, $r^2 = 0.593$, $F = 192.43$, $P < 0.001$) and Molopo ($y = 0.0469x - 0.4494$, $r^2 = 0.767$, $F = 204.66$, $P < 0.001$) areas (Fig. 2.1). Species number increased with stem circumference more than twice as fast in the Molopo area than in the Nossob valley. The slopes of the species - stem circumference curves were significantly different ($t_{(2) 194} = 9.292$, $P < 0.001$) also when the data set for the Nossob area was reduced to trees ≤ 195 cm stem circumference, which is the maximum size for the Molopo area ($t_{(2) 176} = 9.753$, $P < 0.001$) and when the latter data set was reduced to five species shared between the two sites that could be unequivocally identified (*Boscia albitrunca*, *Ehretia rigida*, *Grewia flava*, *Pollichia campestris*, *Solanum capense*, $t_{(2) 176} = 12.356$, $P < 0.001$).

To determine tree occupancy only trees larger than the minimum size for which all species have been recorded were included in the analysis. Thus ensuring that abiotic conditions were suitable for all species and minimizing the chance that differences in occupancy were due to different habitat requirements. For the Nossob area small seeds occupied more trees than large seeded species ($r = -0.605$, $n = 13$, $P < 0.05$). But in the Molopo area this was not the case ($r = -0.475$, $n = 11$, n.s. Fig. 2.2). For the smallest tree circumference for which a species was recorded (time of arrival) and seed mass no significant

correlations were found (Nossob area $r = 0.339$, $n = 13$, n.s., Molopo area $r = 0.465$, $n = 11$, n.s. Fig. 2.3). However, if species are divided in two groups, one with seed mass < 5 mg and one with seed mass > 5 mg the minimum stem circumference of *Acacia erioloba* trees where species were found was actually lower for small seeded species than for large seeded species for the Nossob site (Mann-Whitney-U = 4.0, $P < 0.05$), but no difference was found for the Molopo site.

Species shared between the two study sites reacted different to the difference in rain fall. *Solanum capense* seems to be little influenced. *Pollichia campestris* and *Grewia flava* however, colonize the subcanopy earlier in the Molopo area with higher rain fall (Fig. 2.4, Table 2.2). *Solanum capense* has very persistent seeds while the viability of *Pollichia campestris* seeds seems to decrease steadily with time and burial also has a negative effect (Fig. 2.5).

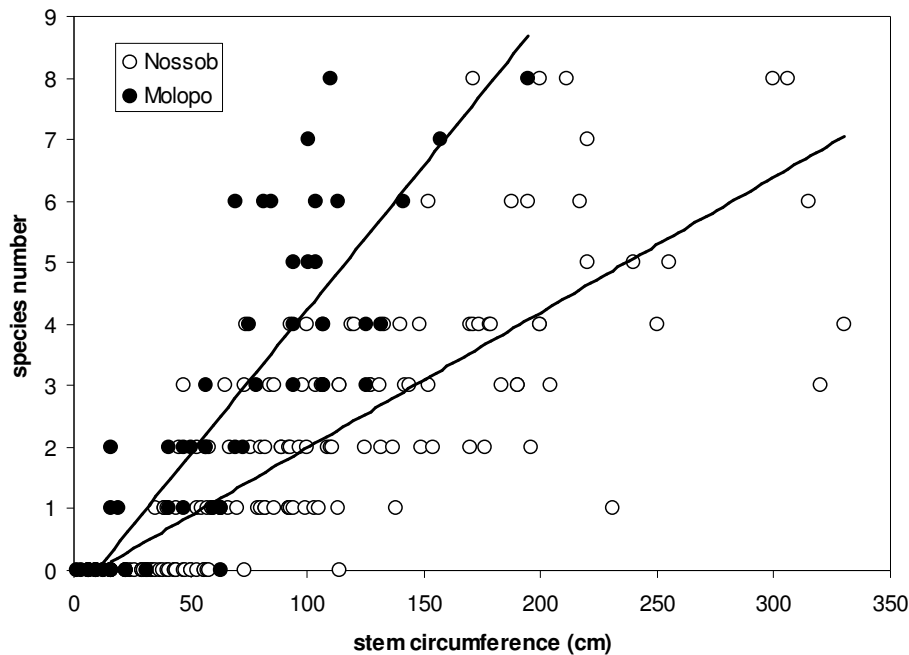


Fig. 2.1 Relation between tree circumference and number of fleshy-fruited plant species growing under it for the Nossob ($y = 0.022 x - 0.207$, $r^2 = 0.593$, $F = 192.43$, $P < 0.001$) and Molopo ($y = 0.0469 x - 0.4494$, $r^2 = 0.767$, $F = 204.66$, $P < 0.001$) areas. The slopes of the species - stem circumference curves were significantly different ($t_{(2) 194} = 9.292$, $P < 0.001$).

Discussion

The data are partly consistent with the hypothesis that small seeded species are superior colonizers. For the low rain fall site a significant negative correlation between tree occupancy and seed size was found. The absence of a significant correlation between minimum stem

circumference of the host tree and seed mass in both sites is probably due to the sensitivity of this measurement to outliers. The fact that under higher rain fall no significant correlation between tree occupancy and seed mass was found indicates that small seeded species are not always superior colonizers. A possible explanation is that when rain fall increases, persistence

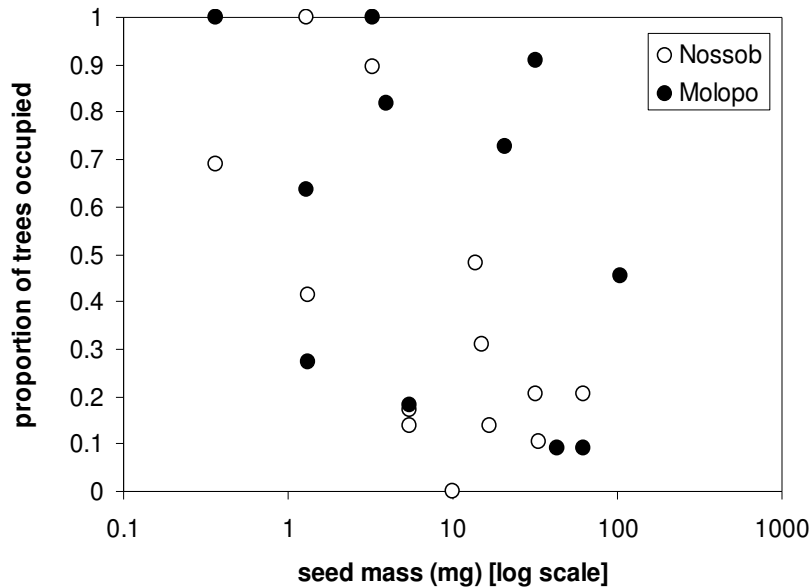


Fig. 2.2 Proportion of trees occupied by fleshy-fruited species in relation to their seed mass for the Nossob area ($r = -0.605$, $n = 13$, $P < 0.05$, annual precipitation 200 mm, trees > 171 cm stem circumference) and the Molopo area ($r = -0.475$, $n = 11$, n.s., annual precipitation 332 mm, trees > 105 cm stem circumference).

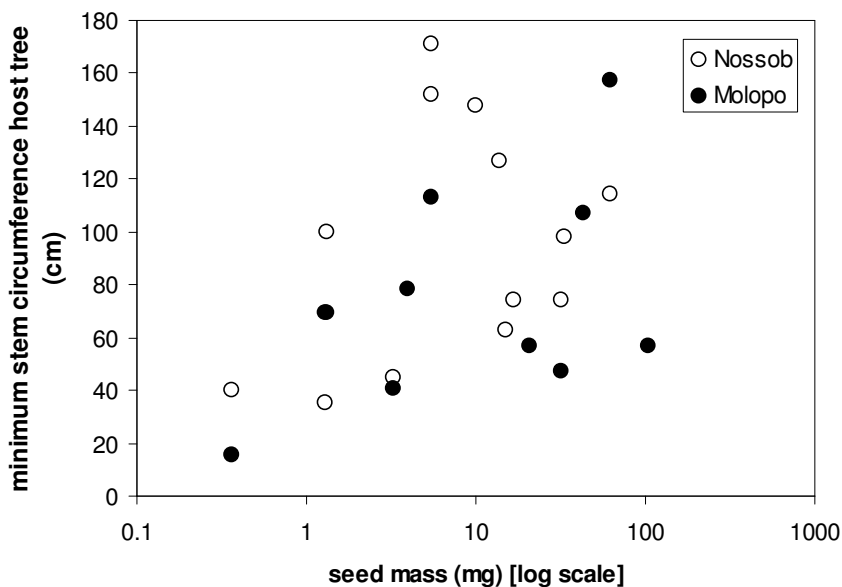


Fig. 2.3 Smallest stem circumference of *Acacia erioloba* trees where the species was recorded in relation to seed mass for the Nossob area ($r = 0.339$, $n = 13$, n.s., annual precipitation 200 mm) and the Molopo area ($r = -0.465$, $n = 11$, n.s., annual precipitation 332 mm).

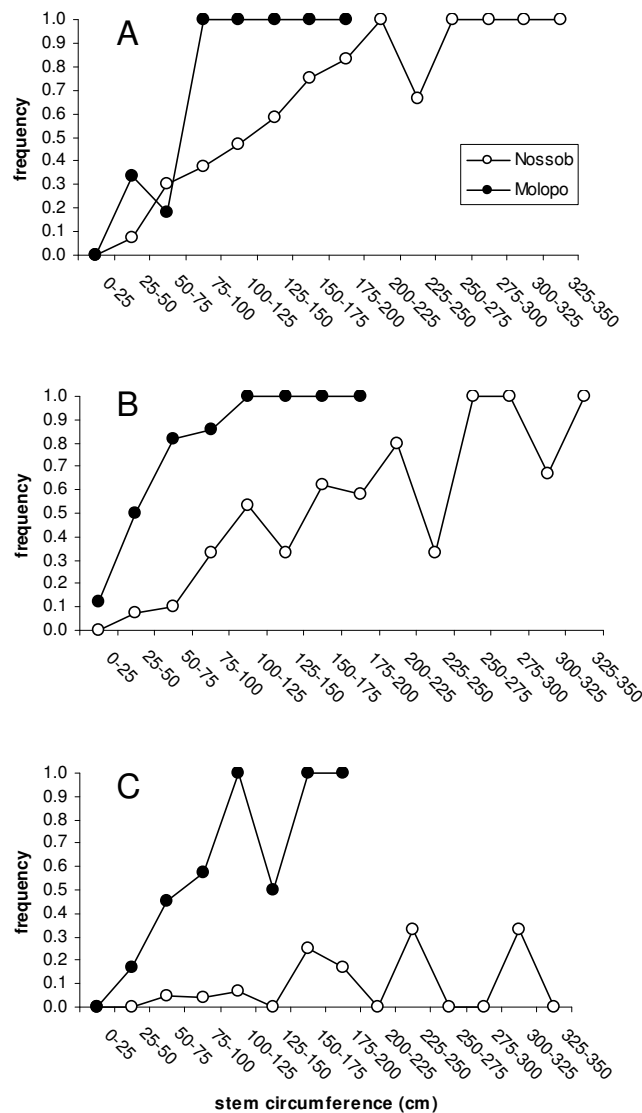


Fig. 2.4 Frequency of tree occupancy for different tree size classes for the three most common fleshy-fruited species present at both study sites: *Solanum capense* (A), *Pollichia campestris* (B) and *Grewia flava* (C). Note that *Grewia flava* forms no seed bank and has the largest seeds, *Pollichia campestris* has the smallest seeds but these are less persistent than those of *Solanum capense*.

becomes a less important aspect of the colonization potential of plant species. The faster increase of species number with tree size at the higher rain fall site suggests the larger establishment window available for species there. Though large seeded species still produce less seeds the higher resistance against environmental hazards of large seeds (Leishman *et al.* 2000), compensates for this. In this way both large seeded and small seeded species may be equally successful colonizers using different strategies. It is conspicuous that the only case known to us where no relation was found between seed size and number of habitat patches

Table 2.2 The smallest stem circumference for which a species was recorded and tree occupancy (%) at the high and low rain fall sites for the three most common fleshy-fruited species shared between the sites.

	Site	First arrival (cm stem circumference)	Tree occupancy (%)
<i>Pollichia campestris</i>	High rain	16	100
	Low rain	40	69
<i>Solanum capense</i>	High rain	41	100
	Low rain	45	90
<i>Grewia flava</i>	High rain	47	91
	Low rain	74	21

occupied was undertaken in the tropics (Hovestadt 1997). Similarly Kelly (1995) did not find a relationship between seed size and the successional stage of tropical forest. Under high rainfall large and small seeded species may be equally effective colonizers. This hypothesis is supported by the seed persistence and colonizing behaviour of the three most common species occurring at both sites. Under high rain fall the species with smallest seeds, *Pollichia campestris*, occupies most trees and arrives fastest, followed by *Solanum* and the largest seeded species *Grewia* respectively. Under low rainfall *Solanum*, which has larger but more persistent seeds than *Pollichia*, becomes the best colonizer. *Grewia*, which has seeds about 10 and 100 times heavier than *Solanum* and *Pollichia*, is the poorest colonizer at both sites. *Grewia* is also a species that germinates better in the dark than in light (Weiersbye & Witkowski 2003). A light requirement for germination is seen as a prerequisite for forming a persistent seed bank (Baskin & Baskin 1989; Pons 1991) which suggests it has no long term persistent seeds. This is confirmed by the observed lack of survival in the soil (F. Schurr, personal communication).

The fact that the smaller seeded *Pollichia campestris* has less persistent seeds than the larger seeded *Solanum capense* suggests that seed persistence may not be strongly correlated with seed size. There is no conclusive evidence that the relation between seed size and persistence found in many parts of the world also exists in arid and semi-arid ecosystems. Price & Joyner (1997) found large seeds to be under-represented in the seed bank relative to their density in the seed rain in the Mojave desert, California. But Moles *et al.* (2003) found no relationship between seed size and persistence in arid Australia. However, this may well be due to different behaviour of seed predators in Australia. However, for our study species the available information suggests that larger seeds are indeed less persistent. The large seeded (> 13 mg) *Asparagus* spp. (see Chapter 4) and *Grewia flava* (Weiersbye & Witkowski 2003) germinate as well or even better in the dark as in the light. The very large seeds of *Boscia*

albitrunca survive only one or two seasons in the soil (Briers 1988). The small seeded (< 4 mg) *Pollichia campestris*, *Solanum capense* and *Lycium bosciifolium* all have a complete or partial light requirement for germination and are the only species found in the seed bank (see Chapter 4).

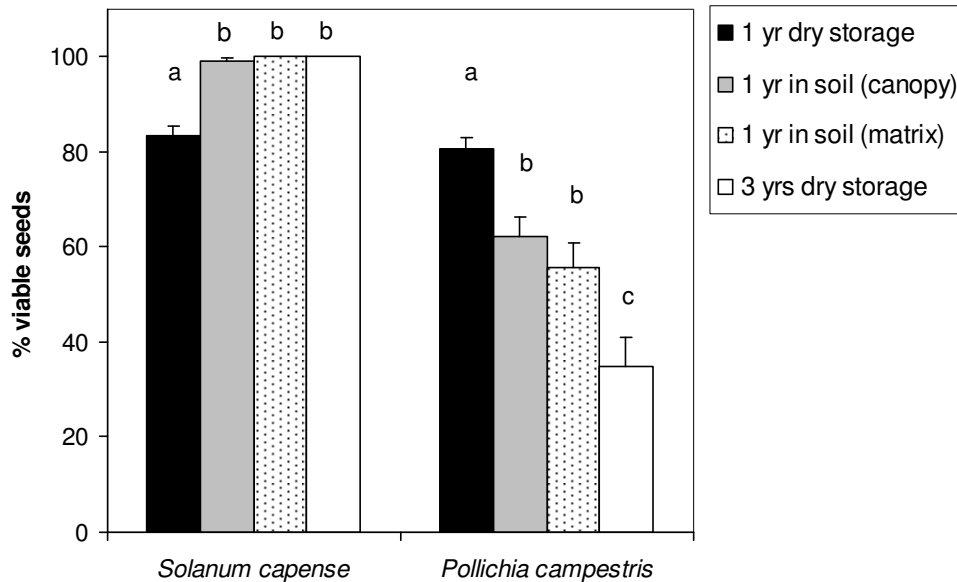


Fig. 2.5 Viability of seeds of *Solanum capense* and *Pollichia campestris* after varying periods of storage in the soil and the lab (see legend), indicated is the mean plus one standard error. Different letters indicate significant differences between treatments within a species (one-way ANOVA followed by Tukey-test).

Conclusion

This study demonstrates the importance of seed size as a correlate of colonization potential and that the amount of annual precipitation influences this relationship. However, it is not possible to distinguish clearly between the different ways by which seed size influences colonization potential. Both seed number and seed persistence may be important. More studies in (semi-) arid environments are needed to separate between the relative effects of different seed traits correlated with seed size like seed bank persistence, seed number and resistance of seedlings against environmental hazards.

Chapter 3

Directed dispersal of fleshy fruited plants to *Acacia erioloba* trees in the Southern Kalahari

Abstract

In arid environments fleshy-fruited plants are often associated with nurse plants. Disproportional dispersal to canopies, favorable conditions for germination and establishment and reduced seed predation under canopies have all been proposed as mechanisms to explain such patterns. These hypotheses were tested in a dry river bed in the Southern Kalahari where fleshy fruited plants are associated with camelthorn (*Acacia erioloba*) trees. Seed rain of *Lycium* was found to be higher under *Acacia erioloba* trees than in the open matrix and seed rain was higher under mature trees than under saplings in 2002. In 2003 there was no difference between mature trees and saplings, but seed rain under both was higher than in the matrix. Seed rain of *Solanum capense* was higher under saplings than under mature trees in 2003, no differences between microhabitats were observed in 2002. No emergence of sown seeds of *Lycium bosciifolium* and *Pollichia campestris* took place in the matrix. Though the difference was not significant seedlings only emerged under the canopy of mature trees. For *Lycium* no significant differences between the number of seeds collected from the soil and from traps excluding predators were observed for all microhabitats. For *Solanum* there was only a significant difference for saplings, where the number of seeds collected from the soil was less than that from traps, suggesting more predation under saplings than under mature trees. This could be due to litter hiding seeds as litter is practically absent under saplings. The sparrow weaver, a mainly insectivorous bird, may be an important disperser of fleshy fruited plants in the Kalahari. Seed rain of *Lycium* and *Solanum* under nests of this species was higher than the average seed rain under mature trees and seeds of *L. bosciifolium* survive and germinate after ingestion. The results indicate that all three proposed mechanisms are probably responsible for the association of fleshy fruited species under camelthorn canopies.

Introduction

In arid and semi-arid vegetation types, such as deserts and savannas, a distinct assemblage of plant species is commonly associated with the canopies of the initially establishing pioneer

woody species commonly called nurse plants (Tester *et al.* 1987; Milton & Dean 1995; Dean *et al.* 1999; Tewksbury *et al.* 1999). Many of these species have fleshy fruits and are dispersed by birds or bats.

Two main explanations for such patterns have been put forward. First the improved conditions provided by the established vegetation. In arid environments temperature, soil moisture, soil nutrients and radiation differ strongly from open spaces (Belsky *et al.* 1989; Weltzin & Coughenour 1990; Vetaas 1992; Belsky *et al.* 1993; Belsky & Canham 1994). Experimental studies showed that some of these conditions like shading and higher nutrient levels under the canopy improved survival and growth of seedlings under the canopy compared with open spaces (Valiente-Banuet & Ezcurra 1991; Fulbright *et al.* 1995; Carillo-Garcia *et al.* 2000).

Secondly localized dispersal by birds or other animal dispersal agents that preferentially perch roost or nest in nurse trees could be responsible. The seed rain of bird dispersed species tends to be concentrated under isolated trees used by birds for perching, roosting and nesting (McDonnell & Stiles 1983; Tester *et al.* 1987; Hoppes 1988; Izhaki *et al.* 1991; Guevara & Laborde 1993; Debussche & Isenmann 1994; Holl 1998). Nurse plants are often the only perches or nest sites available in arid and semi-arid environments.

It is likely that in most cases both factors are important (Fulbright *et al.* 1995; Milton & Dean 1995; Dean *et al.* 1999; Tewksbury *et al.* 1999) and dispersal by birds to nurse plants in arid and semi-arid ecosystems presents therefore a strong case for directed dispersal e.g. disproportionate arrival in sites especially favourable for survival (Howe & Smallwood 1982; Wenny 2001).

However, most studies on fleshy-fruited species and their nurse plants in arid and semi-arid environments have concentrated on seedling growth and patterns of nurse-protégé associations but did not document the spartial distribution of the seed rain. The few studies that also included the seed rain pattern mostly did so by extrapolating observations on dispersers to the actual seed rain (Tewksbury *et al.* 1999; Godínez-Alvarez *et al.* 2002) but not by measuring the seed rain directly (but see Tester *et al.* 1987). So though directed dispersal of fleshy-fruited plants in arid and semi-arid ecosystems is generally assumed, it has rarely been demonstrated.

A third factor that could have an influence on the association of fleshy fruited plants with nurse plants is nonrandom seed predation. No difference in seed survivorship of columnar cacti depending on nurse plants was found between shaded and open microhabitats by Valiente-Banuet & Ezcurra (1991) and Sosa & Hernandez (unpublished data in Sosa &

Fleming 2002). However, in these studies litter or pebbles had been removed previous to the start of the experiments. When placed on leaf litter and sand more seeds were removed from sand than from leaf litter (V. Sosa & A. Hernandez, unpublished data in Sosa & Fleming 2002). As leaf litter is usually only found under trees or shrubs this could also account for an association of fleshy-fruited species with nurse plants.

The hypotheses mentioned above were tested in the Kalahari, South Africa. In the Southern Kalahari more frugivorous bird species and individuals were seen on mature than sapling or dead trees (Milton & Dean 1995; Dean *et al.* 1999). At the same time plants with fleshy-fruits occurred under 91 % of large trees but under only 17 % of saplings and 8 % of treeless plots (Dean *et al.* 1999). This suggests that seed rain might be more dense under large trees than under sapling trees or the surrounding matrix.

The following questions were addressed in this study:

1. Is the seed rain higher under acacia canopies than in the surrounding open matrix?
2. Is seed rain higher under mature trees than under saplings?
3. Is emergence of seedlings higher in seeds sown under acacia canopies than in seeds sown in the surrounding open matrix?
4. Is seed predation lower under mature trees than under saplings or in the matrix?
5. What are the legitimate dispersers?

To answer these questions the seed rain in different microhabitats was determined using seed traps. To estimate seed predation pressure in different microhabitats seed numbers collected from traps and from the soil were measured and compared for different microhabitats. Observations on dispersers feeding on *Lycium bosciifolium* were made and seed rain was measured under the nests of sociable weavers (*Philetarius socius*), one of the more common feeders on *Lycium* berries. Seeds were extracted from sociable weaver faeces and germination percentage compared with undigested seeds.

Methods

Study species

Fleshy-fruited plant species in the study area that fruited during the study period were *Lycium* spp. (Fig. 3.1), *Asparagus* spp, *Pollichia campestris*, *Solanum capense* and *Tapinanthus oleifolius*.



Fig. 3.1 *Lycium bosciifolium* with flowers and fruits

Seed rain and predation

Seed traps were plastic bowls with a round catching area of 233 mm diameter and about 10 cm deep. They were covered with chicken wire to prevent seed predation by birds or rodents. Seed removal by ants was also prevented as ants could not climb the smooth plastic. Four traps were placed under each mature *Acacia* tree, about half way between trunk and canopy dripline at corners of 90°, forming a cross, but random with regard to cardinal orientation. Four traps were placed in the matrix around the mature tree, along the same line from trunk to canopy trap, 15 paces \approx 12.75 m from the canopy drip line. In 2002 8 mature trees were sampled and 24 saplings, the three saplings closest to the mature tree per large tree plot. Each sapling had one trap at a random cardinal orientation half way between trunk and canopy dripline. In 2003 10 mature trees and 10 saplings were sampled, the saplings in the same way as described for mature trees above, with also four traps per tree. Traps were emptied weekly. Seed rain was measured during the fruiting period of the most common species (depending on rain fall) for two years: 10 May to 9 June and 23 June to 14 July 2002 and 14 March to 9 May 2003, 51 days in 2002, and 56 days in 2003. Seed rain was calculated as $\text{seeds}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Only seeds from bird droppings were used and seeds still in berries were excluded from the calculations. Seed traps under sociable weaver nests were small 2 l buckets with a diameter of 165 mm. Seed rain was measured for 40 days under three nests located in different trees in 2002. Additionally special seed traps were used to determine seed input by birds as described in Grunicke (1996). They consisted of a perching stick, round with a diameter of 13 mm at 1.4

m height above ground level, 15 cm above the centre of a dark green plastic funnel (\varnothing 24 cm) with a bag of nylon mesh attached under it to collect the seeds (Fig. 3.2), 12 traps were set up in 2002, 10 in 2003. To get an estimate of seed predation in different microhabitats wire hoops of the same diameter as the seed traps (233 mm) were positioned in the same manner as the plastic bowls under the canopy of mature and sapling acacias and in the matrix and seeds and bird droppings within the hoops were also collected every week from 30 March 2003 to 9 May 2003, 40 days.



Fig. 3.2 Seed trap to determine ornithochory (after Grunicke 1996)

Sowing experiment

Seeds of *Lycium bosciifolium* and *Pollichia campestris* were sown in plots under mature acacia canopies and in the surrounding matrix. For each of seven plots per micro-habitat 30 seeds of each species were sown in one half of the 30 cm \times 30 cm plots in a grid with distances of 3 cm between seeds. Plots were covered by 30 cm \times 30 cm \times 15 cm cages of chicken wire to prevent seed predation and disturbance by birds and rodents. Seeds were sown

June 2002 and emergence was recorded in March 2003 after a large rain fall event of ± 50 mm in February.

Germination experiment

Seeds of *Lycium bosciifolium* were extracted from faeces collected directly under a sociable weaver nest and from freshly collected fruits. Intact seeds were selected and for each treatment 8 petridishes with 25 seeds per dish were used. Berries for the control and manual scarification treatments were collected from 5 different bushes and each Petri dish contained 5 seeds from each bush. Manual scarification consisted of dragging the seeds over 420 sandpaper, over a distance of 1 cm. Seeds were germinated under shaded conditions in an unheated room in the Kalahari where temperature fluctuated from 10 to 25 ° C over the duration of the experiment but diurnal temperature fluctuations were < 10 °C.

Statistical analysis

The data for seed rain, seed predation and seedling emergence deviated strongly from normality and normality of the data could also not be achieved by transformation. Therefore these data were analysed using non-parametric statistics. For comparing seed rain under mature trees sapling trees and matrix Friedman's test was used: a nonparametric test for more than two connected samples. Each plot (mature tree, surrounding matrix and nearby sapling) was treated as a block. Significant differences between treatments were determined by Tukey-type multiple comparisons for nonparametric repeated-measure ANOVA (Zar 1999). Wilcoxon's test for matched pairs was applied to compare seeds collected from traps with seeds collected directly from a similar surface of soil and to compare seedling emergence under trees and in the matrix. To compare the average seed rain under mature acacias with the seed rain directly under sociable weaver nests the Mann-Whitney-*U* Test was applied. The germination data, being the proportion of viable seeds that germinated, were arcsine transformed prior to analysis. After confirming the homogeneity of variances data were analysed by one-way ANOVA followed by a Tukey-test

Results

Feeding observations

Bird species observed to feed on *Lycium bosciifolium* berries on 16 and 17 May 2002 were Acacia pied barbet (*Tricholaema leucomelas*), Cape Glossy Starling (*Lamprotornis nitens*),

Chestnut-vented Tit-Babbler (*Parisoma subcaeruleum*) Greater Scimitarbill (*Phoeniculus cyanomelas*) and Sociable Weaver (*Philetarius socius*). Acacia pied barbets were also seen feeding on mistletoe berries (*Tapinanthus oleifolius*). Droppings collected under Sociable weaver and White-browed Sparrow Weaver nests contained *Lycium* and *Solanum* seeds. Cape Glossy Starling (*Lamprotornis nitens*) and White-browed Sparrow Weaver (*Plocepasser mahali*) were the only species observed to perch on the artificial perches with seed traps.

Artificial perches

Species found in seed traps with artificial perches are listed in Table 3.1.

Table 3.1 Number of seeds retrieved from traps under artificial perches for 2002 ($n = 12$) and 2003 ($n = 10$). Values given are average \pm standard deviation and the total number of seeds between brackets.

	2002 (24.4 – 9.6)	2003 (21.3 – 10.5)
<i>Lycium</i> spp.	38.9 \pm 43.1 (971)	27.4 \pm 46.1 (486)
<i>Solanum capense</i> L.	0.6 \pm 1.1 (16)	0
<i>Pollichia campestris</i> Ait.	0.4 \pm 0.7 (9)	(1)
<i>Asparagus</i> spp.	0	(2)
<i>Tapinanthus oleifolius</i> (Wendl.)	0.2 \pm 0.4 (4)	0
Danser		

Seed rain in different microhabitats: *Lycium bosciifolium*

In 2002 all habitats differed from each other in seed rain (Friedman-test $n = 8$, $\chi^2 = 8.615$, $df = 2$, $P < 0.05$, followed by Tukey-type multiple comparisons for nonparametric repeated measure ANOVA (Zar 1999), $P < 0.001$). Seed rain was highest under mature trees and lowest in the matrix (Fig. 3.1). In 2003 seed rain under mature trees and saplings did not differ significantly but seed rain under both was significantly higher ($P < 0.001$) than in the open matrix (Friedman-test $n = 10$, $\chi^2 = 7.257$, $df = 2$, $P < 0.05$, followed by Tukey type multiple comparisons for nonparametric repeated-measure ANOVA (Zar 1999) (Fig 3.3).

Seed rain in different microhabitats: *Solanum capense*

In 2002 there were no significant differences in seed rain between habitats (Friedman-test $\chi^2 = 3.895$, $df = 2$, n.s.). In 2003 there were significant differences in seed rain between all habitats (Friedman-test $\chi^2 = 6.333$, $df = 2$, $P < 0.05$, followed by Tukey type multiple comparisons for nonparametric repeated-measure ANOVA (Zar 1999), $P < 0.001$, see Fig 3.4). In contrast

with *Lycium* seed rain was highest under saplings, but like in *Lycium* it was lowest in the matrix.

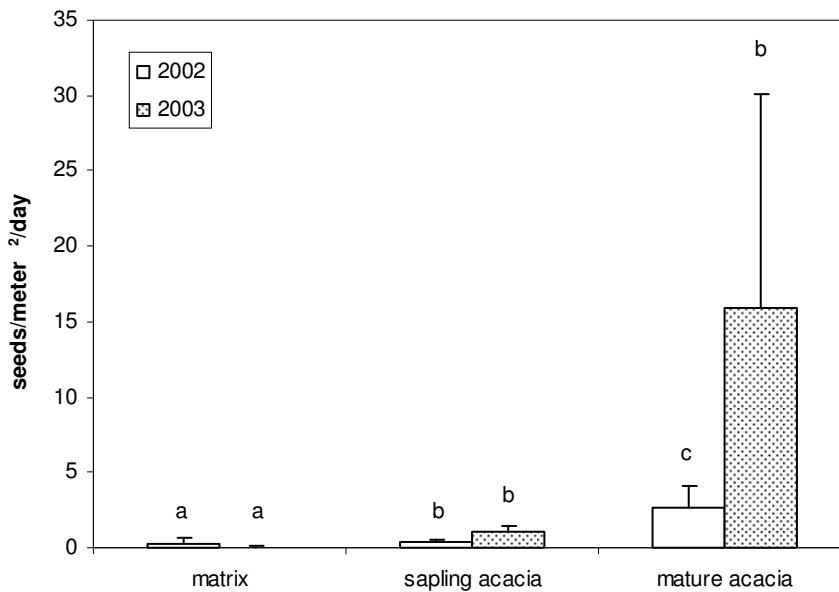


Fig. 3.3 Seed rain (seeds · meter⁻² · day⁻¹) of *Lycium* spp in the matrix, under sapling *Acacia erioloba* trees and under mature *Acacia erioloba* trees (for each habitat $n = 8$ in 2002, $n = 10$ in 2003). Significant differences in seed rain among microhabitats within each year for Friedman-test followed by Tukey-type multiple comparisons for nonparametric repeated-measure ANOVA are indicated by different letters.

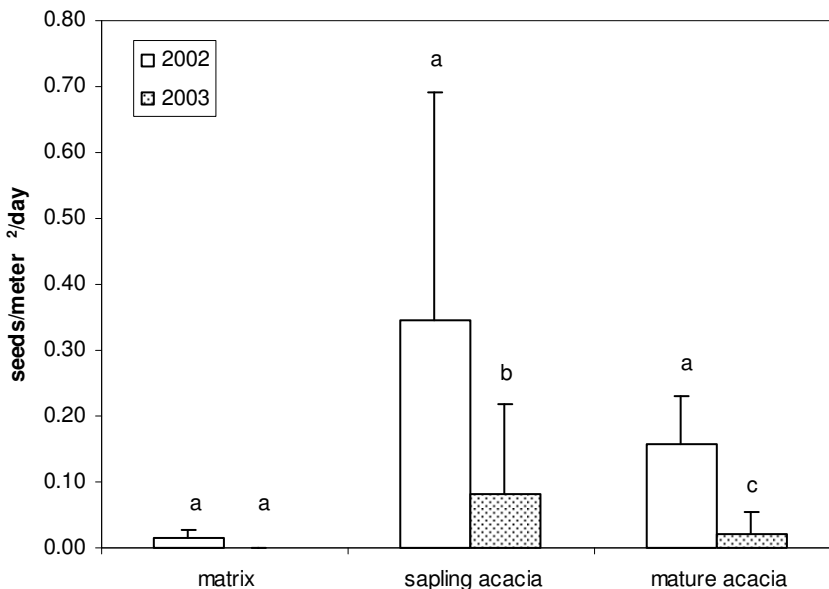


Fig. 3.4 Seed rain (seeds · meter⁻² · day⁻¹) of *Solanum capense* in the matrix, under sapling *Acacia erioloba* trees and under mature *Acacia erioloba* trees (for each habitat $n = 8$ in 2002, $n = 10$ in 2003). Significant differences in seed rain among microhabitats within each year for Friedman-test followed by Tukey-type multiple comparisons for nonparametric repeated-measure ANOVA are indicated by different letters.

The effect of sociable weaver nests on seed rain

Seed rain of both *Lycium* spp. and *Solanum capense* was higher under sociable weaver nests (medians 77.2 and 4.7) than under large mature trees (medians 1.2 and 0, Mann-Whitney Test, $n_1 = 3$, $n_2 = 8$, $U = 0.000$, $Z = -2.449$, $P < 0.05$).

Seed predation

For *Lycium* spp. no significant differences were found between seeds caught in seed traps and from soil in all three microhabitats (Wilcoxon-test: open matrix: $Z = 0.000$, $n = 10$, n.s., sapling acacia: $Z = -0.534$, $n = 10$, n.s., mature acacia: $Z = -0.280$, $n = 10$, n.s.). The number of seeds collected was different between all microhabitats when exposed to predation (Friedman-test $\chi^2 = 7.943$, $df = 2$, $P < 0.05$, followed by Tukey type multiple comparisons for nonparametric repeated-measure ANOVA, $P < 0.001$, see Fig. 3.3), while there was no difference between sapling and mature acacias for seeds from traps (Friedman-test $\chi^2 = 7.257$, $df = 2$, $P < 0.05$, followed by Tukey type multiple comparisons for nonparametric repeated-measure ANOVA, see Fig. 3.5).

For *Solanum capense* there was a significant difference for sapling acacias: the number of seeds collected from the soil was lower than those collected from seed traps (Wilcoxon-test: open matrix: $Z = 0.000$, $n = 10$, n.s., sapling acacia: $Z = -2.060$, $n = 10$, $P < 0.05$, mature acacia: $Z = -0.816$, $n = 10$, n.s.). This resulted in that the significant differences between all microhabitats (Friedman-test $\chi^2 = 6.333$, $df = 2$, $P < 0.05$, followed by Tukey type multiple comparisons for nonparametric repeated-measure ANOVA, see Fig. 3.4) disappeared when seeds were exposed to predation (Friedman-test $\chi^2 = 1.000$, $n = 10$, $df = 2$, n.s, see Fig. 3.6).

Seedling emergence

No significant differences between canopy and matrix in emergence of seedlings was observed for either *Lycium bosciifolium* (Wilcoxon-test: $Z = -1.604$, $n = 7$, n.s.) or *Pollichia campestris* ($Z = -1.000$, $n = 7$, n.s.). However, *Lycium bosciifolium* emerged in three canopy plots (16, 12 and 1 seedlings), and *Pollichia campestris* in one canopy plot (9 seedlings) but no seedlings were observed in matrix plots.

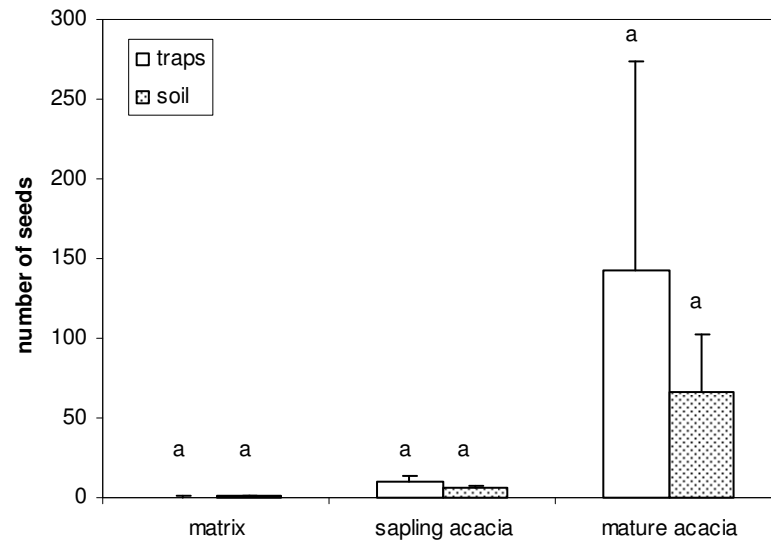


Fig. 3.5 Number of *Lycium spp* seeds collected from seed traps and from soil in the matrix, under sapling *Acacia erioloba* trees and under mature *Acacia erioloba* trees in 2003 ($n = 10$ for each treatment per habitat). Significant differences in seed number between soil and traps for Wilcoxon's test for matched pairs are indicated by different letters.

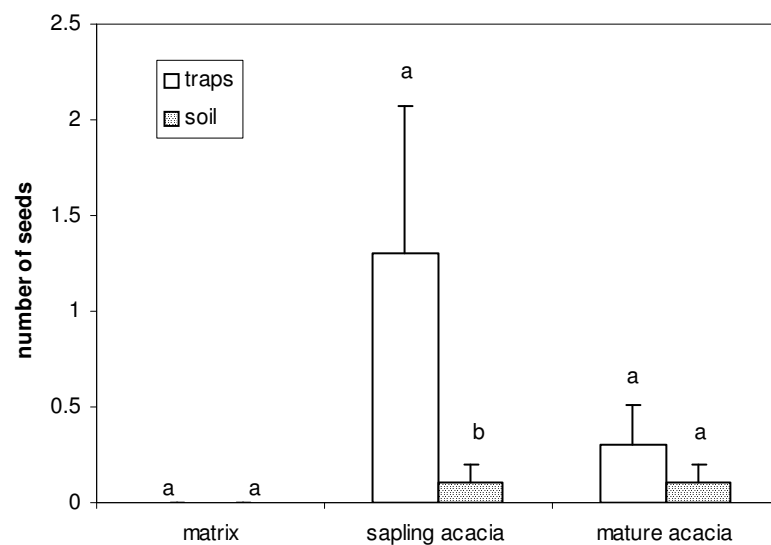


Fig. 3.6 Number of *Solanum capense* seeds collected from seed traps and from soil in the matrix, under sapling *Acacia erioloba* trees and under mature *Acacia erioloba* trees in 2003 ($n = 10$ for each treatment per habitat). Significant differences in seed number between soil and traps for the Wilcoxon's test for matched pairs are indicated by different letters.

Germination

The minimum time to germination was shorter for seeds eaten by sociable weavers compared with manually scarified and control seeds (one-way ANOVA, $F_{2,21} = 6.213$, $P = 0.008$ followed by a Tukey test, Table 3.2, Fig. 3.1). For t_{50} manual scarification and control did not differ significantly but seeds ingested by sociable weavers had a significantly lower t_{50} than

manually scarified seeds (one-way ANOVA, $F_{2,21} = 7.958$, $P = 0.003$ followed by a Tukey test Table 3.2, Fig. 3.7). There were no statistically significant differences between control and manual scarification. The % of viable seeds (germinated + viable at the end of the experiment) did not differ between treatments (one-way ANOVA $F_{2,21} = 0.070$, $P = 0.933$, Table 3.2, Fig. 3.7).

Table 3.2 The effect of different treatments (control, manual scarification and ingestion by sociable weavers) on germination speed, final germination % and % of viable seeds in *Lycium bosciifolium*. Different letters indicate significant differences ($P < 0.05$) for one-way ANOVA followed by a Tukey test.

