DETERMINANTS OF COMMUNITY COMPOSITION AND DIVERSITY IN KWAZULU-NATAL MESIC GRASSLANDS: EVIDENCE FROM LONG-TERM FIELD EXPERIMENTS AND POT AND PLOT COMPETITION EXPERIMENTS

RICHARD WARICK SINCLAIR FYNN

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PREFACE

This thesis is the result of the author's original work except where acknowledged or specifically stated to the contrary in the text. It has not been submitted for any degree or examination at any other university or academic institution.

Signed ....   Date 30 / 04 / 04
Richard Warwick Sinclair Fynn

Signed ....   Date 29 / 04 / 04
Prof. Kevin Kirkman (supervisor)

ABSTRACT

A predictive understanding of plant community response to various environmental influences (e.g. type, timing and frequency of disturbance, site productivity, fertilization, etc.) is a general goal of plant ecology. This study sought to further understanding of mesic grassland dynamics in KwaZulu-Natal using long-term field experiments (> 50 years) and short-term pot and plot competition experiments. The specific objectives were to: 1) examine the effects of long-term burning of grassland on soil organic matter content because of its potential impact on nitrogen cycling and community composition, 2) examine patterns of community composition and species richness in response to different type, timing and frequency of disturbance (burning and mowing) in a long-term grassland burning and mowing experiment and to different type and amounts of fertilizer application in a long-term grassland fertilization experiment, 3) develop hypotheses concerning the response of different species to disturbance and fertilization, and test these hypotheses using pot and plot competition experiments, and 4) provide a general synthesis of the results of the various field, pot and plot experiments that may be used to develop a predictive theoretical framework for mesic grassland dynamics.

Total soil nitrogen was lowest in sites burnt annually, intermediate in sites burnt triennially and highest in sites protected from disturbance and sites mown annually in the dormant-period (spring or winter). Winter burning reduced soil organic carbon and total soil nitrogen more than spring burning. Mineralizable nitrogen was reduced by burning.

The different effects of type, timing and frequency of disturbance on total soil nitrogen appeared to be an important determinant of community composition and species richness. Short-grass species (*Themeda triandra, Eragrostis capensis, Heteropogon contortus, Diheteropogon amplectens and Eragrostis racemosa*) were most abundant in annually burnt sites (especially winter burnt sites), whereas medium and tall-grass species (*Eragrostis curvula, Cymbopogon spp., Hyparrhenia hirta* and *Aristida junciformis*) were most abundant in triennially burnt sites, sites protected from disturbance and sites mown annually in the dormant-period, all of which had higher total soil nitrogen than annually or biennially burnt sites. Species richness and short-grass species declined with increasing levels of nitrogen fertilization in the fertilizer experiment and declined with increasing productivity and nitrogen availability in both the fertilizer and burning and mowing experiments. Thus, it was hypothesized that the type, timing and frequency of disturbance resulted in different

compositional states through different effects on soil resources (especially nitrogen), which affected the competitive balance between short and tall species.

The hypothesis that composition was determined by disturbance-mediated soil nitrogen availability was supported by competition experiments, which revealed that short-grass species were most competitive in low-nutrient/low-productivity treatments and tall-grass species most competitive in high-nutrient/high-productivity treatments. The fertilizer experiment and a competition experiment revealed that tall broad-leaved species were most competitive in sites of highest productivity, fertilized with both nitrogen and phosphorus, whereas tall narrow-leaved species were most competitive in sites of intermediate productivity, fertilized with nitrogen only.

It was hypothesized that summer mowing increased the abundance of short-grass species and decreased the abundance of tall-grass species in the burning and mowing experiment by increasing the competitive ability of short-grass relative to tall-grass species, rather than the tall-grass species being less tolerant of mowing. A competition experiment revealed that tall-grass species (*Hyparrhenia hirta* and *Panicum maximum*) were as tolerant of cutting as a short-grass species (*Themeda triandra*). *Themeda triandra* was shown to become extremely competitive in cutting treatments, reducing the biomass of most other species relative to their monoculture biomass, showing that its dominance of mown sites in the burning and mowing experiment was a result of its superior competitive ability rather than greater tolerance of mowing.

However, many tall erect herbaceous dicots appeared to be intolerant of summer mowing, probably because their meristems are aerial and easily removed by mowing, whereas short creeping herbaceous dicots were increased by summer mowing probably because their meristems were below the mowing height. Further, these short species would be vulnerable to shading in unmown sites. Thus, species with basal meristems (hemicryptophytes) or meristems near the soil surface (geophytes) appear to be more tolerant of mowing than species with aerial meristems (phanerophytes), but the tradeoff is that a low meristem height renders them vulnerable to shading in unmown sites.

