Ecological niches occupied by *Dichapetalum cymosum* (Hook.) Engl. (Gifblaar) in South African rangeland communities

by

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Dedicated to my parents, Alpheus and Gladys Pule,
my beloved wife, Tshepo Bridget Pule,
and my sons, Thuso and Thato Pule

ABSTRACT

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Abstract

Poisonous plants are one of the most important causes of economic losses in the livestock industry throughout the world, especially in those areas where rangeland and pasture grazing are practiced. In the livestock industry in South Africa, total annual costs of plant and fungal poisoning (mycotoxicosis) are conservatively estimated to be R104 506 077, 8% of which is due to *D. cymosum* poisoning.

There is no antidote for *D. cymosum* poisoning of livestock and wide scale eradication by conventional control methods are labour intensive, expensive and often impractical. In South Africa, the communal or emerging farming sectors are the most affected. This is mainly due to the high costs associated with control measures such as fencing, supplementary feeding and veterinary expenses, and / or lack of grazing management with livestock numbers exceeding the biological carrying capacity of the rangeland due to lack of grazing lands.

Proper rangeland management is the surest and most economical means of reducing plant poisoning of livestock. Focused research on the ecology of these poisonous plants in rangeland communities to improve rangeland management would assist in the development of these strategies. This study investigated *D. cymosum* infested savanna communities, focusing on understanding how negative (inter- and intraspecific competition) interactions influence community structure, dynamics and productivity and how plants in *D. cymosum* communities avoid these negative interactions by investigating their seasonal phenological patterns.

Dichapetalum cymosum coexists with trees, such as *Burkea africana*, *Ochna pulchra* and *Terminalia serecia*, as well as shrubs species, such as *Pygmaeothamnus zeyheri* and *Perinari capensis*, in well drained, nutrient poor soils. Some plant ecologists contend that in an environment where water is limited, competition is inevitable amongst plants occupying the same above-ground stratum and the same soil horizon. Others contend that plants avoid competition with each other by sharing resources spatially and temporarily.

Field experiments were conducted to investigate how the above species interact and coexist with each other in two South African savanna communities. Fourteen (100 m x 100 m) *D. cymosum* infested sites were identified in each community. Disperal analysis using nearest neighbour distance was used to investigate competition among species, and above ground flowering phenology along niche axes to determine temporal and spatial sharing of resources.

The dispersal analysis revealed aggregated populations among species when intraspecific and combined (all individuals independent of species) analyses were conducted. However, in all instances, aggregation among species was not significant. No interspecific competition was observed among species when correlation analysis was performed between nearest neighbour distance and combined canopy cover of the nearest neighbour pair. Intraspecific competition was, however, observed for tree species *T. sericea* (n = 128; r = 0.3952; P < 0.0001) and *B. africana* (n = 166; r = 0.49926; P <0.0001) and a shrub species, *D. cymosum* (n = 391; r = 0.39788; P <0.0001). Segregation was found between *O. pulchra* and both *B. africana* (*S* = 0.999, χ^2 = 102.7588, P <0.0001) and *T. sericea* (*S* = 0.999, χ^2 = 57.8571, *P* <0.0001). Shrub species were also segregated, all with interspecific nearest neighbour pairs occurring less often than expected.

The vegetative phenology of all experimental plant species followed the rainfall gradient. Differences in reproductive phenologies were observed between *O. pulchra* and both *B. africana* and *T. sericea*. *Dichapetalum cymosum* also differed from *P. capensis* and *P. zeyheri* in their reproductive phenologies. The differences in the reproductive strategies of at least one of the species in each growth form account for the observed spatial distribution amongst species in these communities. The observed growth patterns shown by the vegetative phenologies, however, suggest that lengthy retention of nutrients is a strategy to avoid competition for nutrient uptake with other species in these communities. Segregation between species and positive correlation between nearest neighbour distance and combined canopy cover of the nearest neighbour pairs suggest that intraspecific competition and interspecific facilitation determine *D. cymosum* woody plant community structure.

This study had limited application to rangeland management. However, it can be concluded that grazing of *D. cymosum* communities should take place during mid-summer, when enough grazing material is available to allow animals to vary their diet. The introduction of animals in poor condition or naïve animals into these lands should be avoided in winter and spring as they will graze non-selectively resulting in *D. cymosum* poisoning. To utilize these areas as grazing lands, supplements need to be provided to assist in the detoxifications of toxins once ingested.

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DECLARATION

I, **Hosia Turupa Pule,** declare that the dissertation, which I hereby submit for the degree MSc (Agric): Pasture Science at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

Signature: …………………………………………..

Date: ……………………………………………….

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CHAPTER 1

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1. INTRODUCTION

1.1. Background

Dichapetalum cymosum (Hook.) Engl., commonly known as gifblaar (Afrikaans for poison leaf), is an underground woody plant (Vahrmeijer 1981, Kellerman et al. 2005). A sole representative in South Africa of the small tropical family, Dichapetalaceae (Mogg 1930), *D. cymosum* also occurs in Angola, Namibia, Zimbabwe and Botswana (Vickery and Vickery 1973, Vahrmeijer 1981, De Sousa Correia and van Rensburg 2000). *Dichapetalum cymosum* interacts and coexists in a community with trees such as *Burkea africana* Hook., *Ochna pulchra* Hook. F and *Terminalia serecia* Burch ex DC (Vahrmeijer 1981, van Wyk et al. 2002). *Dichapetalum cymosum* communities are generally known to occupy the northern side of hills mainly on sandy, well drained and nutrient poor soils (De Sousa Correia and van Rensburg 2000, van Wyk et al. 2002, Kellerman et al. 2005, Hipondoka and Versfeld 2006). *Dichapetalum cymosum* can be confused with other species, which also occur in the same community, such as the shrublet form of *Ochna pulchra* Hook. F., *Pygmaeothamnus zeyheri* (Sond) Robyns var. *zeyheri* and *Parinari capensis* Harv. subsp. *capensis*. In some isolated communities, *D. cymosum* can be confused with ‘gousiektebossies’ (Afrikaans for quick disease shrubs), such as *Pachystigma thamnus* Robyns and *Pachystigma pygmaeum* (Schltr.) Robyns (Vahrmeijer 1981, van Wyk et al. 2002).

Dichapetalum cymosum contains the toxic substance monofluoroacetic acid (Marias 1943). Its poisoning of livestock is well documented (Steyn 1928, Clarke et al. 1981, van Wyk et al. 2002, Minnaar 1997, Kellerman et al.1996, 2005) and generally well understood by South African farmers grazing their livestock on *D. cymosum* infested rangeland communities. However, catastrophic livestock losses, particularly cattle, still occur in the Limpopo, Gauteng, Northwest and Mpumalanga provinces of South Africa (Egyed and Schultz 1986, Kellerman et al. 1996, 2005). These livestock losses occur mainly during the spring season when *D. cymosum* produces new shoots and in autumn when it forms new leaves (Kellerman et al. 2005). The lethal dose for *D. cymosum* in cattle is 0.5g.kg^{-1}, which is the equivalent of 20g dry leave material. *Dichapetalum cymosum* does not lose its toxicity with desiccation and all its plant parts are toxic.

There is no antidote for *D. cymosum* poisoning of livestock and wide scale eradication by conventional control methods are labour intensive, expensive and often impractical (Egyed and Schultz 1986, Kellerman et al. 1996). The difficulty in its eradication is probably due to its enormous deep root system. In South Africa, the communal or emerging farming sectors are the most affected. This is mainly due to 1) the high costs associated with control measures such as fencing, supplementary feeding and veterinary expenses (James et al. 1992, Nielsen & James 1992), and / or (2) lack of grazing management with livestock numbers exceeding the biological carrying capacity of the rangeland due to lack of grazing lands (Ralphs 2002). Proper rangeland management is the surest and most economical means of reducing plant poisoning of livestock (Schuster 1978).

Generally, poisonous plants are the most important cause of economic losses in the livestock industry throughout the world (Holechek 2002), especially in those areas where rangeland and pasture grazing are practiced (Fowler 1983). In the livestock industry in South Africa, total annual costs of plant and fungal poisoning (mycotoxicosis) are conservatively estimated to be R104 506 077, 8% of which is due to *D. cymosum* poisoning (Kellerman et al. 1996). This value is probably underestimated because separating disease, accidents, and predation losses from poisonous plant losses is often difficult (Holechek 2002). This economic impact necessitates research on the development and implementation of cost effective control measures (Kellerman et al. 1996). Cronin et al. (1978) suggested focused research on the ecology of these poisonous plants in rangeland communities to improve rangeland management. In South Africa, this area of research has not being fully explored for *D. cymosum* and its ecology in rangeland communities remains relatively unknown.

1.2. Justification

Two factors that contribute to the occurrence of poisonous plant problems in western United States rangelands are the abundance of toxic plants, both in number of species and density of plants, and overgrazing (Ralphs 2002). The occurrence of poisonous plants in these rangeland communities has been attributed to poor rangeland conditions (Marrill and Schuster 1978, Cronin et al. 1978) and poor rangeland management (Holechek 2002). Studies have described how and why retrogression from palatable to unpalatable plant species has occurred under heavy or severe grazing pressure (Molyneuax and Ralphs 1992). However, there are exceptions and locoweed (Astragalus spp.) and larkspur (Delphinium spp.) have been found to be normal constituents of climax communities and capable of causing livestock losses under any rangeland conditions (Merrill and Schuster 1978).

Generally, under heavy to severe grazing levels, poisonous and unpalatable plants have a competitive advantage over palatable ones. This is because under heavy defoliation levels, the photosynthetic capacity of palatable plants is reduced to a point where they are unable to produce enough carbon compounds to maintain root systems, regenerate leaves, respire and reproduce (Holechek et al. 2001). These plants ultimately shrink and die off and get replaced by unpalatable (Meyer et al. 2008) and/or poisonous plants that can defend themselves against herbivory (Holechek et al. 2001). This is probably what has occurred in plant communities where *D. cymosum* popluations have increased at the expense of other plant species. *Dichapetalum cymosum* is poisonous at all times (Kellerman et al. 2005). The likelihood of livestock poisoning occurring due to hunger and/or by accident increases when *D. cymosum* is the most abundant plant in a community.

To restore and manage ecosystems, there is a need to understand the environmental conditions and interactions between plant species that affect plant establishment (Sanjerehei et al. 2011). Negative interactions, such as competition have long been regarded as key determinants of community dynamics, structure and composition (Fowler 1986, Scholes and Archer 1997). Studies on plant competition in South Africa have relied mainly on nearest neighbour distances (Smith and Grant 1986, Shackleton 2002; Meyer et al. 2008) to avoid costly long-term demographic censuses required by experimental methods. Nearest neighbour distance is based on the theory that if competition takes place in plant communities, there will be a negative spatial correlation in plant sizes (Pieleu 1961). There is also a need to understand how species in the *D. cymosum* community are arranged with respect to each other. For example, regular dispersion will be indicative of competitive interactions, aggregated dispersion will suggest facilitation and random dispersion will suggest that plants are dispersed according to chance (Pieleu 1961, 1962, Scholes and Archer 1997).

Niche separation is a phenomenon where plants use temporal and spatial mechanisms to avoid competing with each other and thereby coexist (Scholes and Archer 1997). Although this mechanism exists in plant communities (Silvertown and Law 1987, Scholes and Archer 1997, Cipriotti and Aguiar 2010), some studies have failed to prove its importance for species coexistence (Mahdi et al. 1989), possibly due to failure to identify the right niche axes. Numerous studies have documented that species differ both in phenology and rooting depth (Fitter 1986, McKane et al. 1990). Chesson (1994) suggested that these differences in phenology and rooting depth could be important for species coexistence. These differences in resource use can be shown by variation in seasonal phenologies amongst coexisting plant species. These mechanisms and their implications for species coexistence have not been explored in communities of *D. cymosum* and associated species.

Facilitation is a mechanism by which species interact and coexist (Bruno et al. 2003), particularly in resource poor environments. However, it has not been given enough research attention. Facilitation is a positive interaction leading to the aggregation of plant species, thereby increasing their densities (Scholes and Archer 1997, Bruno et al., 2003), or the positive effect of plants on the establishment or growth of other plants (Callaway 1995). Facilitation, therefore, plays an important role in community dynamics, structure and composition.

This study will, however, investigate competition and niche separation using seasonal phenology as niche axes among species of the same growth form (trees and shrubs). This study has been limited to tree - tree and shrub - shrub interactions because species within the same growth form often share the same morphological and physiological characteristics that result in a common ecological role.