	Control	Manual scarification	Ingestion by sociable weaver
Minimum time to germination (days)	8 ± 2^a	7 ± 4^a	3 ± 1^b
t_{50} (days)	13 ± 4^{ab}	17 ± 5^a	9 ± 2^b
Final germination %	61 ± 16^a	58 ± 14^a	81 ± 6^b
Viable seeds (%)	75 ± 13^a	74 ± 8^a	75 ± 9^a

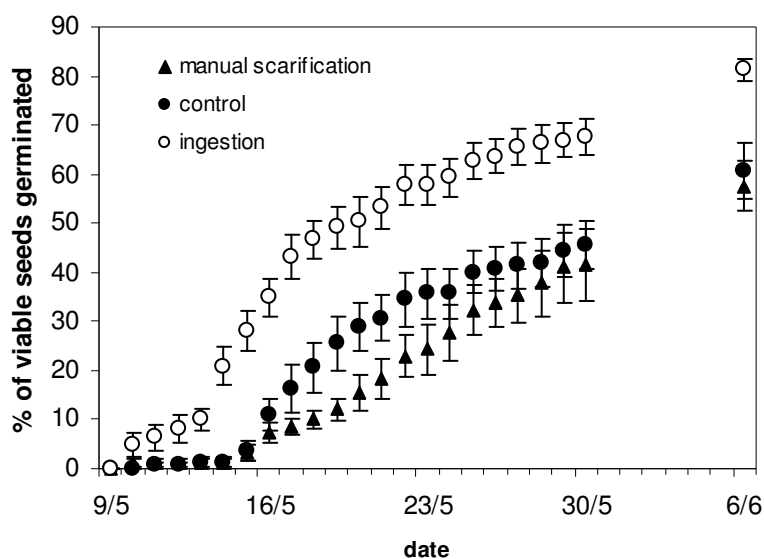


Fig. 3.7 Cumulative % of germinated seeds of *Lycium bosciifolium* for control, manual scarification and ingestion by sociable weavers. $n = 8$ per treatment with 25 seeds per Petri dish. Error bars indicate standard error.

Discussion

The term directed dispersal seems to be valid in the case of *Lycium bosciifolium*. It is associated with the canopy of *Acacia erioloba* (Hoffmann 2001; Zimmermann 2001), seed rain is significantly higher under acacias than in the open matrix and emergence of seedlings only takes place under canopies. It therefore fulfills the conditions for directed dispersal defined as ‘disproportionate arrival in sites especially favourable for survival’ (Howe & Smallwood 1982). Although the differences in emergence between matrix and canopy were not statistically significant, no emergence took place in matrix plots for both *Lycium bosciifolium* and *Pollichia campestris*. Germination studies showed that germination of these species as well as that of *Asparagus* spp and *Solanum capense* is inhibited at diurnal temperature fluctuations at which typical matrix species germinate as well or even better than at lower temperature fluctuations (Chapter 7; Kos & Poschlod 2007).

Dispersal may be even more directed than to *Acacia erioloba* canopies in general. The higher seed rain of *Lycium* under mature trees compared with saplings supports the hypothesis that larger bird activity in mature trees compared with saplings results in higher establishment under mature trees as observed in the vegetation. But temperature fluctuations are higher under saplings (Chapter 7; Kos & Poschlod 2007) and soil nutrients also seem to be less favorable under sapling acacias than under mature acacias (Milton & Dean 1995; Dean *et al.* 1999; Hoffmann 2001).

In *Solanum* the pattern of seed dispersal seems to be less tightly correlated with favourable conditions for establishment. Although seed rain was lower in the matrix than under trees, seed rain was significantly higher for saplings than for mature trees in one year. However, for seeds collected from the soil there was no difference between sapling and mature trees. This approaches more the actual pattern in the vegetation where more plants are found under mature acacias than under sapling acacias (Milton & Dean 1995). For *Lycium* the number of seeds collected from the soil under mature trees was significantly higher than under saplings whereas there was no significant difference between saplings and mature trees for seeds from traps. These results indicate that predation and secondary dispersal can have important effects on the seed shadow. More studies in arid environments are needed to evaluate the effect of these processes on species depending on nurse plants.

The sociable weaver (*Philetarius socius*) appears to be a legitimate dispersal agent of *Lycium bosciifolium* and possibly other fleshy fruited species. Sociable weavers were observed feeding eagerly on *Lycium bosciifolium* berries and seeds can survive passage through its digestive tract and germination is even promoted by ingestion. It's nesting

behaviour aggregates seed rain under large mature trees which also provide the best conditions for germination and emergence of *Lycium*. Seed rain directly under three weaver nests was 20 times higher than the average seed rain under mature acacias. Other species of small birds are probably equally effective in dispersing seeds to large acacia trees but they are not as numerous as the sociable weaver (Dean *et al.* 1999). Though high concentrations of *Lycium* seeds were found in droppings produced by bustards (Otidae), all of these were found in the open and never under *Acacia* canopies. So the dispersal efficiency of these species is presumably low as they deposit seeds mainly in sites unfavorable for germination. Sociable weavers are also resident species, meaning that their dispersal services are always readily available. Frugivorous species like acacia pied barbet (*Tricholaema leucomelas*) or the reдеyed bulbul (*Pycnonotus nigricans*) are nomadic (Maclean 1970). The geographical distributions of the sociable weaver and *Lycium bosciifolium* overlap almost completely which indicates that sociable weavers could have had an important influence on the evolution of *Lycium bosciifolium* fruiting traits and traits related to the association with nurse plants like its germination ecology. It would however, be useful to know how well seeds survive ingestion by sociable weavers compared with other dispersers (Godínez-Alvarez *et al.* 2002). It may be that in general insectivorous birds like sociable weavers play an important role in the dispersal of such species as *Lycium bosciifolium*. Of the other small bird species observed feeding on *Lycium bosciifolium* berries one was an insectivore, two mixed seed and insect feeder frugivores and two frugivores. Frugivorous birds are rare in the Southern Kalahari (Maclean 1970) which is not surprising due to the unpredictability of this resource in arid environments. Under such conditions fleshy-fruited species may be more successful when they produce fruits that are attractive for as many species as possible. The oily fruit pulp of *Lycium* indicates a relatively high fat content which may make them more interesting for insectivores in the same way that elaiosomes are thought to mimic insects for ants (Hughes *et al.* 1994). However, this hypothesis remains to be tested.

It is clear that one can speak of directed dispersal in the case of *Lycium*. But how directed is this dispersal? Some bird species may provide more directed and therefore qualitatively better dispersal than others. For example White-browed Sparrow Weavers (*Plocepasser mahali*) build their nests preferably on the most shaded side of the canopy and may thus also disperse more seed to the more shaded part of the canopy where conditions for germination and establishment are better. Other seed dispersing birds may also perch or nest preferably at the more shaded sides of the canopy during the day similar to the utilisation of *Acacia erioloba* shade by mammals as described by Milton & Dean (1995) and Dean *et al.*

(1999). Valiente-Banuet & Ezcurra (1991) found that in Mexico several succulents that depend on nurse plants for establishment were only found at the (shaded) north side of nurse plants. It is therefore desirable that future studies differentiate between different positions under the canopy.

Chapter 4

Spatial patterns and functional ecology of the soil seed bank of the dry Nossob river valley, Southern Kalahari

Abstract

Little is known about the functional ecology of soil seed banks in arid ecosystems. This study reports on the seed bank of a xeric savannah in the Southern Kalahari. Two aspects were studied: 1) the effect of microhabitat (*Acacia* canopies versus open matrix) on abundance and composition of the seed bank and on filtering species from the seed bank and 2) the vertical distribution and persistence of seeds in the soil in relation to seed morphology and germination biology.

Ordination of seed bank and vegetation data showed that, in contrast to vegetation data, for the seed bank data canopy and matrix did not separate. Matrix species common in the seed bank are anemochorous and/or have small seeds while canopy species common in the seed bank are zoochorous with larger seeds. Matrix species thus have a higher potential to disperse widely to both microhabitats. Species that are more common in the matrix vegetation but are more common in the sub-canopy seed bank have small seed and/or morphological adaptations for wind dispersal. This suggests that matrix species are dispersed to canopy and matrix but environmental filtering restricts growth to the matrix. There was no difference in seed persistence between canopy associated and matrix associated species. Therefore seed persistence does not seem to be important for species sorting.

Seed mass and shape are correlated with depth distribution and persistence in many floras. The hypothesis that smaller and rounder seeds are distributed more deep in the soil was tested. Species that are more common in deeper soil layers are thought to have more persistent seeds than species only found on the surface. On the basis of this assumption species were classified as having persistent or transient seeds. This classification was used to test the hypothesis that smaller and rounder seeds are more persistent than large elongated/flattened seeds.

Depth distribution was correlated with seed shape for the canopy for species and for the matrix for phylogenetically independent contrasts (PICs): species with more elongated or flattened seed had a higher proportion of seeds in the upper soil layer than species with round, compact seeds. Depth distribution was correlated with seed mass and the product of shape and

mass for the matrix for both species and contrasts. Species with persistent seeds had smaller seeds than species with transient seeds, both for species and PICs. No difference in seed shape between persistent and transient species was found for species or PICs.

Introduction

In arid and semi-arid environments the vegetation under the canopies of woody perennial species contrasts often strongly with surrounding open spaces (Flores & Jurado 2003). One possible cause of association with woody perennials is that a larger number of seeds recruits rather under shrubs or trees than on bare soil. This may be through trapping of wind dispersed seeds by the canopy or directed dispersal of seeds to canopies by animals. Alternatively the seed bank can be similar in different microhabitats but contrasting biotic and abiotic filters in both habitats allow only a subset of the species in the seed bank to establish. Pugnaire & Lázaro (2000), for example, found that the soil seed bank under shrubs of different ages is rather uniform, but composition of the vegetation under shrub canopies changes with age because shrubs of different ages filter out different sets of species. Seed persistence could be a trait that determines which species that disperse to a habitat can pass the habitat specific environmental filters and establish grow and reproduce there. One of the filters that could act on persistence is the disturbance regime typical for a habitat. Bet hedging models predict that in variable habitats plants in which only a fraction of one year's seed production germinates will be favoured by natural selection (Cohen 1966; Venable & Brown 1988; Rees 1993). In accordance with theory Thompson *et al.* (1998) showed that species in stable plant communities have generally low seed persistence, while species in highly disturbed habitats have high persistence. *Acacia erioloba* trees attract a variety of animals that use them a.o. for nesting, seeking shade during the heat of the day, cover (Milton & Dean 1995; Dean *et al.* 1999). The concentration of animal activity under acacia trees is likely to result in increased disturbance compared with open spaces. Plants associated with acacia canopies are therefore expected to have more persistent seeds than plants of more stable habitats.

In arid ecosystems, where long periods without sufficient rain for seedling establishment are common, regeneration from seed stored in the soil seed bank is an important component of ecosystem dynamics. Despite the functional importance of seed banks for the vegetation relatively little is known about the functional ecology of seed banks in arid ecosystems. Especially patterns of seed persistence in the soil are not well understood (Thompson 2000; Moles *et al.* 2003). In North-western Europe species with persistent seed banks tend to have smaller, rounder seeds than species that do not form a persistent seed bank

(Thompson *et al.* 1993) and such species are found more deeply buried in the soil (Bekker *et al.* 1998). It has been shown for several other floras around the world that species with persistent seeds have usually smaller seeds than species with transient seeds (Leck 1989; Funes *et al.* 1999; Moles *et al.* 2000; Thompson *et al.* 2001).

However, data on the relationship between persistence and seed mass and shape in arid and semi-arid ecosystems are sparse and inconsistent. Price & Joyner (1997) found that large seeds were under-represented in the seed bank relative to their density in the seed rain in Mojave Desert shrubland. In contrast with these data Moles *et al.* (2003) found a positive relationship between diaspore mass and diaspore viability after being buried in the soil for 1 year in arid Australia. Little is known about the effect of seed shape on persistence in arid and semi-arid plant communities. Knowledge about the relationship of seed mass and seed shape with vertical distribution of seeds in the soil in arid environments is practically absent. Depth distribution may also provide information on persistence in arid floras. Seed predation pressure is high in arid ecosystems (Kemp 1989) and quick burial is thought to aid the accumulation of a seed bank (Thompson *et al.* 1997; Thompson 2000). Here it is attempted to quantify the relationship between seed mass and shape and depth distribution for a dry riverbed in the arid Southern Kalahari. Subsequently depth derived persistence (Thompson *et al.* 1997) is used to determine if persistence is related to seed mass and shape. To verify if depth distribution is correlated with persistence depth distribution is compared with the light requirement for germination as this is seen as a prerequisite for forming a persistent seed bank (Baskin & Baskin 1989; Pons 1991). In another approach to verify if there is a relationship between depth distribution and persistence, survival in the soil after one year burial was determined for selected species.

In summary the questions addressed here are:

1. Does seed bank composition differ among microhabitats?
2. Do canopy associated species have more persistent seeds than matrix species?
3. How do depth derived persistence records compare with predictions on persistence from light requirements for germination and survival during burial in the soil?
4. Is the vertical distribution of seeds in the soil related to seed mass and/or shape?
5. Is seed persistence in the soil related to seed shape and mass?

To answer these questions soil samples were taken at two different depths under acacia canopies and in the surrounding matrix and the germinable seed bank was determined. Seeds

of six common species were buried under canopies and in the matrix and retrieved after one year to compare survival between habitats. Depth distribution is used to assign species to a soil seed bank type. Transient and persistent species are then compared for differences in seed mass and shape. The need for light to germinate was tested for selected species and used to evaluate to accuracy of assignments to persistence class using depth distribution. This was also done by comparing depth distribution and persistence with survival rate data from seeds buried in the soil for one year.

Methods

Vegetation

Percentage cover of each plant species was determined under the canopy and in the surrounding matrix in May 2003. 10 m × 10 m plots were centred on 10 mature *Acacia erioloba* trees (stem circumference > 195 cm). Four 5 m × 5 m subplots, one in each cardinal direction, were established around each tree in the open matrix 15-20 m from the stem. Canopy association was calculated using $(\% \text{ cover under tree} - \% \text{ cover in open}) / (\% \text{ cover under tree} + \% \text{ cover in open})$. This gives a score from -1 (only found in matrix plots) to 1 (only found under canopies). Species that are completely indifferent to microhabitat score 0 (see Appendix 1). To test for a correlation of seed bank with cover only species that occurred in at least 4 plots (Plot = canopy + matrix sub-plots centred on a tree) for both seed bank and vegetation were included in the data set.

Seed bank

To determine the seed bank soil samples were taken under the canopy and in the surrounding matrix of 20 large *Acacia erioloba* trees. Soil samples were collected in June 2002 and May 2003. In both years samples were taken at 0-3 cm depth. In 2003 samples were taken at 0-3 cm and 3-6 cm depth. 10 soil cores (4 cm diameter) per microhabitat per depth were taken. The 10 cores of each depth and microhabitat were pooled and stored in plastic bags. The soil seed bank was estimated by using the seedling-emergence method (ter Heerdt *et al.* 1996). This method includes a concentration step by sieving the samples on a fine sieve of 0.2 mm mesh width. The concentrate was poured in a 5 mm thick layer on 53 cm × 33.5 cm trays filled with sterile sandy to loamy soil. Emerged seedlings were removed once identifiable. After a cultivation period of 6 months trays were left to dry out. When dry, the samples were separated from the potting soil and stored at 50 ° C for 4 weeks, as many species from (semi-)

arid regions are known to lose dormancy under hot and dry storage (Baskin & Baskin 1998). Samples were then cultivated again until no seedlings emerged anymore.

Table 4.1 Key used to allocate species to soil seed bank type after Thompson *et al.* (1997)

		Soil seed bank type
Absent from the seed bank:	Species found in vegetation but not in seed bank	Transient
	Present in the seed bank:	
	Species only found in surface soil	Transient
	Higher densities in upper soil layers	Short-term persistent
	Equal densities in upper and lower soil layers	Long-term persistent
	Higher densities in lower soil layers	Long-term persistent

Depth distribution and persistence

Depth distribution was only determined for species for which a total of 5 or more seeds was found in the seed bank samples. Depth distribution is expressed as the % of seeds of the total number of seeds found in the upper soil layer, 100 % means that seeds are only found in the upper soil layer (Bekker *et al.* 1998). Species were classified as having transient seeds when the species was found in the vegetation but not in the seed bank or when seeds were only found in the surface soil. Species either present or absent from the vegetation but with seeds in both upper and lower soil layers were classified as having persistent seeds (Table 4.1, Thompson *et al.* 1997). Where a distinction between long-term and short-term persistent seeds was made long-term persistent species were those persistent species with equal seed densities in upper and lower soil layers or higher densities in lower soil layers. Species present in fewer than 3 plots (trees) or with fewer than five seeds in the seed bank were not classified. When habitats were pooled the highest persistence class found was used.

Seed measurements

Seed mass was determined for 20 seeds individually according to the protocol in Westoby (1998). Measurements of seeds were made for 20 seeds per species if available, but at least 5 using a binocular microscope with a measuring ocular. Seed shape (variance in seed dimensions, V_s) was calculated using the formula $V_s = \Sigma (x_i - \text{mean}(x))^2/n$. A complete list of species with seed mass and shape is given in Appendix 3. Appendages like papus and awns

were included if they were firmly attached. Appendages extending from the seed in a direction more or less parallel to the length axis were taken into consideration when measuring the length but the same appendages did not contribute to the width while appendages clearly sticking out were added to the width (Götzenberger 2005).

Germination and light

The light requirement for germination was tested by germinating seeds in light (12 hour day) and in darkness. Weekly counts were made until no seeds germinated anymore. Counts of germinated seeds in the darkness treatment were made under a green safety light. Germination percentages in dark and light, based on viable seeds only, were used to calculate a Relative Light Germination (*RLG*) index expressing the light requirement for germination of a species (Milberg *et al.* 2000). $RLG = G_l / (G_d + G_l)$ where G_l = the germination percentage in light, and G_d = the germination percentage in darkness. *RLG* represents a range of values varying from 0 (germination only in darkness) to 1 (germination only in light). Germination test were carried out at a 30/15 °C, 12/12 h day/night regime, except for *Asparagus* and *Pollichia*, which were tested at 22/22 °C and *Solanum* and *Lycium* which were tested at 26/19 °C.

Seed burial

A burial experiment was conducted because this can shed light on the question if persistence is related to the ability to survive in the soil as opposed to, for example, sensitivity to predation. For the burial experiment species were chosen to represent a range of life forms, seed sizes and habitat preferences. Seeds of *Chloris virgata* (annual grass, matrix), *Lycium bosciifolium* (fleshy fruited shrub, canopy), *Peliostomum leucorrhiozum* (dwarf shrub, matrix), *Pollichia campestris* (hemicryptophyte, canopy), *Solanum capense* (hemicryptophyte, canopy) and *Setaria verticillata* (annual grass, canopy) were collected at the end of the rainy season 2002 and buried in July 2002 in nylon mesh bags 3 cm deep under trees and in open spaces. Per microhabitat 8 replications of 25 seeds per bag were used. For each species each canopy bag was buried under a different large *Acacia erioloba* tree, at a random cardinal orientation halfway between stem and canopy dripline. Each matrix bag was buried at a random cardinal orientation, 12.5 m from the canopy dripline. Control seeds were stored dry in the lab at 5° C. After digging the seeds up in May 2003 viability of buried and control seeds was determined by germinating the seeds and then pressing the remaining seeds with tweezers. Firm, intact and germinated seeds were recorded as viable (Baskin & Baskin 1998).

Comparative method

Because two closely related species are more likely to resemble each other on account of common ancestry than are two unrelated species, it is inappropriate to use species as independent points in statistical analysis (Harvey & Pagel 1991). The method of phylogenetically independent contrasts (Felsenstein 1985) was designed to use phylogenetic information to allow enumeration of the number of times relationships have evolved independently.

As a phylogeny for plant families the Angiosperm phylogeny of Davies *et al.* (2004) was used. The phylogeny for the Asteraceae is the supertree published in Funk *et al.* (2005). For grasses the phylogenies in Grass Phylogeny Working Group (2001) and Hilu & Alice (2001) were used. Species were assigned to their respective families and sub-families using the classification in Leistner (2000) and Gibbs Russell *et al.* (1991) for grasses. See Appendix 4 for the resulting super tree.

Contrasts for depth distribution, seed mass, and seed shape were calculated using the computer program CAIC (Comparative Analysis by Independent Contrasts: Purvis & Rambaut 1995) using the assumption of equal branch lengths. To meet the assumptions of normality seed mass was \log_{10} transformed and seed shape $\log \sqrt{\quad}$ transformed prior to calculation of contrasts. Contrasts were first scrutinized to see if the standardization by equal branch lengths was sufficient to render them homoscedastic, and then they were analyzed using Model I multiple regression through the origin (Garland *et al.* 1993).

Data analysis

Seed densities and numbers, seeds per species, species richness and evenness (see Magurran 1988) were calculated for different soil layers and microhabitats. Comparisons between different soil depths and between microhabitats were made using Wilcoxon paired-sample tests. The cross species relationship between depth distribution and seed mass and shape was evaluated using linear regression models. To compare seed mass and shape between persistent and transient species and between canopy and matrix species *t* tests were performed on the log transformed seed mass and $\log \sqrt{\quad}$ transformed shape. To compare seed bank composition with vegetation composition a detrended component analysis (DCA) was carried out on a square root transformed matrix containing seed bank and established vegetation data (PC-ORD 4.0 McCune & Medford 1999).

Results

General

45 species were found in the seed bank for the two study years combined. Of these 15 (33 %) were not found in the vegetation. There was also a large group of 46 species that were found in the vegetation but not in the seed bank. Of the 77 species found in the vegetation 31 were found in the seed bank (40 %). Most species found in the seed bank were annuals (62 %, 28 species), while most of the species absent from the seed bank were perennials (88 %, 36 species). The densities of the most common species in the seed bank are given in Table 4.3 (for complete species list see Appendix 2). Under canopies seed densities were about three times higher than in the matrix, whereas species richness was about twice that found in the matrix. Therefore the number of seeds per species was also higher under canopies (Table 4.2).

Correlation between vegetation and seed bank

The DCA ordination (Fig. 4.1) for data from 2003 shows that for vegetation data plots separate clearly. For the seed bank, however, canopy and matrix plots overlap. This may be related to the high proportion of wind dispersed species (morphological adaptations for wind dispersal or tiny seeds) in the matrix: Of the most common species in the seed bank those that are more common in the vegetation under canopies have significantly heavier ($t = -2.783$, $P < 0.05$) and rounder ($t = -2.881$, $P < 0.05$) seeds than species that are more common in the matrix vegetation (Fig. 4.2).

For the dominant species in vegetation and seed bank, canopy association based on seed bank for 2003 was marginally significantly correlated with canopy association based on cover for 2003 ($r_s = 0.543$, $P < 0.05$, $n = 15$, Fig. 4.3). Especially interesting are the species in the lower right corner of Fig. 4.3. These are more common in the seed bank under canopies than in the matrix. But for cover they are more associated with the matrix. All of these (*Schmidtia*, *Plinthus*, *Geigeria*, *Peliostomum*) have very small and/or wind dispersed seeds. On the other hand the species in the upper right corner tend to have larger seeds and no wind dispersal. Though *Felicia* and *Pentzia* have small wind dispersed seeds, they are associated with the canopy for both seed bank and cover. They are however of all canopy species most weakly associated with the canopy. Actually all species with morphological adaptations for wind dispersal have a lower canopy association based on cover than expected from canopy association based on the seed bank. In accordance with these data there are several species that were consistently more common in the seed bank under canopies in two years, with most

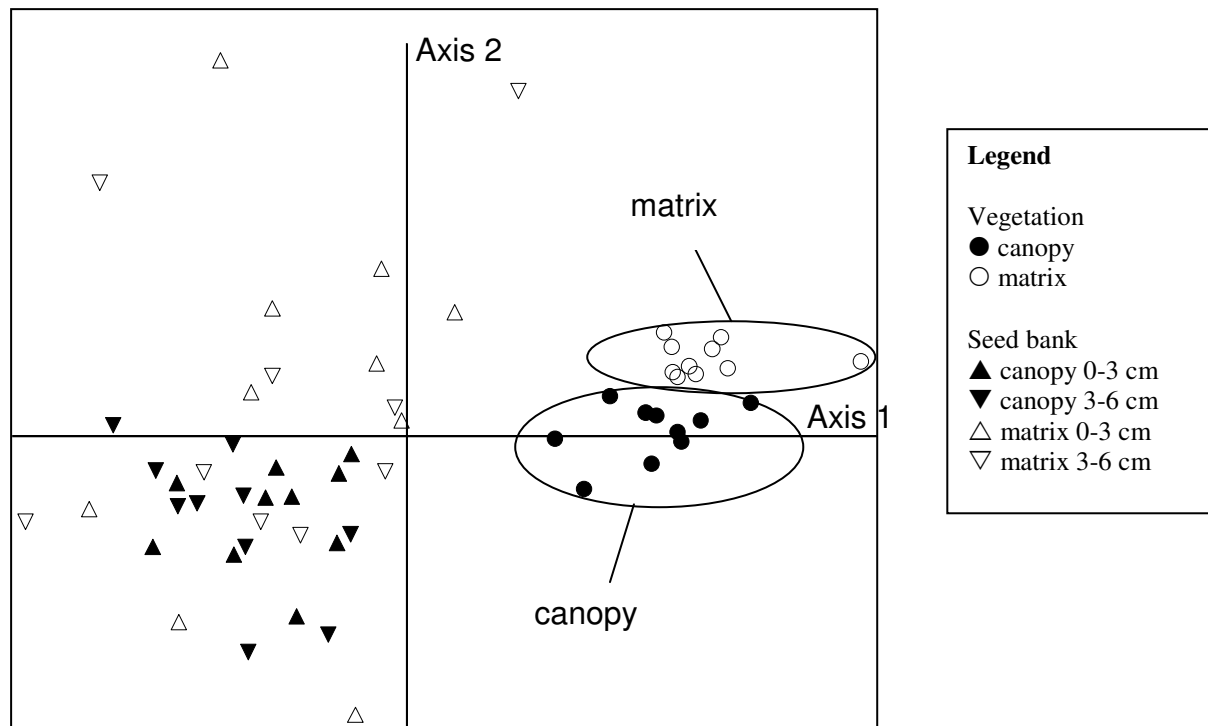


Fig. 4.1 DCA ordination of vegetation and seed bank data. Vegetation data (% cover) of canopy and matrix plots and seed bank data (0-3 and 3-6 cm) of canopy and matrix were analyzed. Only seed bank data for the same plots as the vegetation were used in this analysis ($n = 10$).

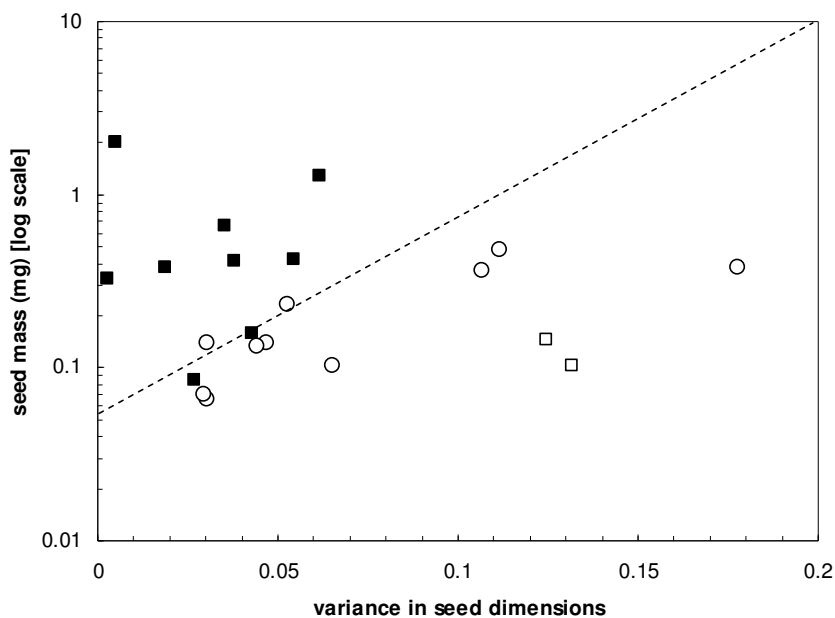


Fig. 4.2 Relationship between canopy association and seed mass and shape for 21 most common species in the seed bank (same species as for depth distribution analysis). Canopy species (black squares) tend to have a higher seed mass and more rounded seeds than matrix species (open circles). The open squares indicate two species (*Felicia clavipilosa*, *Pentzia incana*) that were slightly more common under the canopy but less associated with the canopy than all other canopy associated species.

Table 4.2 Numbers of seeds and species in the soil seed bank under acacia canopies (C) and in the surrounding matrix (M) for 2002 (one soil layer) and 2003. Different letters indicate significant differences within a year between habitats, asterisks between soil layers ($P < 0.05$) for Wilcoxon paired-sample test. Means \pm standard deviation are given ($n = 20$).

	C 2002	M 2002	C 2003	M 2003
<i>Vegetation</i>				
Total number of species in established vegetation	-	-	59	45
Annual species (%)	-	-	32.2	28.9
<i>Soil seed bank</i>				
Species of established vegetation in seed bank (%)	-	-	72.9	68.9
Annual species (%) (0-6 cm)	-	-	61.5	71.0
Annual species (%) (0-3 cm)	64.0	83.3	62.2	70.4
Annual species (%) (3-6 cm)	-	-	69.2	72.7
<i>Species of established vegetation in seed bank</i>				
Total number of species (0-6 cm)	-	-	39	31
Total number of species (0-3 cm)	25	18	37	27
Total number of species (3-6 cm)	-	-	26	22
Mean number of species per sample (0-6 cm)	-	-	11.1 \pm 3.6 ^a	5.8 \pm 2.9 ^b
Mean number of species per sample (0-3 cm)	5.8 \pm 1.9 ^a	2.5 \pm 2.0 ^b	9.0 \pm 3.9 ^a	4.2 \pm 2.8 ^b
Mean number of species per sample (3-6 cm)	-	-	5.9 \pm 2.6 ^a	2.5 \pm 2.2 ^b
Comparison 0-3 and 3-6 cm depth	-	-	*	n.s.
Mean number of seeds per species (0-6 cm)	-	-	6.7 \pm 6.0 ^a	3.9 \pm 5.8 ^b
Mean number of seeds per species (0-3 cm)	5.5 \pm 5.0 ^a	4.6 \pm 4.4 ^a	6.1 \pm 8.1 ^a	3.5 \pm 4.4 ^a
Mean number of seeds per species (3-6 cm)	-	-	4.3 \pm 3.8 ^a	2.7 \pm 4.4 ^b
Comparison 0-3 and 3-6 cm depth	-	-	n.s.	n.s.
Total number of seeds (0-6 cm)	-	-	1502	521
Total number of seeds (0-3 cm)	630	325	993	380
Total number of seeds (3-6 cm)	-	-	509	141
Mean number of seeds per sample (0-6 cm)	-	-	75 \pm 72 ^a	26 \pm 57 ^b
Mean number of seeds per sample (0-3 cm)	32 \pm 30 ^a	16 \pm 31 ^b	50 \pm 47 ^a	19 \pm 41 ^b
Mean number of seeds per sample (3-6 cm)	-	-	25 \pm 26 ^a	7 \pm 16 ^b
Comparison 0-3 and 3-6 cm depth	-	-	*	n.s.
Mean number of seeds m ⁻² (0-6 cm)	-	-	5988 \pm 5699 ^a	2073 \pm 4519 ^b
Mean number of seeds m ⁻² (0-3 cm)	2507 \pm 2313 ^a	1293 \pm 2446 ^b	3951 \pm 3748 ^a	1512 \pm 3259 ^b
Mean number of seeds m ⁻² (3-6 cm)	-	-	2025 \pm 2095 ^a	561 \pm 1301 ^b
Comparison 0-3 and 3-6 cm depth	-	-	*	*
Evenness (0-6 cm)	-	-	0.70 \pm 0.20 ^a	0.76 \pm 0.32 ^a
Evenness (0-3 cm)	0.72 \pm 0.17 ^a	0.55 \pm 0.36 ^a	0.73 \pm 0.20 ^a	0.69 \pm 0.36 ^a
Evenness (3-6 cm)	-	-	0.76 \pm 0.23 ^a	0.68 \pm 0.44 ^a
Comparison 0-3 and 3-6 cm depth	-	-	n.s.	n.s.

other species showing no significant differences between canopy and matrix seed bank. Only *Chloris virgata* was more common in the matrix in 2002 with no significant difference for 2003 (Table 4.3).

Depth distribution and persistence

Depth distribution was correlated across species with seed shape for the canopy alone and habitats pooled (Table 4.4) and for the matrix and habitats pooled for phylogenetically independent contrasts (Table 4.5): species with more elongated or flattened seed had a higher proportion of seeds in the upper soil layer than species with round, compact seeds. Depth distribution was correlated with seed mass and the product of shape and mass for the matrix for both species and contrasts (Table 4.4, 4.5).

Table 4.3 The 19 most common species in the soil seed bank for the upper soil layer (0-3 cm) under canopy and in matrix for 2002 and 2003, seeds per square meter \pm S.D ($n = 20$) and number of trees where the species was observed. In addition habitat where species had the highest % cover in 2003 is given. Different letters indicate significant differences between canopy and matrix for Wilcoxon paired sample test within years.

	Canopy 2002	Canopy 2003	Matrix 2002	Matrix 2003	Habitat
<i>Chenopodium opulifolium</i>	151 \pm 241 (10) ^a	111 \pm 187 (10) ^a	4 \pm 18 (1) ^b	0 ^b	c
<i>Coronopus integrifolius</i>	1027 \pm 1964 (13) ^a	1317 \pm 3360 (11) ^a	64 \pm 248 (3) ^b	0 ^b	c
<i>Setaria verticillata</i>	629 \pm 595 (19) ^a	1035 \pm 1188 (20) ^a	40 \pm 145 (2) ^b	32 \pm 75 (5) ^b	c
<i>Amaranthus praetermissus</i>	107 \pm 135 (11) ^a	179 \pm 195 (14) ^a	52 \pm 183 (2) ^a	111 \pm 338 (6) ^a	c
<i>Argemone ochroleuca</i>	4 \pm 18 (1)	16 \pm 33 (4)	0	0	c
<i>Boerhavia repens</i>	24 \pm 45 (5)	12 \pm 39 (2)	0	4 \pm 18 (1)	c
<i>Lycium bosciifolium</i>	20 \pm 72 (2)	32 \pm 75 (5)	0	4 \pm 18 (1)	c
<i>Felicia clavipilosa</i>	227 \pm 613 (13) ^a	195 \pm 345 (12) ^a	84 \pm 319 (4) ^b	52 \pm 104 (6) ^a	c
<i>Helichrysum argyrosphaerum</i>	32 \pm 54 (6) ^a	219 \pm 245 (15) ^a	24 \pm 52 (4) ^a	64 \pm 80 (9) ^b	-
<i>Geigeria pectidea</i>	36 \pm 125 (3)	28 \pm 47 (6) ^a	0	0 ^b	m
<i>Pentzia lanata</i>	8 \pm 36 (1)	16 \pm 33 (4)	4 \pm 18 (1)	8 \pm 36 (1)	c
<i>Amellus strigosus</i>	12 \pm 39 (2)	151 \pm 421 (9) ^a	0	12 \pm 39 (2) ^a	-
<i>Aptosimum lineare</i>	0	16 \pm 42 (3)	0	95 \pm 243 (5)	m
<i>Enneapogon cenchroides</i>	4 \pm 18 (1)	24 \pm 58 (4) ^a	12 \pm 53 (1)	28 \pm 94 (2) ^a	m
<i>Eragrostis porosa</i>	24 \pm 45 (5) ^a	92 \pm 241 (6) ^a	40 \pm 71 (6) ^a	20 \pm 44 (4) ^a	m
cf. <i>Filago spec.</i>	12 \pm 29 (3)	36 \pm 125 (3) ^a	20 \pm 44 (4)	32 \pm 65 (5) ^a	-
<i>Peliostomum leucorrhizum</i>	0	40 \pm 66 (7) ^a	0	32 \pm 48 (7) ^a	m
<i>Trianthema parvifolia</i>	0	32 \pm 75 (5) ^a	0	60 \pm 106 (7) ^a	m
<i>Chloris virgata</i>	103 \pm 218 (9) ^a	84 \pm 187 (7) ^a	537 \pm 105 (12) ^b	203 \pm 373 (8) ^a	m

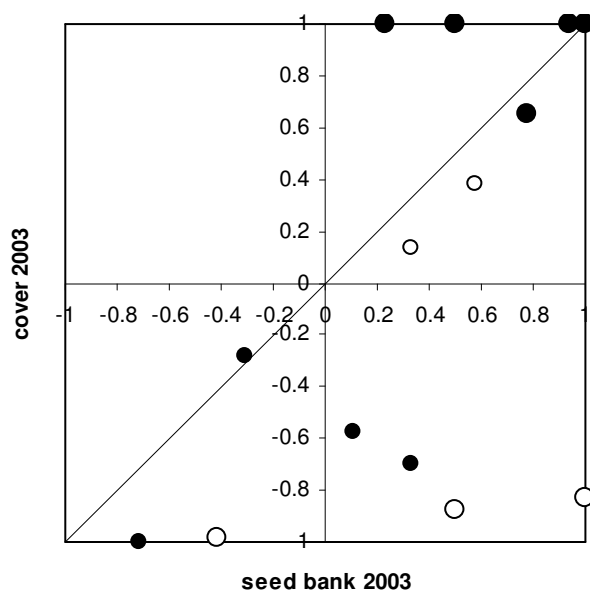


Fig. 4.3 Canopy association $((\text{canopy} - \text{matrix})/(\text{canopy} + \text{matrix}))$ based on cover plotted against canopy association based on seed bank using the same formula ($n = 15$ species). The diagonal line indicates $y = x$. Open circles indicate species with morphological adaptations for wind dispersal, small circles indicate species with seed mass < 0.15 mg. Note that all species with morphological adaptations for wind dispersal have a lower canopy association/higher matrix association based on cover than would be expected from the association based on the seed bank.

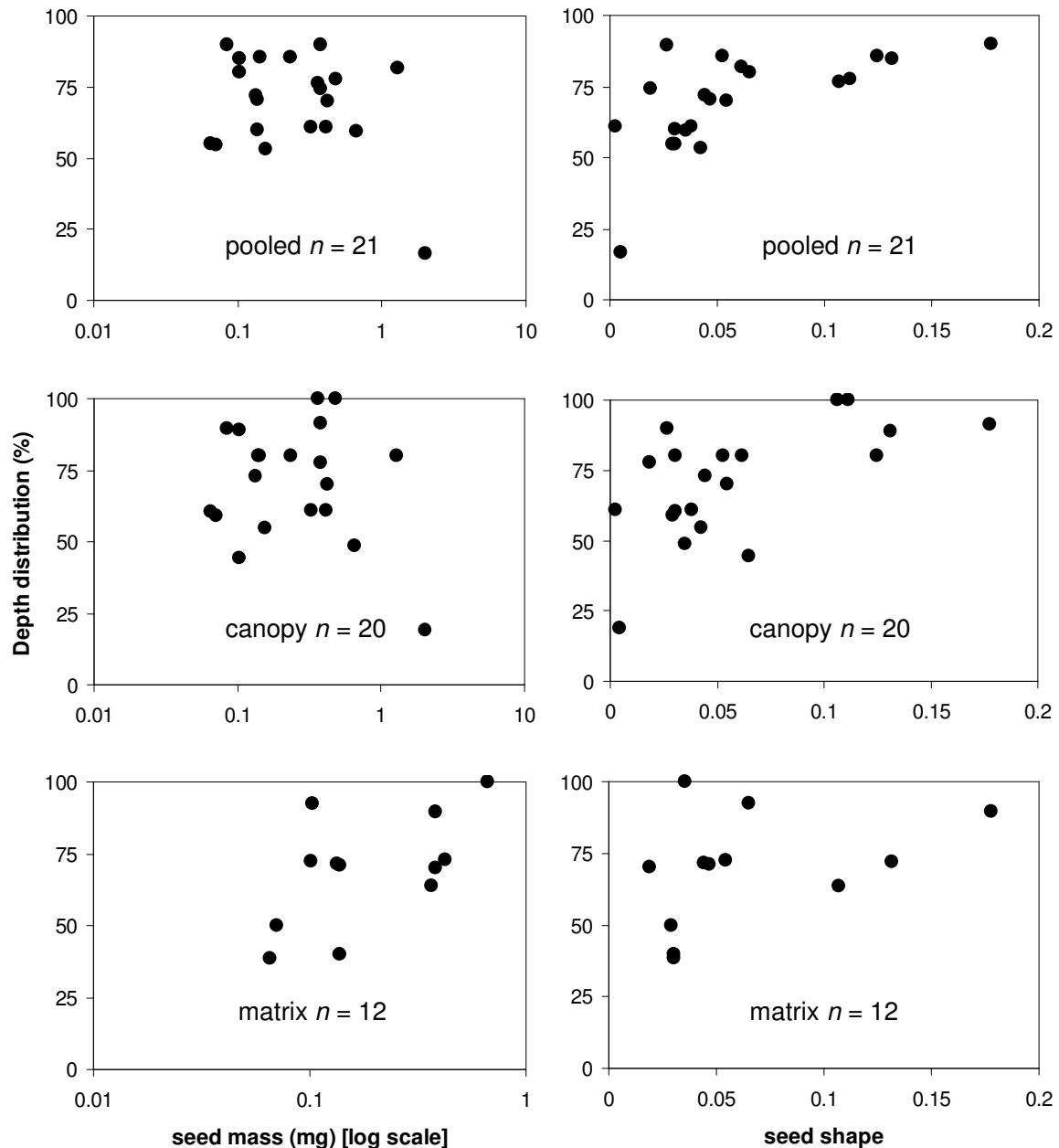


Fig. 4.4 Relation between depth distribution (% of the total number of seeds found in the upper soil layer) and seed mass and seed shape (variance in seed dimensions, V_s) for species in canopy soil, matrix soil and both habitats pooled.