Very high litter accumulation in the sites protected from disturbance appeared to have a direct influence on community composition and species richness. Species that dominated these sites (e.g. *Tristachya leucothrix* & *Aristida junciformis*) initiated tillers below-ground and had sharp erect shoots that appeared to be an adaptation for penetrating litter. Species that initiate tillers below-ground are probably less vulnerable to the effects of shading by litter because their tiller initiation is not dependent on high light availability. The fact that *Aristida*

junciformis was shown to have very low competitive ability in two competition experiments, suggests its dominance of protected sites was through tolerance of high litter levels rather than competitive exclusion of other species. Low grass species richness in these sites was probably a result of an inability of many species to tolerate these high litter levels.

This study has revealed that inherent site productivity and its interaction with the effect of disturbance on soil resources and litter levels is a major determinant of community composition and species richness. The effect of type, timing and frequency of disturbance on soil nitrogen was able to account for the principal changes in community composition. Thus, the influence of disturbance on soil nitrogen is a unifying principle in plant ecological theory that enables greater understanding of disturbance-composition relationships. However, intolerance of certain forms of disturbance (e.g. mowing) by species with aerial meristems, or intolerance of accumulating litter in the absence of disturbance by species without sharp erect shoots, may also have important influences on composition. In addition, this study has revealed that plant traits (height, leaf width, position of tiller initiation, shoot morphology and position of meristems) were well correlated with the various effects of disturbance and fertilization on community composition, indicating that a plant trait-productivity-disturbance framework has great potential for understanding and predicting species response to disturbance and multiple limiting nutrients.

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CHAPTER 1

THEORETICAL AND CONCEPTUAL ISSUES CONCERNED WITH THE DETERMINANTS OF COMMUNITY COMPOSITION IN GRASSLANDS

Introduction

It has been recognized for centuries that repeatable patterns in plant community composition and structure in relation to climate, altitude, soils and disturbance are common in nature (Clements 1916; Whittaker 1980). In other words, species and populations are not just randomly distributed across the landscape. Further, predictable temporal changes in community composition are well recognized (Clements 1916; Odum 1969). Numerous studies of the development of vegetation (succession) dating back to the 1500's are reviewed by Clements (Clements 1916). Many of these authors recognized that plant community development passed through a number of distinct community types or seres. Thus, plant communities are dynamic in both space and time. The mechanisms responsible for spatial and temporal changes in the abundance of a species and community composition are thought to be related to physiological tolerance of various physical factors (e.g. soil pH, salinity, fertility, moisture, temperature, biomass removal etc.) and competition with other species (for pollinators, space, soil resources and light) (Austin 1990). Thus, species are thought to have certain preferred niches beyond the boundaries of which individuals are unable to grow or survive (i.e. their fundamental niche) and core areas within their fundamental niche beyond which they may be able to grow and survive in the absence of competitors but are unable to maintain viable populations in the presence of competitors (i.e. their realized niche). Consequently, interspecific competition has been invoked as a major determinant of the distribution and abundance of plant species. It is clear that a species niche space and optima will vary in space with changes in climate, soil fertility, pH, disturbance etc. and in time as these same factors change as a result of the effect of the species on their environment (autogenic succession) or temporal changes in climate.

Development of Succession theory

The universal phenomenon of changes in the abundance and dominance of different species over time has been named succession. It is a concept that forms the core of plant ecology theory because it provides a framework for understanding and predicting community organization and dynamics. Two forms of succession are recognized: 1) Primary succession which represents vegetation development after new land, without any soil or organic material, is exposed such as the edges of receding glaciers, on volcanic lava flows, wind deposited sand dunes, bare rock exposed after landslides etc. 2) Secondary succession which represents vegetation development after disturbance (i.e. on abandoned croplands, landslides, slash and burn forest clearing, natural disasters, etc.). Thus, the critical difference between primary and secondary succession is that in secondary succession soils are generally well developed with a relatively high level of organic matter and nutrients and an *in situ* seed bank. Consequently, vegetation development is likely to be considerably faster in secondary succession. Further, mechanisms responsible for vegetation change in primary succession may not apply to secondary succession because of differences in initial water and nutrient availability, but this will be discussed later.