1.3. Aims

1. To investigate competitive (intra and interspecific) interaction between common coexisting plant species with similar growth forms in *D. cymosum* communities, and

2. To investigate niche separation using seasonal phenology among common coexisting plant species in *D. cymosum* communities

1.4. Hypothesis

1. If competition takes place among common coexisting plant species with similar growth form within *D. cymosum* communities, there should be a positive relationship between nearest neighbour distance and the combined size of nearest neighbour pairs.

2. Each species will have its own niche, if aggregated species owe their patchiness to the same environmental factors, but differ in their requirements (i.e. their optima).
3. It will be possible to identify plant nutrients requirements using niche separation based on differences in seasonal phenologies, particularly of plant species where within growth-form interspecific competition is observed.

2. Literature review

Dichapetalum cymosum poisoning of livestock is one of the major challenges facing emerging farmers in South Africa. However, very little knowledge exists on how environmental conditions influence the chemistry (nutrients and toxins) of *D. cymosum* and its associated vegetation, general plant species growth, and its interaction and coexistence within a community. Yet, the restoration and management of ecosystems require an understanding of the environmental conditions and the interactions amongst species that affect plant establishment (Sanjerehei 2011).

3. Experimental plant species

Six experimental plant species were selected for this study. The three shrubs species are *D. cymosum*, *Pygmaeothamnus zeyheri*, and *Perinari capensis*, which grow in familial clumps. These shrub species are often called below ground trees (Vahrmeijer 1981) because of their enormous below ground biomass compared to that above ground. The three aboveground or normal savanna trees used for the study are *Burkea africana*, *Terminalia sericea* and *Ochna pulchra*. These trees are winter deciduous and generally unpalatable to wild ungulates. These experimental plant species are described in depth below.

3.1. Shrub species

3.1.1. Dichapetalum cymosum (Hook.) Engl.

This is a counter-seasonal, geoxylic suffrutice (underground tree) that grows on deep, infertile sandy soils (Scholes 1997; De Sousa Correia and van Rensburg 2002). The aerial stem of *D. cymosum* is short, normally 150 mm in length and densely leafy. The secondary veins on the leaves are looped before reaching the leaf-margin, producing an arched effect (Vahrmeijer 1981, Breteler 1986). The leaves are alternate, simple, usually broadly lanceolate and bright green on both surfaces. Young leaves are brown and hairy becoming green, leathery and generally smooth with age (Vahrmeijer 1981).

Dichapetalum cymosum has a taproot-like stem, about 10-70 mm in diameter, which descends obliquely for a great length deep into the soil (Mogg 1930, Kellerman et al. 2005). The fruit are roundish, orange-yellow drupes, which are extremely rarely produced (Mogg 1930, Vahrmeijer. 1981, Breteler. 1986, van Wyk et al. 2002, Kellerman et al. 2005) and contain one to three seeds (Kellerman et al. 2005). *Dichapetalum cymosum* seeds require moisture and a relatively high temperature to survive and germinate (Kellerman et al. 2005).

3.1.2. *Pygmaeothamnus zeyheri* (Sond) Robyns var. *zeyheri*

This species is a dwarf shrub, which grows to about 20 cm in height and has an underground woody rootstock branching profusely in all directions. It has thick, woody subterranean rhizomes and thin upright aerial branches less than 30 cm in height, which appear seasonally. Its shallow underground rhizomes branch and radiate outwards, so that one plant can occupy an area of up to 3 m in diameter. It has alternate deciduous leaves, dark green above and silvery white underneath. The tips of the leaves are slightly twisted and veins are distinct on the underside. Its leaves are bright green, erect and opposite, occurring rarely in whorls of three (Botha and Venter 2002). The base of the leaves taper gradually and merge into the petiole. The stipule is narrow and placed between the petioles. Flowers are small, hairy and greenish to creamy in colour, and are borne in short, densely branched inflorescences occurring in clusters just above the ground during spring to early summer. The fruit are asymmetrical and yellow and succulent when ripe (Botha and Venter 2002). Generally, *P. zeyheri* is found in warm, subtropical regions, usually in dry areas. It occupies acidic, sandy soils often on stony hills. It is often found in communities which include *B.africana*, *T. sericea* and *O. pulchra* (Botha and Venter 2002).

3.1.2. *Parinari capensis* Harv. subsp. *capensis*

Parinari capensis is a suffrutex or creeping shrub, which reaches only a few centimetres in height and grows in colonies (Coates Palgrave 2002). It is commonly found in sandy areas and also on clay soils at the edge of vlei areas.

3.2. Tree species

3.2.1. *Burkea africana* Hook . (Engl.)

This is a medium sized tree, 8 - 10 m in height. It occurs in various types of woodland over a wide range of altitudes and habitats. Its bark is dark grey, rough and flakey, sometimes with very thin pale green lichen looking like a wash of pale green paint. The leaves are bipinnate and crowded at the end of the branchlets with 2 or 3 pairs of pinnae, each having 5 – 9 alternate leaflets. The leaflets are elliptic, 3 – 6 x 1.5 – 3 cm, grey green to dark green, with silvery appressed hairs when very young. The apex is rounded and notched, the base is asymmetric, and the margins entire. The petiole is 4 – 10 cm long. The hermaphrodite flowers, which are a creamy white and about 5 mm in diameter, grow in long graceful pendulous spikes, up to 24 cm long, crowding near the end of branchlets. *Burkea africana* fruit are thin pods, which are about 8 x 2.5 cm, pale brown and indehiscent, and can be seen hanging in conspicuous clusters from the ends of the branches during February to July, although they can remain on the tree for months, frequently until after the leaves have fallen at the end of the growing season (Coates-Palgrave 2002).

3.2.2. *Terminalia sericea* Burch ex DC

Terminalia sericea is a small to medium-sized, well-shaped tree, usually 4 - 6 m in height, but occasionally reaching 10 m. It occurs in open woodland and bushveld, frequently on sandy soils and often at vlei margins, and is a pioneer species. Its bark is dark grey or brownish, which has deep vertical fissures that join and split.. The slender branchlets are dark brown or purplish, peeling and flaking in rings and strips to expose light brown underbark. Its young stems are often parasitized and as a result bears round galls, often up to 2 – 3 cm in diameter, somewhat resembling a lollipop, frequently with leaves growing from them. The leaves, which are clustered towards the tips of the slender branchlets, are narrow and obovate-elliptical (3.5–12 x 1.5 – 4.5 cm), pale green and covered with silvery silky hairs which have a characteristic sheen, although sometimes dull with hairs almost absent. They have 8–16 pairs of obscure lateral veins, sometimes with extra-floral nectaries. The apex is broadly tapered and ends in a short tip and the base is narrowly tapered. Margins are entire, sometimes wavy, and petioles are 2-10 mm long. Flowers are small, cream to pale yellow, heavily or rather unpleasantly scented, and grow in axillary spikes up to 7 cm long during September to December. The fruit are 2.5 – 3.5 x 1.5 – 2.5 cm in size, pink to rose red in colour drying to reddish brown, growing on a stalk up to 5 mm long. They are produced from January – May, but can remain on the tree almost until the next flowering season. The fruit are sometimes parasitized and develop into deformed tangled masses of twisted, rusty hairy structures (Coates-Palgrave 2002).

3.2.3. *Ochna pulchra* Hook. F.

This plant species is small, usually 3 -7 m in height, and occurs at medium to low altitudes in open woodland and bushveld, often on rocky sandstone slopes and sandy areas. The bark of *O. pulchra* is pale grey, rough, flakey and scaly at the base. When the bark peels off thinly, it reveals a beautiful, creamy and opalescent underbark. Its branchlets do not have lenticels. The leaves are elliptic to oblanceolate, usually about 7 – 8 x 2.7 cm (but varying 3.5 – 18.5 x 1.3 – 5.7 cm) , fresh light green to yellowish green in colour and have numerous lateral veins close together, which are not conspicuous, but more clearly defined above than below. The apex is broadly tapering to almost rounded, and the base is narrowly tapered to almost square with entire margins, but sometimes very slightly toothed towards the apex. Its petiole is rather stout and up to 6 mm long. The sweetly scented *O. pulchra* flowers are pale yellow or greenish yellow, occasionally darker, and grow on long slender stalks in a terminal raceme about 2 cm long. Petals are conspicuously narrow, falling very early in the season (August – November). The fruit consist of 1-3 kidney-shaped drupelets, each up to 1.4 cm long, attached laterally on black enlarged persistent sepals 1-2 cm long, becoming showy pink to coral-red, on recurved stalks 1-2.5 cm long (October to January) (Coates-Palgrave 2002).

4. Species Interaction and coexistence

The resource availability hypothesis suggests that in resource poor environments, typical of *D. cymosum* communities in rangelands, the level of plant defence investment increases as the potential for plant growth decreases (Coley et al. 1985, Stamp 2003). As potential plant growth rate becomes more limited by resource availability and replacement of resources lost to herbivores becomes more costly, the benefits of protection outweigh the costs of resource replacement, resulting in higher levels of defence amongst plants.

Observations reveal that inherently slow growing plants in resource poor environments have numerous and varied types of defences, both mechanical and chemical, (Coley et al. 1985) affecting herbivore densities and feeding preferences (McNaughton and Georgiadis 1986).

In resource limited environments, plant species tend to have long-lived leaves and twigs, because these resources are not readily replaced (Coley et al. 1985). Plants also tend to have a slow turnover of plant parts, because each time a plant part is shed, it carries with it approximately half of its maximum nitrogen and phosphorus pool (Chapin 1980). Slow growth rate amongst plants in resource poor environments may result at times from low metabolic demand (Coley et al 1985), and this should be considered as a consequence of nutrient retention rather than a feature on which direct selection takes place (Aerts 1999). Low metabolic demand resulting in low tissue nutrient concentration and high nutrient resorption efficiency are strategies among plants for adaptation to chronically stressful environments. These strategies also provide a competitive advantage for slow growing plants over fast growing and less well defended plant species, which are adapted to resource rich environments (Chapin 1980). Although the resource availability hypothesis explains the presence of species in *D. cymosum* communities fairly well, the factors which determine the structure, dynamics and composition of this community remain unclear.

Plant ecologists have proposed several mechanisms that determine plant community structure, dynamics, composition and productivity. Callaway and Walker (1997) and Callaway et al (2002) proposed negative interactions (competition) and positive interactions (facilitation) between species, as well as abiotic factors such as climate and soil characteristics because they are concurrent in plant communities. Competition on the one hand refers to the tendency of neighbouring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water or volume of space (Grime 1977). Facilitation on the other hand is a positive interaction leading to aggregation of plant species, thereby increasing plant densities (Scholes and Archer 1997, Bruno et al., 2003) or a positive effect of plants on the establishment or growth of other plants (Callaway 1995).

Some authors contend that the importance of facilitation in plant communities increases with increasing environmental stresses (Bruno et al 2003, Callaway et al 2002). Contrary to this, some argue that competition, particularly for water, is important in stressed environments, such as in the arid and semi-arid rangeland communities (Folwer 1986, Seghieri et al. 1995). This disagreement might be due to the fact that facilitation mechanisms may act simultaneously with competition for resources, and the overall effect of one species on another may be a product of multiple, complex interactions (Callaway 1995). For example, the chamaephytic shrub species (Artemisia sieberi) ameliorates micro-environmental conditions and facilitates the establishment and survival of hemicryptophytic species (*Stipa barbata*) and, once established, the hemicryptophytic species compete with each other for limited resources on the basis of their similar life forms (Sanjerehei et al 2011).

Basically, the balance between facilitation and competition appears to vary depending on the life stage of the species (Pugnaire et al. 1996) and the intensity of abiotic stress (Callaway and Walker 1997). However, in cases where competition is more prevalent, competitors avoid competition by separating the use of resources spatially and temporarily in order to coexist (Fargione and Tilman 2005). These mechanisms are true for the communities and conditions under which they were investigated. However, little is known about how they determine species interaction and coexistence in *D. cymosum* communities.

Only a few studies on woody plant species interaction and coexistence in a *D. cymosum* community have been conducted and the results are inconclusive in different ways. A more comprehensive study in *D. cymosum* communities focussed on tree – grass interactions (Knoop and Walker 1985, Scholes and Archer 1997). Yet, tree – tree interactions determine the density and pattern of woody plant distribution across savanna landscapes and hence the pattern of grass biomass and distribution (Scholes and Archer 1997). To better understand woody plant species density and their distribution patterns in *D. cymosum* communities, more research on tree –tree and/or shrub – shrub interactions is required.