For the canopy at least it seems that there is a threshold in seed mass below which all species are persistent (Fig. 4.5B). For the combined data set with species classified according to the most persistent record in both habitats species classified as persistent had significantly lower seed mass than transient species (t -test, $t = 5.45$, $P < 0.001$). Transient and persistent species did not differ in seed shape (t -test, n.s. Fig. 4.5). Using the BRUNCH algorithm of CAIC (Purvis & Rambaut 1995) 12 contrasts were produced. Out of these 12 contrasts 11 showed an increase of seed mass with a transition from persistent to transient seeds (Sign test,

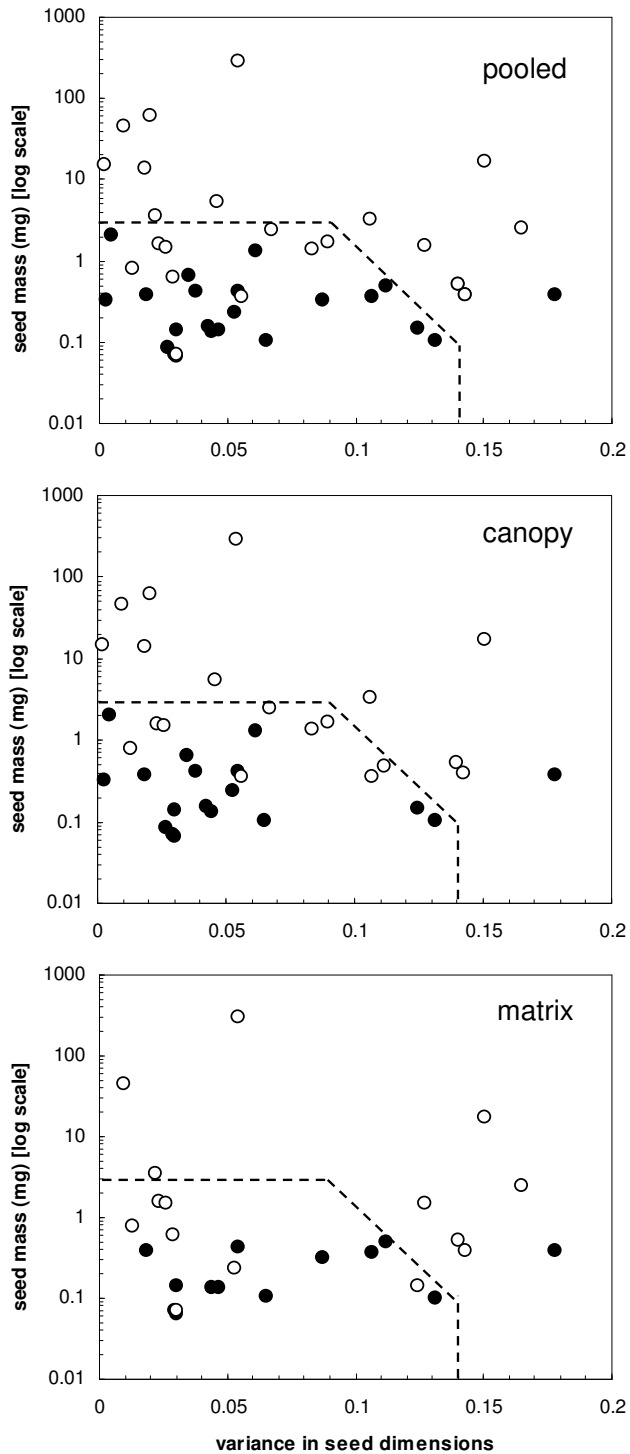


Fig. 4.5 Seed mass and variance of seed dimensions for species from a Southern Kalahari dry river bed flora for microhabitats pooled ($n_{\text{total}} = 44$, $n_{\text{transient}} = 22$, $n_{\text{persistent}} = 22$ species) canopy ($n_{\text{total}} = 37$, $n_{\text{transient}} = 19$, $n_{\text{persistent}} = 18$ species) and matrix ($n_{\text{total}} = 29$, $n_{\text{transient}} = 16$, $n_{\text{persistent}} = 13$ species). Filled circles represent species that are found in upper (0-3 cm) and lower (3-6 cm) soil layers. Open circles represent species whose seeds are not found in the seed bank or only in the upper layer. The dashed line shows the threshold drawn by Thompson *et al.* (1993), below which all species had seeds that could persist in the soil for at least 5 years.

Table 4.4 Linear regressions models of log-transformed seed mass (M), shape (V_s) and their product ($M \times \sqrt{V_s}$) with arcsin transformed depth distribution (Arcsin \sqrt{D}) for canopy and matrix and over both sites. * $P < 0.05$, ** $P < 0.01$.

	Depth distribution (Arcsin \sqrt{D})	Significance
Canopy n = 20		
Log (M)		n.s.
Log ($\sqrt{V_s}$)	arcsin $\sqrt{D} = 0.738 \times \log (\sqrt{V_s}) + 1.549$	$R^2 = 0.378$ **
Log ($M \times \sqrt{V_s}$)		n.s.
Matrix n = 12		
Log (M)	arcsin $\sqrt{D} = 0.447 \times \log (M) + 1.342$	$R^2 = 0.353$ *
Log ($\sqrt{V_s}$)		n.s.
Log ($M \times \sqrt{V_s}$)	arcsin $\sqrt{D} = 0.416 \times \log (M \times \sqrt{V_s}) + 1.589$	$R^2 = 0.401$ *
Pooled n = 21		
Log (M)		n.s.
Log ($\sqrt{V_s}$)	arcsin $\sqrt{D} = 0.597 \times \log (\sqrt{V_s}) + 1.409$	$R^2 = 0.462$ **
Log ($M \times \sqrt{V_s}$)		n.s.

Table 4.5 Linear regressions forced through the origin of phylogenetically independent contrasts in log transformed seed mass (M), shape (V_s) and their product ($M \times \sqrt{V_s}$) with arcsin transformed depth distribution (Arcsin \sqrt{D}) for canopy and matrix and over both sites. * $P < 0.05$, ** $P < 0.01$.

	Depth distribution (Arcsin \sqrt{D})	Significance
Canopy n = 17		
Log (M)		n.s.
Log ($\sqrt{V_s}$)		n.s.
Log ($M \times \sqrt{V_s}$)		n.s.
Matrix n = 11		
Log (M)	arcsin $\sqrt{D} = 0.709 \times \log (M)$	$R^2 = 0.467$ *
Log ($\sqrt{V_s}$)	arcsin $\sqrt{D} = 1.441 \times \log (\sqrt{V_s})$	$R^2 = 0.477$ *
Log ($M \times \sqrt{V_s}$)	arcsin $\sqrt{D} = 0.598 \times \log (M \times \sqrt{V_s})$	$R^2 = 0.593$ **
Pooled n = 18		
Log (M)		n.s.
Log ($\sqrt{V_s}$)	arcsin $\sqrt{D} = 0.760 \times \log (\sqrt{V_s})$	$R^2 = 0.395$ **
Log ($M \times \sqrt{V_s}$)		n.s.

$P = 0.006$). Seed shape, however, increased in only 5 out of 12 transitions from persistent to transient seeds (Sign test, n.s.). Though the difference in seed bank types between habitats seems obvious from Fig.4.6, the H_0 that seed bank type is independent of habitat can not be rejected for this data set ($\chi^2 = 4.96$, n.s.).

Germination and light

Species varied from absolute requirement for light ($RLG = 1.00$) to germination being completely indifferent to light ($RLG = 0.50$, Table 4.6). No relationship between light requirement for germination and depth distribution was observed. Although the species that germinate to relatively high % in the dark compared with germination in light seem to be

found mostly in the upper soil layer. However, species with germination inhibited strongly in darkness include both species with lower depth distribution and species that were found mainly in the upper soil layers. There seems to be a tendency for species classified as transient to have a lower light requirement for germination than those classified as short term persistent and those again seem to have a lower light requirement than long term persistent species (Fig. 4.7). There are however no significant differences in *RLG* between seed persistence classes.

Seed burial

There were clear differences between species in survival after 10 months burial in the soil (Fig 4.8, Table 4.7). Within species there were no significant differences in survival between burial in matrix and canopy, although there seems to be a tendency for higher survival under canopies (Fig 4.8). Species that survived burial in the soil well also tended to be distributed deeper in the soil (Table 4.7), and germination is inhibited more in darkness. Seed bank type seems not directly related to survival of burial.

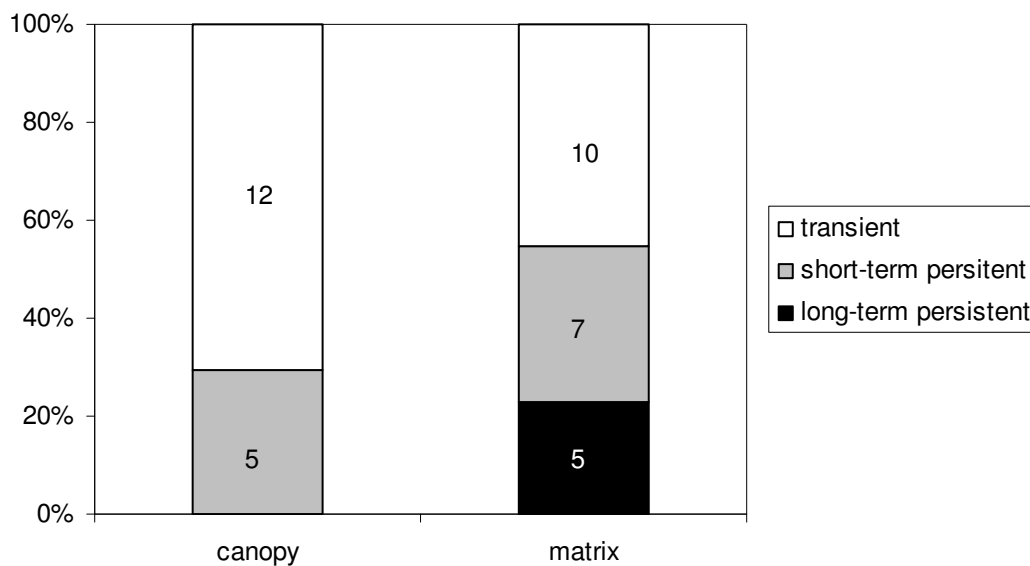


Fig. 4.6 Distribution of soil seed bank type in relation to microhabitat for 39 species. Numbers indicate number of species for that category. Species are all species for which persistence was determined and that were present in the vegetation so that canopy association based on % cover could be determined.

Table 4.6 Germination percentages in light and in darkness (mean \pm s.d., $n = 8$ Petri dishes with 25 seed each, $n = 5$ for *Asparagus*), Relative Light Germination ($RLG = \text{germination percentage in light} / (\text{germination percentage in darkness} + \text{germination percentage in light})$) and soil seed bank type (lp = long-term persistent, sp = short-term persistent, t = transient). Species are sorted according to RLG . Significant differences (t -test) between light and dark treatments are indicated by different letters.

species	% germination in light	% germination in dark	RLG	Seed bank type
<i>Chloris virgata</i>	62 \pm 5a	62 \pm 11a	0.50	sp
<i>Rhigozum trichotomum</i>	100 \pm 0 a	100 \pm 0b	0.50	t
<i>Asparagus africanus</i>	100 \pm 0 a	98 \pm 4b	0.51	t
<i>Schmidtia kalahariensis</i>	66 \pm 8a	48 \pm 14b	0.58	t
<i>Setaria verticillata</i>	40 \pm 13a	22 \pm 8b	0.65	sp
<i>Felicia clavipilosa</i>	24 \pm 8a	10 \pm 12b	0.71	sp
<i>Eragrostis porosa</i>	29 \pm 13a	8 \pm 4b	0.78	lp
<i>Pentzia incana</i>	15 \pm 11a	4 \pm 2b	0.79	sp
<i>Chenopodium schraderianum</i>	91 \pm 6a	24 \pm 12b	0.79	sp
<i>Lycium bosciifolium</i>	25 \pm 14a	6 \pm 9b	0.81	sp
<i>Amaranthus praetermissus</i>	62 \pm 12a	13 \pm 10b	0.83	sp
<i>Amaranthus dinteri</i>	66 \pm 13a	13 \pm 10b	0.84	-
<i>Coronopus integrifolius</i>	77 \pm 9a	12 \pm 9b	0.87	sp
<i>Enneapogon desvauxii</i>	91 \pm 9a	13 \pm 17b	0.88	sp
<i>Aristida congesta</i>	80 \pm 11a	11 \pm 4b	0.88	-
<i>Chenopodium opulifolium</i>	25 \pm 8a	3 \pm 5b	0.89	sp
<i>Geigeria pectidea</i>	100 \pm 0a	10 \pm 5b	0.91	lp
<i>Geigeria ornativa</i>	99 \pm 3a	6 \pm 6b	0.94	-
<i>Pollichia campestris</i>	75 \pm 9a	4 \pm 4b	0.95	t
<i>Aptosimum marlothii</i>	58 \pm 17a	1 \pm 2b	0.98	sp
<i>Aptosimum lineare</i>	93 \pm 6a	0 \pm 0b	1.00	lp
<i>Plinthus karooicus</i>	42 \pm 13a	0 \pm 0b	1.00	lp
<i>Solanum capense</i>	22 \pm 8a	0 \pm 0b	1.00	t

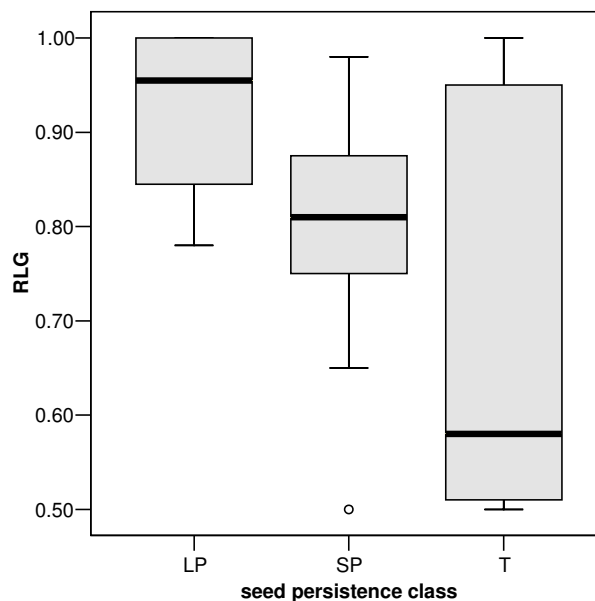


Fig. 4.7 Relative Light Germination (RLG) for species with different classes of seed persistence in the soil (LP = long-term persistent, $n = 4$; SP = short-term persistent, $n = 11$; T = transient, $n = 5$). There are no significant differences in RLG between persistence classes (Kruskal-Wallis test).

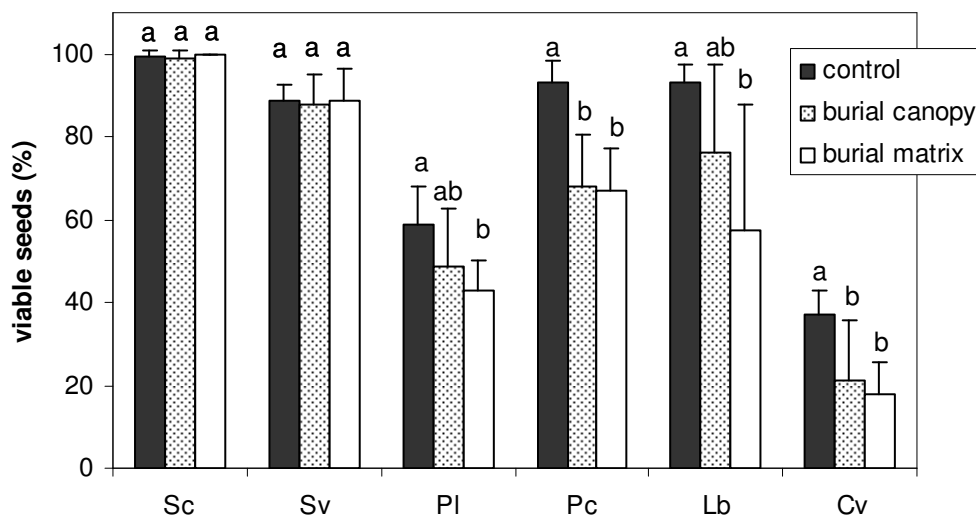


Fig. 4.8 Percentage of viable seeds after dry storage or burial in nylon mesh bags for a 10 month period under canopies or in the matrix. $n = 8$ bags for each treatment with 25 seeds per bag. Significant differences ($P < 0.05$, Tukey test after one-way ANOVA) between treatments within a species are indicated by different letters. Sc, *Solanum capense*; Sv, *Setaria verticillata*; Pl, *Peliostomum leucorrhizum*; Pc, *Pollichia campestris*; Lb, *Lycium bosciifolium*; Cv, *Chloris virgata*.

Table 4.7 Survival in the soil as a % of the lab dry stored control (mean of two microhabitats used), depth distribution (%), relative light germination (RLG) and seed bank class.

	Survival (%)	Depth distribution (%)	RLG	Seed bank class
<i>Solanum capense</i>	100	-	1.00	t
<i>Setaria verticillata</i>	99	70	0.65	sp
<i>Peliostomum leucorrhizum</i>	78	55	-	lp
<i>Pollichia campestris</i>	73	-	0.95	t
<i>Lycium bosciifolium</i>	72	82	0.81	sp
<i>Chloris virgata</i>	53	90	0.50	sp

Discussion

General/Methodology

DCA ordination of vegetation and seed bank data showed that canopy and matrix seed bank samples do not separate but for vegetation canopy and matrix plots are clearly distinct. This suggests that habitat specific environmental filters filter out species present in the seed bank. The most common species in the matrix vegetation have lighter and/or more elongated seeds than species in the canopy vegetation. Matrix species are therefore likely to disperse area-wide by wind to both microhabitats. Indeed comparison of canopy association for seed bank and vegetation show that species that are more common under the canopy for the seed bank

but are more common in the matrix for vegetation have either very small seeds or morphological adaptations for wind dispersal. Actually all species in Fig. 4.3 with morphological adaptations for wind dispersal have a lower canopy association based on cover than that based on the seed bank. It seems thus that seeds of matrix species are literally trapped by the canopy, where conditions for establishment of these species are unfavourable. This filtering effect of woody perennial canopies in (semi-) arid environments has also been described by Pugnaire & Lázaro (2000). They suggested that the soil seed bank is more or less uniform and that shrub canopies determine which species appear under canopies. Our data suggest that for matrix species this is the case but that canopy associated species are also in the seed bank more common under canopies. Directed dispersal by animals to canopies (Milton & Dean 1995) and relatively heavy seeds not easily dispersed by wind prevent these species from building up a large seed bank in the matrix.

That many species were completely absent from the seed bank does not mean that these species do not have a persistent seed bank. Many of these species have large seeds and consequently will produce less seeds than small seeded species for a given amount of resources (Shipley & Dion 1992; Greene & Johnson 1994; Turnbull *et al.* 1999; Jakobsson & Eriksson 2000) which decreases the chance of detecting these species in the soil seed bank. Some species may not have been detected because seeds were dormant and dormancy was not broken by the treatments used in this study, or the conditions for germination of non-dormant seeds were not met. Typical examples where dormancy is a likely cause of apparent absence from the seed bank are species that also did not germinate in the lab, even after various dormancy breaking treatments and by using different incubation temperatures. These include *Limeum aethiopicum*, *Cleome gynandra* and *Heliotropium lineare*.

A sod transplanting experiment (see Chapter 8) showed that *Trianthema parvifolia* germinated better in the matrix than under acacia canopies. The high temperatures and diurnal temperature fluctuations reached at the soil surface in the open may have promoted germination in this species. Interestingly the species was not found in samples taken and cultivated in 2002. However the samples from 2003, a year with a very warm summer that also raised the temperature in the green house, produced quite a lot of seedlings of this species. *Peliostomum leucorrhizum* also a typical species of bare open soils showed the same difference between 2002 and 2003. In future seed bank studies in the area that use the emergence method, care should be taken especially to test at very high temperatures like those found at the soil surface in the Kalahari. However, using only extreme temperatures will have a negative effect on the emergence of species that require lower temperatures and smaller

temperature fluctuations for germination, for example those species that are closely associated with the canopy of camelthorn trees (see Chapter 7) or winter annuals. It is therefore recommendable that future seed bank studies in this area include different temperature regimes for the cultivation of seed bank samples (van Rooyen & Grobbelaar 1982).

Depth distribution general

In contrast with the common assumption that most seeds are found in the top 1-2 cm of the soil in arid environments (Kemp 1989) only 68 % (66 % for canopy soil, 73 % for matrix soil) of the seeds were found in the upper 3 cm (Table 4.2). This proportion would possibly be reduced even more if soil layers deeper than 6 cm would be sampled. This does not correspond with what is known for savannas and arid habitats. For mesic savannah grassland in the eastern Transvaal more than 90 % of the seeds were found in the top 2 cm of soil (O'Connor & Picket 1992). The pattern was the same for a sahelian fallow in Niger (Hérault & Hiernaux 2004). In the Negev Desert nearly all seeds are situated on the soil surface crust and to a depth of 20-25 mm (Gutterman 1993). In North American desert soils 80 to 90 % of seeds occur in the upper two cm of soil of which most are in the litter or top few millimetres of soil (Kemp 1989 and references therein).

The contrast with previous studies may be due to differences in soil texture. In Namaqualand Broken Veld van Rooyen & Grobbelaar (1982) found that for four out of five habitats 67 to 88 % of seeds (sampled from 0-7.5 cm) were found in the upper 2.5 cm of soil. But in the sand plane habitat only 31 % of seeds were found in the top 2.5 cm. They argued that this difference is due to the more unstable character of the sand plane compared to the other habitats. It is more affected by the import and export of sand and seeds by the combined action of wind and water. The loose, sandy soils at the study site could similarly explain the difference in depth distribution between the study site and other arid and semi-arid habitats. Although soils in the dry river beds of the Southern Kalahari are generally more fine than in the surrounding dune veld they still have a sand content from 40 to 85 % (Leistner 1967). The combined action of wind and occasional flooding may therefore bury seeds relatively quickly.

Another explanation is that grasses are poorly represented in the study area. Especially perennial grasses of which no seedlings were found to emerge from the seed bank samples. Perennial grasses made up 85-95 % of the seed bank in mesic savannah grassland (O'Connor & Picket 1992). Grass species with awns are known to become readily anchored and germinate quickly at the soil surface (Peart 1984) instead of developing a seed bank as the seeds of grasses without appendages tend to do (Willems & Huijsmans 1994). Another

explanation for the discrepancy between our data and most other data on depth distribution of seeds in arid ecosystems is that the proportion of seeds present in the upper soil layer can fluctuate strongly depending on the season and year of study. Traba *et al.* (2006) found for Mediterranean grassland and scrubland that soil seed density in the top 1 cm dropped significantly during summer.

The seed bank determination method used may also have influenced the result. The emergence method cannot detect dormant seeds (de Villier *et al.* 1994) which are more likely to occur in the upper soil layers where recently shed seeds are likely to be found. Hérault & Hiernaux (2004) reported that using the emergence method germinating soil samples in the greenhouse only 73 % of the seeds were in the upper 2 cm instead of 90 % for seeds extracted from the soil using flotation. However for Strandveld of the west coast, South Africa, the proportion of seeds found in the top 5 cm of the soil was 79 % for extraction with flotation and 82 % for seedling emergence (de Villiers *et al.* 1994).

Finally higher average seed persistence of species in the system may have contributed to higher seed numbers in deeper soil layers. The species associated with acacias and that do also establish outside canopies under favourable conditions may have more persistent seeds due to the disturbance regime under canopies. Moreover dry riverbeds in the Kalahari are favoured as grazing habitat by antelopes and livestock especially after rains (Leistner 1967). This may also result in higher disturbance compared to other arid systems and have resulted in more persistent seeds as an adaptation to frequent disturbances (Thompson *et al.* 1998).

Depth distribution and seed mass and shape

No consistent pattern in the relationship between depth distribution and seed mass and shape was found for this study. For canopy soil and canopy and matrix soil pooled only seed shape correlated significantly with depth distribution of seeds. For matrix soil no significant correlation of depth distribution with seed shape was found but seed mass was correlated with depth distribution. However, the correlation of depth distribution with seed mass multiplied by the square root of variance of seed dimensions ($M \times \sqrt{V_s}$) was significant for matrix soil and $M \times \sqrt{V_s}$ was a better predictor of depth distribution than seed mass alone.

The inconsistencies in the relation of depth distribution with seed mass and shape between the two microhabitats may also be due to the lower seed densities in the matrix. Several species found in both canopy and matrix were excluded for the matrix due to the low number of seeds recorded there.

For north-western Europe seed mass was found to be the best predictor of depth distribution (Bekker *et al.* 1998). However, all species included in our analysis had a seed mass below the 3 mg threshold below which all species in the British flora that also had relatively compact seeds could persist in the soil for at least 5 years (Thompson *et al.* 1993). Including a wider range of seed sizes might have resulted in a correlation of seed mass with depth distribution for canopy species and canopy and matrix pooled as well.

Other factors than shape and size of seeds may also influence their depth distribution. *Argemone ochroleuca* was the species with the highest proportion of seeds in the deeper soil layer. 81 % of the seeds were found at 3-6 cm. It is likely that this pattern is due to the grazing history of the site. Before 1974 livestock from Botswana could freely graze in the Nossob river bed. This grazing pressure is likely to have caused an increase in unpalatable species like *Argemone ochroleuca*. After the erection of a border fence for veterinary purposes livestock was excluded from the South African part of the river bed as the South African farms were all fenced. The seeds in the soil are probably a legacy of the time when the vegetation was heavily grazed. Today *A. ochroleuca* is only occasionally encountered here. But the species is still very abundant directly on the other side of the fence in Botswana (Zimmerman 2001). *A. ochroleuca* is known to build up a large persistent soil seed bank (Karlsson *et al.* 2003).

Persistence and seed morphology

Species classified as persistent had significantly smaller seeds than species classified as transient, both for species and phylogenetically independent contrasts. Transient species, however, were also found within the boundary found by Thompson *et al.* (1993) where herbaceous species from the British flora all had long-term persistent seeds. Species with seed mass below 0.35 mg were all persistent for the canopy microhabitat. For both habitats combined, classifying species according to the most persistent record, this pattern basically remained, though there was one species found in the matrix with seed mass 0.07 mg that was apparently transient. However, *Eragrostis annulata* is an annual species and must therefore have been classified falsely, maybe due to high dormancy or low seed bank densities, as having transient seeds. The boundary for the matrix seed bank species below which all seeds are persistent is lower than for the canopy seed bank. This is probably due to generally lower seed density in the matrix increasing the chance of not detecting species in the lower soil layer. The pattern that all small seeded species (sometimes below a certain variance of seed shape) are persistent (though the boundary may not correspond with the 3 mg of Thompson *et*

al. (1993)) has been found in several other studies (Funes *et al.* 1999, Moles *et al.* 2000, Peco *et al.* 2003).

Though seed shape was the best predictor of depth distribution no relationship with persistence was found for species or phylogenetically independent contrasts. This may be due to the fact that there were very few species in this study with a variance of seed dimensions > 0.14 , the boundary in Thompson *et al.* (1993) below which all species which had a mass < 3 mg had persistent seeds. However, other studies in contrasting floras including more species with $V_s > 0.14$ also found no difference in seed shape between persistent and transient species (Moles *et al.* 2000; Peco *et al.* 2003).

Persistence and habitat

There were no significant differences in the proportion of persistent species between habitats. Depth distribution also did not differ between habitats and neither did seed mass. It must therefore be concluded that habitat has no effect on persistence. This may be caused by different selective forces in both habitats that both favour persistence: In the matrix more unpredictable conditions, longer unfavourable periods between periods with favourable conditions for establishment, favour species with persistent seeds, while under the canopy disturbance favours persistent seeds. Milton & Dean (1995) suggested that fleshy fruited shrub species may need canopies for establishment because they have no soil seed bank, which would also be a reason for the absence of a difference in seed persistence between habitats. Of seven fleshy-fruited species for which seed bank type was determined 6 were transient and only one short term persistent. Actually all long-term persistent species were matrix associated species so maybe larger data sets may reveal habitat related differences in seed persistence.

How reliable is the soil seedbank type classification

There is the possibility that species beyond the Thompson *et al.* (1993) boundary have persistent seeds: the probability that a species is not found in the seed bank will increase with seed mass as plants with larger seeds tend to produce less seeds. Thus among the species classified as having transient seeds there may be species that have actually persistent seeds. *Acacia erioloba*, for example, which has a seed mass of 295 mg was classified here as transient, has seeds of which a portion has physical dormancy, even after ingestion by large herbivores, its main dispersal agent (Hoffman 1989) and this makes it likely that the species will at least have short term persistent seeds. Witkowski & Garner (2000) found seeds

of the woody savanna species *Acacia nilotica*, *A. tortilis* and *Dichrostachys cinerea*, all with seeds ≥ 25 mg, up to a depth of 6-7 cm in the soil and concluded that all species form at least short-term persistent seed banks (> 1 year). *Acacia mellifera*, another large seeded species also present in the study area, does not have a persistent seed bank (Donaldson 1969; Briers 1988; Hagos 2001) and neither does *Boscia albitrunca* (Briers 1988). It seems therefore that the larger seeded (> 3 mg) species can be either persistent or transient. However, seed predation is also likely to have shaped the relationship between seed mass and persistence observed, as larger seeds are not able to escape predation by burial (Thompson 1987).

Of the smaller seeded species those with a very high to absolute light requirement for germination were found in all three persistence classes (Table 4.6, Fig. 4.7). It is, however, unlikely that species with a high light requirement for germination can not persist in the soil (Baskin & Baskin 1989). The burial experiment suggests a relation between light requirement for germination and survival in the soil (Table 4.7), however, this does not parallel seed bank classification for the species. This leads to the conclusion that the classification for several species is not correct. *Solanum capense* was classified as having a transient seed bank though aspects of its germination behaviour suggest that it has a long term persistent seed bank: seeds have an absolute light requirement for germination (Table 4.6), seeds buried for one year in the soil did not show viability loss (Table 4.7, Fig. 4.8). Seeds that are buried and escape predation will therefore have a high probability to persist in the soil for long periods. *Pollichia campestris* was also classified as transient. It germinates better in light than in dark (Table 4.6) and over 60 % of seeds survived one year burial in the soil (Fig. 4.8) suggesting that this species has at least a short-term persistent seed bank. Both *Solanum* and *Pollichia* were found in the seed bank but in very low numbers and the erroneous classification may therefore be simply due to low sample size. In contrast *Chloris virgata*, the species with the highest variance in seed dimensions in Fig. 4.5, is, contrary to predictions (Thompson *et al.* 1993) classified as having persistent seeds. However, in this case germination behaviour indicates that it might indeed be transient, or at least less persistent than all other small seeded species where seed bank and germination data are available: germination is not sensitive to light (Table 4.6), dormancy loss is relatively fast and accordingly 90% of the seeds are found in the upper soil layer. When *C. virgata* is classified as transient, all species with variance in seed dimensions > 0.14 are transient.

On the other hand the only other species besides *S. capense* with an absolute light requirement *Aptosimum lineare* and *Plinthus karoocicus* (Table 4.6), had seeds that were equally abundant in upper and lower soil layers or more abundant in lower soil layers. The

other species classified as having persistent seeds also all germinated better in light than in dark. This is in accordance with the hypothesis that a light requirement for germination is one of the main determinants of a species ability to accumulate a persistent seed bank (Baskin & Baskin 1989). The combination of no light requirement for germination and no dormancy is expected to prevent the formation of a seed bank and is only found in *Asparagus africanus* and *Rhigozum trichotomum* (see Chapter 5 for dormancy levels) which are, probably correctly, classified as transient.

Conclusions

The picture for seed persistence in this arid environment that emerges is consistent with the view held by Moles *et al.* (2000) that large seeded species can ‘choose’ to have either persistent or transient seeds, but that species below a certain size and shape must have persistent seeds because small rounded seeds are inevitably buried and the only viable strategy for them is to persist until they are brought back to the soil surface.

Though for the Kalahari seed size and shape are not related to persistence in the soil as in Britain (Thompson *et al.* 1993) there seem to be more similarities than with Australia (Leishman & Westoby 1998). Here the species with the largest seeds and the highest variance of seed dimensions actually had persistent seeds and furthermore species with transient and persistent seeds could be found for all other combinations of seed mass and shape. Moles *et al.* (2003) even found a positive relationship between diaspore mass and diaspore viability after being buried in the soil for 1 year in arid Australia. Our findings do seem to be consistent with Price & Joyner (1997) who found that large seeds were under-represented in the seed bank relative to their density in the seed rain in Mojave desert shrub land.

The reports that most seeds in arid desert environments are only found in the top few mm of the soil, may have led to neglecting the vertical distribution of seeds in the soil in arid environments. This study shows that significant amounts of seeds can be found below 3 cm and that the depth distribution of species in the soil seed bank is related to seed mass and shape and probably persistence as supported by data on germination behaviour. It is likely that such differences depend on the type of soil involved. This study also shows that it is important to use several approaches simultaneously to study patterns of persistence in the soil. Burial experiments and especially studies on seed predation would be a further line of study that is likely to give more insights in persistence patterns in arid ecosystems.

Chapter 5

Correlates of inter-specific variation in germination response to water stress in an arid savannah

Abstract

In arid ecosystems large inter-specific variation can be found in the ability to germinate under water stress. Most previous studies did not find correlations with habitat preferences. It is hypothesized that variation in the ability to germinate under osmotic stress is due to variation in seedling drought tolerance rather than differences in habitat use. Large seedlings are thought to be more resistant to drought and a correlation of seed size with the ability to germinate under osmotic stress is therefore expected. Species that are more drought sensitive are expected to have higher dormancy and a correlation of germination fraction with the ability to germinate under osmotic stress can be expected. Hypotheses were tested using 28 plant species from the Southern Kalahari. The water potential needed to reduce germination to 50 % relative to 0 Mpa was determined and the effect of seed mass, germination fraction and habitat preference (canopy association and soil texture association) tested. The data were analysed using phylogenetically independent contrasts. No effect of seed mass was found but there was a strong positive correlation between the ability to germinate under osmotic stress and germination fraction. The correlation was found for all species and perennials, but not for annuals. No correlation with habitat variables was found. The absence of a correlation with seed size can be explained by seedling drought tolerance being composed of many other attributes besides seed mass. The correlation of the ability to germinate under osmotic stress and dormancy supports the hypothesis that seedling tolerance has played a major role in the evolution of germination responses to water stress.

Introduction

Germination is a high-risk event in the life-cycle of most plants (Harper 1977). It is the transition from the most tolerant stage (seeds) to the most sensitive stage (seedlings). Mechanisms reducing the risks associated with germination are therefore expected to be under strong selection pressure (Meyer *et al.* 1997). Accordingly plants have developed a wide array of germination strategies where the response to specific environmental cues ensures germination at the optimal time for establishment (Baskin & Baskin 1998). In (semi-)arid

environments the high risks associated with germination and seedling establishment are mostly related to water availability (Gutterman 1993). One way by which seeds can avoid germinating under inadequate water supplies is by sensing the water potential in the surrounding soil (Koller & Hadas 1982). The need to germinate only at high water availability will increase as precipitation decreases and becomes more erratic. Groves *et al.* (1982) for example, found an increased sensitivity of germination to water stress with decreasing mean annual precipitation in *Themeda australis*. Yet in arid and other habitats large inter-specific variation is found in the ability to germinate under water stress (Evans & Etherington 1990; Briedé & McKell 1992; Flores & Briones 2001; Sy *et al.* 2001). Attempts to correlate this variation with habitat preferences like soil type and moisture conditions have been largely unsuccessful (Evans & Etherington 1990; Briedé & McKell 1992; Sy *et al.* 2001).

It is hypothesized that seedling drought tolerance causes the inter-specific variation in germination responses to water stress by modifying the risks associated with germination. Seedlings from larger seeds are thought to be more tolerant to drought (Leishman & Westoby 1994; Leishman *et al.* 2000) and seed mass is therefore likely to be correlated with the ability to germinate under osmotic stress. Brown & Venable (1986) demonstrated in a modelling study that a decrease in the germination fraction of annuals selects for greater specialization to favourable conditions. Species adapted to favourable moisture conditions will be under higher selective pressure to develop germination mechanisms that prevent germination when conditions are unfavourable for establishment. A correlation between the ability to germinate under osmotic stress and germination fraction is therefore expected. Besides having a bet-hedging function dormancy together with dormancy breaking requirements ensures germination in the season favourable for seedling establishment (Baskin & Baskin 1998; Eira & Caldas 2000). This will promote specialization to the favourable conditions experienced during establishment as well, and result in drought avoiding germination strategies. It is therefore hypothesized that both seed mass and germination fraction are positively correlated with the ability to germinate under osmotic stress.

Different microhabitats may differ in the the risks associated with germination and establishment. Different microhabitat associations could therefore be responsible for inter-specific variation in osmotic stress tolerance of germination. Microhabitat aspects especially likely to exert an influence on the risks associated with germination are the association with woody species ('nurse plants') and soil texture preference. Soils under tree canopies in (semi) arid areas have been reported to be moister than soil in the surrounding matrix (Kennard & Walker 1973; Parker & Muller 1982; Joffre & Rambal 1988; Facelli & Brock 2000). Besides

the effect of shade litter also has a positive effect on soil moisture (Tiedemann & Klemmedson 1977). The risk of encountering adverse conditions is thus larger in open spaces where soil dries out quickly. Species depending on canopies may therefore have a higher ability to germinate under osmotic stress than species preferring open habitat.

Soil texture is also likely to influence water availability. In arid regions coarse soils provide more favourable moisture conditions for plants than fine soils because greater porosity results in smaller run-off, deeper and more rapid penetration, smaller capillary forces resulting in less evaporation, and a lower wilting point (Leistner 1967). It is therefore predicted that species of fine textured soils will cease to germinate at a higher water potential than species from coarse textured soils.

To test the hypotheses the germination response of 28 plant species from the xeric Southern Kalahari savannah to decreasing water potential was determined and the life-history traits seed mass and germination fraction were measured. As habitat variables canopy association was measured and soil texture association was determined from literature data.

In summary the questions addressed in this paper are:

1. Are large seeded species more likely to germinate under osmotic stress than small seeded species?
2. Does the ability to germinate under osmotic stress increase with increasing germination fraction?
3. Are species that are common in sub-canopy habitats more likely to germinate under osmotic stress?
4. Is soil preference related with the ability to germinate under osmotic stress?

Methods

Study area and species

Seeds were collected in austral summer and autumn of 2001-2003, in the Nossob river valley, approximately 40 km south of Twee Rivieren (South Africa). A list of the study species with family and life form after Raunkiaer is given in Table 5.1. See Chapter 1 for a description of the area.

Table 5.1 Study species with family, life form after Raunkiaer, seed mass, clay + silt content in soil where plants are found, canopy association and dry heat pre-treatment applied. See text for details.

Species	Family	Life form	Mean seed mass (mg) \pm S.D.	Clay + silt content (%)	Canopy association	Pre-treatment
<i>Amaranthus dinteri</i>	Amaranthaceae	T	0.481 \pm 0.070	8.4	1.00	50 °C
<i>Amaranthus praetermissus</i>	Amaranthaceae	T	0.380 \pm 0.074	27.3	1.00	50 °C
<i>Aptosimum lineare</i>	Scrophulariaceae	H	0.103 \pm 0.021	15.8	-1.00	-
<i>Aptosimum marlothii</i>	Scrophulariaceae	Ch	0.234 \pm 0.048	22.9	-0.84	-
<i>Aristida congesta</i>	Poaceae	T	0.355 \pm 0.034	43.4	-1.00	70 °C
<i>Asparagus africanus</i>	Asparagaceae	H	14.968 \pm 2.597	34.6	1.00	-
<i>Asparagus pearsonii</i>	Asparagaceae	H	13.7 \pm 1.9	37.3	0.98	-
<i>Boerhaavia repens</i>	Nyctaginaceae	T	2.197 \pm 0.611	49.5	0.94	50 °C
<i>Chenopodium opulifolium</i>	Chenopodiaceae	T	0.413 \pm 0.057	2.0	1.00	-
<i>Chenopodium schraderianum</i>	Chenopodiaceae	T	0.085 \pm 0.014	37.3	1.00	-
<i>Chloris virgata</i>	Poaceae	T	0.331 \pm 0.077	54.4	-0.99	50 °C
<i>Coronopus integrifolius</i>	Brassicaceae	T	0.324 \pm 0.048	37.3	1.00	-
<i>Deverra denudata</i>	Apiaceae	H	1.875 \pm 0.317	59.0	-0.92	-
<i>Enneapogon desvauxii</i>	Poaceae	T	0.274 \pm 0.046	23.4	-1.00	50 °C
<i>Eragrostis porosa</i>	Poaceae	T	0.065 \pm 0.011	21.8	-1.00	50 °C
<i>Felicia clavipilosa</i>	Asteraceae	Ch	0.102 \pm 0.037	13.2	0.38	-
<i>Geigeria ornativa</i>	Asteraceae	T	0.349 \pm 0.049	15.5	-1.00	-
<i>Geigeria pectidea</i>	Asteraceae	H	0.383 \pm 0.082	34.9	-0.83	-
<i>Lycium bosciifolium</i>	Solanaceae	N	1.292 \pm 0.266	4.9	0.65	-
<i>Pentzia lanata</i>	Asteraceae	Ch	0.120 \pm 0.018	6.0	0.14	-
<i>Plinthus karoocicus</i>	Aizoaceae	Ch	0.139 \pm 0.027	26.0	-0.70	-
<i>Pollichia campestris</i>	Illecebraceae	G-H	0.361 \pm 0.062	2.2	1.00	-
<i>Portulaca oleracea</i>	Portulacaceae	T	0.157 \pm 0.033	40.5	1.00	-
<i>Rhigozum trichotomum</i>	Bignoniaceae	N	15.677 \pm 5.323	8.5	-0.51	-
<i>Schmidtia kalihariensis</i>	Poaceae	T	0.615 \pm 0.209	6.9	-0.88	50 °C
<i>Setaria verticillata</i>	Poaceae	T	0.423 \pm 0.074	29.1	1.00	-
<i>Solanum capense</i>	Solanaceae	H	3.299 \pm 0.514	16.7	0.98	-
<i>Tribulus terrestris</i>	Zygophyllaceae	T	1.32 \pm 0.41	25.1	-0.89	50 °C

Germination methods and seed size

To determine the response to decreasing water potentials polyethylene glycol (PEG) was used. PEG is a nonpenetrating, inert osmoticum and forms a colloidal solution which effect is similar to the matric properties of soil particles. The method gives a good estimate of germination behaviour in relation to soil moisture under field conditions (Hadas 1977). PEG 6000 (Merck-Schuchardt for synthesis, average molar mass = 5400 - 6600 g/mol) concentrations were 0, 125, 173, 209, 240 and 267 g/l of solution, these translate into osmotic potentials of 0.0, -0.2, -0.4, -0.6, -0.8 and -1.0 Mpa, respectively. Osmotic potentials were calculated using the formula from Money (1989) for PEG 6000. For each solution 8 replications of 25 seeds per petri dish were used. For each petri dish two 90 mm diameter filter paper discs (Schleicher & Schuell 595) were soaked in solution. Petri dishes were closed

with two strips of Parafilm to minimize evaporation of water from the solutions. Germination for most species was at a 30/15 °C, 12/12 h day night. Because of better germination results *Asparagus* and *Pollichia* were germinated at 22/22 °C and *Solanum* and *Lycium* at 26/19 °C. Some species had very low germinability and this was improved using dry heat treatments of 2 weeks at 50 or 70 °C (indicated in Table 5.1). Seeds were stored at 5 °C prior to experiments.