Although, temporal changes in vegetation have been probably recognized for thousands of years, the phenomenon of succession was first formally organized into a conceptual framework by Frederick Clements less than a hundred years ago (Clements 1916). He related succession to the development of an organism in which the process of succession was the growth and maturing of a super organism or climax community where the degree of maturity is determined by the site and climate. He termed distinct plant communities that develop during the development of the climax community as Sere's from the Latin word *sero,* to join or connect. He considered succession to be a predictable deterministic process with a single end point or climax state for a particular climatic zone and site. He recognized the importance of soil depth, moisture and nutrient content and the effect of plants on the soil (reaction) and its implications for further vegetation development. In other words, he concluded that during primary succession it was necessary for earlier species to modify the soil sufficiently for later successional

species to be able to establish. He recognized that seed mobility and production have an important influence on the pattern of succession. He proposed that competition was an important mechanism controlling successional replacement of species, with competition for water being important in early succession and competition for light becoming increasingly important in the later stages of succession. This viewpoint is essentially similar to many popular contemporary theories of succession (e.g. Tilman 1985, 1988). Others have also emphasized the increasing importance of shade-tolerance as a mechanism of replacement as succession proceeds (MacArthur & Connell 1966). In fact, both Clements (1916) and MacArthur & Connell (1966) make reference to the fact that foresters tables of shade tolerance agree well with patterns of forest succession.

Later developments in succession theory began to consider the relationship between successional maturity and complexity, information content, diversity and stability (Margalef 1963; Odum 1969; Whittaker 1970). Clements did not ever really consider these relationships in his theory probably because he considered succession to be the maturing of a "super organism" analogous to the development of an individual seedling into a mature tree. If this analogy is true then complexity and diversity should not change much during succession because a seedling is as complex as a mature tree, it is only the size that differs. Margalef (1963) proposed that as ecosystems mature (during the process of succession) they become more diverse and complex. He proposed that more mature later successional communities require less energy per unit biomass. In his words: "*An ecosystem that has a complex structure, rich in information, needs a lower amount of energy for maintaining such structure. If we consider the interrelations between the elements of an ecosystem as communication channels, we can state that such channels function on average more effectively, with a lower noise level, if they are multiple and diverse, linking elements not subjected to great changes. Then, loss of energy is lower, and the energy necessary for preventing decay of the whole ecosystem amounts relatively to less.*" Thus, he considered later successional communities to be more efficient. He proposed an energetic mechanism of succession: "*Let us remember that succession is simply the exchange of an excess available energy in the present, for a future increase of biomass. An ecosystem in its present state is less mature and has an excess production that goes to the future and helps reorganize the ecosystem in a more*

mature form. If there is no available excess production or it is drained out of the system, succession proceeds no further." He also proposed that abiotic control over ecosystem dynamics became relatively weaker, whereas internal control through biotic factors became stronger as succession proceeds. Thus, early successional communities have stronger abiotic control over population dynamics than later successional communities. These ideas were essentially echoed by Odum (1969) and Whittaker (1970). Certain studies have supported these theories (e.g. Naeem et al. 1994; Tilman & Downing 1994; Tilman 1996) but their conclusions have been criticized (Huston 1997).

One of the largest areas of dispute in the theories of succession proposed by Clements is the question of the mechanism of successional advance. Clements proposed that later successional species can only successfully establish at a site (ecesis) after the site has been modified (reaction) by earlier succession species (Clements 1916). Numerous studies have failed to support this notion. Many studies reviewed by Drury & Nisbet (1973) showed that a large proportion of the late successional species were present at the start of succession. In fact, some studies showed that late successional species grew far better when the early successional species were removed. They concluded that many successional patterns simply reflect differential growth rates of species, with smaller species dominating early in succession because of higher maximal growth rates. In the light of this sort of evidence, Connell & Slatyer (1977) proposed that successions may follow a number of different pathways. In some cases later succession species are only able to establish at a site once earlier succession species have sufficiently modified the site (facilitation model). In other cases, any species is able to establish at the site but will modify the site making it unsuitable for early- but not late-successional species (tolerance model) or may modify the site making it unsuitable for both early- and late-successional species (inhibition model).