5. Models of species interaction and coexistence

Species interaction and coexistence in a community is explained by niche separation and balance competition models (Scholes and Archer 1997, Sankey 2007). Evidence exists that these models are at least partly correct in explaining mechanisms of species interaction and coexistence. However, Scholes and Archer (1997) acknowledge that no single model can account for the variety of phenomena in all savanna locations or even the range of behaviours exhibited at one location in different seasons or stages of succession. This is probably because different mechanisms of coexistence may predominate in different communities (Bazzaz 1991).

5.1. Niche separation model

The niche separation model has received substantial research attention in the past (Silvertown and Law 1987, Silvertown et al. 1999, McKane et al. 2002, Silvertown 2004, Cipriotti and Aguiar 2010). This model argues that competitors avoid competition by using resources that are slightly different, obtained in different places or obtained at different times (Walter 1971, Scholes and Archer 1997). These separations into niches are generally believed to reduce intensity of competition amongst species and thereby promote species coexistence (Tilman 1982, Fowler 1986, Mckane et al. 2002). If a variable, such as water, is a limiting factor within a plant community, woody and herbaceous species will have to make use of the water (variable) at different times or in a separate space. For example, in order to coexist grasses and shrubs can have root systems extending to different depths in the soil profile to access soil water (Walter et al 1981, Knoop and Walker 1985).

In theory, this hypothesis is sensible and is supported by some field studies. McKane et al. (2002) documented that the composition of a plant community is related to the partitioning of differentially available forms of a single limiting resource. However, some ecologists have failed to find evidence of its expression in natural communities (Mahdi et al 1989, Fargione and Tilman 2005). Mahdi et al (1989) suggested that either inappropriate or insufficient niche axes are examined and/or species are not competing. Despite this inconsistency in research results, it is still believed that coexistence by separation in niches is important, particularly in species rich plant communities (Newman 1982, Tilman 1982). However, we know very little about the existence and the role of niche separation in species poor communities or environments. Some argue that competition is not important in resource poor environments because traits that lead to higher nutrients retention are far more important for plant performance than traits which lead to a high competitive ability for nutrient uptake (Aerts 1990). As such, this renders niche separation probably unnecessary in such environments.

In plant communities where the niche separation hypothesis has limited application, the use of phenology is a valuable way of understanding the co-ocurrence of plant species (Frankie et al.1974). It is defined by Leith (1974) as the art of observing life cycle phases or activities of plants and animals in their temporal occurrence through the year. In a 6 year field experiment, a dominant prairie bunchgrass, *Schizachyrium scoparium,* excluded species sharing similar niches in the form of phenology and rooting depth, but coexisted with those species with different niches (Fargione and Tilman 2005).

Analysis of community phenology provides information regarding the abiotic and biotic variables that determine the seasonal development and senescence of plant tissues and organs (Shackleton 1999). In addition, the initiation and termination of growth phases represent the boundaries of periods of growth and productivity, and hence resource availability. Little is known about the phenology of *D. cymosum* plant communities as well as resource availability and/or abundance. Research in this field would assist in the development of grazing or browsing plans to reduce the likelihood of livestock over-ingesting *D. cymosum*.

Phenology and rooting depth are related because possession of a large and deep root system is one of the reasons why trees can expand their leaves early and rapidly and retain them for longer in stress periods (Scholes and Archer 1997). However, more studies have made use of phenology, probably because it is difficult to measure the use of underground resources accurately and involves techniques that severely limit sample sizes (Parrish and Bazzaz 1979, Veresoglou and Fitter 1984). Most plant ecologists have followed the experimental route to investigate below ground niche separation (Silvertown et al 1999, Fargione and Tilman 2005), which provides experimental evidence that supports alternative conceptual approaches, but is not necessarily a true reflection of natural communities.

Although water stress is seen to be a limiting factor to plant growth, it does not constitute the sole trigger for phenological stages or phases (Seghieri et al. 1995). Plants may alter their use of water by being physiologically active at different times (Solbrig and Orians 1977). In addition, co-occurring species that show similar phenological rhythms in the vegetative phases often differ in the timing of their reproductive phases (Seghieri et al. 1995). These can be investigated using niche axes such as the phenology of growth and flowering (Veresoglou and Fitter 1984). The phenology of plant species in *D. cymosum* communities is not well understood, and more research is needed to better understand seasonal patterns and trends in plant.

5.2. Balance competition model

The balance competition model allows for interspecific (e.g. grasses and shrubs) competition, but proposes that it is weaker than intraspecific (grasses-grasses and shrubs-shrubs) competition (Scholes and Archer 1997). This model suggests that individuals compete most strongly with individuals that are more similar to themselves, which causes intraspecific competition to be stronger than interspecific competition, thereby leading to coexistence (Fargione and Tilman 2005). This model is consistent with a majority of studies on competition between plants species in communities (Smith and Grant 1986, Rathogwa 2000, Shackleton 2002).

Plant ecologists agree that interspecific competition is an important determinant of the structure and the dynamics of plant communities (Aerts 1999). Some ecologists have discovered and quantified competition in plant communities and determined that it is important in determining the spatial arrangement of woody plant species (Knoop and Walker 1985, Fowler 1986, Smith & Goodman, 1986, Smith and Grant 1986), whilst others argue that the importance of competition in communities is over emphasised (Shackleton 2002, Welden and Slauson 1986). Shackleton (2002) believes that the majority of such studies on competition are based on small sample numbers. Welden and Slauson (1986) argue that these studies probably overlooked the distinction between the intensity of competition among individuals of one or more species and the importance of competition to individual fitness, community structure, and the coevolution of species.

In nutrient limited environments, such as those in which *D. cymosum* occurs, it is believed that competition, particularly between individuals of different species, is unimportant (Grime 1979, 1988, Aerts 1999). These findings are supported by Fowler (1986) who stated that in environments where desert plant communities occur, plants usually compete with relatively few neighbours as compared to neighbours in more mesic environments. The argument is that in nutrient poor environments, traits which lead to high nutrient retention are far more important for plant performance than traits which lead to higher competitive ability for nutrient uptake (Aerts 1990, Berendse 1994a). However, further research is needed to understand the role of competition in determining community structure, dynamics and composition of *D. cymosum* communities.

There are several techniques for investigating competitive interactions amongst woody plants species in communities. Nearest neighbour analysis is the most preferred for arid and semi-arid regions (Smith and Grant 1986, Scholes and Archer 1997, Rathogwa 2000, Shackleton 2002, Meyer et al. 2008). The choice of nearest neighbour analysis is probably based on its ability to differentiate between intensity and importance of competition (Welden and Slauson 1986). The use of nearest neighbour distance is based on the premise that if competition takes place in a plant population, unsuccessful competitors will either be small or stunted, or else completely unable to establish themselves. Furthermore, if competition is sufficiently intense amongst plant species in communities, each plant's maximum size becomes a function of the proximity and size of its neighbours (Pielou 1962). As such, the combined size of a plant and its nearest neighbour will generally be positively correlated with the distance between them (Smith and Grant 1986, Smith and Walker 1983).

In woody plant communities, individuals of a species may either be lumped together in clumps, or randomly or regularly distributed (Pielou 1960). In random population patterns, the position of each individual plant is independent of all other individuals, in clumped/aggregated population patterns (suggesting facilitation) there is a tendency for the individuals of a species to occur close together with the distance between neighbouring individuals being minimized (Scholes and Archer 1997), while in regular/over dispersed populations (suggesting competition) plants are more evenly spaced than they would be had they been distributed according to chance (Pielou 1960, Archer and Scholes 1997).

A regular distribution of plants and a positive correlation of the distances between neighbouring plants and their sizes (canopy), indicate the prevalence of competition (Pielou 1960). However, the absence of such patterns of distribution is not necessarily evidence of the absence of competition (Fowler 1986). The reason being that both spatial heterogeneity of the environment and restricted seed dispersal can override the tendency for competition to produce a regular distribution of plants and a positive correlation between plant size and distance apart. Furthermore, a positive correlation between the size of competing plants and their distances apart may also be absent because plants may have to compete with many neighbouring plants (Fowler 1986).

There is also evidence, although only from few a studies, that competition can restrict the distribution of a plant species. For example, the grass *Stipa mexicana* was restricted to a ridge crest in a site in Arizona by interspecific competition (Gurevitch 1986). Furthermore, the forb *Machaeranthera canescens* was absent or rare in all but disturbed sites due to competition from *Gutierrezia microcephala* (Parker and Root 1981). However, the nature and magnitude of the effects of both intra- and interspecific competition upon population size and population dynamics in arid and semi-arid regions are still not clear (Fowler 1986), probably because only a relatively small number of studies have examined the direct effect of competition upon individual plants and plant populations in arid and semiarid regions.

6. Study outline

To understand mechanisms of species interaction and coexistence in *D. cymosum* communities we proposed that 1) multiple-species (tree-tree and shrub-shrub) interactions be investigated and that 2) evolutionary consequences involving differentiation that permits a reduction in the extent of interactions among species also be investigated. To do so, we undertook ecological research on *D. cymosum* communities, focusing on understanding how negative (inter- and intraspecific competition) interactions influence community structure, dynamics and productivity and/or how plants in *D. cymosum* communities avoid these negative interactions by investigating their seasonal phenological patterns.

We predicted that 1) intraspecific or intra-growth form competition would be more prevalent in *D. cymosum* communities and would manifest itself through positive correlation between the distance separating two nearest neighbours and their combined canopy cover and that 2) each species would have its own niche, if both aggregated species owed their patchiness to the same environmental factors, but differed in their resource requirements (i.e. their optima) (Pielou 1962) and that, such differences in requirements would be shown by differences in their seasonal phenologies, particularly amongst species where within life form interspecific competition was observed.

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CHAPTER 2

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Competitive interaction among common plant species occurring in *Dichapetalum cymosum* (Hook.) Engl. communities

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Abstract

Competition within growth form among commonly occurring plant species in *D. cymosum* communities in South African savannas were investigated using nearest neighbour analysis. A field experiment was conducted on fourteen sites in two veld types with six woody plants species, trees : *Burkea africana*, *Ochna pulchra* and *Terminalia serecia*; shrubs : *D. cymosum*, *Pygmaeothamnus zeyheri* and *Perinari capensis*. A significant positive correlation was found between nearest neighbour distance and combined canopy cover of nearest neighbour pair for intraspecific comparisons of the tree species *T. sericea* (n = 128, r = 0.3952, P < 0.0001) and *B. africana* (n = 166, r = 0.49926, P <0.0001), and shrub species *D. cymosum* (n = 391, r = 0.39788, P <0.0001). However, no significant correlation was found for interspecific comparisons for either trees or shrubs. Significant segregation was found between *O. pulchra* and both *B. africana* (*S* = 0.999, χ^2 = 102.7588, P <0.0001) and *T. sericea* (*S* = 0.999, χ^2 = 57.8571, *P* <0.0001). Shrub species also segregated, interspecific nearest neighbour pairs occurring less often than expected. These results suggest that both intraspecific competition and interspecific facilitation determine *D. cymosum* woody community structure.

Key words: Facilitation, nearest neighbour distance, interspecific competition, intraspecific competition, segregation.

1. Introduction

Dichapetalum cymosum is commonly known by South African livestock farming communities as gifblaar or poison leaf. This is because of its extreme toxicity to livestock, particularly cattle (Kellerman 1996). *D.ichapetalum cymosum* contains toxins called monoflouroacetic acid (Marias 1943, Minnaar 1997) and animals die within 24 hours of ingesting the plant (Kellerman et al. 2005). There is no antidote for *D. cymosum* and conventional control measures are labour intensive, expensive and often ineffective (Kellerman et al. 1996). In South Africa, emerging farmers are the most affected, and stock losses are prevalent in Limpopo, Gauteng, Mpumalanga and the NorthWest Province (Kellerman 1996). This is probably because farmers do not 1) have enough land to defer grazing during dry periods in autumn and winter when livestock are most likely to be poisoned by *D. cymosum* (Kellerman et al. 1996, 2005), and / or 2) have sufficient financial resources to pay the high costs associated with control measures such as fencing, supplementary feeding and veterinary expenses (Nielsen & James 1992).

In South African, *D.cymosum* interacts and coexists with trees such as *Burkea africana*, *Ochna pulchra* and *Terminalia serecia* (Vahrmeijer 1981). *Dichapetalum cymosum* can be confused with some species that also occur in its community such as the shrublet form of *Ochna pulchra*, *Pygmaeothamnus zeyheri* and *Perinari capensis*. In some isolated communities, *D. cymosum* can be confused with plants such as *Pachystigma thamnus* and *Pachystigma pygmaeum*, which cause ‘gousiekte’, meaning ‘quick disease’ (Vahrmeijer 1981). *D.ichapetalum cymosum* grows mainly on the northern aspects of hills, often on coarse textured, well drained and very marginal soils (Vahrmeijer 1981). However, little is known about what determines *D. cymosum* community dynamics, structure, and composition and how species in *D. cymosum* communities interact and coexist.