Germination fraction was the proportion of viable seeds that germinated in the first germination test within 6 months after collecting, without any pretreatments. The number of seeds germinated after two weeks was used in the analyses. This time span can be used to simulate the expected number of germinated seeds after a single rain fall event (Jurado & Westoby 1992). The final number of germinated seeds was recorded and the number of still viable seeds determined by pressing remaining seeds with tweezers. Firm, intact seeds were recorded as viable (Baskin & Baskin 1998). The ability to germinate under osmotic stress was defined as the water potential at which within 2 weeks 50% of the seeds relative to the 0 Mpa treatment germinated. This value was determined by linear interpolation. Seed mass was determined for 20 seeds individually according to the protocol in Westoby (1998) (see Table 5.1).

Canopy association

Percentage cover of each plant species was determined under the canopy and in the open in May 2003 (see Appendix 1). 10 m × 10 m plots were centred on 10 mature *Acacia erioloba* trees (stem circumference > 195 cm). Four 5 m × 5 m subplots, one in each cardinal direction, were established around each tree in the open matrix 15-20 m from the stem. Canopy association was calculated using $(\% \text{ cover under tree} - \% \text{ cover in open}) / (\% \text{ cover under tree} + \% \text{ cover in open})$. This gives a score from -1 (only found in open plots) to 1 (only found under tree canopies). Species that are indifferent to microhabitat score 0 (see Table 5.1).

Soil texture

For each species an average value for the proportion of fine particles (clay plus silt fraction) in the soils on which it was found growing was determined using data in Leistner & Werger (1973). In calculating the average, values for each soil type were weighted by the proportion of releves occupied by the species on each soil type. For *Aptosimum marlothii*, *Coronopus integrifolius* and *Solanum capense* with no records in Leistner & Werger (1973), the average proportion of fine particles was calculated using the soil types indicated for each species in

Leistner (1967) and the fine particle fraction of these soils from Leistner and Werger (1973), relative representation on each soil type could therefore not be included in this calculation because Leistner (1967) provided no data to enable this. *Asparagus pearsonii* and *Chenopodium schraderianum* were not represented in either Leistner (1967) or Leistner & Werger (1973) and were classified from own observations as only occurring in the river bed and average fine particle proportion was calculated using the average of riverbed soils in Leistner and Werger (1973) (see Table 5.1 for details).

Comparative method

Because two closely related species are more likely to resemble each other on account of common ancestry than are two unrelated species, it is inappropriate to use species as independent points in statistical analysis (Harvey & Pagel 1991). The method of phylogenetically independent contrasts (Felsenstein 1985) was designed to use phylogenetic information to allow enumeration of the number of times relationships have evolved independently.

See Chapter 4 and Appendix 4 for the phylogeny used. Contrasts in drought tolerance, germination fraction and seed size, canopy association and soil preference were calculated using the computer program CAIC (Comparative Analysis by Independent Contrasts: Purvis & Rambaut 1995) using the assumption of equal branch lengths. To meet the assumptions of normality seed mass was \log_{10} transformed and the proportions germination fraction and fine grain fraction of soil arcsine transformed prior to calculation of contrasts. Contrasts were first scrutinized to see if the standardization by equal branch lengths was sufficient to render them homoscedastic, and then they were analyzed using Model I multiple regression through the origin (Garland *et al.* 1993). Annuals and perennials were also analyzed separately.

Results

Cross species data

Drought tolerance was significantly correlated with germination fraction for all species together ($r = -0.636$, $P < 0.001$, $n = 28$), annuals only ($r = -0.548$, $P < 0.05$, $n = 15$) and perennials only ($r = -0.763$, $P < 0.01$, $n = 13$) (see Fig. 5.1). There was an unexpected correlation of drought tolerance with seed size for annuals (0.671 , $P < 0.01$, $n = 15$): larger seeded species are less tolerant to drought during germination. No correlations with seed size were found for all species or perennials only. No correlation of the ability to germinate under

osmotic stress was found with soil type or canopy association for all species or annuals and perennials separate.

Phylogenetically independent contrasts

For all species and perennials, partial regression coefficients showed a significant relationship between osmotic stress tolerance and germination fraction, but not between osmotic stress tolerance and seed mass, canopy association or soil texture (see Fig. 5.2, Table 5.2). For annuals partial regression coefficients showed no significant relationship between osmotic stress tolerance and germination fraction, nor seed mass, canopy association or soil texture (Table 5.2).

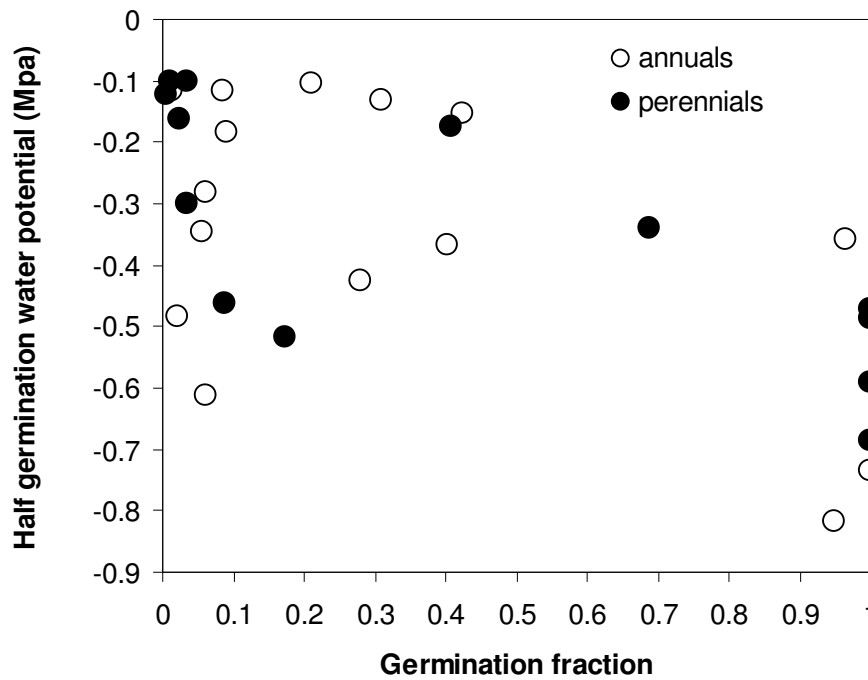


Fig. 5.1 Relation between germination fraction and water potential reducing germination 50 % compared with the control (0 MPa). Annuals: $n = 15$, $r^2 = 0.306$, $P < 0.05$ perennials: $n = 13$, $r^2 = 0.536$, $P < 0.01$ (arcsine transformed germination fraction).

Table 5.2 Multiple regression (through the origin) models for PIC's in 'drought tolerance' of the equation 'drought tolerance = $\beta_1 \times$ germination fraction + $\beta_2 \times$ seed mass + $\beta_3 \times$ canopy association + $\beta_4 \times$ soil texture' (all species: $r^2 = 0.516$, $F_{4,23} = 6.121$, $P = 0.002$, annuals cover: $r^2 = 0.667$, $F_{4,10} = 4.510$, $P = 0.028$, annuals seed bank $r^2 = 0.703$, $F_{4,8} = 4.733$, $P = 0.03$, perennials: $r^2 = 0.567$, $F_{3,9} = 3.931$, $P = 0.048$). For perennials a significant model could only be produced after exclusion of the least significant variable 'canopy association'.

Variable	β	n	t	P
All species				
germination fraction	-0.310	27	-4.327	0.000
seed mass	0.094	27	1.554	0.134
canopy association	-0.061	27	-1.221	0.235
soil texture	-0.121	27	-0.718	0.480
Annuals				
germination fraction	-0.305	13	-1.832	0.100
seed mass	0.226	13	1.386	0.199
canopy association	-0.029	13	-0.366	0.723
soil texture	-0.053	13	-0.196	0.849
Perennials				
germination fraction	-0.227	12	-2.370	0.042
seed mass	-0.055	12	-0.669	0.520
soil texture	0.289	12	1.187	0.265

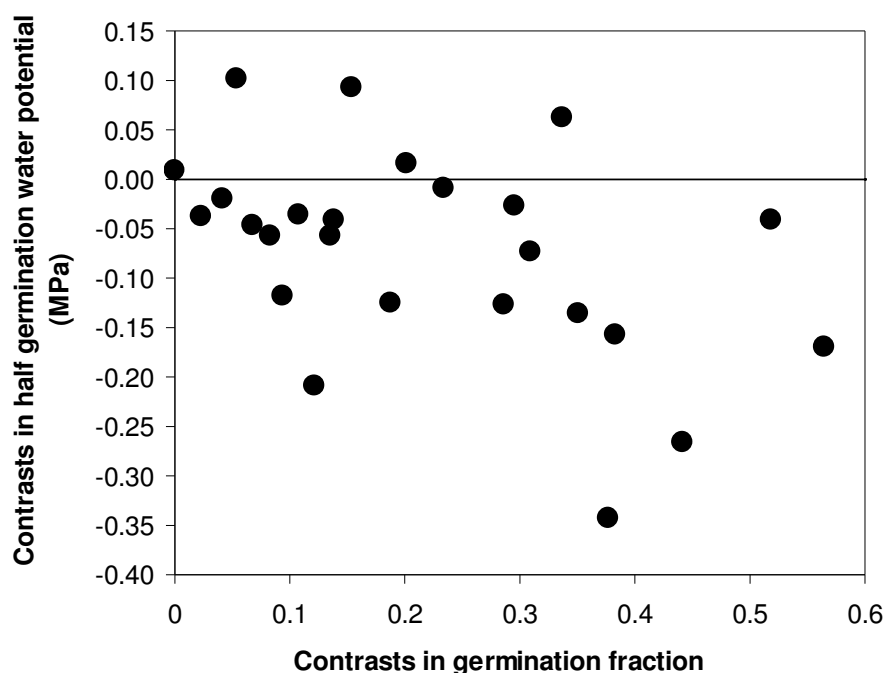


Fig. 5.2 Relation between phylogenetically independent contrasts in arcsine transformed germination fraction and in water potential reducing germination 50 % compared with the control for 28 Southern Kalahari species. $n = 27$ contrasts. All contrasts in germination fraction are set positive. Negative values of contrasts in water potential indicate that drought tolerance during germination increases (as water potential is always negative) when germination fraction increases.

Discussion

A strong correlation of osmotic stress tolerance during germination with germination fraction independent of phylogeny and the absence of a correlation with the most important habitat variables lends strong support to the hypothesis that variation in the ability to germinate under water stress is caused by differences in seedling drought tolerance rather than microhabitat preferences.

Using independent contrasts there was no significant effect of germination fraction on osmotic stress tolerance for annuals. This lack of a significant result can be attributed to the fact that (1) all annuals in arid regions are likely to have some kind of dormancy and variation in dormancy is therefore smaller between annual species, (2) the measure of dormancy used was relatively crude, (3) sample size for annuals was small.

It might be argued that the dry heat pre-treatment for more than half of the annual species influenced the result as these were also the species with low initial germination fractions. However, even without these species a linear regression model including all variables was highly significant ($r^2 = 0.634$, $F_{4, 13} = 5.642$, $P = 0.007$) and only germination fraction was significantly correlated with the ability to germinate under osmotic stress ($P = 0.003$).

Other studies also confirmed this study's findings for osmotic stress tolerance and germination fraction. Germination in *Citrullus lanatus*, which has zero initial germination (unpublished data) germinates to 50 % at a waterpotential > -0.2 Mpa and is completely inhibited at a water potential of -0.43 Mpa (Botha *et al.* 1984). Of seven Sahelian legume species the species with the lowest germination fraction had its relative germination reduced to 50 % at a higher water potential than all other species, which all had a germination fraction about twice as high (Sy *et al.* 2001). In a study of four *Eucalyptus* species, the species with the highest germination fraction had the highest relative germination % at -1.05 Mpa, the lowest water potential tested (Facelli & Lad 1996). Three of six perennial grasses from central New South Wales reached maximum germination soon after harvest. These included the two species that germinated over a wider range of water potentials than the other species (Maze *et al.* 1993). The pattern may also be found in temperate floras. Out of 15 British species only *Rumex crispus*, which had 100 % germinability at the highest water potential, had still 100 % germinability at -1.5 Mpa (Evans & Etherington 1990).

Seed mass did not behave as hypothesized. According to the hypothesis that larger seeds germinate under drier conditions, osmotic stress tolerance should increase with seed size. However, a significant correlation of seed mass with osmotic stress tolerance was only

found for annuals in the cross-species analysis, but not with the anticipated sign. Osmotic stress tolerance decreased with seed size. For independent contrasts there was no significant effect of seed mass. Only in perennials the partial regression coefficient had the predicted sign. For all species and annuals the partial regression coefficients for seed mass were in the opposite direction from what was predicted.

Relatively few studies have been carried out on interspecific relations between seed size and germination traits (But see Grime *et al.* 1981; Shipley & Parent 1991; Schütz 1999; Schütz & Rave 1999). Neither of the within habitat studies, both for wetland species (Shipley & Parent 1991; Schütz & Rave 1999), found a relation between seed size and germination traits. Seed size is correlated with many aspects of plant ecology (Leishman *et al.* 2000), which may explain the results in this study and those of others. For example animal dispersed seeds are generally larger than species with wind or unassisted dispersal (Leishman *et al.* 2000). Such effects could easily obscure other correlations with seed size. Drought tolerance can also be achieved by other means than large seedlings, for example by increasing root to shoot ratios, and by various physiological and morphological adaptations.

The absence of a relation between soil texture and drought tolerance during germination may be due to two different features of sandy and fine soils leading to similar adaptations. Though coarse soils generally provide more favourable moisture conditions for plants than fine soils (Leistner 1967) capillary rise will provide a higher moisture level for a longer time near the surface in fine soils rather than in sands (Scheffer 1998). Accordingly Elberse & Breman (1989) found higher germination percentages under experimental conditions on loam compared with sand in several species. So seeds in sand have to germinate at high water potentials to ensure that they will be able keep up with the rapidly descending water while seeds in fine soil have to germinate at high water potentials to maximize the chances that enough water will be available for establishment. Accordingly Schütz *et al.* (2002) also did not find a relation between drought tolerance during germination and soil type in the natural habitat for *Eucalyptus* species.

No relationship between the ability to germinate under osmotic stress and canopy association was found. Though several studies found higher soil moisture under tree canopies (see introduction), other studies found no significant differences in soil moisture between open and tree canopy areas (Shreve 1931; Tiedemann & Klemmedson 1977; Haworth & McPherson 1995; Anderson *et al.* 2001). The seasonal effects on soil moisture are also complex. Early in the season in Kenya soils are drier under canopies than in the open due to rainfall interception (Belsky *et al.* 1989) later in the growing season soils are wetter below

canopies because of reduced temperature and evapotranspiration in the shade, while still later in the growing season soils below trees and in the matrix are equally dry as plants in both habitats use all available moisture. Species growing mostly under canopies may therefore be exposed to similar soil moisture regimes as those growing in open places.

Germination responses to osmotic stress are often used to evaluate the adaptation of plant species to a certain habitat. This study shows that the results of such tests should be interpreted cautiously. Plants that coexist in the same micro-habitat can vary widely in their ability to germinate under osmotic stress, and presumably, in seedling drought tolerance. Though it was demonstrated that at a micro-scale habitat seems to have no effect on the ability to germinate under osmotic stress this still needs to be evaluated at larger scales. Further studies are also needed to verify the presence of a general correlation between the ability to germinate under osmotic stress and seedling drought resistance.

Chapter 6

Slow germination in annuals growing in association with *Acacia* canopies in an arid Kalahari savannah

Abstract

Reduced germination speed can be seen as a mechanism reducing the risk of germination in arid environments. The longer water has to be available for germination, the more likely it is that water will be available for subsequent growth. In arid environments large variation in germination speed is found among plant species. It is likely that part of this variation is related to microhabitat variation. Woody plants in arid environments are generally assumed to affect water availability under their canopies positively and will alter the risk for germinating seeds. If water stress is less limiting there will be selection for faster germination as fast germinating seedlings have a competitive advantage over slow germinating seedlings. It is hypothesized that due to improved water availability under canopies, which reduces the risk associated with germination, species associated with the canopy habitat germinate faster than species typically found in the surrounding open matrix. Contrary to the hypothesis a significant positive relationship between canopy association based on cover and the delay of germination was found. This could be caused by 1.) canopy interception of rain reducing water availability under canopies compared with the matrix 2.) very fast drying of the top soil in open areas, which makes fast germination necessary or, 3.) plant traits affecting drought tolerance, like root elongation rate, that differ between canopy and matrix species. No correlation was found when canopy association was based on seed bank data which can be attributed to either dispersal or establishment in both microhabitats in favourable years. To determine how much each mechanism contributes to the observed pattern in germination speed the study of other traits related to the response to water availability, manipulative experiments and a better understanding of the soil hydrology in the different microhabitats and the effect of canopy interception of rain are needed.

Introduction

Plant species vary widely in their speed of germination (Grubb 1977; Grime *et al.* 1981; Elberse & Breman 1989, 1990; Jurado & Westoby 1992; Gutterman 1993). Grubb (1977)

recognized germination speed as a potentially important source of variation in the regeneration niche that can contribute to the maintenance of diversity in plant communities: fast germinating species might gain a competitive advantage if subsequent conditions remain favourable, but slow germinating species, which may fail to germinate in short favourable periods could benefit in the long run as the fast germinating species are killed in a subsequent catastrophe.

In plant communities in arid and semi-arid environments in particular considerable variation in germination speed is found among species (Elberse & Breman 1989, 1990; Jurado & Westoby 1992; Gutterman 1993). Elberse & Breman (1989, 1990), in support of Grubb (1977), concluded that in the Sahel fast germinating species are at an advantage in years when small rain fall events at the beginning of the rainy season are followed up fast enough by more rain, if, however, the intermittent periods of drought are too long the germinable seeds are depleted and more slowly germinating species are at an advantage. Despite the apparent importance for the maintenance of species-richness, one of the more important questions in plant ecology, relatively little attention has been given to this topic in seed ecology. Grubb (1977) emphasized temporal variation in favourable conditions as a reason for the coexistence of different germination speed strategies. However, life history and (micro-) habitat are expected to affect germination speed. Grime *et al.* (1981) found germination speed to be negatively correlated with seed mass and germination speed has been found to differ with slope aspect (Gutterman & Agami 1987; Gutterman & Edine 1988; Boeken & Gutterman 1990). However, knowledge about determinants of germination speed is still very limited. Especially in arid environments, where spatial variation in the availability of moisture is likely to have the strongest influence on germination speed. Variation in moisture conditions experienced by seeds could be caused by soil type, slope aspect, or canopies of nurse plants.

In arid ecosystems annual plant species are often associated with canopies of woody plant species (Went 1942; Flores & Jurado 2003). Hydrological conditions are likely to vary strongly between the sub-canopy zone and the surrounding open habitat. Soils under tree canopies in (semi-) arid areas have been reported to be moister than soil in the surrounding matrix (Kennard & Walker 1973; Parker & Muller 1982; Joffre & Rambal 1988; Facelli & Brock 2000). Besides the effect of shade, litter also has a positive effect on soil moisture (Tiedemann & Klemmedson 1977). Due to favourable moisture conditions and higher nutrient availability, densities of seedlings are usually also higher under these woody plants than in the open matrix (own observations) and competition may therefore be more intensive under canopies. Germination speed may determine the outcome of competitive interactions between

seedlings through its effect on the size of seedlings at time of encounter (Ross & Harper 1972), fast germinating seeds therefore being at an advantage.

Due to improved water availability under canopies which reduces the risk associated with germination and more intense competition it is predicted that species associated with the canopy habitat germinate faster than species typically found in exposed habitat. In addition soil texture may also be an important habitat aspect influencing germination speed. Water will descend more rapidly in sand than in clay and species on sand may therefore have to germinate more rapidly than species associated with clayey soils (Schütz *et al.* 2002).

There may be trade-offs between germination speed and other life history traits. Dormancy, like slow germination, is another important risk avoiding strategy in arid environments (Gutterman 1993; Baskin & Baskin 1998) and there may be a trade-off between dormancy and germination speed. Jurado & Westoby (1992), found that faster germination tends to be associated with high dormancy and suggest the existence of a continuum with species that have high dormancy and high germination speed on the one hand to species that have low dormancy and low germination speed on the other hand. The former risking only a small number of seeds in each rain fall event, the latter risking all seeds after large rainfall events. As large seed size is like slow germination a way to reduce risk in variable environments (Venable & Brown 1988) a trade off between seed size and germination speed may also be expected. Large seed size is therefore expected to be associated with high germination speed, while smaller seeds should germinate more slowly. Such trade-offs may confound a relationship between canopy association and germination speed. Dormancy and seed mass were therefore included as co-variables in this study.

The hypothesis, that annual plant species associated with the canopy habitat germinate faster than species typically found in exposed habitat, was tested in the Southern Kalahari savannah. Here a suite of annuals is typically found associated with *Acacia erioloba* trees (Leistner 1967; Milton & Dean 1995; Leistner 1996) while other species are associated with the surrounding open matrix. Germination speed was determined in the lab and habitat association was determined based on the standing vegetation and based on the seed bank for two years. In addition the covariables soil texture preference, germinability and seed size were determined.

Methods

Seed collection and study area

Seeds were collected in austral summer and autumn of 2001-2003, in the dry Nossob river valley, appr. 40 km south of the Kgalagadi Transfrontier Park entrance at Twee Rivieren. See Chapter 1 for a description of the area.

Germination methods and seed mass

To determine germination pattern in time the number of germinated seeds was counted daily until no seeds germinated anymore. For each species 8 replications were used with 25 seeds each. The time related variables that were determined are minimum germination lag (the minimum time to germination from the start of the experiment of all replications together), average germination lag (the average minimum time to germination from the start of the experiment for eight replications) and t_{50} , the time needed to reach 50 % of total germination (average of eight replications).

For each petri dish two 90 mm diameter filter paper discs (Schleicher & Schuell 595) were soaked in deionized water. Germination was at a 30/15 °C, 12/12 h day night. The 30/15°C regime was chosen because all species germinated best at this temperature regime. Besides it is the optimum for germination in most tested open land species from arid southern Africa (Veenendaal & Ernst 1991). In some species dormancy had to be broken and this was done using dry heat treatments of 2 weeks at 50 °C or 70 °C (indicated in Table 6.1). Seeds were stored at 5 °C prior to experiments.

As a measure of dormancy germinability ($\text{germinability} = 1 - \text{dormancy}$) was used. Germinability was measured as the proportion of viable seeds that germinated within two weeks of the start of the treatment within 6 months after collecting, and without any pretreatments. The time span of two weeks can be used to simulate the expected number of germinated seeds after a single rain fall event (Jurado & Westoby 1992; Flores & Briones, 2001). The number of viable seeds was measured at the end of the experiment as the number of germinated seeds plus the number of ungerminated seeds that felt firm and intact when squeezed by tweezers (Baskin & Baskin 1998). Seed mass was weighed for 20 seeds individually according to the protocol in Westoby (1998) (see Table 6.1).

Canopy association

Percentage cover of each plant species was determined under the canopy and in the open in May 2003 (see Appendix 1). 10 m × 10 m plots were centered around 10 mature *Acacia erioloba* trees (stem circumference > 195 cm). Four 5 m × 5 m subplots, one in each cardinal direction, were established around each tree in the open matrix 15-20 m from the stem. An index of canopy association was calculated using the formula $(\% \text{ cover under tree} - \% \text{ cover in open}) / (\% \text{ cover under tree} + \% \text{ cover in open})$. This gives a score from -1 (only found in open plots) to 1 (only found under tree canopies). Species that are indifferent to microhabitat score 0 (see Table 6.1). Data collected in 2001 by Zimmerman (2001) were also used as it is known that association of annuals with shrubs and trees can fluctuate strongly between years (Tielbörger & Kadmon 2000). For 4 of the 15 species found in 2003 no data from 2001 were available.

Seed bank

To determine the seed bank soil samples were taken under the canopy and in the surrounding matrix of 20 large *Acacia erioloba* trees. Soil samples were collected in June 2002 and May 2003. Samples were taken at 0-3 cm depth, 10 soil cores (4 cm diameter) per microhabitat were taken. The 10 cores per tree were pooled for each microhabitat and stored in plastic bags. The soil seed bank was estimated by using the seedling-emergence method (ter Heerd *et al.* 1996). This method includes a concentration step by sieving the samples on a sieve of 0.2 mm mesh width. The concentrate was poured in a 5 mm thick layer on 53 cm × 33.5 cm trays filled with sterile compost. Emerged seedlings were removed once identifiable. After a cultivation period of 6 months trays were left to dry out. When dry the samples were separated from the potting soil and stored at 50 °C for 4 weeks, as many species from (semi-) arid regions are known to lose dormancy under hot and dry storage (Baskin & Baskin 1998). Samples were then cultivated again until no seedlings emerged anymore. An index of canopy association based on the seed bank was calculated using the formula $(\text{seeds under tree} - \text{seeds in open}) / (\text{seeds under tree} + \text{seeds in open})$. This gives a score from -1 (only found in open plots) to 1 (only found under tree canopies). Species that are indifferent to microhabitat score 0 (see Table 6.1).

Soil texture

For each species an average value for the proportion of clay in the soils it grows on was determined using data in Leistner & Werger (1973). In calculating the average, values for each soil type were weighted by the proportion of releves occupied by the species on each soil type. For four species with no records in Leistner & Werger (1973), the average proportion of clay particles was calculated using the soil types indicated for each species in Leistner (1967) and the clay particle fraction of these soils from Leistner & Werger (1973), relative representation on each soil type could therefore not be included in this calculation. Two species were not represented in either Leistner (1967) or Leistner & Werger (1973) and were classified from own observations as only occurring in the river bed and average clay particle proportion was calculated using the average of riverbed soils in Leistner & Werger (1973) (see Table 6.1 for details).

Table 6.1 Study species with family, life form after Raunkiaer, seed mass, germinability after 2 weeks, water potential (Ψ) reducing germination 50 % compared to $\Psi = 0$, average clay fraction, canopy association. See text for details.

Species	Family	Min. lag (days)	Average lag (days) (n = 8)	t ₅₀ (days) (n = 8)	Soil clay fraction (%)	Germinability after 2 weeks	Mean seed mass (mg) ± S.D.
<i>Amaranthus dinteri</i>	Amaranthaceae	2	2±0	2.3±0.3	6.7	42.3 ± 12.1	0.481 ± 0.070
<i>Amaranthus praetermissus</i>	Amaranthaceae	2	2.3±0.5	3.2±0.9	18.6	9.0 ± 5.6	0.380 ± 0.074
<i>Aristida congesta</i>	Poaceae	1	1±0	1.3±0.2	27.0	8.7 ± 9.8	0.355 ± 0.034
<i>Boerhaavia repens</i>	Nyctaginaceae	1	1.6±0.5	2.0±0.6	33.5	21.0 ± 10.0	2.197 ± 0.611
<i>Chenopodium opulifolium</i>	Chenopodiaceae	3	4.8±1.0	7.0±0.3	2.0	31.0 ± 17.7	0.413 ± 0.057
<i>Chenopodium schraderianum</i>	Chenopodiaceae	1	1±0	1.0±0.2	24.0 ¹	94.9 ± 4.1	0.085 ± 0.014
<i>Chloris virgata</i>	Poaceae	1	1±0	0.6±0.2	37.0	6.2 ± 4.5	0.331 ± 0.077
<i>Coronopus integrifolius</i>	Brassicaceae	4	4.5±0.5	6.5±1.7	24.0 ²	40.3 ± 14.6	0.324 ± 0.048
<i>Enneapogon desvauxii</i>	Poaceae	1	1.3±0.5	1.6±0.2	15.4	27.9 ± 9.7	0.274 ± 0.046
<i>Eragrostis porosa</i>	Poaceae	1	1.9±0.4	1.5±0.0	15.3	2.0 ± 2.2	0.065 ± 0.011
<i>Geigeria ornativa</i>	Asteraceae	1	1.3±0.5	1.7±0.4	10.6	96.6 ± 5.9	0.349 ± 0.049
<i>Portulaca oleracea</i> L.	Portulacaceae	1	1±0	0.6±0.1	28	100.0 ± 0.0	0.157 ± 0.033
<i>Schmidtia kalahariensis</i>	Poaceae	1	1.1±0.4	0.8±0.6	5.4	6.0 ± 5.2	0.615 ± 0.209
<i>Setaria verticillata</i>	Poaceae	2	2.4±0.5	2.4±0.4	20.9	5.5 ± 2.9	0.423 ± 0.074
<i>Tribulus terrestris</i>	Zygophyllaceae	1	1.9±0.4	1.4±0.4	16.6	1.36 ± 1.45	1.32 ± 0.41

¹Not in Leistner & Werger (1973) nor Leistner (1967) only observed in river bed, values for river soil taken from Leistner & Werger (1973)

²Not in Leistner & Werger (1973) value calculated using values from Leistner & Werger for the soil types indicated for these species in Leistner (1967) therefore not weighed by proportion of releves occupied.

Comparative method

See Chapter 4 and Appendix 4 for information on the phylogeny used for calculating contrasts. Contrasts in germination lag, germination speed, germinability and seed size, canopy association and soil preference were calculated using the computer program CAIC (Comparative Analysis by Independent Contrasts: Purvis & Rambaut 1995) using the assumption of equal branch lengths. To meet the assumptions of normality germination lag, germination speed and seed mass were \log_{10} transformed and the proportions germinability and fine grain fraction of soil arcsine square root transformed prior to calculation of contrasts. Contrasts were first scrutinized to see if the standardization by equal branch lengths was sufficient to render them homoscedastic, and then they were analyzed using Model I multiple regression through the origin (Garland *et al.* 1993).

Results

Canopy association based on plant cover generally explained most of the variation in germination speed parameters (Table 6.2, 6.3, 6.4, Fig. 6.1). Soil texture and germinability also had a significant effect, but only for canopy association the partial regression coefficient was significant in both years and for all measures of germination speed. The effect of germinability was not consistent between years. In 2001 the regression coefficient was positive for models for all three speed measures, in 2003 it was negative. This difference can only be explained by the lower number of species used for 2001. The significant positive correlation of germinability and germination speed parameters found for the 2001 standing vegetation data is therefore probably an artefact of small sample size. Seed mass never had a significant effect on germination speed.

Although there was a cross species correlation between canopy association based on the seed bank for 2002 and germination speed (Fig. 6.2), using PICs no effect of germination speed on canopy association based on the seed bank was found. Neither did any of the covariables in the models with seed bank based canopy association as the main predictor variable show a significant relationship with germination speed parameters (Table 6.2, 6.3, 6.4).

Discussion

Interestingly the opposite of what was expected was found: species associated with acacia canopies germinate more slowly than those growing mostly in the surrounding open matrix.

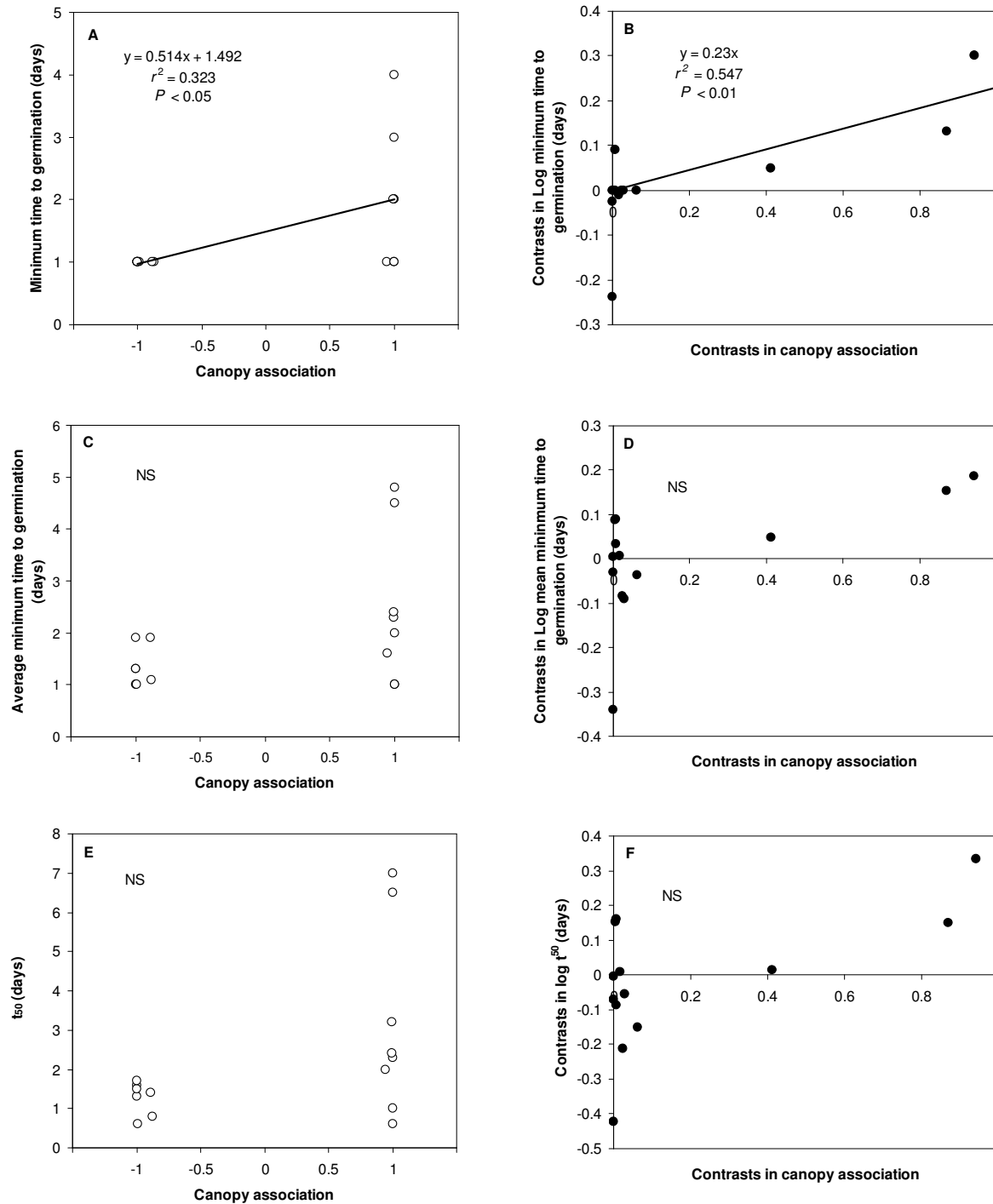


Fig. 6.1 Cross species relationship ($n = 15$) between canopy association based on cover in 2003 and (A) absolute minimum time to germination, (C) average time to germination, and (E) t_{50} and relationships between Phylogenetically Independent Contrasts (PICs, $n = 13$) in canopy association based on cover in 2003, and PICs in (B) absolute minimum time to germination, (D) average time to germination and (F) t_{50} .

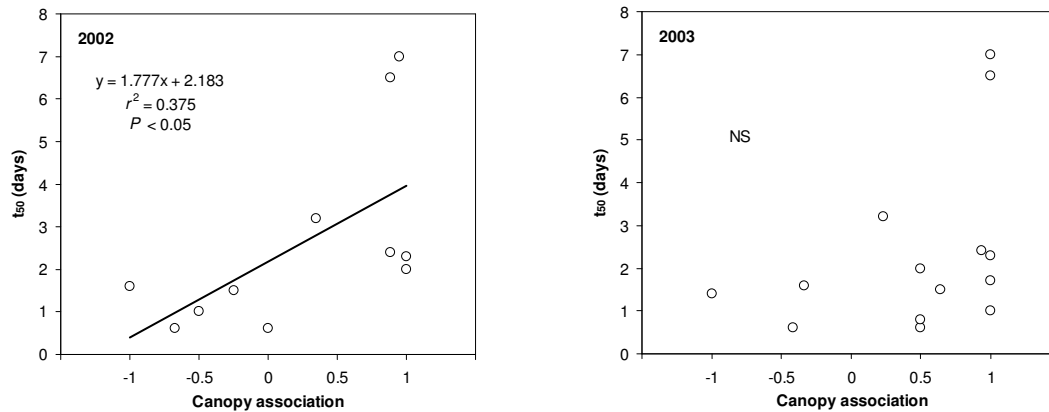


Fig. 6.2 Cross species relationship between t_{50} and canopy association based on seed bank data for 2002 ($n = 11$) and 2003 ($n = 14$).

One possible explanation is that water availability under canopies is actually lower than in the open. It has been suggested that rain interception might result in lower water availability under shrub canopies in (semi-) arid regions. Species growing under canopies exploit the increased nutrient content found there, but can only do so in years when rain is sufficient to overcome the effect of canopy interception of rain (Tielbörger & Kadmon 2000). Canopy interception of rain might increase the proportion of rain events that are insufficient for establishment and thereby promote more risk-avoiding germination strategies.

An alternative explanation for the observed pattern is that in the matrix the top soil dries out very quickly. In the Negev desert it was found for geophytes and shrubs inhabiting different habitats (north or south facing slopes and wadis inbetween) that in species from more exposed and extreme habitats, the onset of germination is earlier and germination is faster because the top soil remains moist only for a relatively short period (Gutterman & Agami 1987; Gutterman & Edine 1988; Boeken & Gutterman 1990). Though species growing in open areas between acacia trees might also benefit from germinating slowly to ensure adequate water supplies, fast drying top soil may constrain the evolution of germination speed in species growing on exposed sites. The observed slower germination of canopy associated species may therefore not be a special adaptation to the canopy environment but species germinate more slowly just because it is possible as top soil dries out more slowly under the canopy. The fact that under the canopy the whole range of very fast up to very slow germinating species is found, but in the open only fast germinating species are found (for this study's sampling dates) supports the hypothesis that species are limited to fast germination by fast top soil drying in open spaces but less so under the canopy. If there would be selective

Table 6.2 Multiple regression (through the origin) models for PIC's in 'minimum time to germination' of the equation 'minimum time to germination = $\beta_1 \times$ canopy association + $\beta_2 \times$ soil + $\beta_3 \times$ germinability + $\beta_4 \times$ seed size' (cover 2001: $r^2 = 0.888$, $F_{4,4} = 7.921$, $P < 0.05$, cover 2003: $r^2 = 0.718$, $F_{4,9} = 5.734$, $P < 0.05$, seedbank 2002: $r^2 = 0.629$, $F_{4,6} = 2.542$, n.s., seedbank 2003: $r^2 = 0.474$, $F_{4,8} = 1.805$, n.s.).

Variable	β	n	t	P
Cover 2001				
canopy association	0.274	8	2.656	0.057
clay content	-0.692	8	-2.298	0.083
germinability	0.308	8	1.433	0.225
seed size	-0.184	8	-0.864	0.436
Cover 2003				
canopy association	0.243	13	4.313	0.002*
clay content	-0.533	13	-1.893	0.091
germinability	-0.113	13	-0.906	0.388
seed size	-0.055	13	-0.444	0.668
Seedbank 2002				
canopy association	0.116	10	0.933	0.387
clay content	-0.458	10	-1.051	0.334
germinability	-0.075	10	-0.488	0.643
seed size	0.007	10	0.045	0.965
Seedbank 2003				
canopy association	0.213	12	2.259	0.054
clay content	-0.138	12	-0.307	0.767
germinability	-0.145	12	-0.797	0.448
seed size	0.022	12	0.119	0.908

pressure for slow germination in canopy associated species fast germinating species are expected to be absent there.

A third explanation is that species under canopies differ from species in the open in traits related to drought sensitivity. Root system development may be related to more efficient extraction of available nutrients and water (Lloret *et al.* 1999). Under canopies nutrient concentrations are much higher than in the open matrix (Dean *et al.* 1999, Hoffmann 2001) and water availability may be higher (see introduction). Species under acacia canopies may therefore be less nutrient and water limited and thus can reduce allocation to roots. Higher relative investment in photosynthetic tissues may enable faster biomass accumulation and higher competitive ability which will be especially important under canopies where seedling and adult plant densities of annuals can be very high. Preliminary results suggest that most canopy species have slower initial root elongation than matrix species (M. Kos unpublished results). This is likely to make them more vulnerable to drought stress and may have resulted in low germination speed in this group of species.

Table 6.3 Multiple regression (through the origin) models for PIC's in 'average minimum time to germination' of the equation 'average minimum time to germination = $\beta_1 \times$ canopy association + $\beta_2 \times$ soil + $\beta_3 \times$ germinability + $\beta_4 \times$ seed size' (cover 2001: $r^2 = 0.969$, $F_{4,4} = 30.806$, $P = 0.003$, cover 2003: $r^2 = 0.735$, $F_{4,9} = 6.245$, $P = 0.011$, seedbank 2002: $r^2 = 0.826$, $F_{4,6} = 7.123$, $P = 0.018$, seedbank 2003: $r^2 = 0.568$, $F_{4,8} = 2.625$, $P = 0.114$).