Clearly, mechanisms of succession can only be understood by differentiating between primary and secondary succession and the degree of disturbance. If disturbance only removes the vegetation cover but leaves the soil with its organic matter, nutrients, moisture and propagules intact then it is clear that a facilitation model will not be applicable because seeds of most species should be present and sufficient resources available for them to establish. If however, disturbance removes all the soil leaving only

bare rock or deposits a deep layer of infertile sand, then clearly not all species will be able to establish at these sites and a facilitation model will apply. This important distinction was well recognized by Clements who noted: "*If denudation consists of the destruction of the vegetation alone, the soil factors are changed relatively little. The sere thus initiated is relatively short, consisting of fewer stages and reaching the climax in a short time. If the soil is much disturbed, however, the conditions produced approach much nearer the original extreme, and the resulting sere is correspondingly longer and more complex. The degree of disturbance may be so great as to bring back the original extreme conditions, in which case the normal course of development is repeated. This amounts to the production of a new area, both with respect to the extreme condition and the lack of germules*" (Clements 1916; page 60).

There are numerous examples showing that later successional species cannot establish at sites where there are insufficient resources to sustain them. It is not even necessary to use widely different life-forms such as an early-successional grass and a late-successional tree as examples. Even within a life-form, such as amongst grasses, species may differ in their ability to establish at sites. For example, it was shown that the late-successional grasses, *Andropogon scoparius* and *Panicum virgatum*, were unable to colonize abandoned fields in Oklahoma because their requirements for nitrogen were higher than the early-successional grass, *Aristida oligantha* (Rice et al. 1960). Nitrogen levels in these oldfields have become so low that *Andropogon scoparius* and *Panicum virgatum* are unable to establish without the addition of fertilizer. Likewise, in KwaZulu-Natal mesic grasslands the late successional grass *Panicum maximum* cannot establish unless the grassland is fertilized with both nitrogen and phosphorus (Le Roux & Mentis 1986). The fact that species richness increased with succession in Minnesota old fields of extremely low soil nitrogen content suggests that many species were not able to establish in the youngest fields owing to their low soil nitrogen contents but were able to establish later when nitrogen availability had increased (Inouye et al. 1987).

Studies of primary successions have revealed that many of the late successional species are rare in the youngest sites where nitrogen availability is extremely low. In Alaska, vegetation development after retreating glaciers follows a sequence of herbs (*Epilobium latifolium*, *Equisetum variegatum* and *Lupinus nootkatensis*) and some

shrubs, followed by nitrogen fixing alder (*Alnus crispa*) and finally cottonwood (*Populus trichocarpa*) and spruce (*Picea sitchensis*). This sequence is accompanied by an associated increase in soil nitrogen, especially after colonization by nitrogen fixing alder. It is only after sufficient nitrogen has accumulated that conditions are suitable for spruce to dominate (Crocker & Major 1955; Crocker & Dickson 1957). Similar patterns of replacement in plant life form with increasing soil nitrogen on a successional sequence below the Franz Josef Glacier in New Zealand have been observed (Wardle & Ghani 1995). On lake Michigan sand dunes, several grass species such as *Ammophila breviligulata, Calamovilfa longifolia* and *Andropogon scoparius* and also dune building shrubs such as *Prunus pumila* appear to be necessary to prepare the way for the establishment of *Pinus banksiana* and *Pinus strobes* and especially for the later succession species, *Quercus velutina* (Olson 1958). The mechanism of facilitation appears to be related to dune stabilization as well as increased nutrient and moisture availability. That facilitation, through increased nutrient and moisture availability, is important is demonstrated in the fact that the low tissue nutrient contents of these species and the high leaching rates in the dunes, resulted in nitrogen never reaching levels high enough (even on 10 000 year old dunes) to support further succession to oak-hickory and sugar maple-beech forest. These species only occured in localized zones that allow moisture and nutrient accumulation (Olson 1958). During primary succession on dunes in the Netherlands, tall late-successional grasses and certain shrub species only became established and rose to dominance after earlier succession species had increased the nitrogen and moisture content of the dune soils (Olff et al. 1993). This again suggests that facilitation was an important mechanism in succession.

The evidence so far reviewed indicates that later successional species (grasses or trees) have high nutrient demands that do not allow them to establish in nutrient-limited environments. There is clear evidence that the facilitation model of Connell & Slatyer (1977) is valid probably for most primary successions and some secondary successions on extremely low nitrogen soils. In most secondary successions, however, nutrient availability appears to be high enough that later successional species can establish without the need for site modification (reaction) by earlier successional species. It appears that under these conditions of higher nutrient availability growth rates of species

determine the pattern of succession with fast growing competitive ruderals often dominating early in succession (e.g. Grime 1979; Bazzaz 1996). These species may suppress later successional species initially but eventually will be replaced by shade-tolerant later successional species (e.g. Clements 1916; Drury & Nisbet 1973). The importance of growth rate early in succession and shade-tolerance later in succession has been predicted mathematically and theoretically (Huston & Smith 1987; Tilman 1985, 1988). The phenomenon of initial domination of sites by fast growing competitive ruderals has been coined "transient dominance" (e.g. Clements 1916; Tilman 1988).