Negative interactions (competition) and positive interactions (facilitation) between species as well as abiotic factors, such as climate and soil characteristics, are common and concurrent in plant communities, and have long been regarded as important factors determining community dynamics, structure and composition (Callaway and Walker 1997, Callaway et al 2002). Most studies have, however, emphasized the importance of competition (Fowler 1986, Scholes and Archer 1997, Silvertown 2004, Meyer et al 2008), with fewer studies focussing on facilitative interactions. The majority of studies on competition argue that competitive interactions are stronger between individuals and or species of the same growth form (e.g., tree – tree interactions) than they are for individuals and/or species of different growth forms (e.g., trees – grass interactions) (Yeaton et al. 1977, Aarssen 1989, Scholes and Archer 1997, Shackleton 2002). Furthermore, studies have found that the importance of competition in plant communities tends to increase in less stressful environments, e.g., high productivity conditions (Callaway et al. 2002), whereas facilitative interactions increase with increasing environmental stresses (Callaway and Walker 1997, Callaway et al. 2002).

In many cases evidence has been found that competition occurs and is important in determining the spatial pattern of woody plants (Fowler 1986). A few studies have been conducted in communities in which *D. cymosum* is present, woody-herbaceous species (Knoop and Walker 1985) and/or tree-tree interactions (Rutherford and Panagos 1982, Smith and Grant 1986). They were not specifically on interaction of *D. cymosum* and its associated shrubs or multiple species of this community. In addition, studies of competition, particularly in broad leaved savanna communities are incomplete and inconclusive in many ways (Shackleton 2002). Therefore, the occurrence and importance of competition in determining the structure, dynamics and composition of *D. cymosum* communities is still unclear.

In South African savannas, the presence and / or absence of competition in a woody plant community has always been studied using spatial techniques, such as nearest neighbour distance (Smith and Walker 1983, Fowler 1986, Smith and Goodman1986, Smith and Grant 1986, Meyer et al 2008). Spatial techniques are basically favoured over non-spatial techniques because they retain more information (Meyer et al. 2008). For example, nearest neighbour distance can differentiate between the intensity and importance of competition in plant communities (Welden and Slauson 1986). It can also be used to investigate how species are arranged with respect to members of other species in the community (segregation), i.e. two species may be regarded as “segregated” if individuals of either species are found near the individuals of the same species more frequently than expected. Spatial pattern techniques provide an indirect approach to evaluating interaction amongst plants without the need for costly, long-term demographic censuses (Meyer et al 2008).

The nearest neighbour distance technique is based on the assumption that if competition takes place among plant species in a community, there will be a positive correlation between the distance separating two neighbouring plants and the sum of their sizes (Pielou 1962). Ultimately, if space (as a source of light, water, nutrients, etc.) is limiting plant growth, each individual plant should grow until its weight is proportional to the size of its immediate, available space (Franco and Harper 1988). Furthermore, if combined occurrences of species are less (more) frequent than random expectation, the two species are regarded as being negatively (positively) associated. These negative and positive associations are a result of ecological processes indicative of competition and mutualism amongst plants species (Schluter 1984).

The aim of this study was to investigate competitive (inter- and intraspecies and within growth form) interactions amongst *D. cymosum* and its associated species with two contrasting growth forms (i.e. shrubs and trees) using nearest neighbour distances. Interactions between growth forms were excluded due to differences in structural architecture (canopy cover or volume versus patch size). We predicted that 1) intraspecies or growth form competition would be stronger than interspecies or growth form competition (Scholes and Archer 1997) and that 2) if competition takes place within species of similar growth form, there will be a positive correlation between the distance separating two neighbouring plants and the sum of their canopies (Pielou 1962, Smith and Grant 1986).

2. Materials and Methods

2.1.1. Location of the study sites

Fourteen experimental sites were selected in the savanna biome of South Africa, falling within the Central Sandy Bushveld (CSB) and the Western Sandy Bushveld (WSB) (Mucina and Rutherford 2006). These experimental sites are located at Kwa-Mhlanga and Klipfontein in Gauteng and at Ga-rasai near Brits in the North West Province (Figure 1).

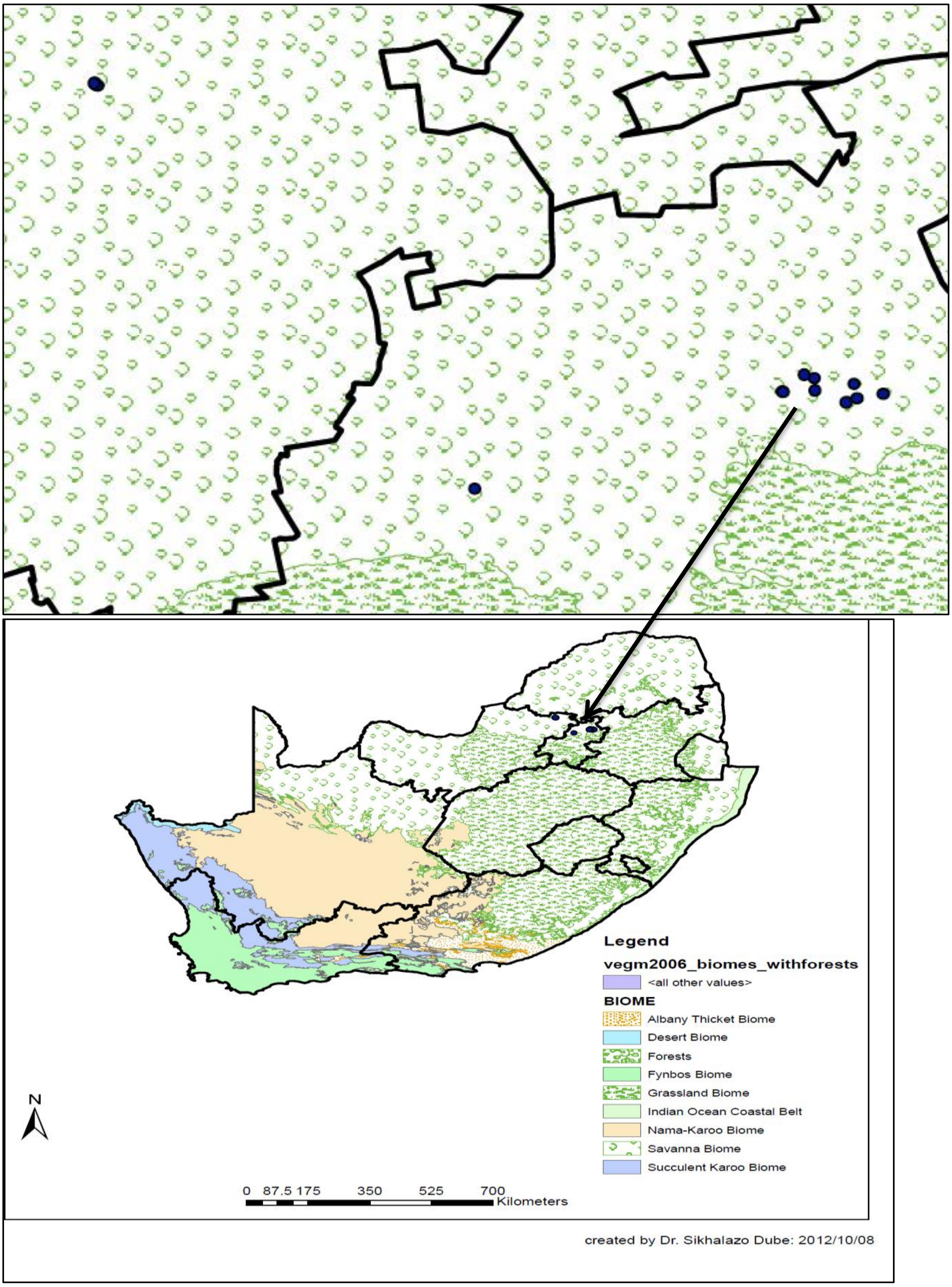

Figure 1: A map showing South Africa's biomes and the location of experimental sites in Gauteng and the Northwest Province

2.1.2. Abiotic characteristics.

A number of abiotic characteristics were recorded at each site at the beginning of the study. These included altitude, latitude and longitude, and soil characteristics. Soil samples consisted of topsoil collected using a soil auger from five points per site and grouped together. These were analysed for sand (Hydrometer), percentage organic matter content (Walkley Black), Ca, Mg, Na, K, P (Ambic I extraction followed by AA spectroscopy) (Table 1).

Table 1: Abiotic characteristics of the experimental sites in the Central Sandy Bushveld (CSB) and Western Sandy Bushveld (WSB)

Sites Numbers	ALTITUDE (m) (GPS)	LONGITUDE	LATITUDE	SAND %	SILT %	CLAY %	Organic Carbon %
CSB 1	1410	28.629833	-25.5413	70.5	9.2	20	1.07
CSB 2	1400	28.679667	-25.5491	66.4	19.6	14	0.98
CSB 3	1389	28.669883	-25.5735	73	15	12	0.73
CSB 4	1369	28.683033	-25.5687	72.5	15.5	12	0.5
CSB 5	1419	28.716517	-25.5629	66.1	19.9	14	0.7
CSB 6	1382	28.61695	-25.5367	75.8	12.2	12	0.96
CSB 7	1400	28.630633	-25.558	73	12.3	14	1.02
CSB 8	1292	28.588883	-25.5594	83.7	8.3	8	2.3
CSB 9	1293	28.59045	-25.5601	83.8	6.2	10	0.92
WSB 1	993	27.723733	-25.1425	90	4	6	0.27
WSB 2	1002	27.724567	-25.1441	92	2	6	0.45
WSB 3	1003	27.7255	-25.1453	90	2	8	0.33
WSB 4	1014	27.726567	-25.147	82	10	8	0.6
WSB 5	998	27.72304	-25.1435	90	2	8	0.38

The average altitude of the experimental sites is 1250m, with the lowest (998m) located in the Western Sandy Bushveld and the highest (1410m) in the Central Sandy Bushveld. The soils are very sandy with the highest (90%) and the lowest (64%) contents in the Western Sandy Bushveld and the Central Sandy Bushveld, respectively. Organic matter content ranged from 0.33% in the Western Sandy bushveld to 1.7% Central Sandy Bushveld (Table 1).

2.1.3. Biotic characteristics.

Biotic site characteristics recorded for the grass component included basal cover, grass species composition, tuft diameter and distance to the point (Hardy and Tainton, 1993b). The mean basal cover of the grasses was 14% and 9% for the Central Sandy Bushveld and Western Sandy Bushveld, respectively (See Appendix 1). In the Central Sandy Bushveld, dominant grass species were *Setaria sphacelata* (16%), *Tristachya leucothrix* (13%), *Eragrostis curvula* (11%) and *Digitaria eriantha* (10%). In the Western Sandy Bushveld the dominant grass species were *Digitaria eriantha* (49.8%), *Panicum maximum* (21%) and *Eragrostis rigidor* (20.8%) (See Appendix 1). The mean grass tuft diameter was 10 cm and 7 cm for Central Sandy Bushveld and Western Sandy Bushveld, respectively. Mean distance from the point to the grass tuft was 6 cm, and 8 cm for Central Sandy Bushveld and the Western Sandy Bushveld, respectively.

For the tree component, tree species composition, height classes (<2m, 2 – 5m and >5m), density and percentage canopy cover were recorded. In the Central Sandy Bushveld, total canopy cover for tree species was 43% of which 40.2 % was from species in height class between 2 m – 5 m. The dominant tree species were *Burkea africana* (26%), *Acacia caffra* (4.5 %) and *Combretum molle* (3.9%). In the Western Sandy Bushveld, total canopy cover for the tree species was 34.6% of which 24.7 % was from species in the height class <2 m. The dominant trees were *Terminalia sericea* (10%), *Dichrostachys cinerea* (8.6%) and *Grewia flava* (7.9%). (See Appendix 2.)

2.1.4. Climate of the study sites

The Central Sandy Bushveld and the Western Sandy Bushveld enjoy a mild climate, characterized by warm, moist summers and cool dry winters. Both veld types receive similar rainfall from October to April, with a mean annual precipitation of 712.75mm^{-1} and 712.50 mm^{-1} for the Central Sandy Bushveld and Western Sandy Bushveld, respectively. The Western Sandy Bushveld receives relatively high rainfall in the beginning of the rainy season and less towards the end of the season. The Central Sandy Bushveld, on the other hand, receives low rainfall in the beginning of the rainy season and relatively higher rainfall towards the end of the season (Figure 2).