Variable	β	n	t	P
Cover 2001				
canopy association	0.259	8	5.911	0.004**
clay content	-0.829	8	-6.506	0.003**
germinability	0.364	8	3.995	0.016*
seed size	0.024	8	0.262	0.806
Cover 2003				
canopy association	0.204	13	3.423	0.008**
clay content	-0.764	13	-2.556	0.031*
germinability	-0.320	13	-2.414	0.039*
seed size	-0.152	13	-1.153	0.278
Seedbank 2002				
canopy association	0.136	10	1.215	0.270
clay content	-0.703	10	-1.781	0.125
germinability	-0.248	10	-1.783	0.125
seed size	-0.076	10	-0.534	0.612
Seedbank 2003				
canopy association	0.160	12	1.719	0.124
clay content	-0.440	12	-0.986	0.353
germinability	-0.348	12	-1.937	0.089
seed size	-0.097	12	-0.521	0.617

Seed bank

No relationship between germination speed and canopy association based on the seed bank was found for PICs, though for 2002 the cross species correlation was significant. Whereas for canopy association based on the standing vegetation species occurred either under the canopy or in the matrix (Fig. 6.1), there were several species in the seed bank that were more evenly distributed between canopy and matrix (Fig. 6.2). There are two possible causes for the presence of species in the seed bank where they were not found in the standing vegetation. Either seeds were dispersed to unsuitable habitat (canopy and matrix species) or species established and produced the seeds in the 'unfavourable habitat' during years with sufficient rain fall (canopy species).

The degree of canopy association in a particular year may depend on rain fall. Tielbörger & Kadmon (1997) found for 29 annuals over a period of three years with contrasting rain fall that only one species was consistently more abundant under shrubs. On the other hand several of the canopy species are nitrophilous species that are consistently more common under *Acacia erioloba* canopies in the standing vegetation and in the seed bank. For example *Setaria verticillata*, *Amaranthus* and *Chenopodium* spp (Leistner 1967;

Table 6.4 Multiple regression (through the origin) models for PIC's in 't₅₀' of the equation 't₅₀ = $\beta_1 \times$ canopy association + $\beta_2 \times$ soil + $\beta_3 \times$ germinability + $\beta_4 \times$ seed size' (cover 2001: $r^2 = 0.930$, $F_{4,4} = 13.264$, $P = 0.014$, cover 2003: $r^2 = 0.537$, $F_{4,9} = 2.610$, $P = 0.107$, seedbank 2002: $r^2 = 0.768$, $F_{4,6} = 4.968$, $P = 0.041$, seedbank 2003: $r^2 = 0.459$, $F_{4,8} = 1.696$, $P = 0.243$).

Variable	β	n	t	P
Cover 2001				
canopy association	0.353	8	3.241	0.032*
clay content	-0.989	8	-3.113	0.036*
germinability	0.789	8	3.475	0.025*
seed size	0.046	8	0.203	0.849
Cover 2003				
canopy association	0.275	13	2.401	0.040*
clay content	-0.815	13	-1.420	0.189
germinability	-0.381	13	-1.494	0.169
seed size	-0.128	13	-0.504	0.626
Seedbank 2002				
canopy association	0.101	10	0.552	0.601
clay content	-1.026	10	-1.596	0.162
germinability	-0.357	10	-1.575	0.166
seed size	0.058	10	0.250	0.811
Seedbank 2003				
canopy association	0.268	12	1.732	0.122
clay content	-0.293	12	-0.396	0.703
germinability	-0.450	12	-1.510	0.170
seed size	-0.043	12	-0.138	0.894

Milton & Dean 1995; our data).

The sod transplant experiment (Chapter 8) suggests that slow germinating canopy species may not only germinate slowly because they are associated with canopies but that slow germination enforces the association with canopies by reducing the chance of germination under matrix conditions. Of course it is not clear if germination or early seedling growth is inhibited by matrix conditions as these cannot be distinguished in the field. Slow root growth may be as likely a cause of finding no seedlings as the absence of conditions that allow germination.

Soil texture

Clay content was positively correlated with germination speed. The higher the clay content of the soil where plants grow the faster the germination. In arid regions coarse soils provide more favourable moisture conditions for adult plants than fine soils because greater porosity results in smaller run-off, deeper and more rapid penetration, smaller capillary forces resulting in less evaporation, and a lower wilting point (Leistner 1967). However, water descends rapidly in coarse soils, with favourable moisture conditions in the seed zone persisting only

shortly compared to clayey soils. In accordance with this Allen *et al.* (2000) found that psammophytes needed high water potentials to germinate while generalists with regard to soil texture germinated over a wide range of water potentials. One would therefore expect to find more slow germination in species associated with more clayey soils where favourable moisture conditions at the soil surface persist longer. It is possible that the process of run-off is important here. After rain fall large areas are only wetted at the surface, while most water drains to channels and local depressions. To allow establishment outside channels and local depressions germination would need to be fast, before the superficially penetrated water has evaporated.

Germinability

A significant relationship between germinability and germination speed was found. However, the sign of the regression coefficient varied between years. This difference can only be explained by the lower number of species used for 2001. The significant positive correlation of germinability and germination speed parameters found for the 2001 standing vegetation data is therefore probably an artefact of small sample size. If only the 2003 data are considered (and the sign of the relationship for 2002 and 2003 seed bank data) germination speed increases with germinability. The data do therefore not show a trade-off between germination speed and dormancy as suggested by Jurado & Westoby (1992).

Seed mass

The absence of a relationship between seed size and germination speed does not support the hypothesis that there is a trade off between germination speed and seed size. Other studies also failed to find a correlation between seed mass and germination speed (Shipley & Parent 1991; Morgan 1998). However, Grime *et al.* (1981) found germination speed to be negatively correlated with seed mass. But they included species from a much wider range of seed sizes than represented in this study, ranging from annuals to trees. It is possible that large seeded species germinate more slowly because they have a competitive advantage over smaller seeded species in the community. The size of seedlings at time of encounter determines the outcome of competitive interactions between seedlings (Ross & Harper 1972), and large seeded species in a community may be less constrained by the effects of competition.

Conclusions

It was shown that differences in germination speed can be related to microhabitat use. It is conspicuous that standard texts (Baskin & Baskin 1998; Fenner 2000) neglect this aspect of seed ecology although the importance of this trait has been recognised before (Grubb 1977; Grime 1981). However, this reflects a general attitude towards this aspect of germination ecology, which is reflected in a very limited body of literature. This study provided additional evidence that germination speed is an important aspect of the regenerative biology of plants, especially in (semi-) arid regions, that deserves more attention.

At present it is not possible to say if selective pressure for fast germination in the matrix, selective pressure for slow germination under canopies or certain traits related to drought resistance like root elongation rate are responsible for the observed relationship between canopy association and germination speed. More field observations in years with contrasting rain fall are needed together with manipulative experiments in the field and in the lab.

Chapter 7

Seeds use temperature cues to ensure germination under nurse plant shade in xeric Kalahari savannah

Abstract

In arid environments many plant species are found associated with the canopies of woody perennials. Favourable conditions for establishment under canopies are likely to be associated with shade but under canopies shade is distributed patchily and differs in quality. Diurnal temperature fluctuations and maximum temperatures could be reliable indicators of safe sites. Here it is examined if canopy associated species use temperature cues to germinate in shade patches, rather than matrix areas between trees. Perennial and annual species associated with *Acacia erioloba* trees and matrix species were germinated at temperature regimes resembling shaded and un-shaded conditions. Soil temperature was measured in the field. Germination of all fleshy fruited perennial Acacia-associated species and two annual Acacia-associated species was inhibited by the temperature regime resembling un-shaded conditions compared with at least one of the regimes resembling shaded conditions. Inhibition in perennials decreased with seed mass, probably reflecting that smaller seedlings are more vulnerable to drought. Germination of matrix species was not inhibited by the un-shaded temperature regime and in several cases it increased germination compared with shaded temperature regimes or constant temperature. Using Phylogenetically Independent Contrasts there was a significant positive relationship between canopy association and the germination at shade temperatures relative to un-shaded temperatures. The data support the hypothesis that canopy species have developed mechanisms to prevent germination in open sun conditions. This study and data from the literature show that inhibition of germination at temperature regimes characteristic of open sun conditions can be found in fleshy-fruited species of widely divergent taxonomic groups. It is predicted that germination mechanisms to detect canopy shade based on temperature cues are widespread in species depending on nurse plants, especially bird dispersed species.

Introduction

In vegetation characterised by discontinuous tree or shrub layers a distinct assemblage of plant species ranging from annuals to trees is commonly associated with the canopies of the initially establishing pioneer woody species. Such patterns are most commonly found in arid regions (Went 1942; Archer *et al.* 1988; Pugnaire *et al.* 1996; Facelli & Brock 2000) where facilitation is most important (Callaway & Walker 1997; Holmgren *et al.* 1997; Flores & Jurado 2003), but can also be found in several other environments (reviewed in Flores & Jurado (2003)). The establishment of many species in arid areas depends completely on their so called nurse plants, a phenomenon which has been especially well studied for Cactaceae (Steenberg & Lowe 1969; Valiente-Banuet & Ezcurra 1991; Valiente-Banuet *et al.* 1991; Godínez-Alvarez *et al.* 2002). In arid environments local conditions, like temperature, soil moisture, soil nutrients and radiation are different under canopies compared with open spaces (Belsky *et al.* 1989; Weltzin & Coughenour 1990; Vetaas 1992; Belsky *et al.* 1993; Belsky & Canham 1994). Experimental studies showed that some of these conditions under the canopy, such as shading and higher nutrient levels, improved survival and growth of seedlings under the canopy compared with open spaces (Valiente-Banuet & Ezcurra 1991; Carillo-Garcia *et al.* 2000).

At the same time dispersal probably plays an important role in the development of such associations. Many of the perennial species associated with canopies are bird dispersed (McDonnell & Stiles 1983; Tester *et al.* 1987; Dean *et al.* 1999; Facelli & Brock 2000), and the seed rain of bird dispersed species tends to be concentrated under isolated trees used by birds for perching, roosting and nesting (McDonnell & Stiles 1983; Tester *et al.* 1987; Hoppes 1988; Izhaki *et al.* 1991; Guevara & Laborde 1993; Debussche & Isenmann 1994; Holl 1998). For annuals epizoochory and endozoochory by large herbivores that rest and defaecate under trees while seeking shade has been suggested as a cause for this pattern (Janzen 1984; Milton & Dean 1995).

When both the seed rain and the optimal conditions for establishment show a patchy distribution and are spatially correlated one can speak of directed dispersal (Howe & Smallwood 1982). Wenny (2001) hypothesized that directed dispersal is especially common in arid regions. It can be expected that in canopy associated species in arid environments directed dispersal, i.e. an interaction between dispersal pattern and favourable local conditions, has led to the development of germination responses to detect these conditions. Tree canopies in savannas reduce maximum soil temperature and daily temperature fluctuations (DTF) (Tiedemann & Klemmedson 1977; Belsky *et al.* 1989). These temperature

parameters under canopies are likely to be highly correlated with favourable conditions for establishment and growth like reduced daytime temperatures, reduced radiation and higher soil moisture. Temperature fluctuation has long been recognized as a cue that seeds use for gap detection (Thompson & Grime 1983; Bullock 2000). Germination of gap colonizing species in tropical rain forests for example, is stimulated by increased temperature fluctuation typical of gaps (Vázquez-Yanes & Orozco-Segovia 1982; Pearson *et al.* 2002). Likewise canopy specialists could use temperature cues to detect a canopy patch. In this case germination should be inhibited by high temperature fluctuations or maximum temperatures as found in open spaces.

It might seem redundant to develop a mechanism that ensures germination under canopies when directed dispersal ensures the deposition of the majority of seeds under trees. But these factors are not mutually exclusive because the sub-canopy patch is not a homogeneous environment. For example the amount of shading under the canopy differs depending on cardinal orientation (Belsky *et al.* 1989; Belsky & Canham 1994). Valiente-Banuet & Ezcurra (1991) found that in Mexico several succulents that depend on nurse plants for establishment were only found at the north side of nurse plants. However, seed rain of fleshy-fruited cacti might still be considerable on other sides due to birds perching overhead. Sapling and mature trees also differ in the shade they provide, adding further to heterogeneity in the canopy layer (Dean *et al.* 1999). It could therefore be profitable for a seed to wait until secondary dispersal or growth of the canopy results in more favourable conditions for establishment. Animal activity in arid landscapes is often concentrated under shrubs and trees as they provide services like cover, shade and food, which increases the chance of secondary dispersal (Dean *et al.* 1999).

It is hypothesized that canopy species have developed mechanisms to avoid germination at temperatures characteristic of open un-shaded spaces in response to the heterogeneous distribution of shade favourable for establishment under the canopy. Matrix species are expected to be stimulated by temperature regimes characteristic of open conditions and inhibited by low DTF or maximum temperatures. Their mainly wind dispersed seeds will frequently land under canopies where establishing seedlings would be out competed by canopy species adapted to exploit high nutrient levels under shaded conditions. These hypotheses were tested with plants from the semi-arid savannah of the Southern Kalahari where a distinct set of species, mainly annuals and fleshy fruited perennials, is associated with the canopy of *Acacia erioloba* trees growing in dry river beds (Dean *et al.* 1999).

A relationship between habitat association and germination response to temperature could be confounded by a relationship between seed mass and response to alternating temperatures. Pearson *et al.* (2002) found for pioneer rainforest trees that small seeded species did not use DTF as a gap detection cue, though large seeded species did. Alternatively small seeded species might also be more affected by DTF than large seeded species as small seedlings are less tolerant to environmental hazards like drought (Leishman *et al.* 2000). Therefore seed mass was also measured to evaluate its effect on germination behaviour.

In particular the questions addressed in this paper are:

1. Do soil temperature regimes differ between mature trees, saplings and matrix?
2. Do soil temperature regimes differ between different cardinal orientations under the canopy?
3. Do soil temperature regimes characteristic of open spaces inhibit germination of canopy associated species?
4. Do soil temperature regimes characteristic of open spaces stimulate germination of matrix species?
5. Is the germination response to soil temperature dependent on seed mass?

To answer these questions cover and presence of each species in canopy and matrix plots was recorded to enable classification of species according to their pattern of association with *Acacia erioloba*, temperature was measured in the field, seed mass was measured and germination tests were conducted in the lab for 29 Kalahari plants, both canopy and matrix species, at different temperature regimes characteristic of canopies or openings.

Methods

Seed collection

Seeds were collected in the summer and autumn of 2001-2003, in the dry Nossob river valley, South Africa, appr. 40 km south of the Kalahari Gemsbok National Park entrance at Twee Rivieren. See Chapter 1 for a detailed description of the area.

Vegetation pattern

To be able to classify species according to their association with *Acacia erioloba* the presence and percentage cover of each plant species was determined under the canopy and in the open

in May 2003. Plots were centered around ten mature *Acacia erioloba* trees (stem diameter > 60 cm measured at 30 cm above ground level as this species tends to branch at a very low level). Under the canopy of each tree a 10 m × 10 m plot centered around the base was established. Around each tree, in the open matrix 15-20 m from the stem, four 5 m × 5 m subplots, one in each cardinal direction, were established.

Temperature measurements

To measure temperature the Thermochron iButton DS1921L-F51 (Maxim Dallas, Texas) was used. Thermobuttons were buried one cm deep, halfway between trunk and canopy drip line and 10-15 m away from the canopy drip line of five mature trees (stem diameter 96 ± 9 cm) and halfway between trunk and canopy drip line under five saplings (stem diameter 20 ± 7 cm). For each sample unit a thermo button was buried in each cardinal direction. Measurements were made every 20 minutes starting at 1800 h, 12 Mar.2003 and ending at 1740 h, 8 Apr. 2003. However, as no rain fall was recorded for this period another data set, originally collected for other purposes, was used to evaluate the effect of rain fall on soil temperature. For the period 1 Oct. 2002 - 30 Dec. 2002 soil temperature was recorded with eight thermo buttons each buried under a different mature acacia halfway between stem and canopy drip line at a random cardinal orientation and eight buried in the matrix at a random cardinal orientation, 10-15 m from the canopy drip line. Measurements were made every two hours starting 0000 h. Rain fall data were provided by Prof. Dr. A.O.E. Rasa on the farm Alpha, about four km from the study site. The average of three rain gauges on the farm was used.

Minimum temperature, maximum temperature and daily temperature fluctuation were determined for every 24 hours from from the start of measurements. Daily temperature fluctuation was calculated as the difference between the maximum and minimum temperature within 24 hours from the start of measurements. For statistical evaluation the average of all days was used.

Germination methods

Prior to germination tests seeds were stored at 5 °C. Tests were carried out within 6 months of seed collection. Seeds were germinated at day/night temperatures of 30/15 °C, 26/19 °C, 22/15 °C, 22/22 °C, with a 12 hour day/night regime. Wet soils have lower maximum temperatures and daily temperature fluctuations (Nobel & Geller 1987) and comparison of the temperature data with rain fall showed that after rain maximum temperatures and DTF

decreased (Fig. 7.1). The temperature of the soil under moist conditions allowing imbibition would be the temperature that seeds use to tune their germination. Therefore temperature regimes were chosen on the basis of observed temperatures after rain fall. DTF decreased to between 6 and 8 °C under canopies after rain and 7 °C was therefore chosen as the DTF resembling canopy conditions. In the matrix DTF dropped to a minimum of 13 °C but fluctuated more widely than DTF under the canopy with DTF above 20 °C also occurring several times after rain. According to our hypothesis seeds of canopy species will use temperature mainly as a shade indicator under the canopy. The maximum temperatures and DTF that inhibit germination may therefore be lower than those typically found for matrix conditions. Therefore 15 °C was taken to represent DTF of the soil after rain, not as an average but more as a threshold value above which canopy species should prevent germination. This was also the maximum DTF observed after rain for the most exposed measuring point under the canopy. Minimum temperature was found to differ only very slightly for different microhabitats and was somewhat arbitrarily set at 15 °C which is within the range of minimum temperatures observed after rain. Because seasonal changes in minimum and maximum temperatures could cause differences between canopy species a 4 °C higher canopy regime also with DTF of 7 °C was included. As not enough seeds and climate chambers were available it was not possible to do the same for the matrix regime. However, as a 30/15°C regime was found to be the optimum for germination in the majority of open land species from arid southern Africa (Veenendaal & Ernst 1991) this was not considered critical. A constant 22 °C regime was also included.

Some species had initially a very low germinability and this was improved using dry heat treatments of 2 weeks at 50°C (*Amaranthus dinteri*, *Amaranthus praetermissus*, annual grasses except *Aristida congesta* and *Setaria verticillata* or 70°C (*Aristida congesta*).

For each temperature eight (five in *Asparagus africanus* and *Asparagus pearsonii* because less seeds were available) replications of 25 seeds per Petri dish were used. For *Pentzia lanata* and *Asparagus pearsonii* the 22/15 °C treatment is absent because not enough seeds were available. For each Petri dish two 90 mm diameter filter paper discs (Schleicher and Schuell 595) were soaked with deionized water. Germinated seeds were counted each week until no seeds germinated anymore with a maximum incubation period of 8 weeks. Finally the number of still viable seeds was determined by pressing remaining seeds with tweezers. Firm, intact seeds were recorded as viable (Baskin & Baskin 1998). The final value used was the % of viable seeds (germinated + not germinated but viable) that germinated.

Comparative method

To be able to statistically evaluate the relationship between germination response and habitat association and seed mass indices of germination response and canopy association were calculated and seed mass was measured. An index of germination response (R) was calculated with the % germination at 26/19 °C (G_c) and the % germination at 30/15 °C (G_m) using the formula ' $R = G_c / (G_c + G_m)$ '. A value of 1 means that the species germinates only at 26/19 °C, a value of 0.5 that the species germinates equally well at both temperature regimes, a value of 0 that the species germinates only at 30/15 °C. 26/19 °C was used because only for this canopy temperature simulating regime data were available for all species. An index of canopy association (A) was calculated with the % cover under the canopy (C_c) and the % cover in the matrix (C_m) using ' $A = C_c / (C_c + C_m)$ '. Here a value of 1 means that the species is only found under *Acacia erioloba* canopies, a value of 0.5 that the species is equally common under canopies and in the surrounding matrix and a value of 0 that the species only occurs in the matrix. *Verbesina encelioides* was not included in this analysis because it was not found directly in the study plots and a precise measure of canopy association was therefore not available. Seed mass was determined for 20 seeds individually according to the protocol in Westoby (1998). See Chapter 4 and Appendix 4 for information on the comparative method and the phylogeny used to calculate phylogenetically independent contrasts (PICs).

Results*Vegetation pattern*

Cover and frequency (number of plots) for both microhabitats are given in Table 7.1. Species were classified as 'canopy' or 'matrix' species when their cover values were significantly associated with one of these microhabitats (Wilcoxon paired-sample test). In addition, species with no significant microhabitat association were classified as 'matrix' species, and sparsely occurring species were classified as 'canopy' species when individuals were only found beneath canopies.

Table 7.1 Study species with family, life form after Raunkiaer (taken from Leistner (1967), T = therophyte, H = hemicryptophyte, G = geophyte, Ch = chamaephyte, N = nanophanerophyte), % cover and frequency (number of plots) for 10 canopy and 10 matrix plots, significance level for a Wilcoxon paired-sample test for differences between canopy and matrix cover (-, not enough pairs available for test, ns, not significant, * $P < 0.05$, ** $P < 0.01$), seed mass (mg) \pm 1 s.d. and dispersal mode.

Species	Family	Life form	Canopy	Matrix		Seed mass	Dispersal mode
<u>Perennial canopy species</u>							
<i>Asparagus africanus</i>	Asparagaceae	H	0.2 (4)	0 (0)	-	14.968 \pm 2.597	birds
<i>Asparagus pearsonii</i>	Asparagaceae	H	0.2 (6)	< 0.1 (1)	*	13.7 \pm 1.9	birds
<i>Pollichia campestris</i>	Illecebraceae	G-H	0.2 (8)	0 (0)	**	0.361 \pm 0.062	birds
<i>Lycium bosciifolium</i>	Solanaceae	N	6.4 (10)	1.4 (3)	*	1.292 \pm 0.266	birds
<i>Solanum capense</i>	Solanaceae	H	0.2 (10)	< 0.1 (1)	**	3.299 \pm 0.514	birds
<u>Annual canopy species</u>							
<i>Setaria verticillata</i>	Poaceae	T	1.3 (9)	< 0.1 (2)	**	0.423 \pm 0.074	adhesion
<i>Chenopodium opulifolium</i>	Chenopodiaceae	T	0.1 (6)	0 (0)	*	0.413 \pm 0.057	unassisted, herbivore
<i>Chenopodium cf schraderianum</i>	Chenopodiaceae	T	-	-	⁻¹	0.085 \pm 0.014	unassisted
<i>Amaranthus dinteri</i>	Amaranthaceae	T	< 0.1 (3)	0 (0)	-	0.481 \pm 0.070	unassisted, herbivore
<i>Amaranthus praetermissus</i>	Amaranthaceae	T	0.5 (10)	< 0.1 (1)	**	0.380 \pm 0.074	unassisted, herbivore
<i>Portulaca oleracea</i>	Portulacaceae	T	< 0.1 (4)	0 (0)	-	0.157 \pm 0.033	ants
<i>Coronopus integrifolius</i>	Brassicaceae	T	-	-	⁻²	0.324 \pm 0.048	unassisted
<u>Perennial matrix species</u>							
<i>Plinthus karoocicus</i>	Aizoaceae	Ch	0.1 (9)	0.5 (10)	**	0.139 \pm 0.027	rain
<i>Deverra denudata</i>	Apiaceae	H	< 0.1 (1)	< 0.1 (1)	-	1.875 \pm 0.317	unassisted
<i>Aptosimum lineare</i>	Scrophulariaceae	(T-)H	0 (0)	< 0.1 (3)	-	0.103 \pm 0.021	unassisted
<i>Aptosimum marlothii</i>	Scrophulariaceae	Ch	0.5 (10)	5.2 (10)	*	0.234 \pm 0.048	unassisted
<i>Rhigozum trichotomum</i>	Bignoniaceae	N	0.2 (5)	0.6 (5)	ns	15.677 \pm 5.323	wind
<i>Felicia clavipilosa</i>	Asteraceae	Ch	0.4 (10)	0.2 (10)	ns	0.102 \pm 0.037	wind
<i>Geigeria pectidea</i>	Asteraceae	H	< 0.1 (3)	< 0.1 (5)	ns	0.383 \pm 0.082	wind
<i>Pentzia lanata</i>	Asteraceae	Ch	< 0.1 (6)	< 0.1 (5)	ns	0.120 \pm 0.018	wind
<u>Annual matrix species</u>							
<i>Aristida congesta</i>	Poaceae	T(-)H	0 (0)	< 0.1 (1)	⁻³	0.355 \pm 0.034	wind, adhesion
<i>Boerhavia repens</i>	Nyctaginaceae	T	0.1 (6)	< 0.1 (2)	ns	2.197 \pm 0.611	adhesion
<i>Chloris virgata</i>	Poaceae	T	< 0.1 (2)	0.2 (3)	-	0.331 \pm 0.077	wind
<i>Enneapogon desvauxii</i>	Poaceae	T	0 (0)	0.1 (6)	*	0.274 \pm 0.046	wind
<i>Eragrostis porosa</i>	Poaceae	T	0 (0)	< 0.1 (1)	⁻⁴	0.065 \pm 0.011	unassisted
<i>Schmidtia kalihariensis</i>	Poaceae	T	< 0.1 (1)	< 0.1 (5)	-	0.615 \pm 0.209	wind
<i>Geigeria ornativa</i>	Asteraceae	T	0 (0)	< 0.1 (9)	**	0.349 \pm 0.049	wind
<i>Tribulus terrestris</i>	Zygophyllaceae	T	< 0.1 (9)	0.5 (9)	*	1.32 \pm 0.41	adhesion
<i>Verbesina encelioides</i>	Asteraceae	T	-	-	⁻³	1.145 \pm 0.116	wind

¹ Found in 15 out of 20 canopy plots but in only two of the 20 matrix plots in a nearby area in 2002.

² Some seedlings were found under other trees. Otherwise only found in seed bank samples, over 90 % of all seeds were found under the canopy (unpublished data).

³ Only observed growing in the open outside the study plots.

⁴ Recorded by Weltzin & Coughenour (1990) to have higher cover in the open than under trees

Temperature measurements

For the October-December 2002 measurements (see Fig. 7.1) canopy and matrix were significantly different for minimum temperature (t -test for matched pairs, $t = 8.371$, $n = 91$, $P < 0.001$), maximum temperature ($t = -45.882$, $P < 0.001$) and DTF ($t = -52.505$, $P < 0.001$).

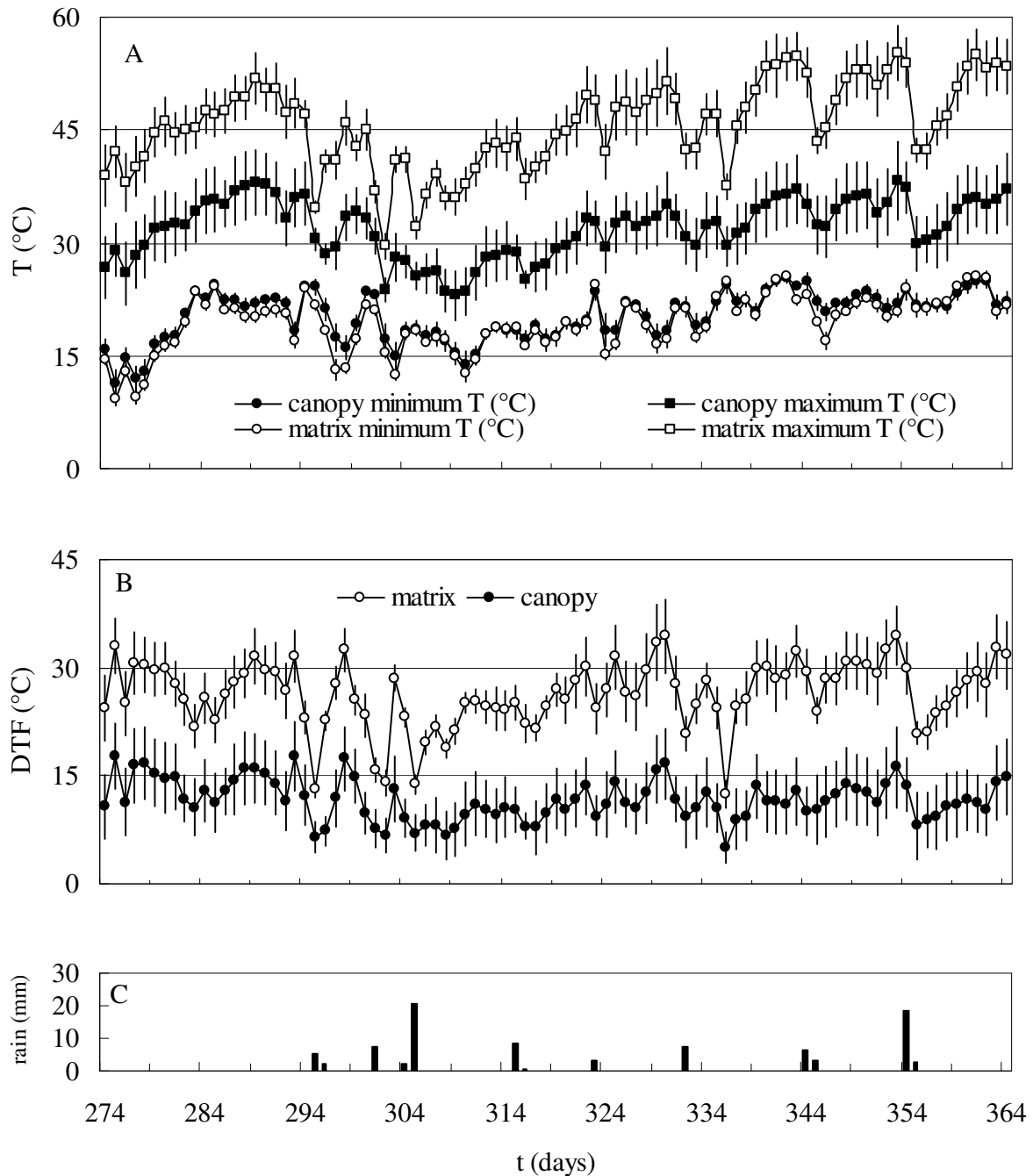


Fig. 7.1 Temperature parameters (mean \pm s.d., $n = 8$) and rain fall on a 24 h basis for the period 1 Oct. 2002 – 30 Dec. 2002. Temperature parameters based on 2 h interval measurements. (A) Maximum and minimum temperature in the matrix and under mature acacia canopies (B) Daily temperature fluctuation in the matrix and under mature acacia canopies (C) Rain fall. Time scale indicates day of the year.

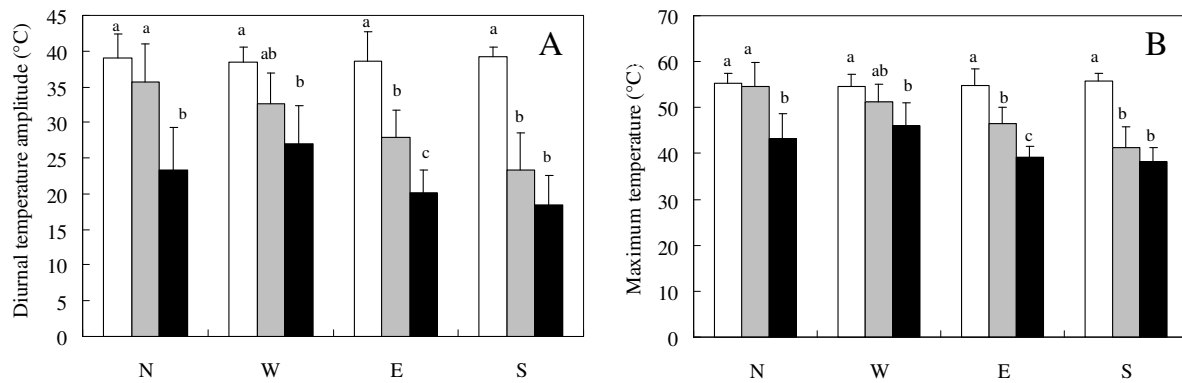


Fig. 7.2 Daily temperature fluctuation (A) and maximum temperature (B) in three different microhabitats: matrix (white), sapling canopy (grey) and mature canopy (black) for each cardinal orientation (N = north, W = west, E = east, S = south). For each combination of habitat and cardinal orientation $n = 5$. Measurements were taken 12 March – 8 April 2003. Significant differences ($P < 0.05$, Tukey-test after one-way ANOVA) between habitats within one cardinal orientation are indicated by different letters. See text for details.

Over the whole period average minimum temperature ranged from 11 to 25 °C (average 20 °C) under the canopy and 9 to 26 (average 19 °C) in the matrix. Maximum temperature ranged from 23 to 38 °C (average 32 °C) under the canopy and 30 to 55 (average 46 °C) in the matrix. DTF ranged from 5 to 18 °C (average 12 °C) under the canopy and 13 °C to 34 °C (average 26 °C) in the matrix. Drops in DTF were associated with rain events. The number of consecutive days with a DTF less than 10 °C was significantly positively correlated with the amount of rain ($r = 0.726$, $n = 8$, $P < 0.05$). This is important because most species growing under canopies have been found to germinate rather slowly (M. Kos, unpub. res.) and soil should remain wet and at the same time below a critical DTF for long enough to allow germination.

For the April-March 2003 data set mature trees also had significantly smaller DTFs than the matrix for all cardinal orientations (Tukey-test after one-way ANOVA, for this and further results reported below, see Fig. 7.2A), but saplings only for the east ($P < 0.01$) and south side ($P < 0.001$) of the canopy. Saplings had significantly larger DTF under their canopies than mature trees for the north ($P < 0.01$) and east side ($P < 0.05$) of the canopy. There were no significant differences between cardinal orientations for both the matrix and mature trees. For saplings north and south side ($P < 0.01$) and west and south side ($P < 0.05$) differed significantly in DTF. Maximum temperature showed essentially the same pattern described for DTF between habitats (see Fig. 7.2B). But in addition there were significant differences between the east and north side of saplings ($P < 0.05$) and the south and west side of mature trees also differed significantly ($P < 0.05$). Minimum temperature did not differ significantly between cardinal orientations for all habitats. Minimum temperatures were

significantly lower in the matrix compared with canopies of sapling and mature trees for all cardinal orientations except for the south side where matrix and sapling did not differ significantly. There were no significant differences in minimum temperature between sapling and mature trees except for the south side ($P < 0.05$).

Germination tests

Differences between treatments within species were determined by one-way ANOVA followed by a Tukey test (see Fig. 7.3). All fleshy fruited perennial canopy species showed reduced germination at 30/15 °C compared with 26/19 °C. *Pollichia campestris* and *Lycium bosciifolium* germinated better at 22/15 °C compared with 26/19 °C, while *Solanum capense* showed the opposite pattern. Constant temperature inhibited germination in *Lycium bosciifolium* but did not differ from 26/15 °C and/or 22/15 °C in the other fleshy fruited species. For matrix perennials germination rate was highest at 30/15 °C in only one species: *Aptosimum lineare*. In *Plinthus karoocicus* both 22/15 °C and 30/15 °C produced higher germination than 26/19 °C. In the other matrix perennials no differences between treatments were found. Among the annual canopy species *Chenopodium opulifolium* germinated better at 22/15 °C than at any other temperature but there were no differences between the other treatments, though 30/15 °C did have the lowest mean germination. *Coronopus integrifolius* germinated also better at 22/15 °C than at 26/19 °C or 30/15 °C, but germination was negligible at constant temperature. In both *Amaranthus dinteri* and *A. praetermissus* germination was stimulated by 30/15 °C compared with other treatments. No differences between treatments were found in *Chenopodium schraderianum*, *Portulaca oleraceae* and *Setaria verticillata*. Of the matrix annuals *Aristida congesta* germinated best at 30/15 °C. *Chloris virgata* had reduced germination at constant temperature. *Eragrostis porosa* showed a pattern similar to *Plinthus karoocicus* although the difference between 26/19 °C and 30/15 °C was not significant. No differences between treatments were found for the other five matrix annuals.

Comparative analysis

Multiple regression models using phylogenetically independent contrasts for all species, perennials and annuals with germination response as the dependent variable and both seed mass and canopy association as independent variables were all not significant. A simple linear regression model with germination response (R) as the dependent variable and canopy

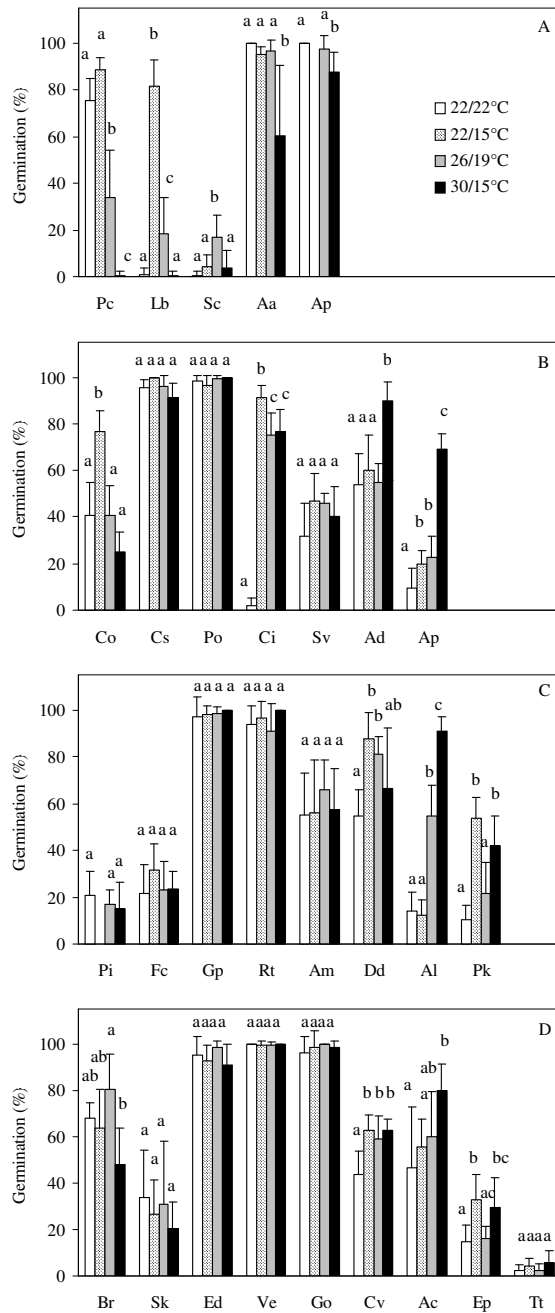


Fig. 7.3 Germination response (% of viable seeds germinating) of Kalahari plants to different temperature regimes. Significant differences between treatments within a species are indicated by different letters. **Canopy perennials (A)**: Pc = *Pollichia campestris*, Lb = *Lycium bosciifolium*, Sc = *Solanum capense*, Aa = *Asparagus africanus*, Ap = *Asparagus pearsonii*. **Canopy annuals (B)**: Co = *Chenopodium opulifolium*, Cs = *Chenopodium schraderianum*, Po = *Portulaca oleraceae*, Ci = *Coronopus integrifolius*, Sv = *Setaria verticillata*, Ad = *Amaranthus dinteri*, Ap = *Amaranthus praetermissus*. **Matrix perennials (C)**: Pi = *Pentzia lanata*, Fc = *Felicia clavipilosa*, Gp = *Geigeria pectidea*, Rt = *Rhigozum trichotomum*, Am = *Aptosimum marlothii*, Dd = *Deverra denudata*, Al = *Aptosimum lineare*, Pk = *Plinthus karoocicus*. **Matrix annuals (D)**: Br = *Boerhavia repens*, Sk = *Schmidtia kalihariensis*, Ed = *Enneapogon desvauxii*, Ve = *Verbesina encelioides*, Go = *Geigeria ornativa*, Cv = *Chloris virgata*, Ac = *Aristida congesta*, Ep = *Eragrostis porosa*, Tt = *Tribulus terrestris*.

association (A) as the only independent variable was significant for perennials ($\arcsin \sqrt{R} = 0.330 \times \arcsin \sqrt{A}$, $r^2 = 0.400$, $F_{1, 11} = 7.327$, $n = 12$, $P < 0.05$) and all species together ($\arcsin \sqrt{R} = 0.171 \times \arcsin \sqrt{A}$, $r^2 = 0.158$, $F_{1, 25} = 4.708$, $n = 26$, $P < 0.05$), but not for annuals. Linear regression models with seed mass as the only independent variable were not significant for annuals, perennials and perennials and annuals combined.

Discussion

Canopy species were the only species where germination was inhibited by the matrix temperature regime. Using phylogenetically independent contrasts it was found that germination at the canopy temperature regime of 26/19 °C relative to the matrix temperature 30/15 °C increased significantly with an increase in canopy association. Comparison with temperature measurements in the field show that maximum temperatures and daily temperature fluctuation are usually well above those inhibiting or preventing germination in the lab. Even DTF and maximum temperature marginally smaller than the tested matrix regime during and after rain don't last longer than one 24 h cycle. Considering the slow germination of canopy associated species (M. Kos, unpub. res.) this germination behaviour is very likely to prevent germination in the matrix or relatively sun exposed patches under the canopy. Our temperature measurements also show that DTF and maximum temperatures under the canopy vary strongly with cardinal orientation, which confirms the results of other studies (Belsky *et al.* 1989; Belsky & Canham, 1994). These results support the hypothesis that maximum temperatures or DTF are used as cues to detect safe sites under the canopy in this group of plants.