Contemporary theories of community organization

Habitat productivity and disturbance have been recognized as the principal determinants of community composition, diversity and structure (Grime 1979; Huston 1979; Tilman 1988; Bazzaz 1996). Habitat productivity has the potential to influence community organization because it is linked to soil nutrient and light availability, both of which are essential resources for plants. Because different plant species have different requirements for these resources, it is a logical conclusion that habitat productivity must influence community organization. However, the actual mechanisms behind compositional changes along productivity gradients are more complex than the differing resource requirements of various species and has resulted in a longstanding and unresolved debate in ecological theory.

Increasing habitat productivity generally results in decreasing light availability (Tilman 1988; Schimel et al. 1991; Twolan-Strutt & Keddy 1996; Peltzer et al. 1998; Cahill 1999; Rajaniemi 2002). Thus, nutrient and light availability are generally inversely correlated. Consequently, plant strategies in fertile productive habitats, where light is often a limiting resource, generally tend to be orientated towards rapid growth rates, tall growth form, broad leaves and shade tolerance, whereas the strategies of plants in infertile unproductive habitats, where soil resources are strongly limiting, tend towards slow growth rates, short growth form and large root allocation (Chapin 1980; Grime 1979; Tilman 1988). Grime, in his well-known competitor, stress tolerator, ruderal (CSR)

model, proposed that plants have three primary strategies (Grime 1977, 1979). For fertile productive habitats, plants adopt a competitive strategy by growing tall and taking up space but also producing large root biomass for the uptake of water and nutrients to support rapid growth, large above-ground biomass and photosynthetic mechanisms. For infertile unproductive habitats, plants adopt a stress tolerant strategy but slow growth rates, low nutrient demands and conservation of nutrients. Grime maintains that plants do not compete in these habitats but rather tolerate the conditions. In extremely disturbed habitats where a perennial growth form is impossible, plants adopt a ruderal strategy. In this CSR framework Grime allows for some hybridization of strategies where an environment may be midway between fertile and infertile or undisturbed and highly disturbed. For example, in a productive habitat with a moderate disturbance frequency plants may have a competitive-ruderal strategy.
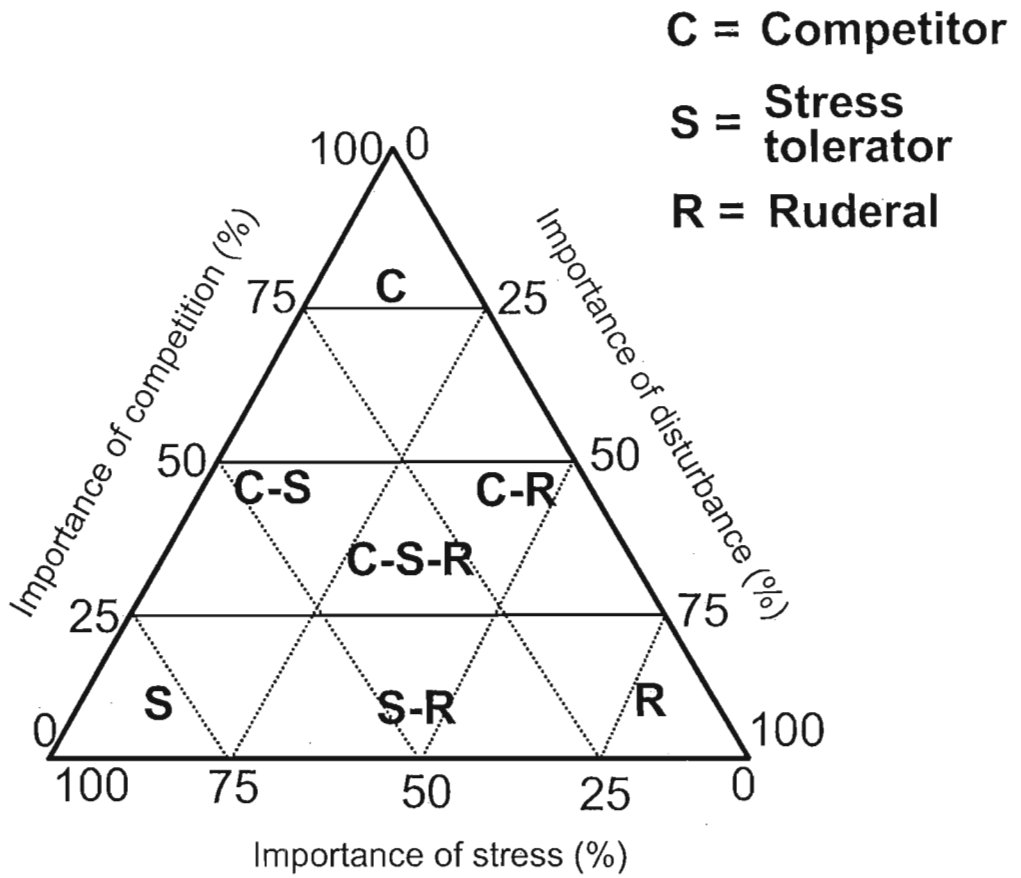
Fig. 1.1. Grime's three primary strategies of plants (competitors, stress tolerators and ruderals) and their various combinations as influenced by fertility, stress and disturbance (Grime 1977).