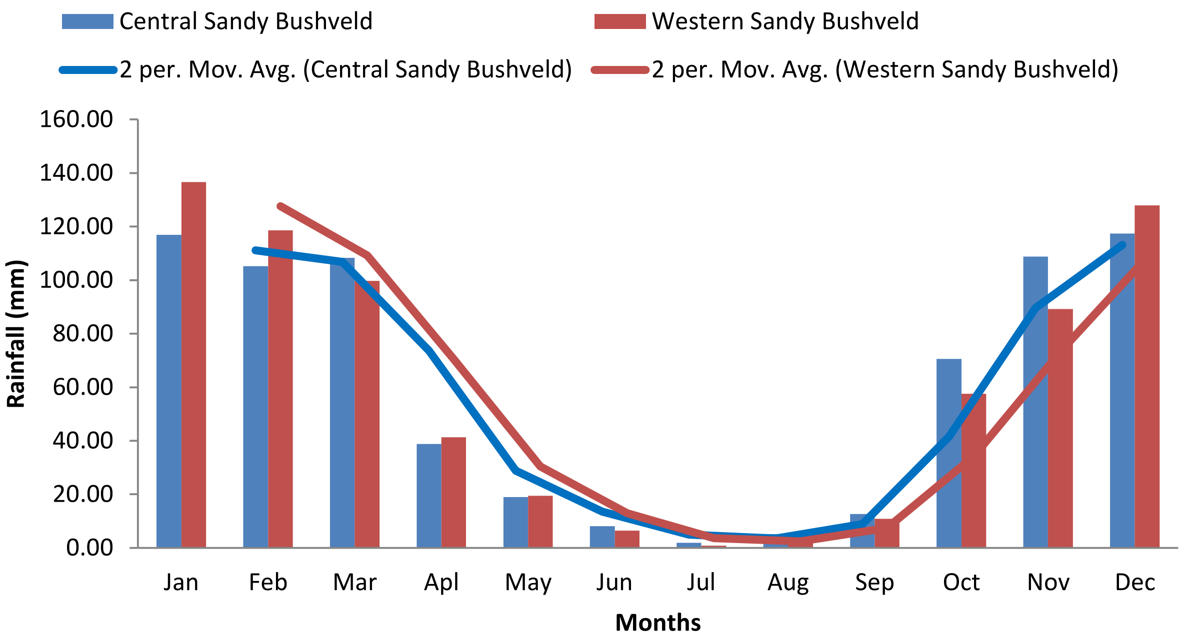

Figure 2: Long term rainfall distribution and quantities in the Central Sandy Bushveld and the Western Sandy Bushveld

2.1.5. Sampling techniques

Nearest neighbour analysis was used during this study to investigate competitive interactions amongst plant species. This method was chosen because it can detect both the intensity and the importance of competition in plant communities (Welder and Slauson 1986, Shackleton 2002). In each of the fourteen experimental sites, ten 100 m line transects, 10 m apart, were systematically placed in each hectare plot and only experimental plants that intercepted (canopy) the line were sampled. Sampling was done by pairing species to allow ease of analysis (i.e. shrubs: *D. cymosum* – *P. zeyheri; D. cymosum* – *P. capensis* and *P. zeyheri* – *P. capensis*), and trees: *B. africana* – *T. sericea*, *B. africana* – *O. pulchra* and *O. pulchra* – *T. sericea*). Selected pairings were, therefore, dependent on which of the experimental plant species were present at a particular site.

Distance to the nearest neighbouring plant of the same growth form (i.e. tree or shrub), regardless of species and direction, was recorded from the centre of canopy (trees) / patch (shrubs) to the centre of canopy/ patch of the nearest neighbouring plant using a 50m tape. If the nearest neighbouring plant was of another species (interspecific nearest neighbour pair), the distance to the nearest neighbouring plant of the same species (intraspecific nearest neighbour pair) was also recorded. If the nearest neighbouring plant was outside the quadrat, it was also included for the purpose of analysis. Canopy cover (C) was then calculated as though the canopy were an ellipse: $C = ab\pi / 4.0$, (Smith and Grant 1986), where a and b are the major and the minor horizontal canopy axes. Nearest neighbouring pairs were then grouped into intra- and interspecific observations. Data was subjected to logarithmic transformation (Log_{10}) to normalize it before it was analysed using correlation analysis.

2.1.6. Analysis

2.1.6.1. Dispersal analysis

The significance of departure from randomness towards aggregated or regular dispersion was tested using the Clark and Evans (1954) dispersal index, $R = (\check{r}a / \check{r}e)$, where $\check{r}a$ is the mean observed nearest neighbour distance ($\Sigma\, r / n$), r is the measured nearest neighbour distance; n the number of observations; and $\check{r}e$ the expected mean nearest-neighbour distance, given a random dispersion ($\frac{1}{2} \sqrt{\rho}$), where ρ is the density expressed as individuals per unit area. The density estimates were obtained from the quadrat data. The index R was then used as a measure of the degree to which the observed distribution departs from random expectation. In a random dispersion, $R = 1$. Under conditions of aggregation values approach 0, whereas values > 1 suggest over dispersion (i.e. regular dispersion). The significance of departure from randomness was tested using the standard normal variate, $Z = (\check{r}a - \check{r}e) / \sigma\, \check{r}e$, where $\sigma\, \check{r}e = 0.26136 / \sqrt{N\rho}$, and N is the number of nearest- neighbour measurements made. Indices were calculated for each species independently, as well as for combined species to examine the dispersion of individual independence of species.

2.1.6.2. Nearest - neighbour analysis

To examine the role of competition in the spacing of shrubs and trees within *D. cymosum* communities, comparisons were made between nearest neighbour distance and the combined sizes (i.e., canopy cover) of the nearest-neighbour pair, using Pearson's product moment correlation (Pielou 1962). Both inter- and intraspecific comparisons were made. The method of segregation (Pielou 1962) was used to examine the relative distribution of the experimental shrubs (*D. cymosum*, *P. capensis*, and *P. zeyheri*) and experimental trees (*B. africana*, *T. sericea* and *O. pulchra*). Assuming two species of known density to be unsegregated, the expected proportion of AA, AB, BA and BB nearest neighbour pairs was calculated. Observed and expected distributions were compared using chi-square (χ^2) statistics. If the observed departure from expectation was significant, the species were regarded as segregated. To determine the degree of segregation, a co-efficiency of segregation (S) (Pielou 1962), was calculated using the following equation:

$$S = 1- \frac{\text{Observed number of AB and BA pairs}}{\text{Expected number of AB and BA pairs}} \qquad \textbf{Equation 1}$$

When S = 0, the population is said to be unsegregated (interspecific nearest-neighbour pairs expected under random occupancy). Value of $S < 0$ reflect negative segregation (interspecific nearest-neighbour pairs occur more often than expected), whereas values of $S > 0$ reflect segregation (interspecific nearest neighbour pairs occur less often than expected).

3. Results

The dispersal analysis revealed aggregated populations for both the intraspecific and combined (all individuals independent of species) analyses, although no results were significant. (Table 2). The seven interspecific comparisons made showed no significant positive correlation between nearest neighbour distances and combined canopy cover of nearest neighbour pairs.

Table 2: Coefficiency of dispersion (R) for both intraspecific and combined (all individuals independent of species) analyses.

Species Name	R	P
All species grouped	0.001	0.239162
D. cymosum	0.006	0.463746
P. capensis	0.015	0.443935
P. zeyheri	0.029	0.398589
B. africana	0.012	0.441961
T. sericea	0.017	0.434472
O. pulchra	0.114	0.367682
D. cymosum-P.capensis	0.052	0.400907
D. cymosum-P. zeyheri	0.107	0.36092
P. capensis-P.zeyheri	0.504	0.349748
B. africana-others	0.009	0.450658
B. africana-O. pulchra	0.764	0.41099
T. sericea-O.pulchra	1.634	0.180884

A significant positive correlation was found between nearest neighbour distance and combined canopy cover of the nearest neighbour pair for three out of six intraspecific comparisons: the two tree species *T. sericea* (n = 128, r = 0.3952, P < 0.0001) and *B. africana* (n = 166, r = 0.49926, P <0.0001), and the shrub species *D. cymosum* (n = 391, r = 0.39788, P <0.0001) (Fig. 3).

Ochna pulchra was partially segregated from *B.africana* (*S* = 0.999, χ^2 = 102.7588, P <0.0001) and *T. sericea* (*S* = 0.999, χ^2 = 57.8571, *P* <0.0001), with interspecific nearest neighbour pairs occurring less often than expected. Although *B. africana* and *T. sericea* were partly segregated (S = 0.999, χ^2 = 6.0828, P = 0.0137), the degree of segregation was insignificant. All shrub species were also partially segregated with interspecific nearest neighbour pairs occurring less often than expected: *D. cymosum* and *P. capensis* (*S* = 0.999, χ^2 = 97.6879, *P* < 0.0001), *D. cymosum* and *P. zeyheri* (*S*=0.999, χ^2 = 288, *P* < 0.0001) and *P. zeyheri* and *P. capensis* (*S*= 0.999, χ^2 = 61.2590, *P* <0.0001).

4. Discussion

The results from this study indicate that intraspecific competition has a strong influence in shaping the dynamics of South African savanna broad leaved woody plant communities. This finding is in agreement with most studies of competitive interaction among plant species in South African savannas (Fowler 1986, Scholes and Archer 1997, Shackleton 2002). The importance, however, of competition in determining the structure of these communities is not convincing. This is probably because the importance of competition between plants tends to increase in less stressful environments (Greiner la Peyre et al. 2001, Callaway et al. 2002).

The woody plant cover in these communities was less than 50 %, suggesting that light was not a limiting resource and that competition was more from below ground resources, such as water and nutrients. Intraspecific competition in this study was influenced by the heterogeneity of the environment. Because individuals of the same species have similar resource requirements, they tend to compete for limited resources in the patches, which they co-occupy in these communities. Rutherford (1983) found that the roots of *B. africana* grow 50 – 60 cm deep and are often 7 times greater in length than the canopy, resulting in root interdigitation within the vertical rooting zone, an explanation for competitive interaction between the *B. africana* trees in this study.

Terminalia sericea, on the other hand, has a shallow (12 -23 cm), lateral spreading root system and, due to a high degree of overlap, individuals of *T. sericea* compete for resources amongst themselves and could also potentially compete with other species with shallow roots such as *O. pulchra* (Rutherford 1983) and / or grasses (Knoop 1982).

Hipondoka and Versfeld (2005) reported that *T. sericea* adapts its rooting system in accordance to the prevailing climatic regime. This strategy potentially results in competition between *T. sericea* and *B. africana*. However, to counteract such interaction, *B. africana* and *T. sericea* tend to occur in one species clumps, so that any individual is more likely to be found near members of its own species than near members of other species, as shown by Smith and Grant (1986) using 60 m x 60 m plot. Such a strategy is scale dependent, as has been shown in this study using 100 m x 100 m plots. Welden and Slauson (1986) also found that as sampling scale increases, the intensity of competition amongst interacting species decreases.