No relationship between seed mass and germination behaviour was found for species or independent contrasts for perennials, annuals and all species combined. However, seed size is correlated with many aspects of plant ecology (Leishman *et al.* 2000) and such correlations could easily obscure a relationship between the germination response to temperature and seed size. However, within the fleshy fruited perennials, though all species are to some extent inhibited by 30/15 °C compared to 26/19 °C this inhibition decreases with seed mass. The species ordering according to their relative inhibition at 30/15 °C in Fig. 7.3 parallels a decrease in seed mass. The smallest seeded *Pollichia campestris* showed the largest relative inhibition of germination at 30/15 °C while the *Asparagus* species still germinate to over 60 % at this temperature (Fig. 7.3). Pearson *et al.* (2002) found that germination of small seeded species of pioneer rainforest trees (< 2 mg) was unaffected by an increasing magnitude of DTF up to a species-specific threshold, above which it declined. They suggested that the

negative germination response to large temperature fluctuations in small-seeded species and at extreme values for some larger seeded species may represent a waiting strategy to avoid large-gap environments where water shortage would constrain seedling establishment. Small-seeded species are thought to be more sensitive to temperature fluctuations because they are especially susceptible to short periods of drought because of their superficial initial rooting depth (Pearson *et al.* 2002). Thus the mechanism that gap colonizing rain forest trees use to avoid extreme gap conditions seems to be similar to that used by acacia associated species to avoid germination in sun exposed sites under the canopy.

All of the fleshy-fruited canopy perennials showed inhibition of germination at matrix conditions. Within the group of annual canopy species however, matrix temperatures had an inhibiting effect only in *Chenopodium opulifolium* and *Coronopus integrifolius*. *Boerhavia repens* also showed a significant higher germination at 26/19 °C compared with 30/15 °C. This species was classified as a matrix species because differences in cover and presence between canopy and matrix were not significant but it is the only matrix species with higher presence and cover under the canopy. The contrast between perennial and annual canopy species in their reaction to the different temperature regimes may be the result of the short life-span of annual species which makes them more flexible than perennials. In good rain years it could be possible for them to complete their life-cycle outside the canopy or at an unfavourable position under the canopy. Perennial species have to establish and grow for a longer period at the same place, which increases the need of germinating in a site where extremes over a longer period of time are avoided.

Most matrix annuals and perennials showed no differences between treatments (63 % of species), indicating that there are no strong selective forces to develop a mechanism preventing germination under canopies. Probably because the chance for a seed to land in a canopy patch is small because the proportion of surface covered by tree and shrub canopies is much lower than the proportion of bare ground.

Despite the fact that many, especially fleshy-fruited, desert and savannah plants are associated with nurse-plants (Tester *et al.* 1987; Archer *et al.* 1988; Valiente-Banuet *et al.* 1991) few other studies exist that tried to relate the effect of temperature on germination with an association with nurse plants (but see Fulbright *et al.* 1995; Godínez-Alvarez & Valiente-Banuet 1998). Fulbright *et al.* (1995) found inhibition of germination of the fleshy fruited shrub *Celtis pallida* associated with the tree *Prosopis glandulosa* at high temperatures characteristic of interspaces whereas a species characteristic for interspaces, *Acacia smallii*, still germinated at these temperatures. They conclude that an association of *Celtis* with its

nurse-plant is caused in part by dispersal by birds and in part because of inhibition of germination in interspaces. Godínez-Alvarez & Valiente-Banuet (1998) studied the effect of DTF on germination and its relation to nurse plant associations. They however, did not find a negative effect of DTF in nurse plant associated cacti. Moreover, some species germinated better under fluctuating temperatures than at constant temperatures. However, DTF was only 5 ° C. The response may therefore just be a mechanism that prevents germination too deep in the soil. A positive effect of 7 °C fluctuation compared with constant temperature was also found in this study for *Solanum* and *Lycium*, but germination was inhibited at higher DTF. This is also indicated by other studies. Rojas-Aréchiga *et al.* (1997) studied the effect of light on germination of cacti. They used three different temperature regimes (25/25, 30/20 and 30/15° C). The data were, however, not analyzed with regard to temperature. This probably would have revealed a decrease of germination with increasing DTF in columnar cacti as suggested by the mean values. One of the species for which the data in Rojas-Aréchiga *et al.* (1997) suggest that it germinates best at constant temperature is *Neobuxbaumia tetetzo*. This species is completely dependent on nurse plants for establishment (Valiente-Banuet & Ezcurra 1991; Godínez-Alvarez *et al.* 2002). Rojas-Aréchiga *et al.* (1998) propose that, based on their preference for high temperatures and light, barrel cacti may also establish in open areas whereas columnar cacti establish mainly under the shade of shrubs. In accordance with this observation Nolasco *et al.* (1997) found that in *Stenocereus thurberi*, a columnar cactus species commonly associated with nurse trees, emergence of seedlings from seeds sown in full sun was nil even when ample water was available. This suggests that modification of soil temperature by nurse plant canopies may be required for germination of this species.

It can be concluded that for fleshy fruited perennials the available data from the literature support the hypothesis that species which occur under tree canopies have developed mechanisms to prevent germination in open sun conditions. The results presented in this study and data from the literature show that inhibition of germination at temperature regimes characteristic of open spaces can be found in fleshy-fruited species of widely divergent taxonomic groups. It is therefore predicted that more studies in other parts of the world will reveal the universality of such mechanisms in bird dispersed species depending on nurse plants. The variation in favourable conditions for establishment under the canopy is most likely the selective pressure that caused the evolution of this type of germination response. Therefore such future studies should preferably be accompanied by studies that also record the spatial pattern of seed rain, seedling emergence and seedling survival under the canopy in combination with spatial variation in microclimate under the canopy.

Chapter 8

The importance of abiotic filters versus seed dispersal for species sorting: A soil sod transplanting experiment in an arid Kalahari savannah

Abstract

In arid ecosystems characterized by a discontinuous tree or shrub layer distinct groups of species are usually found under canopies and in open interspaces. The mechanisms behind the observed vegetation patterns are, however, not well known. Dispersal, abiotic factors and biotic interactions are all thought to be potentially important. However, canopy and matrix microhabitat contrast strongly in abiotic conditions and plants are expected to have adapted to either one of them due to various trade-offs. As the process of germination basically forms the only possibility for a plant to 'choose' more or less precisely under which conditions it will grow, germination behaviour is expected to have evolved to direct germination and establishment to favoured microhabitat. Transplanting seeds to another microhabitat should therefore result in lower seedling emergence compared with the original habitat. The hypothesis that habitat specific filters acting on germination are more important for species sorting than dispersal processes was tested in an arid Kalahari savannah. Soil sods were transplanted from acacia canopy to matrix and vice versa and emerged seedlings were recorded after a natural rain event. In canopy sods transplanted to the matrix seedling number was significantly reduced compared with control sods. No difference was found for matrix sod transplants and controls. However, for the only typical matrix species where seedling numbers allowed statistical testing emergence was also significantly reduced in matrix sods transplanted to the canopy compared with controls. The similar seedling number in matrix sod transplants and controls may be caused by seed input from the canopy vegetation and seedbank which are both much denser under canopies than in the matrix. This study supports the hypothesis that filtering by abiotic factors at the germination and early seedling stage is of prime importance for the maintenance of vegetation pattern and is likely to overrule dispersal effects.

Introduction

In arid ecosystems characterized by a discontinuous tree or shrub layer distinct groups of species are usually found under canopies and in open interspaces (Archer *et al.* 1988; Milton & Dean 1995; Dean *et al.* 1999; Facelli & Brock 2000; Pugnaire & Lázaro 2000; López-Pintor *et al.* 2003). Woody species thus contribute considerably to biodiversity in such systems. The mechanisms behind the observed vegetation patterns are, however, not well known.

According to the species pool concept only a certain set of species from a specified region or landscape is able to colonize and persist in a habitat within that region or landscape (Zobel 1997). Which species are able to coexist in a habitat is in the first place determined by the ability of species to disperse to that habitat. Species that arrive in a community subsequently have to pass the filter formed by the local abiotic factors and biotic interactions. Both dispersal and abiotic factors (e.g. reduced radiation and temperature, higher water availability, higher nutrient availability under canopies) and biotic interactions (e.g. protection from herbivores, competition) have been recognized as potentially important determinants of vegetation patterns mediated by the woody vegetation in arid environments (Flores & Jurado 2003). However, there are reasons to assume that abiotic factors are the primary drivers behind these patterns. The strongly contrasting conditions found under canopies and in the surrounding open matrix are due to various trade-offs likely to result in adaptation of plant species to one of the two microhabitats. It is therefore important for plants to track favourable habitat in such a system. Because plants are largely immobile and dispersal depends on external factors (e.g. animals, wind), dispersal will be a relatively imprecise mechanism of habitat 'choice' even in the case of 'directed dispersal'. Germination responses to habitat specific cues offer the main opportunity for plants to precisely 'choose' their habitat. Abiotic filters are therefore likely to act in the germination phase. This is supported by Weiher & Keddy (1995) who by the experimental filtering of 20 wetland species showed that the filter that prevented germination or early establishment or both was of primary importance for community assembly. It is therefore expected that the germination biology of species will overrule dispersal patterns.

However, the multitude of environmental factors that follow steep gradients going from the open matrix to the area under canopies, both abiotic and biotic, makes it difficult to pinpoint the causes for the distribution of species. If, for example, trees attract animals that disperse seeds mainly to canopies where at the same time microclimatic conditions prevail that contrast strongly with the open matrix, the correlation between vegetation pattern and

these factors cannot provide evidence for either of them having an effect on vegetation pattern. The effects of dispersal and various abiotic and biotic factors on vegetation patterns affected by the mosaic of canopies and open spaces can therefore only be disentangled using manipulative experiments.

The hypothesis that germination biology determines vegetation pattern in arid ecosystems characterized by a two-phase pattern of trees and open spaces was tested in the arid southern Kalahari savannah where distinct sets of species are associated with the canopy of *Acacia erioloba* trees and the surrounding open matrix (Milton & Dean 1995; Dean *et al.* 1999; Zimmermann 2001; Seymour 2006). If abiotic factors acting on germination are the main determinant of vegetation patterns affected by acacias, the emergence of seedlings is expected to be reduced when soil sods are transplanted from one habitat to the other. When, on the other hand, dispersal and/or increased seed production under canopies due to nutrient enrichment (i.e. seed limitation) is the main factor determining vegetation pattern transplanting should have no effect or even a positive effect on seedling emergence/establishment. To determine the relative importance of habitat specific filters acting on germination and/or early seedling establishment (as these cannot be distinguished in the field) and dispersal soil sods were therefore transplanted from canopy to matrix and vice versa and emerged seedlings were recorded after natural rain.

Methods

16 large *Acacia erioloba* trees were selected (stem circumference >150cm, spreading canopy). Transplants had a surface of 30 × 30 cm and were 15 cm deep. Subcanopy plots were positioned halfway between stem and canopy dripline and matrix plots 15 paces of ~ 85 cm from the canopy dripline. Plots were close together on a line perpendicular to the canopy radius. The soil which was dug out was kept aside for transplanting; litter layer and the upper soil crust were kept separate from each other and the rest of the soil. Soil was put back in the designated spot with soil layers in original order. Subcanopy soil was transplanted to the matrix and vice versa and for both matrix and subcanopy a control treatment was installed where soil was put in its original position after digging out. Plots were installed July 2002, in February/March 2003. Seedlings were determined to species if possible and counted about two weeks after a good rain of about 40 mm on 18.2.2003. Adult plants that established earlier in the season were also recorded. Habitat association of species is based on cover and the index used is as in Chapter 5 and 6.

Statistics

A detrended component analysis (DCA) was carried out on the raw data (PC-ORD 4.0, McCune & Mefford 1999). Plots and species frequencies were ordinated. The effect of source habitat and transplanting on total seedling numbers were analyzed by two-way univariate analysis of variance (ANOVA) using the general linear model (GLM) design in SPSS version 12.0 (SPSS Inc., Standard Version). A Tukey-test at 5% confidence level was used for comparisons of treatments. As there were zero counts seedling number data were arcsinh transformed prior to analysis to meet the assumptions of homogeneity of variance. For individual species homogeneity of variances was not achieved after transformation, and data were analysed using the Wilcoxon paired-sample test. Significance levels were corrected for multiple comparisons using the Bonferroni correction.

Results

The separation of the sods in the DCA in two clusters, one of canopy control sods and transplanted matrix sods and another cluster of matrix control sods and transplanted canopy sods (Fig. 8.1) suggest that abiotic filters related to the presence or absence of a canopy have a stronger effect on community structure than seed availability. Transplanting had a significant effect on seedling number, but there was no significant interaction between original habitat and transplanting (Table 8.1). However, for canopy soil transplantation resulted in a significantly lower number of seedlings, but for matrix soil no difference was found (Fig. 8.2). Seedling emergence was significantly higher in untransplanted canopy soil compared with untransplanted matrix soil (Fig. 8.2). Of the canopy associated species 14 showed a negative response to transplanting sods to the matrix (based on average number of seedlings per plot), against only two that showed a positive response ($P = 0.004$, binomial test, Table 8.2). Matrix associated species showed a negative response to transplanting to the canopy in six cases and a positive response in four cases ($P = 0.754$, binomial test, Table 8.2).

For five species enough seedlings emerged to allow a statistical comparison between soil left in place and transplanted soil for at least one microhabitat (Fig. 8.3). Three species associated with canopies, *Amaranthus praetermissus*, *Boerhavia repens* and *Setaria verticillata*, showed a very similar pattern with most seedlings emerging under the canopy in canopy soil. The number of seedlings was significantly reduced when canopy soil was transplanted to the matrix where very few seedlings emerged. *Indigofera alternans* which is associated with the open matrix showed the opposite pattern with most emergence taking place in the matrix, and transplanting to the canopy having a significant negative effect.

Table 8.1 Effect of original habitat and transplanting on total seedling numbers in a two-way univariate analysis of variance.

Source of variation	SS	d.f.	MS	<i>F</i>	<i>P</i>
Original habitat	1.295	1	1.295	0.422	0.519
transplant	28.944	1	28.944	9.422	0.003
Original habitat × transplant	9.217	1	9.217	3.000	0.089
Within	172.030	56	3.072		
Total	642.435	60			

Table 8.2 Numbers of species that respond negative, positive, or neutral in terms of seedling numbers on transplanting soil sods from one microhabitat to the other. Canopy species have higher cover under trees, matrix species have higher cover in the matrix.

Soil being transplanted	Effect of transplanting	Canopy species	Matrix species	Total
Canopy soil	negative	14	4	18
	positive	2	7	9
	neutral	0	1	1
Matrix soil	negative	0	6	6
	positive	9	4	13
	neutral	0	0	0

Table 8.3 Seedling numbers and diversity and litter cover for sod transplants to the other habitat and controls for matrix and canopy ($n = 15$ plots per treatment). Different letters indicate significant differences for a one-way ANOVA followed by a Tukey-test. Litter cover was arcsine transformed prior to analysis.

	Canopy control	Canopy transplanted	Matrix control	Matrix transplanted
Number of seedlings/plot	46.3±11.4 ^a	10.0±3.6 ^b	30.7±19.4 ^b	30.6±15.8 ^b
Number of species/plot	5.7±0.8 ^a	2.2±0.6 ^b	2.0±0.5 ^b	4.2±1.0 ^b
Total species	29	15	12	23
Litter cover (%)	63.3±31.0 ^a	14.1±12.0 ^b	1.9±3.2 ^c	28.8±17.8 ^b

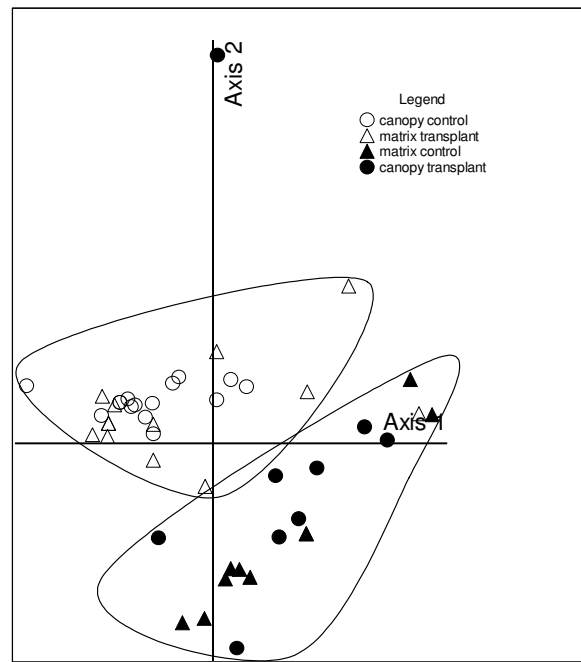


Fig. 8.1 DCA ordination of the seedling community in soil sods transplanted from below *Acacia erioloba* canopies to the open matrix (canopy transplants, $n = 9$) and vice versa (matrix transplants, $n = 13$) and controls receiving the same treatment as transplants but remaining in the original microhabitat (canopy control, $n = 15$; matrix control, $n = 10$). Matrix: 32 species, 47 plots. Originally $n = 15$ plots for each treatment, total $n = 60$, but plots with zero seedlings are not included here.

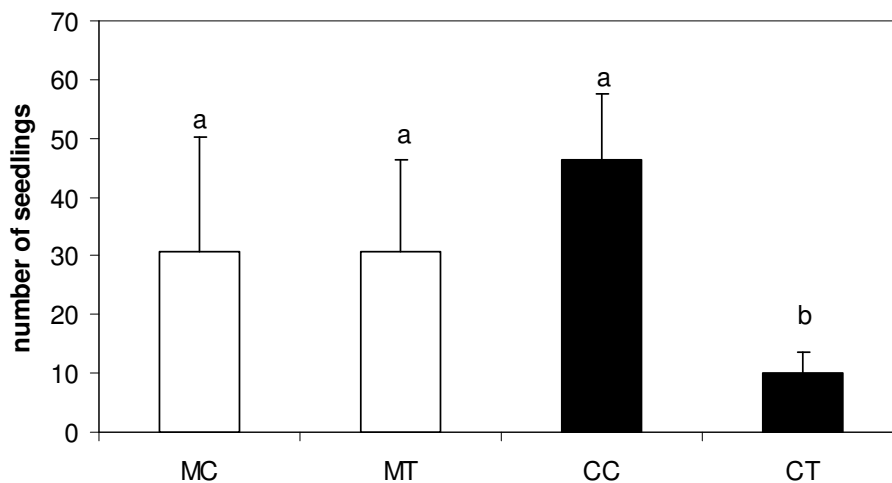


Fig. 8.2 Mean seedling number (error bar indicates 1 standard error) under canopies and in the matrix, transplanted and not transplanted. MC = matrix control, MT = matrix soil transplanted to canopy, CC = canopy control, CT = canopy soil transplanted to matrix. Different letters indicate significant differences for a one-way ANOVA followed by a Tukey-test.

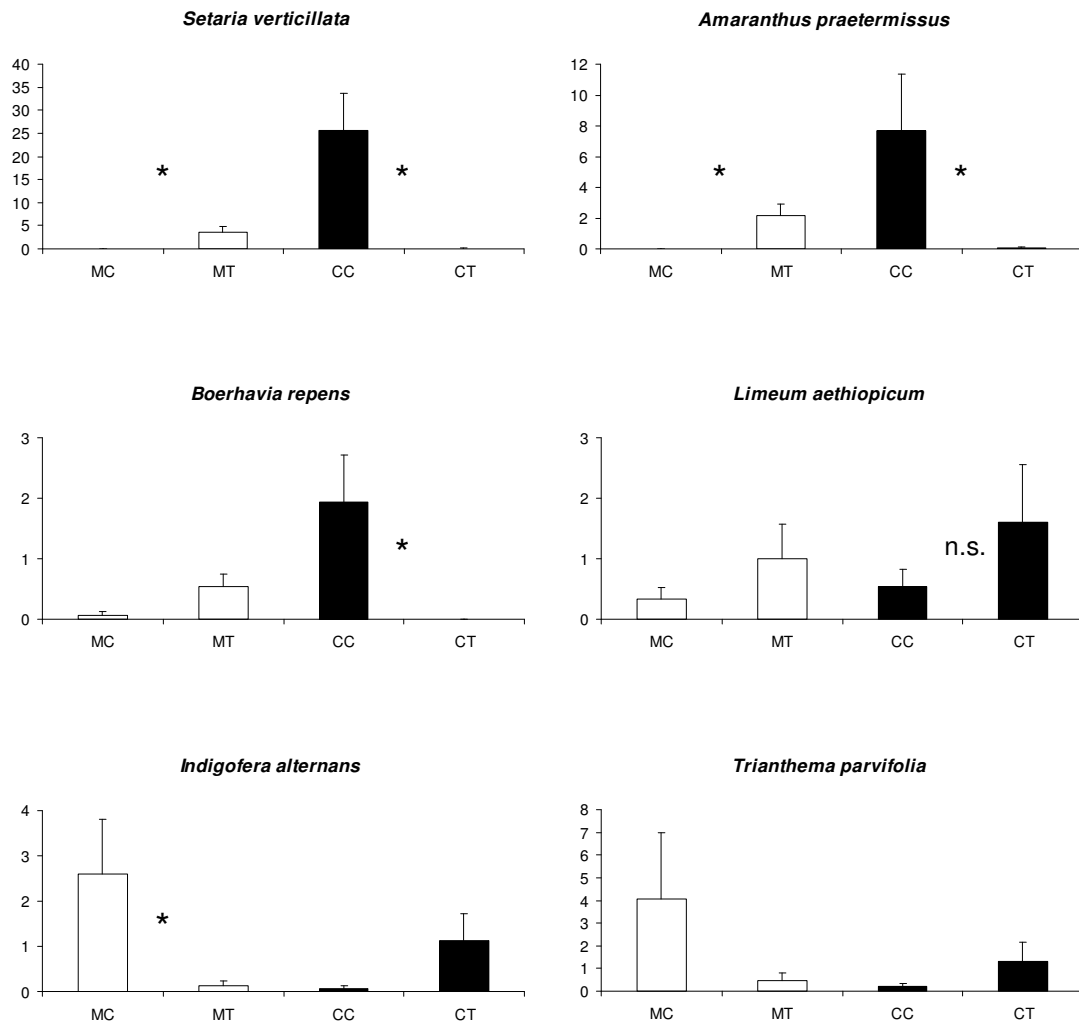


Fig. 8.3 Mean seedling number (error bar indicates 1 standard error) under canopies and in the matrix, transplanted and not transplanted. MC = matrix control, MT = matrix soil transplanted to canopy, CC = canopy control, CT = canopy soil transplanted to matrix. Asterisks indicate significant differences between control and transplant for soil from a given microhabitat ($P < 0.05$, Wilcoxon paired sample test, significance levels were corrected for multiple comparisons using the Bonferroni correction, n.s. means no significant difference, no significance indication means that sample sizes were too small for statistical testing)

Trianthena parviflora was included in Fig. 8.3 although the data for this species did not allow a statistical test. This was done for illustrative purposes, because it shows exactly the same pattern as *Indigofera alternans*. For *Limeum aethiopicum* there was no significant difference between canopy soil left in situ and canopy soil transplanted to the matrix. Data for adult plants that established earlier in the season indicate that the pattern of seedling emergence and establishment in relation to microhabitat depends also on rain fall and season. Here most plants were found in canopy soil transplanted to the matrix (Table 8.5). For *Amaranthus praetermissus* actually all four plants were found in these plots and none under trees. A list with all species recorded in the experimental plots with seedling numbers can be found in Table 8.4.

Table 8.4 Mean numbers of seedlings per plot \pm s.d. ($n = 15$) and number of plots where seedlings were found between brackets. cc: canopy control, mt: matrix sods transplanted to canopy, mc: matrix control, ct: canopy sods transplanted to matrix. Habitat preference is based on cover values in 2003 (Appendix 1) except for some species not observed in that year where data were extracted from Zimmerman (2001): ‘c’ more common under canopies, ‘m’ more common in the matrix.

	cc	mt	ct	mc	habitat
<i>Chenopodium schraderianum</i>	0.2 \pm 0.8 (1)				c
<i>Solanum capense</i>	0.3 \pm 1.3 (1)				c
<i>Coronopus integrifolius</i>	2.9 \pm 8.1 (2)				c ¹
<i>Acrotome inflata</i>	0.1 \pm 0.4 (2)				c
<i>Argemone ochroleuca</i>	0.1 \pm 0.3 (1)				c ¹
<i>Acacia erioloba</i>	0.1 \pm 0.3 (1)				c
Dicot spec. 1	0.1 \pm 0.3 (1)				-
<i>Amaranthus dinteri</i>	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)			c
<i>Chenopodium opulifolium</i>	0.2 \pm 0.6 (2)	0.1 \pm 0.4 (1)			c
<i>Lycium bosciifolium</i>	0.5 \pm 0.8 (5)	0.3 \pm 0.9 (2)			c
<i>Portulaca oleracea</i>	0.4 \pm 0.9 (3)	0.1 \pm 0.3 (1)			c
<i>Felicia clavipilosa</i>	1.3 \pm 4.4 (3)	1.7 \pm 4.5 (3)			c
<i>Setaria verticillata</i>	25.6 \pm 30.8 (14)	3.5 \pm 4.5 (12)	0.1 \pm 0.3 (1)		c
<i>Amaranthus praetermissus</i>	7.7 \pm 14.4 (12)	2.1 \pm 3.0 (10)	0.1 \pm 0.3 (1)		c
<i>Crotalaria</i> spec.	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)		m
<i>Aptosimum</i> spec.	0.1 \pm 0.3 (1)	0.1 \pm 0.4 (2)	0.7 \pm 1.8 (2)		m
<i>Chloris virgata</i>	1.0 \pm 2.3 (3)	15.7 \pm 58.5 (3)	1.9 \pm 7.5 (1)	18.9 \pm 73.3 (1)	m
<i>Enneapogon</i> spec.	1.6 \pm 2.8 (6)	2.2 \pm 3.8 (7)	0.1 \pm 0.5 (1)	0.5 \pm 1.8 (1)	m
<i>Eragrostis</i> spec.	0.5 \pm 1.1 (3)	1.1 \pm 2.4 (4)	2.1 \pm 4.5 (4)	3.3 \pm 6.5 (6)	m
<i>Trianthema parvifolia</i>	0.2 \pm 0.6 (2)	0.5 \pm 1.3 (3)	1.3 \pm 3.2 (4)	4.1 \pm 11.3 (4)	m
<i>Indigofera alternans</i>	0.1 \pm 0.3 (1)	0.1 \pm 0.4 (2)	1.1 \pm 2.3 (4)	2.6 \pm 4.6 (7)	m
<i>Limeum aethiopicum</i>	0.5 \pm 1.1 (4)	1.0 \pm 2.2 (4)	1.6 \pm 3.7 (5)	0.3 \pm 0.7 (3)	c
<i>Chamaesyce inaequilatera</i>	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)	0.1 \pm 0.3 (1)	-
<i>Boerhavia repens</i>	1.9 \pm 3.0 (7)	0.5 \pm 0.8 (5)		0.1 \pm 0.3 (1)	c
<i>Tribulus</i> spec.	0.3 \pm 0.9 (2)	0.4 \pm 0.9 (3)		0.7 \pm 2.3 (2)	m
<i>Schmidtia kalahariensis</i>	0.1 \pm 0.5 (1)		0.4 \pm 1.5 (1)		m
<i>Peliosostomum leucorrhizum</i>	0.1 \pm 0.5 (1)		0.1 \pm 0.3 (1)		m
<i>Dicoma</i> spec.	0.1 \pm 0.3 (1)			0.1 \pm 0.4 (2)	m
<i>Geigeria</i> spec.		0.3 \pm 0.8 (2)	0.2 \pm 0.6 (2)	0.1 \pm 0.3 (1)	m
<i>Tragus</i> spec.		0.1 \pm 0.4 (2)	0.3 \pm 0.6 (3)		c ¹
<i>Hermannia</i> spec.		0.1 \pm 0.3 (1)			-
<i>Enneapogon desvauxii</i>		0.2 \pm 0.8 (1)			m
Various unidentified species	0.1 \pm 0.4 (2)	0.2 \pm 0.4 (3)	0.3 \pm 0.7 (2)	0.1 \pm 0.3 (1)	-

Table 8.5 Mean number of adult plants per plot \pm s.d. ($n = 15$) and number of plots where adult plants were found between brackets. Cc: canopy control, mt: matrix sods transplanted to canopy, mc: matrix control, ct: canopy sods transplanted to matrix.

	cc	ct	mc	mt
<i>Chenopodium opulifolium</i>	0.3 \pm 1.0 (1)			
<i>Salsola kali</i>	0.1 \pm 0.3 (1)			0.1 \pm 0.3 (1)
<i>Setaria verticillata</i>	0.8 \pm 1.7 (4)	0.3 \pm 0.8 (2)		0.1 \pm 0.4 (2)
<i>Tribulus</i> spec.	0.3 \pm 0.7 (3)	0.9 \pm 1.1 (7)	0.3 \pm 0.8 (2)	
<i>Schmidtia kalahariensis</i>		0.7 \pm 2.8 (1)		
<i>Amaranthus praetermissus</i>		0.9 \pm 2.1 (4)		
<i>Trianthema parvifolia</i>		0.1 \pm 0.3 (1)		
<i>Dicoma capensis</i>		0.1 \pm 0.3 (1)		
<i>Indigofera alternans</i>			0.1 \pm 0.3 (1)	
Total number of plants	22	44	5	3

Discussion

Seedling emergence in soil sods transplanted from canopy to matrix was significantly reduced compared with controls left under the canopy. This is also reflected in the response of individual species to transplanting to the matrix. Several species did not germinate at all when transplanted to the matrix. At least for canopy associated species it seems that abiotic factors acting on dormancy breaking, germination and/or early seedling establishment reduced establishment in the matrix and in some species even prevented establishment altogether. For matrix sods, however, no difference between total seedling emergence in soil transplanted from the matrix to the canopy, and the control remaining in the matrix, was found. Possibly abiotic filters act on life stages beyond the early seedling stage in matrix associated species. However, in contrast with total seedling numbers some species (*Indigofera alternans*, *Trianthema parvifolia*) found mainly in the matrix did have lower seedling establishment in sods transplanted to canopies compared with the control remaining in the matrix (Fig. 8.3). This suggests that also in matrix species abiotic filters acting on dormancy breaking, germination and/or early seedling establishment can reduce or prevent establishment of matrix species under canopies. The lack of a significant difference in total seedling number between matrix sod transplants and controls could be due to other matrix species reacting positively to, for example, moisture conditions under canopies. But this can also be explained by a combination of seed trapping of matrix species by acacia canopies before the start of the experiment that cancels out lower emergence % under canopies (see Chapter 4) and input of seeds from the surrounding canopy soil in the transplanted matrix sods. Seed density in the soil and plant densities are higher under the canopy than in the matrix (Chapter 4) and the soil under canopies tends to be looser so that this effect is likely to be stronger under the canopy.

It may be argued that dispersal processes taking place after installation of the experimental plots have resulted in the observed patterns. Higher emergence of seedlings in the favoured habitat could be due to the higher seed rain in that habitat and this is an important point to consider. However, seedling densities of species were generally lower in the transplants in the favoured habitat than in the control in the favoured habitat (canopy sods transplanted to the matrix had lower seedling number than matrix controls), so seed limitation can still be observed (Fig. 8.2). Even when seedlings in the matrix transplant (new seeds) are subtracted from the canopy control seedling numbers are significantly higher for the canopy control than for canopy transplanted in *Amaranthus praetermissus* (Wilcoxon paired sample test, $P = 0.008$), *Boerhavia repens* ($P = 0.017$) and *Setaria verticillata* ($P = 0.003$). Only for

Indigofera alternans the significant difference between matrix control and matrix transplanted to canopy disappeared ($P = 0.089$). Also seed densities are actually higher under canopies for some species favouring matrix habitat (Chapter 4)

The exact mechanisms that reduced emergence in transplants are unknown. However, the available knowledge about the germination biology of the species suggests several realistic scenarios. One possible explanation of reduced emergence in canopy sods transplanted to the matrix is the relatively long induction time of some species associated with canopies (Chapter 6). As soil dries out more slowly in the shade these species can germinate under the canopy, but it might be that in the matrix top soil usually dries out too fast for them to germinate and establish. In fleshy-fruited perennial species inhibition of germination at high daily temperature fluctuations and/or maximum temperatures may prevent germination in the matrix (Kos & Poschlod 2007). Species that showed reduced emergence in matrix sods transplanted to the canopy may have seed dormancy that is broken by dry heat or large temperature fluctuations. Due to shading by the canopy the requirements for dormancy breaking may not be met for these species. This may function as a gap-detection mechanism or maybe for a sparsely vegetated arid savannah more appropriately called a tree avoiding mechanism. In a similar way the dormancy loss of seeds of the tropical forest tree *Heliocarpus donnell-smithii* in response to fluctuating temperatures ensures that they germinate in gaps where solar irradiance is high and not in the shade of mature trees where seedlings are unlikely to survive (Vazques-Yanes & Orozco-Segovia 1982). Alternatively germination under canopies may be inhibited by light filtered through leaves (Pons 2000) or the litter found under the canopy may pose a problem for emergence of germinating seedlings, especially those with small seeds (Leishman *et al.* 2000). Mortality during early seedling establishment may also have contributed to the reduced seedling numbers observed in transplants. As this will like germination also mainly take place underground it is actually not possible to say if this or no germination is the cause for reduced seedling emergence.

It must be kept in mind that this study provides only a snapshot. In fleshy-fruited perennial species that use temperature cues to germinate in shade under canopies (Kos & Poschlod 2007) germination in the open matrix is likely to be consistently prevented. Indeed seedlings of fleshy-fruited species were never observed in plots situated in the matrix. This is also supported by the observation that in two of these species sown under canopies and in the matrix seedling emergence was only observed in canopy plots (Chapter 3). This may also be the case for *Chenopodium opulifolium* (Kos & Poschlod 2007, Chapter 7). However, most annual species associated with canopies did not show inhibition by matrix temperatures (Kos

& Poschlod 2007, Chapter 7). The longer induction times in most of these species compared with matrix species may prevent germination in the open matrix after relatively small amounts of rain (Chapter 6), but when rain fall is above a certain threshold soil may stay wet long enough for them to germinate and establish. This is also suggested by the fact that larger individuals of *Amaranthus praetermissus* that established during an earlier rain event were only found in sods transplanted from canopy to matrix although seedlings were only very sparsely found in the matrix (Table 8.5). Tielbörger & Kadmon (1997) found for a three year study period only one species out of 29 annuals from a sandy desert that was consistently more common under shrubs than in the matrix. This suggests that for annuals the association with shrubs may fluctuate with precipitation. After high rain fall seed availability becomes more likely as a limiting factor for annual canopy species distributions and is in this way expected to have a stronger influence on vegetation pattern in general. To determine the relative importance of seed availability and abiotic factors on annual community assemblage further studies that determine the effect of transplanting sods under different rain fall scenarios, or using artificial watering, are therefore needed.

The results presented in this study lend support to the hypothesis that filtering by abiotic factors will overrule dispersal effects. Many studies document correlations between seed dispersal patterns and the distribution of adult plants and suggest that there exists a causal link between the two (e.g. Westelaken & Maun 1985; Fragoso 1997; Bleher & Bohning-Gaese 2001). However, as argued by Schupp & Fuentes (1995) and indicated by the present study such correlative evidence for dispersal driven patterns should be interpreted very cautiously and should not be readily accepted as evidence for dispersal driven patterns due to the primacy of processes occurring between seed arrival and maturity to adult plants.

Chapter 9

Conclusions and perspectives

“Germination responses to environmental factors can be exquisitely precise mechanisms of habitat choice in plants”

Donohue (2005)

This study clearly shows that aspects of the regeneration niche, notably those related to dispersal in space (Chapter 3) and germination behaviour (Chapter 5, 6 and 7), are important for filtering species from the species pool and thereby maintain vegetation patterns affected by camelthorn trees in the Southern Kalahari. In addition it shows that the ecological function of *Acacia erioloba* changes with its life history: The seed rain density and species diversity of fleshy fruited species increases with *A. erioloba* size (Chapter 2 and 3) and large trees offer more suitable conditions for germination of fleshy fruited species (Chapter 3 and 7).

What maintains vegetation pattern in Kalahari savannah: Dispersal versus abiotic factors

Can something be said about the relative contribution of different processes (dispersal, germination, seedling establishment) to species filtering? The general picture that emerges from the first part of this study (Chapter 3 and 4) and earlier studies (Milton & Dean 1995, Dean *et al.* 1999) is that canopy associated species are dispersal limited while matrix associated species tend to be more widely dispersed and filtering at other life stages determines distribution patterns. However, as Schupp & Fuentes (1995) argued such correlative evidence cannot demonstrate that patterns are dispersal driven because of the primacy of processes taking place between seed arrival and maturity to adult plants. Indeed several studies have found that the pattern of distribution of seeds tends to disappear as seedlings mature (Schupp & Fuentes 1995, Rey & Alcantara 2000, Balcomb & Chapman 2003).

The effects of dispersal and abiotic filters on vegetation patterns affected by the mosaic of canopies and open spaces can therefore only be disentangled using manipulative experiments. In Chapter 3 and 8 it was attempted, using sowing and sod transplant experiments, to distinguish between the effect of seed limitation and abiotic factors to vegetation patterns. The results suggested that abiotic filters acting on dormancy breaking,

germination and/or early seedling establishment rather than dispersal limit both canopy and matrix associated species to their respective microhabitats. The studies on germination biology (Chapter 6 and 7 in particular) indicate likely mechanisms. However the data presented in Chapter 8 provide only a snapshot. The main difficulty here is that many canopy associated species have very long induction times. The soil therefore has to remain moist for a sufficient long time to allow germination. The apparent lack of germination in the matrix may thus be related to the fact that not enough rain had fallen to fulfil the requirements for germination in these species. Under acacias shading by the canopy may have kept the soil moist long enough to allow germination there. For the guild of fleshy fruited perennials the additional inhibition of germination at temperatures resembling open sun conditions (Chapter 7, Kos & Poschlod 2007) suggests that they may indeed be limited by abiotic factors acting on germination.

Overall the results strongly suggest that germination biology is of major importance for vegetation pattern. However, germination and seedling emergence have also been found to be inadequate predictors of plant distribution in single species (Rey & Alcantara 2000) or at the community level (Figueroa & Lusk 2001). To demonstrate germination-driven pattern more reciprocal sowing experiments are needed under a variety of different watering regimes either artificial or natural and like for seed dispersal (Levine & Murrell 2003) it is necessary to describe the consequences for later life stages and link patterns of germination among multiple life stages.

However, it is still likely that the preliminary results will be confirmed: It is the imprecise nature of the dispersal process in plants (i.e. that they are due to their immobility not able to select habitat in a proximal sense) that has resulted in the wide range of germination mechanisms that we can observe in plants. These do provide very precise mechanism of habitat choice because of the specific environmental requirements for dormancy breaking and germination. Even when dispersal is directed (Howe & Smallwood 1982, Wenny 2001) it can not reach the same precision of habitat 'choice' that is achieved by germination responses to environmental cues. It is therefore not surprising that where more or less steep environmental gradients are found distribution patterns are in a proximate, mechanistic sense germination driven.

Even when in a proximal sense germination may be the driving force behind the vegetation pattern affected by trees in the arid Kalahari, in an ultimate (evolutionary) sense dispersal may still be considered as the factor responsible for present day vegetation patterns. This is particularly clear for fleshy fruited species. Most perennial canopy associated species have fleshy fruits and this trait is relatively conserved in evolution (Bolmgren & Eriksson

2005). The presence of fleshy fruits is likely to have caused the initial association of these species with *Acacia* canopies due to the behaviour of dispersers that resulted in dispersal of the majority of seeds to canopies (Jordano 2000, Kos & Poschlod 2007, Chapter 3). Germination traits, in contrast with fruit morphology, can evolve quickly as the variation among populations of the same species demonstrates (Meyer *et al.* 1995, Meyer *et al.* 1997, Baskin & Baskin 1998) and subsequently adaptations in germination behaviour to the microhabitat where most seeds landed may have occurred. The hypothesis that dispersal by herbivores is responsible for the association of certain annual species with acacias (Milton & Dean 1995) either in a proximal or ultimate sense, remains to be tested in a comparative framework. Survival after gut passage (Bonn 2004), epizoochorous attachment capacity (e.g. Römermann *et al.* 2005) combined with deposition patterns of dung and habitat use patterns of animals need to be quantified for a large set of species.

The general importance of germination for vegetation pattern

Under which conditions will germination be equally important for species sorting? Besides the present study most support for the importance of germination for species filtering comes from tropical rainforest pioneer communities (Daws *et al.*, 2002; Pearson *et al.*, 2002) where temperature and light requirements for germination allow species to distinguish between gaps and understory and between gaps of different sizes. Another example are wetlands where species differ in their germination response to cues that indicate water depth which results in species sorting to areas with different water tables (Moore & Keddy 1988; Seabloom *et al.* 1998). The importance of germination behaviour for vegetation pattern is therefore likely to increase where steep, relatively stable abiotic gradients can be found such as gaps in tropical lowland rainforest, arid ecosystems characterized by a discontinuous tree or shrub layer, or wetlands with variations in water depth. Often such gradients will be indicated by conspicuous features in the landscape (savanna trees, forest gaps). Another factor that will promote species sorting by differences in germination requirements is that contrasting habitats exhibit a relatively small scale mosaic-type spatial distribution. This will increase the chance that seeds land in the 'wrong' habitat and will therefore promote the evolution of mechanisms to avoid germination there. This does, however, require a relatively high probability that seeds landing in an unsuitable spot reach a suitable spot within their life span.

Germination is thus expected to be most important for species sorting in landscapes with a mosaic-like spatial distribution of habitats at a relatively small scale, with steep relatively stable abiotic gradients between habitats or microhabitats. At larger scales and in

other types of environments germination may still be important but sorting by germination requirements may not be as efficient because there is no direct adaptive link between germination behaviour and the environment. However, the requirements for dormancy breaking and germination are very specific for each species and so there are many opportunities for differences in factors that influence germination e.g. differences in soil texture, soil moisture, shading or the chemical environment (Baskin & Baskin 1998, Fenner 2000). This makes it likely that in general seeds dispersed outside a species natural habitat will have suboptimal germination behaviour in the new habitat: they will not be able to germinate or have strongly reduced germination, or may even germinate 'better' but in the wrong place or at the wrong moment.