Tilman (Tilman 1985, 1988) has disputed Grime's unified concept of competitive ability noting that there is good theoretical and empirical evidence to support the notion that plants compete for limiting soil resources in infertile habitats. He has developed a theory of competition for limiting soil resources based originally on models of algal nutrient competition but extended to competition for limiting nutrients by higher plants (Tilman 1982). Tilman has proposed that plants make tradeoffs for competitive ability in fertile or infertile habitats through above- or below-ground allocation patterns (Tilman 1985, 1988). Thus, plants make tradeoffs for competitive ability in fertile habitats through allocation to stems, height, above-ground biomass and photosynthetic mechanisms at the expense of competitive ability in infertile habitats, and tradeoffs for competitive ability in infertile habitats through large allocation to roots and nutrient uptake mechanisms at the expense of competitive ability in fertile habitats. This is because a proportion of total energy available to the plant allocated to one function or structure results in less energy to allocate to other functions or structures. Thus in Grime's model, root, shoot and total competition intensity increase with increasing habitat productivity (Fig. 1.2a), whereas in Tilman's model, root competition intensity decreases, shoot competition intensity increases and total competition intensity is unchanging with increasing productivity (Fig. 1.2b).
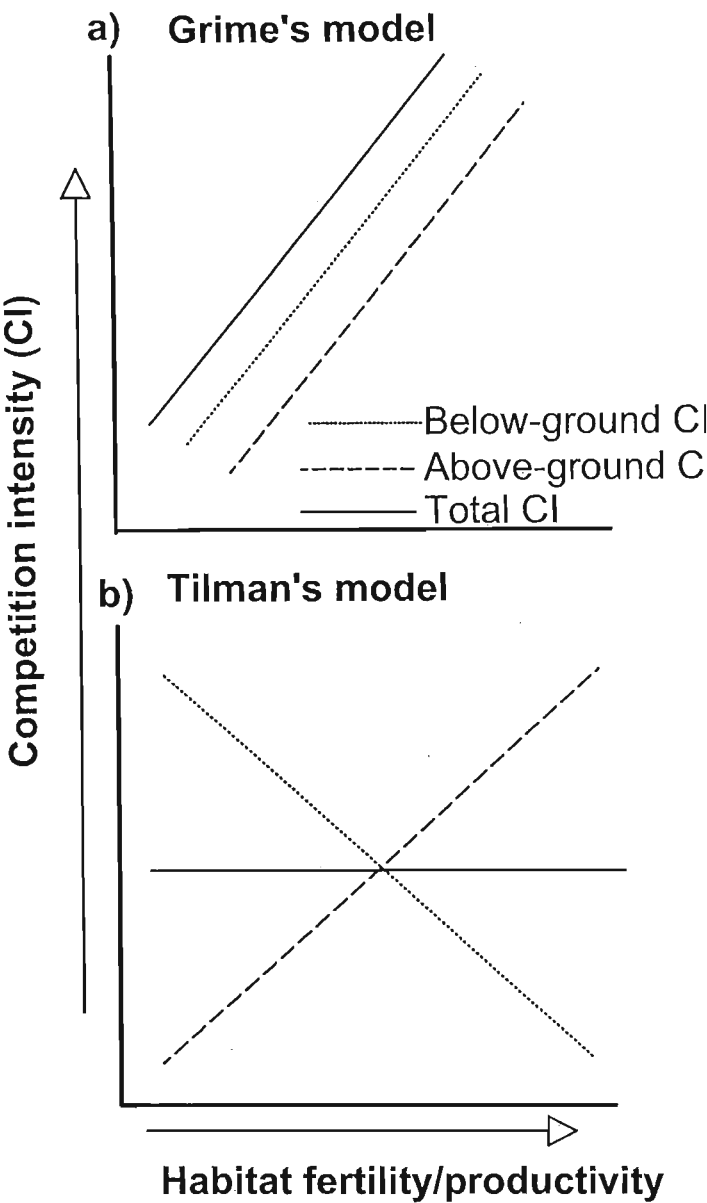
Fig. 1.2. Comparison of Grime (a) and Tilman's (b) models of predicted trends in above, below and total competition intensity along productivity gradients.