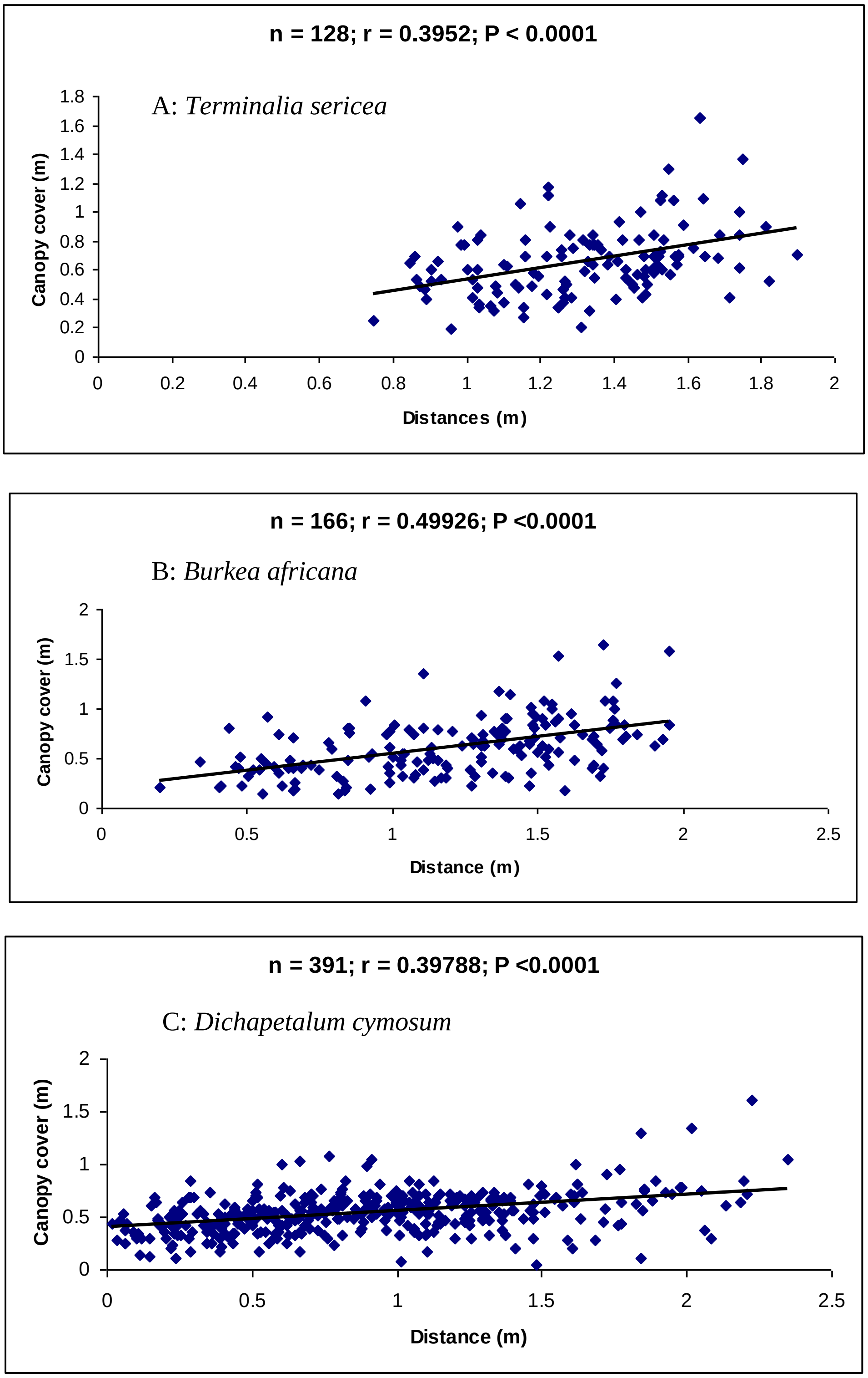

Figure 3: Relationship between nearest neighbour distance and combined canopy cover for intraspecific comparisons

Dispersal analysis revealed no regular or random patterns among species when both intraspecific and combined analyses were performed, but insignificantly aggregated populations. This may also suggest competition among the experimental plants, since competition may lead to a regular or less aggregated pattern of plant dispersion (Duncan 1991). Partial segregation among species in *D. cymosum* communities suggest that the following clump dispersal patterns may occur: 1) a clump may contain more of one species than another, with the dominant species varying between clumps (e.g., one clump may contain more members of *D. cymosum* than *P. capensis* and another more members of *P capensis* than *D. cymosum*) and 2) single species clumps may overlap. Either or both patterns may be present. A contributing factor to the partial segregation of the experimental species in the *D. cymosum* communities is their occurrence in familial clumps as a result of vegetative reproduction and/or crowding of a large number of seedlings around their parents (Pielou 1962). *Ochna pulchra* reproduces vegetatively (Rutherford 1983) and *D. cymosum* also reproduces vegetatively, rarely producing seeds (Vahrmeijeir 1983, Kellerman et al. 2005). These similarities in reproductive strategies in at least in one species of both growth forms (trees and shrubs) permit positive association (partial segregation) and coexistence amongst common plants species in *D. cymosum* communities. Vegetative reproduction may also provide a competitive advantage among species: *D. cymosum* and/or *O. pulchra* are able to tolerate a greater departure from more moderate local conditions, since they can re-sprout efficiently from well-developed root systems. The partial segregation of *T. sericea* and *B. africana* from *O. pulchra*, could indicate that both *B. africana* and *T. sericea* facilitate the growth of *O. pulchra*. The observed association among species and the positive correlation between distance separating two neighbouring plants and their combined canopy suggests that both interspecies facilitation and intraspecies competition are responsible for *D. cymosum* community dynamics.

5. Conclusion

In conclusion, this study argues that, despite complex interactions amongst woody and herbaceous plants and the influence of livestock and abiotic factors, intraspecific competition and interspecies facilitation are key determinants in the structure and functioning of broad leaved savanna communities in which *D. cymosum* occurs. Furthermore, coexistence of species within these communities is permitted by differences in their reproductive strategies, growth forms and, to a certain degree, niche separation, particularly belowground.

Our understanding of how competition influences the structure, dynamics and productivity of plant species in *D. cymosum* communities will help clarify the adaptive and evolutionary behaviour of species in the flora of this still poorly understood community, providing the insight necessary for the development of ecologically sound methods for the control of *D. cymosum* that can be used in the management of grazing lands.

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CHAPTER 3

Prepared according to the guidelines of the African Journal of Range and Forage Science

Seasonal flowering phenology of common plant species in *Dichapetalum cymosum* (Hook.) Engl. communities.

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Abstract

The seasonal flowering phenology of six co-existing plant species, occurring in two South African savanna communities infested by *Dichapetalum cymosum* was investigated during the growing season. At each of fourteen (100m x 100m) sites, 12 points at 15 m intervals were used to record phenophases of experimental tree and shrub species within four 90º quadrants. The vegetative phenology of tree species *Burkea africana, Terminalia sericea* and *Ochna pulchra* showed no evidence of niche separation. Reproductive phenologies revealed no niche separation between *B. africana* and *T. sericea*, but was present between *O. pulchra* and both *B. africana* and *T. sericea*. The vegetative phenology of shrubs species *D. cymosum*, *Perinari capensis* and *Pygmaeothamnus zeyheri* showed no evidence of niche separation. However, reproductive phenologies revealed niche separation between *D. cymosum* and both *P. capensis* and *P. zeyheri*. *Dichapetalum cymosum* produces its reproductive buds/flowers early in the rainy season and then aborts, while the others produce dehiscing fruit late in the rainy season. Lack of clear phonological niche separation among species in *D. cymosum* communities suggests that species can coexist without trophic niche separation, i.e. habitat preferences and/or resource utilization.

Key words: niche separation, vegetative phenology, reproductive phenology, savannas, coexistence

1. Introduction

Plant ecologists have had a long standing interest in understanding the conditions under which plant species coexist (Mahdi et al. 1989). In an environment where water is limited, competition is inevitable among plants occupying the same above-ground stratum and same soil horizon (Folwer 1986). However, plant species have evolved through natural selection and the development of temporal and spatial mechanisms for aquiring resources in order to avoid or minimize competition with each other and promote coexistence (Fargione and Tilman 2005). Temporal and spatial resource aquiring mechanisms enable a plant to develop, grow and flower at slightly different times, depending on the environmental conditions (Gunster 1994).

In plant ecology, phenology is a valuable tool for understanding the co-ocurrance of plant species (Frankie et al.1974). Phenology is the study of the rhythm of repetative biological events, the biotic and abiotic causes for this rhythm and the relationship between phenophases of different species or a single species (Leith 1974).The majority of studies have focussed on the use of phenology rather than below ground techniques, probably because it is difficult to measure underground resources accurately and sample sizes are severely limited (Parrish and Bazzaz 1979). Nonetheless, Scholes and Archer (1997) argue that phenology and rooting depth are not unrelated because possession of a large and deep root system is one reason why trees can expand their leaves early and rapidly and retain them for longer into stress periods.

Timing of plant reproductive cycles affects not only plants, but also the animals that depend on plants resources for forage availability (Archibald and Scholes 2007). For example, a delay of a few weeks in the production of new leaves can make a difference to the survival and reproductive success of the herbivores that depend on them (Owen-Smith & Cooper 1989). The timing of plant reproductive cycles also impinges on plant-plant interactions such as competition for resources or pollinators. Therefore, phenological differences between species that result in a temporal division of resources may mitigate competitive interaction, promote coexistence and increase local species richness. This mechanism of species interaction has not been explored in *D. cymosum* communities in South Africa and our understanding of how species in *D. cymosum* interact and coexist is limited.

Water is a limiting resource, particlularly in South African savanna communities where *D. cymosum* occurs, and plant species are forced to optimize their use of water both in both time and space. Plants may alter their use of water by being physiologically active at different times (Solbrig and Orians 1977). Furthermore, co-occuring species, which have a similar phenological rhythm in the vegetative phase, will often differ in their timing of their reproductive phase (Seghieri et al. 1995). Accepting that water is the limiting resource in the semi-arid savanna communities, particularly in areas where *D. cymosum* occurs, we asked the following question: do common, co-ocuring species of similar growth form, partition available water in such a way as to minimize competition for this resource? We hypothesized that if they do, there will be some differences in vegetative and/or reproductive phenology amongst species of the same growth form.

2. Materials and Methods

The seasonal phenology of 6 experimental plants with contrasting growth forms (trees: *Burkea africana*, *Terminalia sericea* and *Ochna pulchra*; shrubs: *D. cymosum*, *Perinari capensis* and *Pygmaeothamnus zeyheri*) was investigated in relation to seasonal rainfall, October 2010 – March 2011 (Figure 4) .

Fourteen (100m x 100m) experimental sites selected for this experiment were those used previously to investigate competitive interaction (See chapter 2). During this experiment 15 permanent points 20m apart were identified. At each of the 15 points, the nearest experimental tree and shrub within 4 x 90º quadrants were inspected with respect to their phenological state. In order to promote the inclusion of less abundant experimental species, no more than two of the trees and / or shrubs at each point could be of the same species. Therefore, if the nearest experimental tree species in the third quadrant had already been recorded in the previous two, the second nearest experimental tree / shrub in that quadrant was then considered.

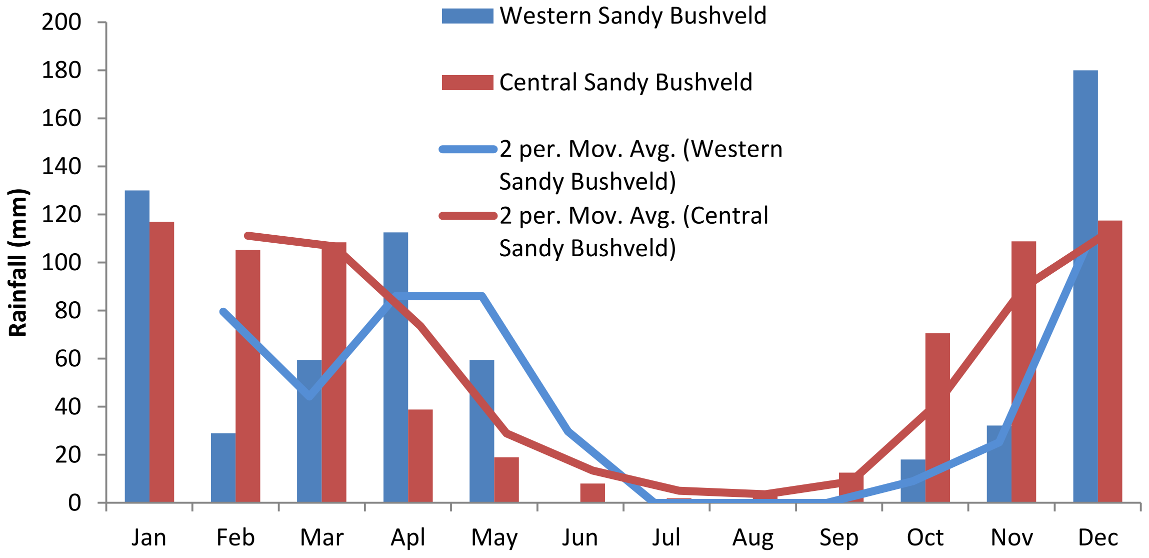

Figure 4: Rainfall for the experimental sites in both veld types during the year 2010/11 rainy season

Each of the selected experimental trees was classified into one of three height classes; <2m, 2-5m and >5m. Then the phenological state of both trees and shrubs was recorded according to one or more of the following phenophases: 1) leaf initials/ buds present; 2) leaves emerging from buds; 3) mature leaves present; 4) leaves senescing; 5) leafless; 6) reproductive buds / flowers present; 7) immature fruit present; 8) mature / dehiscing fruitpresent; 9) fruit from previous season present; 10) shoot elongation evidence (Shackleton 1999). Data was expressed as the frequency of phenophases per plant type along the rainfall gradient. (See Appendices 3 and 4.)

3. Results

The vegetative phenologies of tree species showed no evidence of niche separation. All trees had higher proportion of mature leaves and shoot elongation at the beginning of the experiment (October). Although, there were some inconsistencies at various times during the observation period, vegetative phenology generally followed the rainfall gradient throughout the study period (Figure 5).