What is needed to determine the contribution of germination to vegetation patterns are sowing experiments, based on a knowledge of abiotic gradients occurring in the landscape, with monitoring of plants from seedling through to reproductive adult life stages combined with determination of germination responses to the same abiotic gradients under laboratory conditions. At present there are no studies that fulfil all these requirements.

Links between germination and seedling traits

It should always be kept in mind that germination behaviour has evolved in relation to seedling requirements. Interspecific differences in germination behaviour will often reflect trade-offs at the seedling stage. Correlations between germination and seedling traits may therefore provide clues to the adaptive value of germination behaviour as the main function of germination cueing is to reduce mortality of seedlings. Though in this study seed mass was used as an approximation of seedling resistance against environmental hazards such as drought (Leishman *et al.* 2000) no PIC relationships between seed mass and germination traits were found (Chapter 5, 6 and 7). Among species of fleshy-fruited perennials the magnitude of inhibition by temperature typical of un-shaded soil increased with decreasing seed size, suggesting that smaller seedlings are indeed more vulnerable to drought (Chapter 7). However, an unexpected correlation of drought tolerance during germination with seed size was also found for annuals: germination of larger seeded species was more inhibited at lower water potentials than germination of smaller seeded species (Chapter 5). Besides seedling size, which is strongly correlated with seed size (Leishman *et al.* 2000) drought resistance could also be related to seedling differences in allocation pattern between roots and shoots, or physiological (e.g. photosynthetic pathways) and anatomical adaptations. Direct

measurements of seedling traits may thus increase understanding of the adaptive value of germination behaviour.

Importance of *Acacia erioloba* life history for associated species

The importance of *Acacia erioloba* life history for its key-stone function has been shown by Milton & Dean (1995), Dean *et al.* (1999) and Seymour (2006). This study identified aspects of the regeneration niche that are likely to be related to the difference in ecological function of saplings and mature trees.

The results presented in Chapter 7 suggest that temperature requirements for germination will limit establishment of fleshy-fruited species to acacia canopies. Germination of small seeded fleshy-fruited species is more inhibited at temperatures resembling open, unshaded conditions than germination of larger seeded species (Chapter 7). But this germination behaviour could also affect the relative importance of different life stages of *Acacia erioloba* for these species. The temperature measurements for saplings show that diurnal temperature fluctuations and maximum temperature are consistently higher than under the canopy of mature trees. Temperature measurements were taken halfway between canopy drip line and bole and this suggests that at least the proportion of suitable area for germination and establishment is smaller under saplings. The fact that small seeded species like *Lycium bosciifolium* and *Solanum capense* are also found under saplings (Chapter 2) suggests however that safe sites for establishment can still be found under sapling canopies, though probably at lower frequencies.

It could be argued that due to the higher inhibition of small seeded species by temperatures found in open sunny spots they might be less likely to establish under small trees than large seeded species. There was, however, no significant relationship between seed mass and the smallest stem circumference of *Acacia erioloba* trees where species were found (Chapter 2). However, if species are divided in two groups, one with seed mass < 5 mg and one with seed mass > 5 mg the minimum stem circumference of *Acacia erioloba* trees where species were found was actually lower for small seeded species than for large seeded species for the Nossob site, but no difference was found for the Molopo site. Species with small seeds seem therefore better colonizers. This suggests that dispersal in time and space limit larger seeded species to large trees, while small seeded species are not limited to large trees to the same extent in spite of the higher occurrence of safe sites. This is also supported by 1.) that species with seed mass > 5 mg were practically absent from the seed rain (Chapter 3), 2.) that the large seeded *Asparagus* species have dormancy and germination characteristics that

prevent them from forming a seed bank (Chapter 4) and 3.) that species that form a persistent seed bank generally tend to have smaller seed mass than species with transient seeds (Chapter 4). The results for colonization speed and seed mass could not yet be confirmed using PICs and more data are needed to enable a sound statistical evaluation of the hypothesis that small seeded species are better colonizers.

This study supports the hypothesis that the key stone species function of *A. erioloba* in the Southern kalahari is context dependent and is limited to large camelthorns (Milton & Dean 1995; Dean *et al.* 1999; Seymour 2006). Not only the presence of *Acacia erioloba* in the southern Kalahari savannas increases biodiversity, also its population structure limits plant diversity. The last decades have seen a dramatic increase in the harvesting of *Acacia erioloba* for firewood and charcoal production (Anderson & Anderson 2001; Liversidge 2001; Raliselo 2002) which is likely to take place on the basis of larger trees. In the past large specimens became rare in certain areas, because most of them were cut down for fuel for the Kimberley diamond mines (Barnes *et al.* 1997 and references therein). Management strategies that maintain a healthy population structure of *Acacia erioloba* are vital for biodiversity conservation in the Southern Kalahari dry river beds. A shift in the population structure of *Acacia erioloba* to a population that consists mainly of young trees is expected to have strong negative effects on the populations of plant species associated with its canopy.

Germination traits should be included in functional trait databases

The germination biology of species is not only important for species sorting. This study, for example, not only demonstrates the importance of germination behaviour for maintaining vegetation pattern, but also indicates the importance of germination behaviour for coexistence within plant communities. The dependence of the temperature response of fleshy fruited species on seed size, is one example. Small seeded species are more specific in their requirements for germination and will thus have a more limited number of suitable safe sites available under trees. The trade-off may be that small seeded species have a higher probability to reach suitable spots than larger seeded species. This assumption is supported by a large body of literature and the data in Chapter 2 suggest that smaller seeded fleshy-fruited species do indeed occupy more canopy patches, and this is likely to be the same at a more local scale. On the other hand germination behaviour may be important at larger scales: a correlation between distributional range size and germination patterns found by Brändle *et al.* (2003) suggests that germination traits may be useful in exploring macroecological relationships in

plants and germination biology may determine the outcome of interactions between local flora and invasive species (Levine & Rees 2004).

It is clear that germination behaviour is relevant for plant ecology over a range of spatial scales: from species coexistence in communities, to succession to plant distributional range and invasive species ecology. This study indicates the large potential of germination traits for the prediction of species distributions and changes in distributions in arid ecosystems. Römermann (2006) emphasized that for north-western Europe germination traits, in spite of their importance for plant establishment and the prediction of plant species distributions, are hardly available or accessible. This may not be much different for most arid regions. The aspects of germination ecology found in this study that were not yet described in the literature are also indicative of the relative scarcity of data on plant regeneration in arid regions. The advantage of germination traits is that they can often be relatively easily measured in the lab. This means that the direct effect of environmental factors on the process of germination can be measured under controlled conditions. Measuring processes like for example seedling and adult plant growth and survival responses to environmental factors is much more cumbersome. The chapter on germination speed (Chapter 6) shows that easily measured germination traits can have a high predictive value. Standardized protocols (Knevel *et al.* 2005) that enable the measurement of germination requirements for large numbers of species should therefore be developed in addition to existing protocols for dispersal traits (Bonn 2004, Römermann *et al.* 2005, Römermann 2006).

The scarcity and poor accessibility of data on germination biology (Römermann 2006) reflects a more general tendency to neglect the regeneration niche when explaining spatial vegetation patterns or species richness in plant communities (Grubb 1977, Schütz 2000). However, the importance of the regeneration niche has traditionally been recognized by plant ecologists working in arid ecosystems and the relative scarcity of data (but see Gutterman 1993) may mainly be due to inaccessibility and hard conditions for field work in arid regions. Traits related to regeneration processes, like seed persistence, germination and seedling establishment are expected to increase in importance in more arid environments due to the increasing risks associated with seedling establishment caused by low and unpredictable rain fall (Chapter 2).

The Southern Kalahari is expected to become increasingly more arid over the next decades due to global climate change (Rutherford *et al.* 1999). This is expected to lead at the same time to the remobilisation of the Kalahari dunes, due to increasing drought and associated loss of vegetation cover (Thomas *et al.* 2005). Increased mobility of sand will on

itself also have strong effects on the vegetation, so this is a self enforcing process. Combined with increasing pressure from human populations with increasing numbers of life stock (Thomas & Shaw 1991) it is clear that changes in the Kalahari vegetation could be dramatic. The compilation of a database on plant regenerative traits for the Southern Kalahari, (and other arid environments) would help to predict effects of climate change and land use on the vegetation and to determine which levels of land use are sustainable under different scenarios of vegetation change. In addition such a database would allow large scale comparative studies that lead to a better general understanding of vegetation dynamics and mechanisms of coexistence in arid ecosystems. As the the southern Kalahari flora consists of only about 600 species (Leistner 1967, van Rooyen & Bezuidenhout 1997), such a database for this region could be within easy reach.

Summary

In arid ecosystems with a discontinuous shrub or tree layer distinct groups of plant species are usually associated with the area under woody perennials and the open interspaces respectively. The processes behind such patterns are not completely understood. Most studies on the effects of woody species on plants in arid environments focus on species found under canopies and are motivated by the current interest of plant ecologists in facilitation. However, to understand the mechanisms behind vegetation patterns comparative studies are needed. The species pool concept provides a useful framework to do so. According to the species pool concept only a certain set of species from a specified region or landscape is able to colonize and persist in a habitat within that landscape. Which species can coexist in a habitat is in the first place determined by the ability of species to disperse to that habitat but abiotic and biotic factors form a habitat specific environmental sieve that determines which of the arriving species can establish and maintain a population there. For plants the regeneration niche is expected to be of major importance for filtering species from the species pool. Being largely immobile plants can track habitat mainly by seed dispersal and germination cueing. Because canopy and matrix contrast strongly in abiotic conditions plants are expected to have adapted to either one of them due to various trade-offs. As the process of germination basically forms the only possibility for a plant to 'choose' more or less precisely under which conditions it will grow, germination behaviour is expected to have evolved to direct germination and establishment to favoured habitat. The aim of this study was to determine the effect of regenerative traits (seed dispersal, seed persistence and germination) on the origin and maintenance of vegetation patterns affected by *Acacia erioloba* in arid Southern Kalahari savannah.

Chapter 2 described the colonization of acacia trees by fleshy fruited plants. It is expected that seed mass is a major determinant of colonization potential because small seeded species produce higher numbers of seeds that are more persistent in the soil. The strength of such a correlation is expected to increase with increasing aridity due to the increased importance of seed persistence. All fleshy-fruited species found under individual *Acacia erioloba* trees were recorded at two sites with different annual precipitation and seed mass was determined for each species. Seed persistence of two selected species was studied by burying seeds for one year in the soil and one and three years dry storage in the lab. Species number increased twice as fast with stem circumference at the high rain fall site, demonstrating the increased

establishment opportunities there. Tree occupancy was significantly correlated with seed size only at the low rain fall site. Of the three most common species shared between the two sites tree occupancy decreased most with decreasing rain fall in species with the least persistent seeds even though the species with the most persistent seeds had larger seeds than the second most persistent species. Under more arid conditions the relevance of seed persistence for colonization potential increases. This might explain the absence of a correlation between seed size and tree occupancy under more humid conditions but more studies about persistence and its relation to seed size in (semi-) arid regions are needed.

In Chapter 3 the pattern of seed rain of fleshy fruited plants was examined. In arid environments plants associated with woody perennials often have fleshy-fruits. Disproportional dispersal to canopies, favourable conditions for germination and establishment and reduced seed predation under canopies have all been proposed as mechanisms to explain such patterns. The seed rain of *Lycium* was found to be higher under *Acacia erioloba* trees than in the open matrix and seed rain was higher under mature trees than under saplings in 2002. In 2003 there was no difference between mature trees and saplings, but seed rain under both was higher than in the matrix. Seed rain of *Solanum capense* was higher under saplings than under mature trees in 2003, no differences between microhabitats were observed in 2002. No emergence of sown seeds of *Lycium bosciifolium* and *Pollichia campestre* took place in the matrix. Though the difference was not statistically significant seedlings only emerged under the canopy of mature trees. For *Lycium* no significant differences between the number of seeds collected from the soil and from traps excluding predators were observed for all microhabitats. For *Solanum* there was only a significant difference for saplings, where the number of seeds collected from the soil was less than that from traps, suggesting more predation under saplings than under mature trees. This could be due to litter hiding seeds as litter is practically absent under saplings. The sparrow weaver, a mainly insectivorous bird, may be an important disperser of fleshy fruited plants in the Kalahari. Seed rain of *Lycium* and *Solanum* under nests of this species was higher than the average seed rain under mature trees and seeds of *L. bosciifolium* survive and germinate after ingestion. The results indicate that both dispersal and abiotic filters contribute to the association of fleshy fruited species with acacia canopies.

In Chapter 4 two aspects of the seed bank were studied: the effect of microhabitat (*Acacia* canopies versus open matrix) on abundance and composition of the seed bank and on filtering

species from the seed bank and the vertical distribution and persistence of seeds in the soil in relation to seed morphology.

Ordination of seed bank and vegetation data showed that for seed bank data canopy and matrix did not separate. For vegetation data canopy and matrix were clearly separated. Matrix species common in the seed bank are anemochorous and/or have small seeds while canopy species common in the seed bank are zoochorous with larger seeds. Matrix species thus have a higher potential to disperse widely to both microhabitats. Species that are more common in the matrix vegetation but are more common under the canopy for the seed bank all have small seed and/or morphological adaptations for wind dispersal. This suggests that matrix species are dispersed to canopy and matrix but environmental filtering restricts growth to the matrix. There was no difference in seed persistence between canopy associated and matrix associated species. Therefore seed persistence does not seem to be important for species sorting.

Seed mass and shape are correlated with depth distribution and persistence in many floras. But knowledge of this aspect of seed ecology is sparse and equivocal for arid environments. The hypothesis that smaller and rounder seeds are distributed more deep in the soil was tested. Species that are more common in deeper soil layers are thought to have more persistent seeds than species only found on the surface. On the basis of this assumption species were classified as having persistent or transient seeds. This classification was used to test the hypothesis that smaller and rounder seeds are more persistent than large elongated/flattened seeds. Depth distribution was correlated with seed shape for the canopy for species and for the matrix for phylogenetically independent contrasts (PICs): species with more elongated or flattened seed had a higher proportion of seeds in the upper soil layer than species with round, compact seeds. Depth distribution was correlated with seed mass and the product of shape and mass for the matrix for both species and contrasts. Species with persistent seeds had smaller seeds than species with transient seeds, both for species and PICs. No difference in seed shape between persistent and transient species was found for species or PICs.

Chapter 5,6 and 7 focused on germination behaviour (responses to water potential, duration of wetting and temperature respectively) and how it is influenced by habitat association and life history traits. Chapter 5 is a study on the effect of water potential on seed germination. In arid ecosystems large inter-specific variation can be found in the ability to germinate under water stress. Most previous studies did not find correlations with habitat preferences. It was

predicted that variation in the ability to germinate under osmotic stress is due to variation in seedling drought tolerance rather than differences in habitat use. Large seedlings are thought to be more resistant to drought and a correlation of seed size with the ability to germinate under osmotic stress is therefore expected. Species that are more drought sensitive are expected to have higher dormancy and a correlation of germination fraction with the ability to germinate under osmotic stress can be expected. To test this hypothesis the water potential needed to reduce germination to 50 % relative to 0 Mpa was determined for 28 species and effect of seed mass, germination fraction and habitat preference (canopy association and soil texture association) were tested. No effect of seed mass was found but there was a strong positive correlation between the ability to germinate under osmotic stress and germination fraction. The correlation was found for all species and perennials, but not for annuals. No correlation with habitat variables was found. The absence of a correlation with seed size can be explained by seedling drought tolerance being composed of many other attributes besides seed mass. The correlation of the ability to germinate under osmotic stress and dormancy supports the hypothesis that seedling tolerance has played a major role in the evolution of germination responses to water stress.

In chapter 6 the effect of habitat preferences and life history variables on germination speed was investigated. Reduced germination speed can be seen as a mechanism reducing the risk of germination in arid environments. The longer water has to be available for germination, the more likely it is that water will be available for subsequent growth. Woody plants are thought to affect water availability under their canopies positively and will alter the risk for germinating seeds. If water stress is reduced there will be selection for faster germination as fast germinating seedlings have a competitive advantage over slow germinating seedlings. It was hypothesized that due to improved water availability under canopies which reduces the risk associated with germination species associated with the canopy habitat germinate faster than species typically found in the surrounding open matrix. Contrary to the hypothesis a significant positive relationship between canopy association based on cover and the delay of germination was found. This could be caused by 1.) canopy interception of rain reducing water availability under canopies compared with the matrix 2.) very fast drying of the top soil in open areas, which makes fast germination necessary 3.) plant traits like root elongation rate that differ between canopy and matrix species. No correlation was found when canopy association was based on seed bank data which can be attributed to either dispersal or establishment in both microhabitats in favourable years.

Favourable conditions for establishment under canopies are likely to be associated with shade but under canopies shade is distributed patchily and differs in quality. Diurnal temperature fluctuations and maximum temperatures could be reliable indicators of safe sites.

In Chapter 7 it was examined if canopy associated species use temperature cues to germinate in shade patches, rather than matrix areas between trees. Species associated with *Acacia erioloba* trees and matrix species were germinated at temperature regimes resembling shaded and un-shaded conditions. Germination of all fleshy fruited perennial *Acacia*-associated species and two annual *Acacia*-associated species was inhibited by the temperature regime resembling un-shaded conditions compared with at least one of the regimes resembling shaded conditions. Germination of matrix species was not inhibited by the un-shaded temperature regime and in several cases it increased germination compared with shaded temperature regimes or constant temperature. Using PICs a significant positive relationship between canopy association and the germination at shade temperatures relative to un-shaded temperatures was found. The data support the hypothesis that canopy species have developed mechanisms to prevent germination in open sun conditions.

Chapter 8 describes a sod transplant experiment that was carried out to test if dispersal or abiotic filters acting on germination and/or early seedling establishment drive vegetation patterns. To test the effects in the chapters on germination soil sods were transplanted from acacia canopy to matrix and vice versa and emerged seedlings were recorded after a natural rain event. Transplanting canopy soil to the matrix had a negative effect on 14 out of 16 canopy species (88 %) but transplanting matrix soil had a negative effect on only 6 out of 10 matrix species (60%) germinated. Similarly total seedling number was significantly higher for control sods under the canopy compared with canopy sods transplanted to the matrix but did not differ between transplanted and control matrix sods. The results can be explained by the germination biology of the species: Canopy species show inhibition of germination by canopy temperatures while matrix species show no inhibition by canopy temperatures (Chapter 7) and canopy associated annuals generally germinate more slowly than matrix associated annuals (Chapter 6). This could prevent canopy species to germinate in the matrix while soil there dries out too fast to allow germination. However, the only matrix species common enough to allow statistical testing *Indigofera alternans* showed a negative response to transplanting to the canopy. This may indicate a vegetation avoiding germination mechanism for this species.

Possibly this is common among matrix species. The similar total seedling emergence in matrix sod transplants and controls may than be caused by seed trapping of matrix species seeds and seed input from the canopy vegetation and seed bank which are both much denser under canopies than in the matrix.

In Chapter 9 conclusions and perspectives for future studies were given. This study supports the hypothesis that dispersal and filtering by abiotic factors at the germination and early seedling stage is of major importance for the maintenance of vegetation patterns affected by *Acacia erioloba* in the Southern Kalahari.

The transplant and sowing experiment (Chapter 3) suggested that the germination responses described in Chapter 6 and 7 provide a mechanism for maintenance of the observed vegetation pattern that overrules dispersal patterns. Dispersal can be seen as an ultimate cause for the observed patterns in the case of fleshy fruited perennials (but possibly also for other functional groups) by directing the evolution of other traits such as germination behaviour, which provides a present day mechanism for the maintenance of vegetation pattern.

Germination biology may be especially important for species sorting in landscapes with a mosaic-like spatial distribution of habitats at a relatively small scale, with relatively steep abiotic gradients between habitats. To determine the contribution of germination to vegetation patterns sowing experiments are needed. These should be based on a knowledge of abiotic gradients occurring in the landscape, and combine monitoring of plants from seedling through to reproductive adult life stages with laboratory studies to determine germination responses to the same abiotic gradients under laboratory conditions. Such studies are virtually lacking in the germination literature.

Besides species sorting at the habitat scale germination biology is also relevant for species coexistence and macroecological relationships. Because of the importance over a wide range of spatial scales germination traits should be included in plant functional trait databases from which they have been conspicuously absent until now. Germination and other traits related to regeneration are expected to increase in importance in arid environments due to the increasing risks associated with seedling establishment caused by low and unpredictable rain fall. Dramatic changes in the Kalahari vegetation are expected to occur over the next decades due to aridization as a result of to global climate change. The compilation of a database on plant regenerative traits would help to predict effects of climate change and land use on the vegetation. Such a database would also allow large scale comparative studies that lead to a better understanding of plant ecology in arid ecosystems.

References

- Acocks, J.P.H. (1953) Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* **28**.
- Adams, W.M., Goudie, A.S. & Orme, A.R. (1996) *The physical geography of Africa*. Oxford University Press, Oxford.
- Allen, P.S., Meyer, S.E. & Khan, M.A. (2000) Hydrothermal time as a tool in comparative germination studies. *Seed biology: advances and applications* (eds M. Black, K. J. Bradford, & J. Vázquez-Ramos), pp. 401–410. CAB International, Wallingford.
- Anderson, M.D. & Anderson, T.A. (2001) Too much, too quickly? Doubts about the sustainability of the camelthorn wood harvest. *African Wildlife* **55**, 21-23.
- Anderson, L.J., Brumbaugh, M.S. & Jackson, R.B. (2001) Water and tree-understorey interactions: a natural experiment in a savanna with oak wilt. *Ecology* **82**, 33-49.
- Archer, S., Scifres, C., Bassham, C.R. & Maggio, R. (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**, 111-127.
- Baker, H.G. (1972) Seed weight in relation to environmental conditions in California. *Ecology* **53**, 997-1010.
- Balcomb, S.R. & Chapman, C.A. (2003). Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. *Ecological Monographs* **73**, 625-642.
- Barnes, M.E. (1999) Acacia woodland ecology and elephants in Northern Botswana. Ph.D. University of Nevada, Reno.
- Barnes, R.D., Fagg, C. W. & Milton S.J. (1997) *Acacia erioloba*: Monograph and annotated bibliography. Tropical forestry papers 35, Oxford Forestry Institute, Oxford.
- Baskin, J.M. & Baskin, C.C. (1989) Physiology of dormancy and germination in relation to seed bank ecology. *Ecology of soil seed banks* (eds M.A. Leck, V.T. Parker & R.L. Simpson), pp. 53-66. Academic Press, San Diego.
- Baskin, C.C. & Baskin, J.M. (1998) *Seeds: ecology, biogeography, and evolution of dormancy and germination*. 1st ed. Academic Press, San Diego.
- Bazzaz, F.A. (1991). Habitat selection in plants. *American Naturalist* **137** (Supplement), 116-130.
- Bekker, R.M., Bakker, J.P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. & Willems, J.H. (1998) Seed size, shape and vertical distribution in the soil: Indicators of seed longevity. *Functional Ecology* **12**, 834-842.
- Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R. & Mwonga, S.M. (1989) The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology* **26**, 1005-1024.
- Belsky, A.J. & Canham, C.D. (1994) Forest gaps and isolated savanna trees: an application of patch dynamics in two ecosystems. *BioScience* **44**, 77-84.
- Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M. & Ali, J.M. (1993) Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. *Journal of Applied Ecology* **30**, 143-155.
- Bleher, B. & Bohning-Gaese, K. (2001) Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* **129**, 385-394.
- Boeken, B. & Gutterman, Y. (1990) The effect of temperature on seed germination in three common bulbous plants of different habitats in the central Negev desert of Israel. *Journal of Arid Environments* **18**, 175-184.
- Bolmgren, K. & Eriksson, O. (2005) Fleshy fruits - origins, niche shifts, and diversification. *Oikos* **109**, 255-272.

- Bonn, S. (2004) *Dispersal of plants in the Central European landscape - dispersal processes and assessment of dispersal potential exemplified for endozoochory*. Ph.D. University of Regensburg, Regensburg.
- Botha, F.C., Grobbelaar, N. & Small, J.G.C. (1984) The effect of water stress on the germination of *Citrullus lanatus* seeds. *South African Journal of Botany* **3**, 111-114.
- Brändle, M., Stadler, J., Klotz, S. & Brandl, R. (2003) Distributional range size of weedy plant species is correlated to germination patterns. *Ecology* **84**, 136-144.
- Briedé, J.W. & McKell, C.M. (1992) Germination of seven perennial arid land species, subjected to soil moisture stress. *Journal of Arid Environments* **23**, 263-270.
- Briers, J.H. 1988. *'n Ondersoek na aspekte van die vestiging van inheemse bome en struike op versteurde gebiede*. M.Sc. thesis Potchefstroom University for Christian Higher Education, Potchefstroom, ZA.
- Brown, J.S. & Venable, D.L. (1986) Evolutionary ecology of seed-bank annuals in temporally varying environments. *American Naturalist* **127**, 31-47.
- Bullock, J.M. (2000) Gaps and seedling colonization. *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd edition (ed M. Fenner), pp. 375-395. CAB International, Wallingford.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**, 1958-1965.
- Canadell, J., Jackson, R.B., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.-D. (1996) Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**, 583-595.
- Carillo-Garcia, Á., Bashan, Y. & Bethlenfalvay, G.J. (2000) Resource-island soils and the survival of the giant cactus, cardon, of Baja California Sur. *Plant and Soil* **218**, 207-214.
- Carr, J.D. (1976) *The South African Acacias*. Conservation Press, Johannesburg.
- Coates Palgrave, K. (1983) *Trees of Southern Africa, 2nd edition*. Struik Publishers, Cape Town.
- Cohen, D. (1966) Optimizing reproduction in a randomly varying environment. *Journal of Theoretical Biology* **12**, 119-129.
- Coomes, D.A. & Grubb, P.J. (2003) Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution* **18**, 283-291.
- Davies, T. J., Barraclough, T.G., Chase, M.W., Soltis, P.S., Soltis, D.E. & Savolainen, V. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proceedings of the National Academy of Sciences of the USA* **101**, 1904-1909.
- Daws, M.I., Burslem, D.F.R.P., Crabtree, L.M., Kirkman, P., Mullins, C.E. & Dalling, J.W. (2002) Differences in seed germination responses may promote coexistence of four sympatric Piper species. *Functional Ecology* **16**, 258-267.
- de Villiers, A.J., van Rooyen, M.W. & Theron, G.K. (1994) Comparison of two methods for estimating the size of the viable seed bank of two plant communities in the Strandveld of the west coast, South Africa. *South African Journal of Botany* **60**, 81-84.
- Dean, W.R.J., Milton, S.J. & Jeltsch, F. (1999) Large trees, fertile islands, and birds in arid savannas. *Journal of Arid Environments* **41**, 61-79.
- Debussche, M. & Isenmann, P. (1994) Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* **69**: 414-426.
- Donaldson, C.H. (1969) *Bush encroachment with special reference to the Blackthorn problem of the Molopo area*. Government Printer, Pretoria.
- Donohue, K. (2005) Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist* **166**, 83-92.

- Donohue, K., Dorn, L.A., Griffith, C., Schmitt, J., Kim, E.-S. & Aguilera, A. (2005) Niche construction through germination cueing: life history responses to timing of germination in *Arabidopsis thaliana*. *Evolution* **59**, 771-785.
- Ehrlén, J. & van Groenendaal, J.M. (1998) The trade-off between dispersability and longevity – an important aspect of plant species diversity. *Applied Vegetation Science* **1**, 29-36.
- Ehrlén, J. & Eriksson, O. (2000) Dispersal limitation and patch occupancy in forest herbs. *Ecology* **81**, 1667-1674.
- Eira, M.T.S. & Caldas, L.S. (2000) Seed dormancy and germination as concurrent processes. *Revista Brasileira de Fisiologia Vegetal* **12**, 85-104.
- Elberse, W.Th. & Breman, H. (1989) Germination and establishment of Sahelian rangeland species I. Seed properties. *Oecologia* **80**, 477-484.
- Elberse, W.Th. & Breman, H. (1990) Germination and establishment of Sahelian rangeland species II. Effects of water availability. *Oecologia* **85**, 32-40.
- Ernst, W.H.O., Veenendaal, E.M. & Kebakile MM. (1992) Possibilities for dispersal in annual and perennial grasses in a savanna in Botswana. *Vegetatio* **102**, 1-11.
- Evans, C.E. & Etherington, J.R. (1990) The effect of soil water potential on seed germination of some British plants. *New Phytologist* **115**, 539-548.
- Facelli, J.M. & Brock, D.J. (2000) Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of South Australia. *Ecography* **23**, 479-491.
- Facelli, J.M. & Lad, B. (1996) Germination requirements and responses to leaf litter of four species of eucalypt. *Oecologia* **107**, 441-445.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1-15.
- Fenner, M. (1987a) Seedlings. *New Phytologist* **106** (Supplement), 35-47.
- Fenner, M. (1987b) Seed characteristics in relation to succession. *Colonization, succession and stability* (eds A.J. Gray, M.J. Crawley & P.J. Edwards), pp. 103-114. Blackwell, Oxford.
- Fenner, M. ed (2000) *Seeds: The Ecology of Regeneration in Plant Communities*. 2nd edition CAB International, Wallingford.
- Fensham, R.J. & Butler, D.W. (2004) Spatial pattern of dry rainforest colonizing unburnt Eucalyptus savanna. *Austral Ecology* **29**, 121-128.
- Figueroa, J.A. & Lusk, C.H. (2001) Germination requirements and seedling shade tolerance are not correlated in a Chilean temperate rain forest. *New Phytologist* **152**, 483-489.
- Fleming, T.H. & Valiente-Banuet, A. (2002) *Columnar cacti and their mutualists: evolution, ecology, and conservation*. The University of Arizona Press, Tucson.
- Flores, J. & Briones, O. (2001) Plant life-form and germination in a Mexican inter-tropical desert: effects of soil water potential and temperature. *Journal of Arid Environments* **47**, 485-497.
- Flores, J. & Jurado, E. (2003) Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science* **14**, 911-916.
- Flynn, S., Turner, R.M. & Dickie, J.B. (2004) *Seed Information Database* (release 6.0, October 2004). URL: <http://www.rbgbkew.org.uk/data/sid> [Royal Botanical Gardens, Kew, UK].
- Fragoso, J.M. (1997) Tapir-generated seed shadows: scale dependent patchiness in the Amazon rain forest. *Journal of Ecology* **85**, 519-529.
- Fulbright, T.E., Kuti, J.O. & Tipton, A.R. (1995) Effects of nurse-plant canopy temperatures on shrub seed germination and seedling growth. *Acta Oecologia* **16**, 621-632.
- Funes, G., Basconcelo, S., Diaz, S. & Cabido, M. (1999) Seed size and shape are good predictors of seed persistence in soil in temperate mountain grasslands of Argentina. *Seed Science Research* **9**, 341-345.

- Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N.T., Susanna, A. & Jansen, R.K. (2005) Everywhere but Antarctica: Using a supertree to understand the diversity and distribution of the Compositae. *Plant diversity and complexity patterns -Local, regional and global dimensions* (eds I. Friis & H. Balslev), pp. 343-373. *Biologiske Skrifter / udg. af det Kgl. Danske Videnskabernes Selskab*, vol. **55**. Munksgaard, København.
- Garland, T.J., Dickerman, A.W., Janis, C.M. & Jones, J.A. (1993) Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* **42**, 265-292.
- Gibbs Russell, G.E., Watson, L., Koekemoer, M., Smook, L., Barker, N. P., Anderson, H. M. & Dallwitz, M. J. (1991). Grasses of Southern Africa. *Memoirs of the Botanical Survey of South Africa* **58**. National Botanical Institute, Pretoria.
- Godínez-Alvarez, H. & Valiente-Banuet, A. (1998) Germination and early seedling growth of Tehuacan Valley cacti species : the role of soils and seed ingestion by dispersers on seedling growth. *Journal of Arid Environments* **39**, 21-31.
- Godínez-Alvarez, H., Valiente-Banuet, A. & Rojas-Martínez, A. (2002) The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* **83**, 2617-2629.
- Götzenberger, L. (2005) Seed weight and seed shape. *The LEDA Trait base Collecting and measuring standards of life-history traits of the northwest European flora*. (eds I.C. Knevel, R.M. Bekker, D. Kunzmann, M. Stadler & K. Thompson), pp. 101-104. LEDA Traitbase project, University of Groningen Community and Conservation Ecology group, Groningen.
- Grass Phylogeny Working group (2001) Phylogeny and Subfamilial Classification of the Grasses (Poaceae). *Annals of the Missouri Botanical Garden* **88**, 373-457.
- Greene, D.F. & Johnson, E.A. (1994) Estimating the mean annual seed production of trees. *Ecology* **75**, 642-647.
- Grime, J.P., Mason, G., Curtis, A.V., Rodman, J., Band, S.R., Mowforth, M.A.G., Neal, A.M. & Shaw, S. (1981). A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**, 1017-1059.
- Groves, R.H., Hagon, M.W. & Ramakrishnan, P. S. (1982) Dormancy and germination of seed of eight populations of *Themeda australis*. *Australian Journal of Botany* **30**, 373-386.
- Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* **52**, 107-145.
- Grunicke, U. (1996) *Populations- und ausbreitungsbiologische Untersuchungen zur Sukzession auf Weinbergsbrachen am Keuperstufenrand des Remstals*. J Cramer in der Gebrüder Borntraeger Verlagsbuchhandlung, Berlin/Stuttgart.
- Guevara, S. & Laborde, J. (1993) Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. *Vegetatio* **107/108**, 319-338.
- Gutterman, Y. & Agami, M. (1987) A comparative study of seeds of *Helianthemum vesicarium* Boiss. And *H. ventosum* Boiss. Perennial desert shrub species inhabiting two different neighbouring habitats in the Negev desert highlands. Israel. *Journal of Arid Environments* **12**, 215-221.
- Gutterman, Y. & Edine, L. (1988) Variations in seed germination of *Helianthemum vesicarium* and *H. ventosum* from populations of two different altitudes in the Negev highlands, Israel. *Journal of Arid Environments* **15**, 261-262.
- Gutterman, Y. (1993) *Seed germination in desert plants*. Springer Verlag, Berlin/Heidelberg.
- Hadas, A. (1977) A simple laboratory approach to test and estimate seed germination performance under field conditions. *Agronomy Journal* **69**, 582-585.

- Hagos, M.G. (2001) The influence of tree thinning and subhabitat differentiation on the reproductive dynamics of *Acacia mellifera* subsp. *detinens*. MSc (Agric) thesis, University of the Free State, Bloemfontein.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, New York.
- Harvey, P.H. (1996) Phylogenies for ecologists. *Journal of Animal Ecology* **65**, 255-263.
- Harvey, P.H. & Pagel, M. D. (1991) *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- Harvey, P.H., Read, A.F. & Nee, S. (1995) Why ecologists need to be phylogenetically challenged. *Journal of Ecology* **83**, 535-536.
- Haworth, K. & McPherson, G.R. (1995) Effects of *Quercus emoryi* trees on precipitation distribution and microclimate in a semiarid savanna. *Journal of Arid Environments* **31**, 153-170.
- Hérault, B. & Hiernaux, P. (2004) Soil seed bank and vegetation dynamics in Sahelian fallows; the impact of past cropping and current grazing treatments. *Journal of Tropical Ecology* **20**, 683–691.
- Hilu, K.W. & Alice, L.A. (2001) A phylogeny of Chloridoideae (Poaceae) based on matK sequences. *Systematic Botany* **26**, 386-405.
- Hoffman, M.T., Cowling, R.M., Douie, C. & Pierce, S.M. (1989) Seed predation and germination of *Acacia erioloba* in the Kuiseb River Valley, Namib Desert. *South African Journal of Botany* **55**, 103-106.
- Hoffmann, J. (2001) *Dynamics and structure of the woody vegetation in the Nossob river bed, Southern Kalahari*. Diploma thesis Philipps Universität Marburg, Marburg.
- Holl, K.D. (1998) Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology* **6**, 253-261.
- Holmes, P.M. & Newton, R.J. (2004) Patterns of seed persistence in South African fynbos. *Plant Ecology* **172**, 143-158.
- Holmgren, M., Scheffer, M., Huston, M.A. (1997). The interplay of facilitation and competition in plant communities. *Ecology* **78**, 1966-1975.
- Hoppes, W.G. (1988) Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* **69**, 320-329.
- Hovestadt, T. (1997) *Fruchtmerkmale, endozoochore Samenausbreitung und ihre Bedeutung für die Zusammensetzung der Pflanzengemeinschaft. Untersuchungen im Wald Savannenmosaik des Comoé Nationalparks, Elfenbeinküste*. Wissenschaft und Technik Verlag, Berlin.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**, 201-228.
- Hughes, L., Westoby, M. & Jurado, E. (1994) Convergence of elaiosomes and insect prey: evidence from ant foraging behaviour and fatty acid composition. *Functional Ecology* **8**, 358-365.
- International Seed Testing Association 1999. International rules for seed testing. *Seed Science and Technology*, 27, Supplement, 333 pp.
- Izhaki, I., Walton, P.B. & Safriel, U.N. (1991) Seed shadows generated by frugivorous birds in an eastern mediterranean scrub. *Journal of Ecology* **79**, 575-590.
- Jacquemyn, H., Butaye, J. & Hermy, M. (2003) Influence of environmental and spatial variables on regional distribution of forest plant species in a fragmented and changing landscape. *Ecography* **26**, 768-776.
- Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* **88**, 494-502.
- Janzen, D.H. (1984) Dispersal of small seeds by big herbivores – foliage is the fruit. *American Naturalist* **123**, 338-353.

- Joffre, R. & Rambal, S. (1988) Soil water improvement by trees in the rangelands of southern Spain. *Acta Oecologica* **9**, 405-422.
- Jordano, P. 2000. Fruits and frugivory. *Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition* (ed M. Fenner), pp. 31-57. CAB International, Wallingford.
- Jurado, E. & Westoby, M. (1992) Germination biology of selected Central Australian plants. *Australian Journal of Ecology* **17**, 341-348.
- Kahmen, S. & Poschlod, P. (2004) Plant functional trait responses to grassland succession over 25 years. *Journal of Vegetation Science*. **15**, 21-32.
- Karlsson, L.M., Tamado, T. & Milberg, P. (2003) Seed dormancy pattern of the annuals *Argemone ochroleuca* and *A. mexicana* (Papaveraceae). *Flora* **198**, 329-339.
- Kelly, C.K. (1995) Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* **102**, 377-388.
- Kemp, P.R. (1989). Seed banks and vegetation processes in deserts. *Ecology of soil seed banks* (eds M.A. Leck, V.T. Parker & R.L. Simpson), pp. 257-281. Academic Press, San Diego.
- Kennard, D.G. & Walker, B.H. (1973) Relationships between tree canopy cover and *Panicum maximum* in the vicinity of Fort Victoria. *Rhodesian Journal of Agricultural Research* **11**, 145-153.
- Knevel, I.C., Bekker, R.M., Kunzmann, D., Stadler, M. & Thompson, K. (eds) (2005) *The LEDA Trait base Collecting and measuring standards of life-history traits of the northwest European flora*. LEDA Traitbase project, University of Groningen Community and Conservation Ecology group, Groningen.
- Koller, D. & Hadas, A. (1982) Water relations in the germination of seeds. *Encyclopedia of Plant Physiology, New Series 12 B* (eds A. Pirson & M. H. Zimmermann), pp. 401-431. Springer Verlag, Berlin/Heidelberg/New York.
- Kos, M. & Poschlod, P. (2007) Seeds use temperature cues to ensure germination under nurse-plant shade in xeric Kalahari savannah. *Annals of Botany* **99**, 667-675.
- Leck, M.A. (1989) Wetland seed banks. *Ecology of soil seed banks* (eds M.A. Leck, V.T. Parker & R.L. Simpson), pp. 283-305. Academic Press, San Diego.
- Leishman, M.R. & Westoby, M. (1994) The role of large seeds in seedling establishment in dry soil conditions – experimental evidence from semi-arid species. *Journal of Ecology* **82**, 249-258.
- Leishman M.R. & Westoby, M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology* **12**, 480-485.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition* (ed M. Fenner), pp. 31-57. CAB International, Wallingford.
- Leistner, O.A. (1967) The plant ecology of the Southern Kalahari. *Memoirs of the Botanical Survey of South Africa* **38**. Pretoria: Botanical Research Institute.
- Leistner, O.A. (1996) The subcanopy flora in the dynamics of the Kalahari Thornveld. *The biodiversity of African Plants* (eds L.J.G. van der Maesen, X. M. van der Burgt, and J. M. van Medenbach de Rooy), pp. 163-179. Proceedings XIVth AETFAT congress, 22-27 August 1994, Wageningen, The Netherlands.
- Leistner, O.A. (ed) (2000) Seed plants of southern Africa: families and genera. *Strelitzia* **10**. Pretoria: National Botanical Institute.
- Leistner, O.A. & Werger, M. J. A. (1973) Southern Kalahari phytosociology. *Vegetatio* **28**, 353-399.
- Levine, J.M. & Murrell, D. (2003) Community-level consequences of seed dispersal patterns. *Annual Reviews of Ecology and Systematics* **34**, 549-574.
- Levine, J.M. & Rees, M. (2004) Effects of temporal variability on rare plant persistence in annual systems. *American Naturalist* **164**, 350-363.