Wilson & Tilman (1991; 1993) showed that below-ground competition was greatest in infertile habitats, above-ground competition was greatest in fertile habitats and total competition intensity remained the same in fertile and infertile habitats. These results support Tilman's model (Tilman 1985, 1988). However, in another study, using one type of phytometer species, total, above- and below-ground competition intensity increased with increasing habitat productivity, in support of Grime's hypothesis, whereas when using another phytometer species, above-ground competition intensity increased, below-ground competition intensity decreased, and total competition intensity remained constant along a productivity gradient, in support of Tilman's hypothesis (Twolan-Strutt & Keddy 1996). How can these two contrasting results be reconciled? One possibility is that if the phytometer species performs poorly in infertile habitats, it will show very little effects of compeition on it, irrespective of the competitive ability of the competitor.

Results of recent studies, however, have suggested that studies examining the strength of root and shoot competition along productivity gradients may have given contrasting results because most of these studies have assumed that below- and above-ground competition are additive. Cahill (1999, 2002) has shown that positive and negative interactions between above- and below-ground competition may occur. If negative interactions occur then the competitive response of target species experiencing both root and shoot competition may be less than the response predicted by an additive model (e.g. Cahill 2002). The reverse will be true if interactions are positive (e.g. Cahill 1999). The problem with most studies of competition intensity is that they did not directly measure shoot competition intensity but obtained it by indirect means (total competition intensity − root competition intensity). In other words they assumed that below- and above-ground competition are additive (root competition intensity + shoot competition intensity = total competition intensity), whereas they may be interactive (Cahill 1999, 2002). Negative interactions occurred only for those species that were short rossete forming species and not for the taller species possibly because these rossete forming species are shade-tolerant sub-canopy species. They showed large effects of root competition because in the absence of shoot competition they allocated large biomass to roots (Cahill 2002). When they experienced root and shoot competition, however, they allocated more biomass to shoots because increased photosynthetic capability was

necessary (i.e. they had high plasticity). Positive interactions occurred only in high productivity sites when the initial effects of root competition reduced the growth of target species, allowing them to be shaded by neighbors, resulting in greater asymmetric competition for light (Cahill 1999). In other words root competition caused the target species to be subjected to more intense shoot competition than they would have been in the absence of root competition. Thus, these interactive effects of root and shoot competition may explain the contrasting results of the two different target species in the Twolan-Strutt & Keddy (1996) study as well as the contrasting results of all the other studies. Cahill (1999) has proposed a model where there will be no interactions between root and shoot competition at low productivity because competition is mainly below ground and symmetric. At intermediate productivity there is a potential for positive interactions because a target species has the potential to reach the canopy in the absence of root competition resulting in very little shoot competition. At the highest levels of productivity no interactions or negative interactions can occur because of plasticity responses of targets (negative interaction) and the fact that targets have little chance of reaching the canopy at such high productivity (hence no positive interaction). The model is similar to Tilman's (Tilman 1985, 1988) in that below-ground competition intensity decreases with increasing productivity, whereas above-ground competition intensity increases at the highest levels of productivity. It appears, therefore, that models of positive correlation between above- and below-ground competition intensity (e.g. Grime 1979) are losing support amongst ecologists.

Do plants compete in infertile habitats?

Most ecologists are in agreement that competition plays an important role in structuring plant communities in fertile productive habitats (Clements 1916; Grime 1979; Tilman 1988; Gaudet & Keddy 1995; Bazzaz 1996; Goldberg 1996) but there is very little agreement over the role of competition in infertile habitats (Grime 1979; Thompson 1987; Tilman 1987; Tilman 1988; Twolan-Strutt & Keddy 1996).