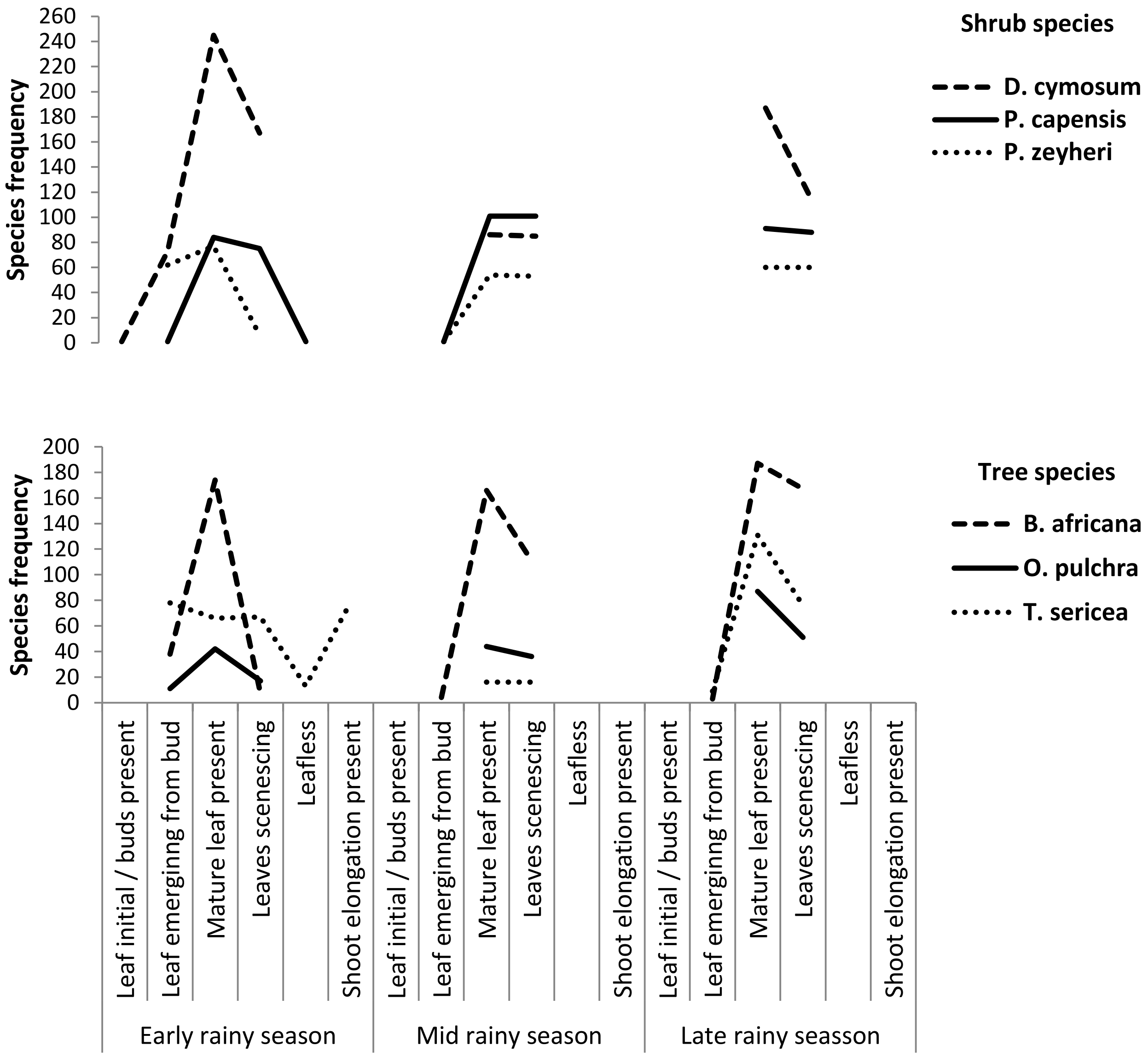

Figure 5: Vegetative phenology of experimental tree and shrub species along the rainfall gradient

Reproductive phenologies revealed no niche separation between *B. africana* and *T. sericea*, but was observed between *O. pulchra* and both *B. africana* and *T. sericea*. *Burkea africana* and *T. sericea* produced reproductive buds early in the season, which continued to grow until mature dehiscing fruit were present at the end of the rainy season. *Ochna pulchra* developed reproductive buds at the beginning of the rainy season, but aborted immature fruit. (Figure 6).

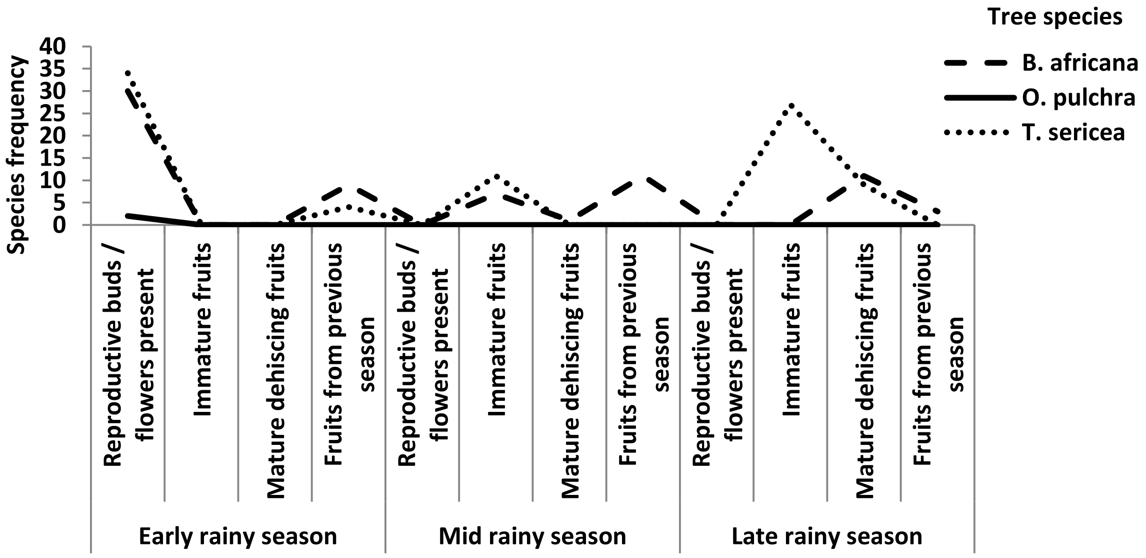

Figure 6: Reproductive phenology of experimental tree species along the rainfall gradient.

There was no niche separation by vegetative phenology observed amongst the shrubs species (See Figure 5). However, niche separation based on reproductive phenologies was observed between *D. cymosum* and both *P. capensis* and *P. zeyheri*. *Dichapetalum cymosum* produced its reproductive buds/flowers early in the rainy season and then aborted, while *P. zeyheri* continued to produce immature and mature dehiscing fruit at the end of the experiment. *Parinari capensis* only produced immature fruit, and no mature dehiscing fruit were observed during the experiment (Figure 7).

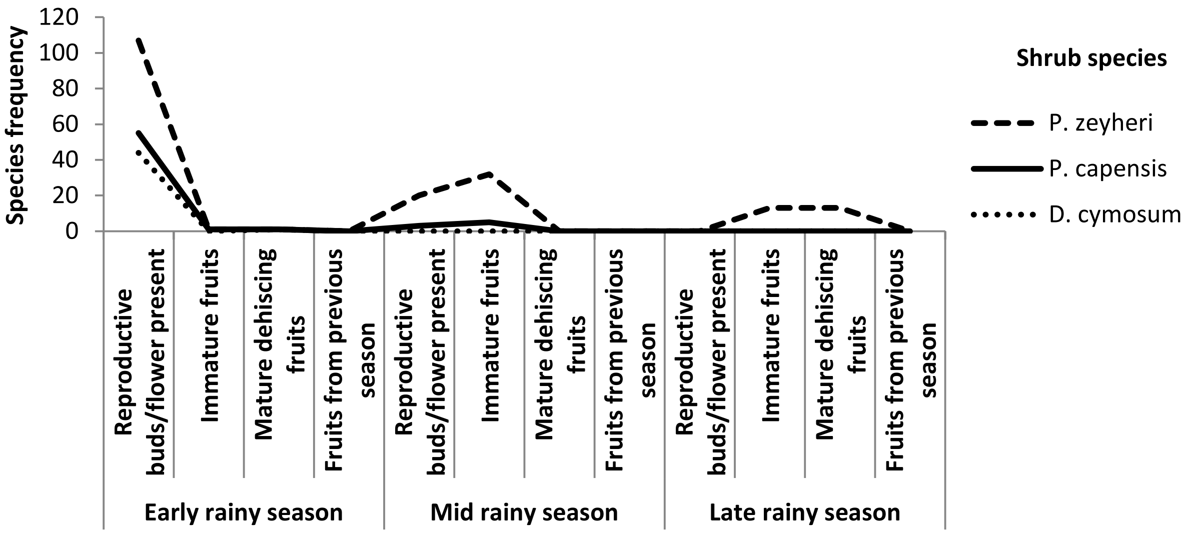

Figure 7: Reproductive phenology of experimental shrub species along the rainfall gradient

4. Discussion

Tree and shrub species in *D. cymosum* communities generally follow the same vegetative growth pattern. This is probably because the seasonal responses of woody (trees and shrubs) plant species are closely linked to their structure and function. Generally, woody plant species tend to produce leaves before the commencement of the rainy season (Milton 1987; Shackleton 1999). This is in contrast to the pattern followed by grasses, whose onset of current season's growth seems to depend on availability of rain (Dye & Walker 1987; Prins 1988). In semi-arid regions with cold winters, the growing season is short and woody plants use stored carbohydrates to produce new leaves, flowers and shoots early in the growing season (Milton 1987).

Although the trees in the *D. cymosum* communities showed slightly variable growth patterns in their vegetative phenology at different time intervals, the overall patterns were the same. These differences could be due to the range of different strategies that plants have for dealing with their seasonally arid and highly variable environments (Singh and Kushwaha 2005). So, for example, evergreen, deciduous, semi-deciduous, and facultative deciduous trees may occur in the same plant community and demonstrate different strategies in response to resource availability (Borchert 1999).

Ochna pulchra employs a relatively shallow root system and has a tendency to reproduce both sexually and reproductively (Rutherford 1983), an explanation for its observed niche separation by reproductive phenology from both *B. africana* and *T. sericea*, which have deep root systems and only reproduce reproductively. Lack of interspecific interferences observed between *B. africana* and *T. sericea* and negative segregation, with interspecific nearest neighbour pairs occurring more often than intraspecific ones (Smith and Grant 1986), provides a basis for them to interact and coexist without competing for resources. This is demonstrated by their ability to reproduce successfully without negatively affecting each other.

The three experimental shrub species are evergreen and so had mature leaves at the beginning of the rainy season and maintained them through to the end of the rainy season. This may be attributed to their enormous deep root systems (Scholes and Archer 1997), which enable them to use water stored deep in the soil profile. No shoot elongation was observed on the shrub species during the entire experiment. This confirms the work by Coley et al (1985), that in resource poor environments, plants with inherently slow growth rates are more successful than fast growing ones because slow growth favours large investment in anti-herbivore defenses.

The differences in reproductive phenology between *D. cymosum* and both *P. zeyheri* and *P. capensis* are due to differences in their mode of reproduction. *Dichapetalum cymosum* employs vegetative and sexual reproduction depending on habitat conditions. Although it produces reproductive buds and / or flowers these are usually aborted before mature fruit are produced. However, mature seeds have been found in some instances (Kellerman et al. 2005).The condititons under which *D. cymosum* aborts are unknown. *Parinairy capensis* and *P. zeyheri* produce immature fruit during the mid rainy season, but only *P. zeyheri* continues to produce mature dehiscing fruit. This could be a result of resource competition between *P. capensis* and other species in a community, since no competition was detected between the *P. zeyheri* and *P. capensis*.

5. Conclusion

Tree and shrub species in *D. Cymosum* infested savanna rangelands exhibit phenological niche separation based on their reproductive and growth strategies, which allows species coexistence due to differences in their resource requirements, both spatially and temporarily.

The timing, duration, and degree of synchrony of the various phenological phases have major implications for savanna plant community structure, function, regeneration, the quantity and quality of resources available for consumer organisms, as well as the adaptive and evolutionary behavior of species in this poorly understood ecosystem. Knowledge gained about these phenological phases is important for rangeland management not only for grazing strategies but also because *D. Cymosum* is one of the major causes of livestock poisoning and losses in South Africa. Development of ecological rangeland management strategies to reduce or eradicate it on rangelands would be beneficial, especially for emerging farmers, who are most affected by stock losses. There is also a possibility that some of the temporal phenological trends may be correlated with concentrations of plant toxins. This knowledge would be valuable for planning grazing strategies.