- Liversidge, R. (2001) A unique habitat threatened. *African Wildlife* **55**, 24-25.
- Lloret, F., Casanovas, C. & Peñuelas, J. (1999) Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Functional Ecology* **13**, 210-216.
- López-Pintor, A., Espigares, T. & Rey Benayas, J.M. (2003) Spatial segregation of plant species caused by *Retama sphaerocarpa* influence in a Mediterranean pasture: a perspective from the soil seed bank. *Plant Ecology* **167**, 107-116.
- Maclean, G.G. (1970) An analysis of the avifauna of the southern Kalahari Gemsbok National Park. *Zoologica Africana* **5**, 249-273.
- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Croom Helm, London.
- Maze, K. M., Koen, T. B. & Watt, L. A. (1993) Factors influencing the germination of six perennial grasses of central New South Wales. *Australian Journal of Botany* **41**, 79-90.
- McCune, B., Mefford, M.J. (1999) *PcOrd. Multivariate analysis of ecological data. User's Guide*.
- McDonnell, M.J., Stiles, E.W. (1983) The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* **56**, 109-116.
- Meyer, J. (2004) *The impact of habitat structures on some small rodents in the Kalahari Thornveld (South Africa)*. Ph.D. thesis Philipps-Universität Marburg, Marburg.
- Meyer, S.E., Kitchen, S. G. & Carlson, S. L. (1995) Seed germination timing patterns in intermountain *Penstemon* (Scrophulariaceae). *American Journal of Botany* **82**, 377-389.
- Meyer, S.E., Allen, P.S. & Beckstead, J. (1997). Seed germination in *Bromus tectorum* and its ecological significance. *Oikos* **78**, 475-485.
- Milberg, P., Andersson, L. & Thompson, K. (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99-104.
- Milton, S.J. & Dean, W.R.J. (1995) How useful is the keystone species concept, and can it be applied to *Acacia erioloba* in the Kalahari Desert? *Zeitschrift für Ökologie und Naturschutz* **4**, 147-156.
- Moles, A.T., Hodson, D.W. & Webb, C.J. (2000) Seed size and shape and persistence in the soil in the New Zealand flora. *Oikos* **89**, 541-545.
- Moles, A.T., Warton, D.I. & Westoby, M. (2003) Seed size and survival in the soil in arid Australia. *Austral Ecology* **28**, 575-585.
- Money, N.P. (1989) Osmotic pressure of aqueous polyethylene glycols- relationship between molecular weight and vapor pressure deficit. *Plant Physiology* **91**, 766-769.
- Moore, D.R.J. & Keddy, P.A. (1988) Effects of a water-depth gradient on the germination of lakeshore plants. *Canadian Journal of Botany* **66**, 548-552.
- Morgan, J.W. (1998) Comparative germination response of 28 temperate grassland species. *Australian Journal of Botany* **46**, 209-219.
- Niering, W.A., Whittaker R.H. and Lowe C.H. (1963) The saguaro: a population in relation to environment. *Science* **142**, 15-23.
- Nobel, P.S. & Geller, G.N. (1987) Temperature modelling of wet and dry desert soils. *Journal of Ecology* **75**, 247-258.
- Nolasco, H., Vega-Villasante, F. & Díaz-Rondero, A. (1997) Seed germination of *Stenocereus thurberi* (Cactaceae) under different solar irradiation levels. *Journal of Arid Environments* **36**, 123-132.
- O'Connor, T.G. & Picket, 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.
- Parker, V.T. & Muller, C.H. (1982) Vegetational and environmental changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist* **107**, 69-81.

- Pearson, T.R.H., Burslem, D.F.R.P., Mullins, C.E., Dalling, J.W. (2002). Germination ecology of neotropical pioneers: interacting effects of environmental conditions and seed size. *Ecology* **83**, 2798-2807.
- Peart, M.H. (1984) The effects of morphology, orientation and position of grass diaspores on seedling survival. *Journal of Ecology* **72**, 437-453.
- Peco, B., Traba, J., Levassor, C., Sánchez, A.M. & Azcárate, M. (2003) Seed size, shape and persistence in dry Mediterranean grass and scrublands. *Seed Science Research* **13**, 87-95.
- Pons, T.L. (1991) Induction of dark dormancy in seeds: its importance for the seed bank in the soil. *Functional Ecology* **5**, 669-675.
- Pons, T.L. (2000) Seed responses to light. *Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition* (ed M. Fenner), pp. 31-57. CAB International, Wallingford.
- Poschod, P., Tackenberg, O. & Bonn, S. (2005) Plant dispersal potential and its relation to species frequency and coexistence. *Vegetation Ecology* (ed van der Maarel), pp. 147-171. Blackwell, London.
- Price, M.V. & Joyner, J.W. (1997) What resources are available to desert granivores: Seed rain or soil seed bank? *Ecology* **78**, 764-773.
- Pugnaire, F.I., Haase, P. & Puigdefábregas, J. (1996) Facilitation between higher plant species in a semiarid environment. *Ecology* **77**, 1420-1426.
- Pugnaire, F.I. & Lázaro, R. (2000) Seed bank and understory species composition in a semi arid environment: the effect of shrub age and rainfall. *Annals of Botany* **86**, 807-813.
- Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applications in Biosciences* **11**, 247-251.
- Raliselo, M. (2002) Camelthorn (*Acacia erioloba*) firewood industry in Western Cape, South Africa. M.Sc. University of Stellenbosch, Stellenbosch.
- Rees, M. (1993) Trade-offs among dispersal strategies in the British flora. *Nature* **366**, 150-152.
- Rees, M. (1994) Delayed germination of seeds: a look at the effects of adult longevity, the timing of reproduction, and population age/stage structure. *American Naturalist* **144**, 43-64.
- Rees, M. (1995) EC-PC comparative analyses? *Journal of Ecology* **83**, 891.
- Rey, P.J. & Alcantara, J.M. (2000) Recruitment dynamics of fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology* **88**, 622-633.
- Ricklefs, R. (1987) Community diversity: relative roles of local and regional processes *Science* **235**, 167-171.
- Rojas-Aréchiga, M., Orozco-Segovia, A. & Vázquez-Yanes, C. 1997. Effect of light on germination of seven species of cacti from the Zapotitlán Valley in Puebla, México. *Journal of Arid Environments* **36**, 571-578.
- Rojas-Aréchiga, M., Vázquez-Yanes, C. & Orozco-Segovia, A. (1998) Seed response to temperature of Mexican cacti species from two life forms: an ecophysiological interpretation. *Plant Ecology* **135**, 207-214.
- Römermann, C. (2006) Patterns and processes of plant species frequency and life-history traits. *Dissertationes Botanicae* **402**.
- Römermann, C., Tackenberg, O. & Poschod, P. (2005) How to predict attachment potentials of seeds to sheep and cattle coat from simple morphological traits? *Oikos* **110**, 219-230.
- Ross, M.A. & Harper, J.L. (1972) Occupation of biological space during seedling establishment. *Journal of Ecology* **60**, 77-88.

- Rutherford, M.C., Powrie, L.W. & Schulze, R.E. (1999) Climate change in conservation areas of South Africa and its potential impact on floristic composition: a first assessment. *Diversity and Distributions* **5**, 253-262.
- Rydin, H. & Borgegård, S.-O. (1991) Plant characteristics over a century of primary succession on islands: Lake Hjälmaren. *Ecology* **72**, 1089-1101.
- Salisbury, E.J. (1942) *The reproductive capacity of plants*. Bell, London.
- Sankaran M., Hanan N.P., Scholes, R.J., Jayashree, R., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature* **438**, 846-849.
- Scheffer, F. (1998) *Lehrbuch der Bodenkunde*. Enke, Stuttgart.
- Schupp, E.W., Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* **2**, 267-275.
- Schütz, W. (1999) Germination responses of temperate *Carex*-species to diurnally fluctuating temperatures - a comparative study. *Flora* **194**, 21-32.
- Schütz, W. (2000) The importance of seed regeneration strategies for the persistence of species in the changing landscape of Central Europe. *Zeitschrift für Ökologie und Naturschutz* **9**, 73-84.
- Schütz, W., Milberg, P. & Lamont B.B. (2002) Germination requirements and seedling responses to water availability and soil type in four eucalypt species. *Acta Oecologica* **23**, 23-30.
- Schütz, W. & Rave, G. (1999) The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. *Plant Ecology* **144**, 215-230.
- Seabloom, E.W., van der Valk, A.G. & Moloney, K.A. (1998) The role of water depth and soil temperature in determining initial composition of prairie wetland coenoclines. *Plant Ecology* **138**, 203-216.
- Sekercioglu, C.H. (2006) Increasing awareness of avian ecological function. *Trends in Ecology and Evolution* **21**, 464-471.
- Seymour, C. L. (2006) *The influence of size and density of the Camelthorn (Acacia erioloba) on its keystone role in the Xeric Kalahari*. PhD thesis, University of Cape Town, Cape Town.
- Shipley, B. & Dion, J. (1992) The allometry of seed production in herbaceous angiosperms. *American Naturalist* **139**, 467-483.
- Shipley, B. & Parent, M. (1991) Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. *Functional Ecology* **5**, 111-118.
- Shreve, F. (1931). Physical condition in sun and shade. *Ecology* **12**, 96-104.
- Shreve, F. (1951) Vegetation of the Sonoran Desert. Carnegie Institution Publication Number 591, Washington DC.
- Silvertown, J.W. & Dodd M. (1997) Comparing plants and connecting traits. *Plant Life Histories: ecology, phylogeny and evolution*. (eds J. Silvertown, M. Franco & J.L. Harper), pp. 3-16. Cambridge University Press, Cambridge.
- Silvertown J.W., Wilson J.B. (1994) Community structure in a desert perennial community. *Ecology* **75**, 409-417.
- Silvertown, J.W., Charlesworth, D. (2001) *Introduction to plant population biology – fourth edition*. Blackwell Science, London.
- Smit, N. (1999) *Guide to the Acacias of South Africa*. Briza Publications, Pretoria.

- Sosa, V.J. & Fleming, T.H. (2002) Why are columnar cacti associated with nurse plants? *Columnar cacti and their mutualists: evolution, ecology, and conservation*. (eds T.H. Fleming & A. Valiente-Banuet), pp. 306-323. The University of Arizona Press, Tucson.
- Steenberg, W.F., Lowe, C.H. (1969) Critical factors during the first years of life of the saguaro (*Cereus giganteus*) at Saguaro National Monument. *Ecology* **50**, 825-834.
- Steenkamp, C.J. (2000) Age determination of *Acacia erioloba* in the Kalahari Gemsbok National Park. M. Sc. University of Pretoria, Pretoria.
- Sy, A., Grouzis, M. & Danthu, P. (2001) Short communication : seed germination of seven Sahelian legume species. *Journal of Arid Environments* **49**, 875-882.
- Tackenberg, O. (2001) Methoden zur Bewertung gradueller Unterschiede des Ausbreitungspotentials von Pflanzenarten. – Modellierung des Windausbreitungspotentials und regelbasierte Ableitung des Fernausbreitungspotentials. *Dissertationes Botanicae* **347**.
- Taylor, D.R., Aarssen, L.W., Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* **58**, 239–250.
- ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M. & Bakker, J.P. (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. *Functional Ecology* **10**, 144-151.
- Tester, M., Paton, D., Reid, N. & Lange, R.T. (1987) Seed dispersal by birds and densities of shrubs under trees in arid south Australia. *Transactions of the Royal Society of South Australia* **111**, 1-5.
- Tewksbury, J.J. & Lloyd, J.D. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* **127**, 425-434.
- Tewksbury, J.J., Nabhan, G.P., Norman, D., Suzán, H., Tuxill, J. & Donovan, J. (1999) In situ conservation of wild chiles and their biotic associates. *Conservation Biology* **13**, 98-107.
- Thomas, D.S.G., Knight, M. & Wiggs, G.F.S. (2005) Remobilization of southern African desert dune by twenty-first century global warming. *Nature* **435**, 1218-1221.
- Thomas, D.S.G. & Shaw, P.A. (1991) *The Kalahari environment*. Cambridge University Press, Cambridge.
- Thompson, K. (1987) Seeds and seed banks. *New Phytologist* **106** (Supplement), 23-34.
- Thompson, K. (2000) The functional ecology of soil seed banks. *Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition* (ed M. Fenner), pp. 31-57. CAB International, Wallingford.
- Thompson, K., Bakker, J.P. & Bekker, R.M. (1997) *The soil seed banks of North West Europe: methodology, density and longevity*. Cambridge University Press, Cambridge.
- Thompson, K., Bakker, J.P., Bekker, R.M. & Hodgson, J.G. (1998) Ecological correlates of seed persistence in soil in the north-west European flora. *Journal of Ecology* **86**, 163-169.
- Thompson, K., Band, S.R. & Hodgson, J.G. (1993) Seed size and shape predict persistence in the soil. *Functional Ecology* **7**, 236-241.
- Thompson, K. & Grime, J.P. (1983) A comparative study of germination responses to diurnally-fluctuating temperatures. *Journal of Applied Ecology* **20**, 141-156.
- Thompson, K., Jalili, A., Hodgson, J.G., Hamzeh'ee, B., Asri, Y., Shaw, S., Shirvany, A., Yazdani, S., Khoshnevis, M., Zarrinkamar, F., Ghahramani, M.A. & Safavi, R. (2001) Seed size, shape and persistence in the soil in an Iranian flora. *Seed Science Research* **11**, 345-355.
- Tiedemann, A. & Klemmedson, J.O. (1977) Effect of mesquite trees on vegetation and soils in the desert grassland. *Journal of Range Management* **30**, 361-367.

- Tielbörger, K. & Kadmon, R. (1997) Relationships between shrubs and annual communities in a sandy desert ecosystem: a three-year study. *Plant Ecology* **130**, 191-201.
- Tielbörger, K. & Kadmon, R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* **81**, 1544-1553.
- Traba, J., Azcárate, F.M. & Peco, B. (2006) The fate of seeds in Mediterranean soil seed banks in relation to their traits. *Journal of Vegetation Science* **17**, 5-10.
- Turnbull, L.A., Rees, M. & Crawley, M.J. (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. *Journal of Ecology* **87**, 899-912.
- Tweddle, J.C., Dickie, J.B., Baskin, C.C. & Baskin, J.M. (2003) Ecological aspects of seed desiccation sensitivity. *Journal of Ecology* **91**, 294-304.
- Valiente-Banuet, A., Bolongaro-Crevenna, A., Briones, O., Ezcurra, E., Rosas, M., Núñez, H., Barnard, G. & Vázquez, E. (1991) Spatial relationships between cacti and nurse shrubs in a semi-arid environment in central Mexico. *Journal of Vegetation Science* **2**, 15-20.
- Valiente-Banuet, A. & Ezcurra, E. (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse-plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology* **79**, 961-971.
- van Rooyen, M.W. & Grobbelaar, N. (1982) Saadbevolkings in die grond van die Hester Malan-natuurreservaat in die Namakwalandse Gebroke Veld. *South African Journal of Botany* **1**, 41-50.
- van Rooyen, N. & Bezuidenhout, H. (1997) New records of flowering plants and ferns from the Kalahari Gemsbok National Park. *Koedoe* **40**, 105-116.
- van Rooyen, N. & Bredenkamp, G. (1996a) Kalahari Plains Thorn Bushveld. *Vegetation of South Africa, Lesotho and Swaziland*. (eds A.B. Low & A.G. Robelo). Department of Environmental Affairs and Tourism, Pretoria.
- van Rooyen, N. & Bredenkamp, G. (1996b) Shrubby Kalahari Dune Bushveld. *Vegetation of South Africa, Lesotho and Swaziland*. (eds A.B. Low & A.G. Robelo). Department of Environmental Affairs and Tourism, Pretoria.
- van Rooyen, N., Theron, G.K. and Bredenkamp, G.J. (1994) Population trends of woody species in the Kalahari Gemsbok National Park from 1978 to 1994. *Arid Zone Ecology Forum (AZEF)*. National Research Foundation, Karoo National Park, Beaufort West.
- van Rooyen, T.H. (1984) The soils of the Kalahari Gemsbok National Park. *Koedoe* **27** (Supplement), 45-61.
- Vázquez-Yanes, C., Orozco-Segovia, A. (1982) Seed germination of a tropical rain forest tree *Heliocarpus donnell-smithii* in response to diurnal fluctuations in temperature. *Physiologia Plantarum* **56**, 295-298.
- Veenendaal, E.M. & Ernst, W.H.O. (1991) Dormancy patterns in accessions of caryopses from savanna grass species in south eastern Botswana. *Acta Botanica Neerlandica* **40**, 297-309.
- Venable, D.L. & Brown, J.S. (1988) The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *American Naturalist* **131**, 360-384.
- Vetaas, O.R. (1992) Micro-site effects of trees and shrubs in dry savannas. *Journal of Vegetation Science* **3**, 337-344.
- Weiersbye, I.M. & Witkowski, E.T.F. (2003) Seed fate and practical germination methods for 46 perennial species that colonise gold mine tailings and acid mine drainage-polluted soils in the grassland biome. *South African Journal of Botany* **69**, 266-267.
- Weiherr, E. & Keddy, P.A. (1995) The assembly of experimental wetland plant communities. *Oikos* **73**, 323-335.
- Weltzin, J.F. & Coughenour, M.B. (1990) Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *Journal of Vegetation Science* **1**, 325-334.

- Wenny, D.G. & Levey D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest *Proceedings of the National Academy of Sciences of the USA* **95**, 6204–6207.
- Wenny, D.G. (2001) Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research* **3**, 51-74.
- Went, F.W. (1942) The dependence of certain annual plants on shrubs in southern California deserts. *Bulletin of the Torrey Botanical Club* **69**, 100-114.
- Werger, M.J.A. (1986) *The Karoo and Southern Kalahari. Hot deserts and arid shrublands, Ecosystems of the world, vol 12 B.* (eds M. Evenari, I. Noy-meir & D.W. Goodall), pp. 283-359. Elsevier Science Publishers, Amsterdam.
- Westelaken, I.L. & Maun, M.A. (1985) Spatial pattern and seed dispersal of *Lithospermum carolinense* on Lake Huron sand dunes. *Canadian Journal of Botany* **63**,125-132.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213-227.
- Westoby, M., Leishman, M. & Lord, J. (1995a) On misinterpreting the 'phylogenetic correction'. *Journal of Ecology* **83**, 531-534.
- Westoby, M., Leishman, M. & Lord, J. (1995b) Further remarks on phylogenetic correction. *Journal of Ecology* **83**, 727-729.
- Westoby, M., Leishman, M. & Lord, J. (1996) Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London B Biological Sciences* **351**, 1309-1318.
- Willems, J.H. & Huijsmans, K.G.A. (1994) Vertical seed dispersal by earthworms: a quantitative approach. *Ecography* **12**, 124–130.
- Witkowski, E.T.F. & Garner, R.D. (2000) Spatial distribution of soil seed banks of three African savanna woody species at contrasting sites. *Plant Ecology* **149**, 91-106.
- Yarranton, G.A. Morrison R.G. (1974) Spatial Dynamics of a Primary Succession: Nucleation. *Journal of Ecology* **62**, 417-428.
- Zar, J.H. (1999) *Biostatistical analysis, 4th edition*. Prentice Hall, Upper Saddle River.
- Zimmerman, J. (2001) Vegetation patterns in the southern Kalahari affected by *Acacia erioloba* and land use. Diploma thesis, Philipps Universität Marburg, Marburg.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution* **12**, 266-269.

Acknowledgements

First of all I would like to thank Prof. Dr. Peter Poschlod who provided the concept for this study which proved to be a fertile basis for new scientific results, for his motivating enthusiasm and for giving me the freedom to pursue my own ideas.

This study was carried out within the BIOTA Southern Africa project which is funded by the German Federal Ministry of Education and Research (BMBF Förderkennzeichen 01 LC 0024 FuE “Trockensavanne”).

Dr. Steven Higgins is kindly thanked for accepting to be referee for this thesis.

A special big ‘baie dankie’ goes to Bess de Koker for company and friendship under the sometimes difficult conditions of Kalahari Farm life, and to the whole De Koker family in Witdraai for being a second family to me where I was always welcome during the field work periods which made the harsh reality of life in the Kalahari and field work in particular more endurable.

Thank you Jula Zimmermann and John Hoffmann for company and helping me to get around without a driving license during the first field work period. Thank you Niels Blaum for sharing the hardships of Kalahari field work, beers after hot field work and the first Kalahari driving lessons.

Thanks to Prof. Dr. Anne O. E. Rasa who allowed me to live on her farm for the first two years of the field work and to Naas and Alida Mouton for providing a home on their farm Rooiwal in the last year of fieldwork.

The Northern Cape Nature Conservation provided permits to collect and export seeds. The Department of Roads and Public Transport gave permission to work and collect seeds in the road reserve. Naas and Alida Mouton, Prof. Dr. A. O. E. Rasa and Lena and Henry Snyders kindly allowed us to collect seeds on their farms.

The following students assisted with germination experiments, identifying and counting seeds from seed traps and measuring seeds: Manuela Anders, Birgit Blaul, Kristina Fischer, Florian Gmeiner, Jutta Heinrich, Zsuzsa Jenei-Lanzl, Laura Klingseisen, Wolfgang Müller, Lydia Pitzschler, Maximilian Plank, Nicholas Putsch, Christine Richter, Sabine Schmidl, Christine Schneider and Wang Yunxiao.

Thanks to Kirsten Mitlacher who advised on seed bank methods and helped with the seed bank work. Mr. A. Keck is thanked for assistance in the greenhouse.

Steve Higgins, Arne Mooers and Christine Römermann are thanked for reading and providing useful comments on the manuscripts of some chapters.

Many thanks to my present and past colleagues from the chair for Botany at the University of Regensburg for help with computer questions, being pleasant office companions, sharing coffees, scientific discussion and friendship.

Thanks to Carol Baskin and Jerry Baskin for patiently answering questions and discussing about my germination studies and encouraging me in my research on different meetings.

Special thanks to my parents and to my sister for always supporting me. A special thanks to my parents for encouraging from an early age my interests in everything living.

Thank you Mieke, for always believing in me and supporting me even through the most difficult times.



Mieke Gorgels, *Baum in der Sonne*

Appendix 1. Species cover values for 2003 in matrix and canopy microhabitats. Given are mean, s.d. ($n = 10$) and number of plots where species was found. In the last column habitat association calculated on the basis of cover is given (habitat association = (cover canopy – cover matrix) / (cover canopy + cover matrix). See text for details.

	Matrix			Canopy			Habitat association
	mean	s.d.	number of plots	mean	s.d.	number of plots	
<i>Acacia erioloba</i>	0.040	0.118	3	0.151	0.302	7	0.583
<i>Acacia haematoxylon</i>	0.150	0.474	1	0.000	0.000	0	-1.000
<i>Acacia hebeclada</i>	0.000	0.000	0	0.025	0.079	1	1.000
<i>Acrotome inflata</i>	0.000	0.000	0	0.006	0.011	3	1.000
<i>Amaranthus dinteri</i>	0.000	0.000	0	0.001	0.002	2	1.000
<i>Amaranthus praetermissus</i>	0.000	0.000	1	0.462	0.965	10	1.000
<i>Aptosimum lineare</i>	0.001	0.002	1	0.000	0.000	1	-0.905
<i>Aptosimum marlothii</i>	5.171	4.567	10	0.463	0.582	10	-0.836
<i>Aptosimum spinescens</i>	0.002	0.005	1	0.020	0.062	1	0.859
<i>Aristida congesta</i>	0.001	0.003	1	0.000	0.000	0	-1.000
<i>Asparagus africanus</i>	0.000	0.000	0	0.161	0.334	6	1.000
<i>Asparagus pearsonii</i>	0.003	0.008	1	0.219	0.354	6	0.977
<i>Asparagus spec.1</i>	0.000	0.000	0	0.020	0.062	1	1.000
<i>Barleria rigida</i>	0.000	0.001	1	0.000	0.000	0	-1.000
<i>Boerhavia coccinea</i>	0.000	0.000	0	0.001	0.003	1	1.000
<i>Boerhavia repens</i>	0.003	0.005	2	0.086	0.237	5	0.943
<i>Boscia albitrunca</i>	0.000	0.000	0	0.258	0.440	3	1.000
<i>Chenopodium opulifolium</i>	0.000	0.000	0	0.071	0.090	8	1.000
<i>Chloris virgata</i>	0.162	0.483	3	0.002	0.005	1	-0.982
<i>Cleome gynandra</i>	0.000	0.000	0	0.002	0.004	2	1.000
<i>Corallocarpus bainesii</i>	0.000	0.000	0	0.001	0.002	2	1.000
<i>Cucumis africanus</i>	0.000	0.000	0	0.001	0.002	2	1.000
<i>Cullen obtusifolius</i>	0.002	0.005	1	0.000	0.000	0	-1.000
<i>Cynanchum orangeanum</i>	0.000	0.000	1	0.000	0.001	2	0.833
<i>Deverra denudata</i>	0.025	0.079	1	0.001	0.003	1	-0.923
<i>Dicoma capensis</i>	0.027	0.064	8	0.004	0.006	3	-0.757
<i>Ehretia rigida</i>	0.000	0.000	0	0.291	0.786	3	1.000
<i>Enneapogon cenchroides</i>	0.039	0.085	5	0.004	0.009	4	-0.822
<i>Enneapogon desvauxii</i>	0.017	0.025	5	0.000	0.000	1	-0.996
<i>Eragrostis annulata</i>	0.019	0.039	4	0.000	0.000	0	-1.000
<i>Eragrostis porosa</i>	0.001	0.002	1	0.000	0.000	0	-1.000
<i>Felicia clavipilosa</i>	0.172	0.174	10	0.384	0.834	10	0.382
<i>Geigeria ornativa</i>	0.002	0.003	3	0.000	0.000	0	-1.000
<i>Geigeria pectidea</i>	0.049	0.097	4	0.002	0.005	2	-0.931
<i>Geigeria spec.1</i>	0.000	0.000	1	0.000	0.000	0	-1.000
<i>Grewia flava</i>	0.000	0.000	0	0.013	0.041	2	1.000
<i>hairy trilobed Fabaceae</i>	0.000	0.001	1	0.000	0.000	1	-0.818
<i>Heliotropium lineare</i>	0.007	0.012	5	0.079	0.100	5	0.843
<i>Hermannia bicolor</i>	0.001	0.001	2	0.000	0.001	1	-0.333
<i>Hermannia tomentosa</i>	0.000	0.000	0	0.002	0.006	1	1.000
<i>Indigofera alternans</i>	0.019	0.038	6	0.001	0.001	3	-0.942
<i>Indigofera spec.1</i>	0.007	0.017	3	0.000	0.000	0	-1.000
<i>Lebeckia linearifolia</i>	0.000	0.000	0	0.003	0.008	1	1.000
<i>Lessertia physoides</i>	0.000	0.000	0	0.005	0.014	2	1.000
<i>Limeum aethiopicum</i>	0.534	0.827	7	1.849	4.105	8	0.552
<i>Limeum argute-carinatum</i>	0.001	0.002	3	0.001	0.002	3	-0.032

Appendix 1 continued

	Matrix			Canopy			Habitat association
	mean	s.d.	number of plots	mean	s.d.	number of plots	
<i>Limeum spec.1</i>	0.000	0.000	0	0.000	0.000	1	1.000
<i>Lotononis densa</i>	0.078	0.155	4	0.000	0.000	0	-1.000
<i>Lycium bosciifolium</i>	1.219	2.347	3	6.420	2.364	10	0.681
<i>Lycium hirsutum</i>	0.000	0.000	0	0.130	0.257	5	1.000
<i>Lycium spec.1</i>	0.000	0.000	0	0.035	0.082	2	1.000
<i>Lycium spec.2</i>	0.000	0.000	0	0.025	0.079	1	1.000
<i>Monechma genistifolium</i>	0.000	0.000	0	0.040	0.083	3	1.000
<i>Monechma incanum</i>	0.000	0.000	0	0.126	0.396	2	1.000
<i>Peliostomum leucorrhizum</i>	0.053	0.076	9	0.014	0.026	6	-0.575
<i>Pentzia lanata</i>	0.037	0.065	6	0.049	0.085	6	0.136
<i>Phaeoptilum spinosum</i>	1.850	1.789	9	0.356	0.342	9	-0.677
<i>Plinthus karooicus</i>	0.484	0.339	10	0.085	0.082	9	-0.701
<i>Pollichia campestris</i>	0.000	0.000	0	0.179	0.176	8	1.000
<i>Polygala leptophylla</i>	0.006	0.015	3	0.004	0.008	2	-0.222
<i>Portulaca oleracea</i>	0.000	0.000	0	0.002	0.003	4	1.000
<i>Rhigozum trichotomum</i>	0.641	1.262	5	0.207	0.548	6	-0.512
<i>Salsola etoshensis</i>	0.613	1.893	2	0.256	0.808	1	-0.411
<i>Salsola kali</i>	0.000	0.000	0	0.000	0.001	1	1.000
<i>Schmidtia kalahariensis</i>	0.005	0.008	5	0.000	0.001	1	-0.905
<i>Senna italica</i>	0.001	0.002	1	0.000	0.000	0	-1.000
<i>Sericorema</i>	0.000	0.000	0	0.019	0.059	1	1.000
<i>Sesamum triphyllum</i>	0.000	0.000	0	0.000	0.001	1	1.000
<i>Setaria verticillata</i>	0.002	0.005	2	1.307	1.408	9	0.997
<i>Solanum capense</i>	0.005	0.012	2	0.175	0.148	10	0.942
<i>Stipagrostis ciliata</i>	0.011	0.021	3	0.000	0.000	0	-1.000
<i>Stipagrostis obtusa</i>	0.036	0.045	7	0.117	0.344	5	0.529
<i>Stipagrostis uniplumis</i>	0.024	0.038	5	0.004	0.005	4	-0.730
<i>Trianthema parvifolia</i>	0.306	0.588	10	0.142	0.223	9	-0.367
<i>Tribulus terrestris</i>	0.548	1.073	9	0.033	0.035	9	-0.885
<i>Urochloa spec.1</i>	0.000	0.001	1	0.000	0.000	0	-1.000

Appendix 2. Species found in the seed bank in 2002 and 2003 under canopies and in the surrounding matrix, for 2003 samples were taken at two different depths (0-3 cm and 3-6 cm) given are mean \pm s.d. and the number of plots where the species was found in the seed bank between brackets ($n = 20$ per habitat and per depth).

	Canopy 0-3cm 2002	Matrix 0-3cm 2002	Canopy 0-3cm 2003	Matrix 0-3cm 2003	Canopy 3-6cm 2003	Matrix 3-6cm 2003
<i>Amaranthus praetermissus</i>	107 \pm 135 (11)	52 \pm 183 (2)	179 \pm 195 (14)	111 \pm 338 (6)	52 \pm 83 (8)	48 \pm 114 (4)
<i>Amaranthus dinteri</i>	20 \pm 72 (2)	0 \pm 0 (0)	12 \pm 29 (3)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Amellus strigosus</i>	12 \pm 39 (2)	0 \pm 0 (0)	151 \pm 421 (9)	12 \pm 39 (2)	40 \pm 128 (3)	0 \pm 0 (0)
<i>Aptosimum lineare</i>	0 \pm 0 (0)	0 \pm 0 (0)	16 \pm 42 (3)	95 \pm 243 (5)	20 \pm 44 (4)	8 \pm 24 (2)
<i>Aptosimum marlothii</i>	0 \pm 0 (0)	0 \pm 0 (0)	16 \pm 55 (2)	8 \pm 36 (1)	4 \pm 18 (1)	0 \pm 0 (0)
<i>Boerhavia repens</i>	24 \pm 45 (5)	0 \pm 0 (0)	12 \pm 39 (2)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Chamaesyce inaequilatera</i>	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)
<i>Chenopodium opulifolium</i>	151 \pm 241 (10)	4 \pm 18 (1)	111 \pm 187 (10)	0 \pm 0 (0)	72 \pm 159 (6)	0 \pm 0 (0)
<i>Chenopodium cf. schraderianum</i>	4 \pm 18 (1)	12 \pm 39 (2)	103 \pm 407 (4)	0 \pm 0 (0)	12 \pm 39 (2)	0 \pm 0 (0)
<i>Chenopodium murale</i>	0 \pm 0 (0)	0 \pm 0 (0)	72 \pm 320 (1)	40 \pm 178 (1)	76 \pm 338 (1)	0 \pm 0 (0)
<i>Chloris virgata</i>	103 \pm 218 (9)	537 \pm 105 (12)	84 \pm 187 (7)	203 \pm 373 (8)	8 \pm 24 (2)	24 \pm 78 (2)
<i>Coronopus integrifolius</i>	1027 \pm 1964 (13)	64 \pm 248 (3)	1317 \pm 3360 (11)	0 \pm 0 (0)	848 \pm 1881 (11)	0 \pm 0 (0)
<i>Dicoma capensis</i>	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Emneapogon spec.</i>	0 \pm 0 (0)	326 \pm 1459 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Emneapogon desvauxii</i>	0 \pm 0 (0)	44 \pm 178 (2)	4 \pm 18 (1)	8 \pm 24 (2)	0 \pm 0 (0)	4 \pm 18 (1)
<i>Emneapogon cenchroides</i>	4 \pm 18 (1)	12 \pm 53 (1)	24 \pm 58 (4)	28 \pm 94 (2)	0 \pm 0 (0)	16 \pm 71 (1)
<i>Eragrostis brizantha</i>	0 \pm 0 (0)	4 \pm 18 (1)	8 \pm 36 (1)	645 \pm 2883 (1)	8 \pm 24 (2)	263 \pm 1156 (2)
<i>Eragrostis porosa</i>	24 \pm 45 (5)	40 \pm 71 (6)	92 \pm 241 (6)	20 \pm 44 (4)	60 \pm 106 (7)	32 \pm 48 (7)
<i>Felicia clavipilosa</i>	227 \pm 613 (13)	84 \pm 319 (4)	195 \pm 345 (12)	52 \pm 104 (6)	24 \pm 37 (6)	20 \pm 72 (2)
cf. <i>Filago</i>	12 \pm 29 (3)	20 \pm 44 (4)	36 \pm 125 (3)	32 \pm 65 (5)	68 \pm 166 (6)	8 \pm 24 (2)
cf. <i>Filago wooly</i>	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	16 \pm 71 (1)	4 \pm 18 (1)	0 \pm 0 (0)
<i>Geigeria ornativa</i>	0 \pm 0 (0)	0 \pm 0 (0)	8 \pm 24 (2)	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)
<i>Geigeria pectidea</i>	36 \pm 125 (3)	0 \pm 0 (0)	28 \pm 47 (6)	0 \pm 0 (0)	0 \pm 0 (0)	8 \pm 36 (1)
<i>Helichrysum argyrosphaerum</i>	32 \pm 54 (6)	24 \pm 52 (4)	219 \pm 245 (15)	64 \pm 80 (9)	131 \pm 162 (13)	4 \pm 18 (1)
<i>Hermannia tomentosa</i>	8 \pm 24 (2)	0 \pm 0 (0)	16 \pm 42 (3)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Indigofera alternans</i>	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Galenia africana</i>	0 \pm 0 (0)	12 \pm 53 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Lycium bosciifolium</i>	20 \pm 72 (2)	0 \pm 0 (0)	32 \pm 75 (5)	4 \pm 18 (1)	8 \pm 24 (2)	0 \pm 0 (0)
<i>Malva pusilla</i>	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	4 \pm 18 (1)
<i>Argemone ochroleuca</i>	4 \pm 18 (1)	0 \pm 0 (0)	16 \pm 33 (4)	0 \pm 0 (0)	68 \pm 195 (6)	12 \pm 39 (2)
<i>Osteospermum muricatum</i>	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Pentzia lanata</i>	8 \pm 36 (1)	4 \pm 18 (1)	16 \pm 33 (4)	8 \pm 36 (1)	4 \pm 18 (1)	0 \pm 0 (0)
<i>Peliostomum leucorrhizum</i>	0 \pm 0 (0)	0 \pm 0 (0)	40 \pm 66 (7)	32 \pm 48 (7)	28 \pm 53 (5)	32 \pm 54 (6)
<i>Plinthus karoocicus</i>	4 \pm 18 (1)	0 \pm 0 (0)	16 \pm 42 (3)	8 \pm 24 (2)	4 \pm 18 (1)	12 \pm 39 (2)
<i>Pollichia campestris</i>	8 \pm 36 (1)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Portulaca oleracea</i>	8 \pm 24 (2)	8 \pm 36 (1)	24 \pm 73 (3)	8 \pm 24 (2)	20 \pm 44 (4)	8 \pm 24 (2)
<i>Schmidtia kalahariensis</i>	0 \pm 0 (0)	0 \pm 0 (0)	12 \pm 29 (3)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Setaria verticillata</i>	629 \pm 595 (19)	40 \pm 145 (2)	1035 \pm 1188 (20)	32 \pm 75 (5)	446 \pm 520 (19)	12 \pm 39 (2)
<i>Solanum capense</i>	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Stachys spathulata</i>	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	4 \pm 18 (1)	4 \pm 18 (1)
<i>Tragus spec.</i>	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	8 \pm 36 (1)	0 \pm 0 (0)	12 \pm 39 (2)
<i>Trianthema parvifolia</i>	0 \pm 0 (0)	0 \pm 0 (0)	32 \pm 75 (5)	60 \pm 106 (7)	12 \pm 29 (3)	24 \pm 45 (5)
<i>Tribulus terrestris</i>	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Urachloa spec.</i>	8 \pm 36 (1)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
yellow composite fine leave hairy	24 \pm 107 (1)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)
<i>Crotalaria spec.</i>	0 \pm 0 (0)	0 \pm 0 (0)	0 \pm 0 (0)	4 \pm 18 (1)	0 \pm 0 (0)	4 \pm 18 (1)
Unknown dicots	8 \pm 24 (2)	20 \pm 57 (3)	12 \pm 39 (2)	4 \pm 18 (1)	8 \pm 24 (2)	4 \pm 18 (1)
Unknown monocots	8 \pm 24 (2)	8 \pm 24 (2)	40 \pm 111 (3)	4 \pm 18 (1)	68 \pm 174 (4)	-

Appendix 3. List of species used for correlating seed persistence with seed morphology. Given are seed mass (mg) shape (Vs, variance in seed dimensions) and seed bank classification using presence absence in the vegetation and depth distribution (lp = long-term persistent, sp = short-term persistent, t = transient). Seed bank type is given for canopy and matrix soil and the most persistent seed bank type of the two microhabitats is also given. The last column indicates species where classification differed between microhabitats (×). See text for details.

Species	Mass (mg)	Shape	Most persistent	Persistence canopy	Persistence matrix	Conflicting
<i>Acacia erioloba</i>	294.630	0.054	t	t	t	
<i>Acrotome inflata</i>	1.688	0.090	t	t	-	
<i>Amaranthus praetermissus</i>	0.380	0.019	sp	t	sp	
<i>Aptosimum lineare</i>	0.103	0.065	lp	lp	sp	×
<i>Aptosimum marlothii</i>	0.234	0.053	sp	sp	t	×
<i>Argemone ochroleuca</i>	2.022	0.005	lp	lp	-	
<i>Asparagus africanus</i>	14.968	0.002	t	t	-	
<i>Asparagus pearsonii</i>	13.703	0.018	t	t	-	
<i>Boscia albitrunca</i>	62.427	0.020	t	t	-	
<i>Chenopodium cf. schraderianum</i>	0.085	0.027	sp	sp	-	
<i>Chenopodium murale</i>	0.662	0.035	lp	lp	t	×
<i>Chenopodium opulifolium</i>	0.413	0.038	sp	sp	-	
<i>Chloris virgata</i>	0.380	0.178	sp	sp	sp	
<i>Coronopus integrifolius</i>	0.324	0.003	sp	sp	-	
<i>Dicoma capensis</i>	1.356	0.083	t	t	-	
<i>Ehretia rigida</i>	5.453	0.046	t	t	-	
<i>Enneapogon cenchroides</i>	0.364	0.107	sp	t	sp	×
<i>Enneapogon desvauxii</i>	0.320	0.087	sp	-	sp	
<i>Eragrostis annulata</i>	0.071	0.030	t	-	t	
<i>Eragrostis brizantha</i>	0.138	0.047	sp	-	sp	
<i>Eragrostis porosa</i>	0.065	0.030	lp	sp	lp	×
<i>Felicia clavipilosa</i>	0.102	0.131	sp	sp	sp	
<i>Geigeria pectidea</i>	0.484	0.112	lp	t	lp	×
<i>Heliotropium lineare</i>	1.607	0.024	t	t	t	
<i>Indigofera alternans</i>	0.791	0.013	t	t	t	
<i>Limeum aethiopicum</i>	1.471	0.026	t	t	t	
<i>Lotononis densa</i>	3.505	0.022	t	-	t	
<i>Lycium bosciifolium</i>	1.292	0.062	sp	sp	-	
<i>Monechma genistifolium</i>	2.445	0.067	t	t	-	
<i>Peliostomum leucorrhizum</i>	0.071	0.029	lp	sp	lp	×
<i>Pentzia lanata</i>	0.144	0.125	sp	sp	sp	
<i>Phaeoptilum spinosum</i>	45.080	0.010	t	t	t	
<i>Plinthus karoocicus</i>	0.139	0.030	lp	sp	lp	×
<i>Pollichia campestris</i>	0.361	0.056	t	t	-	
<i>Polygala aphylla</i>	1.508	0.127	t	-	t	
<i>Portulaca oleracea</i>	0.157	0.043	sp	sp	-	
<i>Rhigozum trichotomum</i>	17.087	0.151	t	t	t	
<i>Schmidtia kalihariensis</i>	0.615	0.029	t	-	t	
<i>Setaria verticillata</i>	0.423	0.054	sp	sp	sp	
<i>Solanum capense</i>	3.299	0.106	t	t	-	
<i>Stipagrostis ciliata</i>	2.496	0.165	t	-	t	
<i>Stipagrostis obtusa</i>	0.386	0.143	t	t	t	
<i>Stipagrostis uniplumis</i>	0.520	0.140	t	t	t	
<i>Trianthema parvifolia</i>	0.134	0.044	sp	sp	sp	

Appendix 4. Phylogeny used to calculate PICs in Chapter 4, 5, 6 and 7. Sources used to build super tree: the Angiosperm phylogeny of Davies *et al.* (2004) was used as a Backbone; Grass Phylogeny Working Group (2001) Hilu & Alice (2001) for Poaceae, Funk *et al.* (2005) for Asteraceae. Species were assigned to their respective families and sub-families using the classification in Leistner (2000) and Gibbs Russell *et al.* (1991) for grasses.