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CHAPTER 4

1. General Conclusion and Recommendations

This study investigated competitive (intra- and interspecific) interactions and phenological niche separation among plant species of similar growth form (trees and shrubs) in *D. cymosum* infested plant communities in South African savannas. Competitive interactions were investigated using nearest neighbour distances and were limited to within growth forms. Between growth forms were excluded due to the differences in structural architecture (canopy cover or volume versus patch size). Seasonal phenology was investigated in relation to seasonal rainfall. Data was expressed as the frequency of observed phenophases per plant type along the rainfall gradient.

Analysis of competitive intraspecific interactions showed a significant positive correlation between nearest neighbour distance and combined canopy cover of nearest neighbour pair. Significant segregation and slight aggregation found amongst species indicate that intraspecific competition and interspecific facilitation are responsible for the structure of *D. cymosum* communities. Competition is for water and nutrients below ground. These findings are consistent with previous studies on competition in arid and semi-arid savanna communities. Generally, species in these communities avoid competing with each other by occurring in one species clumps, so that any individual is more likely to be found near a member of its own species than near a member of another species. Consequently, individuals within clumps begin to compete with each other for limited resources on the basis of their similar life forms.

Dichapetalum cymosum and its associated shrubs species are segregated, with species occurring in familial clumps. *Dichapetalum cymosum* occurs in familial clumps mainly as a result of vegetative reproduction because it seldom produces seeds. *Parinari capensis* and *P. zeyheri* do produce seeds and so familial clumps are either a result of large numbers of seedlings crowding around their parents, or a result of heterogeneity of the environment. Lack of interspecific competition among species in *D. cymosum* communities is attributed to the spatial distribution patterns of individual plant species, the differences in species growth forms and reproductive strategies. These differences in ecologically important characteristics contribute to species coexistence in *D. cymosum* community.

Lack of interspecific competition and the slow growth rates observed during the vegetative phenology study suggest that in *D. cymosum* communities, natural selection is not necessarily based on a high competitive ability for nutrients, but rather on traits which reduce nutrient losses, such as low tissue nutrients concentrations, slow tissue turn-over rates and high nutrient resorption efficiency. The slow growth rate does, however, have implications for herbivory because it allows plants time to build defense mechanisms, which make them unpalatable. As *D. cymosum* occurs mainly in resource limited environments its defenses are mainly chemical, such as lignins and poly-phenolic compounds, which have dosage-dependent effects on herbivores.

Basically, nearest neighbour analysis remains a useful tool for studying competitive interactions among woody plant species in savanna communities, provided caution is exercised in its use. For example, more than one nearest neighbour pair needs to be measured because the technique is based upon a snapshot of the current situation of the spatial arrangement of individuals in a community. It fails to interpret this within a context of the temporal dynamics, which can be marked within savannas, which are inherently variable systems (Scholes and Walker 1993; Huggins et al 2000). Nearest neighbour analysis has an advantage in that it has the potential to differentiate intensity from the importance of competition in communities. The biggest challenge in the field experiments was the difficulty to recognize the centre of patches. However, the results obtained still provide a reliable indication of how species interact in *D. cymosum* communities.

It can be concluded from this study that interspecific competition is less important than intraspecific competition in resource poor *D. cymosum* savanna communities. This is because the importance of interspecific competition in natural plant communities is highly dependent on nutrient availability. Harmonious species coexistence is due to the spacing patterns of individuals, differences in species growth form and reproductive strategies.

2. Research gaps

In this study all the experimental plants displayed aggregation, although it was not significant in all instances. This suggests facilitation may occur among species (Scholes and Archer 1997; Bruno et al. 2003; Meyer et al 2008). However, facilitation mechanisms were not fully covered by this study, particularly the question of how these species facilitate each other's growth within the community. This is because facilitative mechanisms may act simultaneously with resource competition or allelopathy, and the overall effect of one species on another may be a product of multiple, complex interactions (Callaway 1995).

Intraspecific competition was found to be a key determinant of the structure of woody plant species in this community. However, the direct effect of competition on community structure was not fully investigated due to limitations in by spatial pattern techniques. Suitable techniques such as competitor removal could not be used because they are time consuming (Mayer et al. 2008) and labour intensive. Due to limitation brought by nearest neighbour technique, it was difficult to show the effect of both intra- and interspecific competition upon *D. cymosum* population size and population dynamics. It would have been interesting to investigate and compare different approaches to data collection and analysis as part of this study. However, this would prolong and or exceed the period specified by the university to complete these experiments.

3. Management recommendations

The intraspecific competition observed in this study does not provide a much needed insight into a strategy for the reduction or eradication of *D. cymosum* in rangelands. This is because it is through interspecific competition that certain plants species are excluded in communities (Scholes and Archer 1997). However, its management should entail minimizing soil disturbance in the form of trampling as this favours its vegetative mode of reproduction, with subsequent increases its relative abundance.

The resource availability hypothesis, plant defence strategies are determined by the growth rate of the plant and levels of defence investment increases as potential for growth decreases (Coley et al. 1985; Stamp 2003). This hypothesis holds true for species in *D. cymosum* communities with their inherent slow growth and high level of defences. Grazing of *D. cymosum* communities should take place during mid-summer, when enough grazing material is available to allow animals to vary their diet. The introduction of animals in poor condition or naïve animals into these lands should be avoided in winter as they will graze non-selectively resulting in *D. cymosum* poisoning. To utilize these areas as grazing lands, supplements need to be provided to assist in the detoxifications of toxins once ingested.

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5. APPENDICES

Appendix 1: The top 10 herbaceous species, frequency and mean percentages cover in order of their dominance in each of the veld types.

Veld type	**Species Name**	**Frequency**	**% Cover**
Central sandy bushveld	*Setaria sphacelata*	143	16
	Tristachya leucothrix	114	13
	Eragrostis curvula	102	11
	Digitaria eriantha	91	10
	Schizachyrium sanguineum	59	7
	Themeda triandra	37	4
	Heteropogon contortus	34	4
	Diheteropogon amplectens	33	4
	Urelytrum agropyroides	28	3
	Eragrostis racemosa	26	3
Western Sandy Bushveld	**Species Name**	**Frequency**	**% Cover**
	Digitaria eriantha	249	49.8
	Panicum maximum	105	21
	Eragrostis rigidior	104	20.8
	Aristida difusa	15	3
	Aristida meridionalis	6	1.2
	Eragrostis pallens	4	0.8
	Perotis patens	4	0.8
	Setaria sphacelata	3	0.6
	Schmidtia pappophoroides	2	0.4
	Urachloa mozambicensis	2	0.4

Appendix 2: Woody plant species composition, height classes and mean percentage cover in different veld types

		Height classes			
Veldtype	**Species**	**<2 m**	**2 m - 5 m**	**>5 m**	**Total cover (%) Species**
Central Sandy Bushveld	*Burkea africana*	1.4	24.7	0	26.0
	Acacia caffra	0.3	4.1	0	4.5
	Combretum molle	0.1	3.8	0	3.9
	Ochna pulchra	0.6	1.5	0	2.1
	Vangueria cyanescens	0.0	1.9	0	1.9
	Rhus lancea	0.1	1.3	0	1.4
	Euclea undulata	0.0	1.0	0	1.0
	Dombeya rotundifolia	0.1	0.7	0	0.9
	Combretum apiculatum	0.1	0.7	0	0.8
	Rhus pyroides	0.2	0.3	0	0.6
	Terminalia sericea	0.0	0.1	0	0.1
	Cerephium plumosum	0.1	0.0	0	0.1
	Euclea divinorum	0.1	0.0	0	0.1
	Bachinia galpinii	0.1	0.0	0	0.1
	Hymenodictyon floribundum	0.1	0.0	0	0.1
	Mundulea sericea	0.0	0.0	0	0.0
	Syringa	0.0	0.0	0	0.0
CSB Total Cover		**3.4**	**40.2**	**0**	**43.6**
Western Sandy Bushveld	*Terminalia sericea*	5.2	5.5	0	10.7
	Dichrostachys cinerea	6.1	2.4	0	8.6
	Grewia flava	6.9	1.0	0	7.9
	Combretum apiculatum	2.7	0.2	0	2.9
	Bachinia galpinii	2.0	0.0	0	2.0
	Grewia flavescens	0.4	0.7	0	1.2
	Acacia karoo	0.5	0.0	0	0.5
	Brachystegia boehmii	0.4	0.0	0	0.4
	Combretum molle	0.2	0.0	0	0.2
	Ximenia americana	0.1	0.0	0	0.1
	Sclerocarya birrea	0.1	0.0	0	0.1
	Ochna pulchra	0.0	0.0	0	0.0
	Acacia caffra	0.0	0.0	0	0.0
	Burkea africana	0.0	0.0	0	0.0
WSB Total Cover		**24.7**	**9.9**	**0**	**34.6**

Appendix 3. Phenological data of experimental shrub species along the rainfall gradient

		Shrub species			
Rainfall gradient	**Phenological characteristics**	***D. cymosum***	***P. capensis***	***P. zeyheri***	**Grand Total**
Early Rainy Season	Leaf initial/buds present	1			1
	Leaf emerging from bud	73	1	62	136
	Mature leaf present	245	84	77	406
	Leaves senescing	167	75	6	248
	Leafless		1		1
	Reproductive buds/flowers present	44	11	52	107
	Immature fruit		1		1
	Mature dehiscing fruit present	1			1
	Fruit from previous season				
	Shoot elongation present	7		2	9
	Total	**538**	**173**	**199**	**910**
Mid Rainy Season	Leaf initial/buds present				
	Leaf emerging from bud		1	1	2
	Mature leaf present	86	101	54	241
	Leaves senescing	85	101	53	239
	Leafless				
	Reproductive buds/flowers present		3	17	20
	Immature fruit		5	27	32
	Mature dehiscing fruit present				
	Fruit from previous season				
	Shoot elongation present				
	Total	**171**	**211**	**152**	**534**
Late Rainy Season	Leaf initial/buds present				
	Leaf emerging from bud				
	Mature leaf present	187	91	60	338
	Leaves scenescing	114	88	60	262
	Leafless				
	Reproductive buds/flowers present				
	Immature fruit			13	13
	Mature dehiscing fruit present			13	13
	Fruit from previous season				
	Shoot elongation present				
	Total	**301**	**179**	**146**	**626**

Appendix 4: Phenological data of experimental tree species along the rainfall gradient

		Tree species			
Rainfall gradient	**Phenological characterstics**	***B. africana***	***O. pulchra***	***T. sericea***	**Grand Total**
Early Rainy Season	Leaf initial/buds present	1			1
	Leaf emerging from bud	35	4	13	52
	Mature leaf present	118	28	50	196
	Leaves senescing	65	19	45	129
	Leafless			1	1
	Reproductive buds/flowers present	40	4		44
	Immature fruit			1	1
	Mature dehiscing fruit present				
	Fruit from previous season				
	Shoot elongation present	5			5
	Total	264	55	110	429
Mid Rainy Season	Leaf initial/buds present				
	Leaf emerging from bud				
	Mature leaf present	93	20	9	122
	Leaves senescing	91	20	9	120
	Leafless				
	Reproductive buds/flowers present	3		2	5
	Immature fruit	6		2	8
	Mature dehiscing fruit present				
	Fruit from previous season				
	Shoot elongation present				
	Total	193	40	22	255
Late Rainy season	Leaf initial/buds present				
	Leaf emerging from bud				
	Mature leaf present	104	32	80	216
	Leaves senescing	88	24	39	151
	Leafless				
	Reproductive buds/flowers present				
	Immature fruit	6			6
	Mature dehiscing fruit present	6			6
	Fruit from previous season				
	Shoot elongation present				
	Total	204	56	119	379

Appendix 5: Experimental species, growth form, Accession number and Cabinet number as housed at ARC-Roodeplaat Herbarium

Name	**Growth form**	**Accession no.**	**Cabinet number**
Burkea africana Hook.	Tree	2332	3474000
Ochna pulchra Hook. F.	Tree	4568	5112000
Terminalia sericea Burch ex DC	Tree	4572	5544000
Parinari capensis Harv. subsp. *capensis*	Shrub	2384	3405000
Pygmaeothamnus zeyheri (Sond) Robyns var. zeyheri	Shrub	5021	8351020
Dichapetalum cymosum (Hook.) Engl.	Shrub	1966	4283000