One of Grime's major points of contention over the concept of tradeoffs for competitive ability in infertile habitats is that species that have made a tradeoff for traits associated with competitive ability in infertile habitats do not grow faster in low nutrient treatments than species having traits associated with competitive ability in fertile habitats (Grime 1977, 1979). Many studies have not (e.g. Mahmoud & Grime 1976; Berendse & Elberse 1990) but others have (e.g. Rice et al. 1960; Parrish & Bazzaz 1982; Tilman 1986; Austin et al. 1985; Ghebrihiwot *et al.* in prep) shown evidence of faster growth rates of species characteristic of infertile habitats, when grown in low nutrient treatments, compared with species associated with fertile habitats. *Oenothera biennis* grew much better in monoculture than late-successional species in low nutrient treatments and grew orders of magnitude better when grown in competition with other species compared with its growth in monoculture in low nutrient treatments (Parrish & Bazzaz 1982). Thus, there was clear evidence of competition on low fertility soils. A thistle species, *Carthamus lanatus*, was able to grow better than other thistle species at very low nutrient concentrations (Austin et al. 1985). This appeared to be related to its ability to allocate more to root biomass relative to shoot biomass (narrower shoot/root ratio) at low nutrient concentrations. This growth advantage at low nutrient concentrations translated into greater competitive ability of this species in low nutrient treatments. The growth of annuals in the Sonoran desert was shown to be strongly density dependent, clearly indicating the effects of competition in a soil-resource limited system (Inouye et al. 1980). In a drought year that was severe enough to result in insufficient productivity to cause above-ground competition (as seen in very infertile habitats), transplant mortality was strongly increased by root competition (Cahill 2003). Further, Wilson & Tilman (1991, 1993) and Twolan-Strutt & Keddy (1996) demonstrated the effects of root competition in infertile habitats. Other examples of competition in infertile habitats are given by Tilman (1988), on page 23.

If plants do make tradeoffs, either for greater competitive ability in fertile habitats, or greater competitive ability in infertile habitats, then one would predict that the hierarchy of competitive effect on a phytometer species by a large range of species would be reversed in low and high nutrient treatments. Some studies have shown that hierarchy is consistent across different levels of fertility with the taller species having the greatest

competitive effect in both high and low nutrients (Keddy *et al.* 2000). However, approximately half of the studies reviewed show a reverse in the competitive hierarchy at different levels of fertility (Goldberg 1996). The fact that competition has been demonstrated in many different forms of unproductive habitats shows unambiguously that competition does occur in infertile/unproductive habitats, whereas a lack of evidence for competition in these habitats in other studies is not compelling evidence that competition does not occur in infertile habitats when it is seen in the context of other studies. This point is excellently illustrated in the contrasting results of (Twolan-Strutt & Keddy 1996). Using one type of phytometer species (*Carex crinata*) we might have concluded that competition does not occur in infertile habitats but in exactly the same study but with another phytometer species (*Lythrum salicaria*) we might have concluded the opposite. Lack of evidence in certain situations may be due to the methods used or the species investigated. However, there is the possibility that both Grime's and Tilman's models are correct for certain situations or species (e.g. some species may make tradeoffs for below-ground competitive ability, whereas other species may make tradeoffs to be able to tolerate extremely infertile soils).

Plant traits and competitive ability

Goldberg (1996) has provided a list of some important plant traits and their predicted correlations with competitive ability in different environments. A strong competitive effect in productive environments would be related to the ability to preempt space. Thus, high maximum relative growth rates and large allocation to above-ground biomass would be traits that would facilitate preemption of space. A strong competitive response in productive environments would be related to the ability to avoid being shaded by growing tall or to tolerate shade through broad-leaves, high nitrogen contents in the leaves and low light compensation points. Shade tolerance is especially important in the seedling stage when competition for light will likely be asymmetric. Traits that facilitate a strong competitive effect in productive habitats are likely to be: large allocation to stems, tall plant height and large leaf size, which will allow a plant to overtop and shade

its competitors. Above-ground biomass and plant height have been shown to be good predictors of competitive ability in productive habitats (Goldberg 1987; Gaudet & Keddy 1988; Gaudet & Keddy 1995; Freckleton & Watkinson 2001; Warren et al. 2002). Broad leaves have been shown to be another trait that is correlated with competitive ability in productive habitats (Gaudet & Keddy 1995; Keddy et al. 2002). There is a large amount of evidence to show that tall broad-leaved plants dominate fertile productive environments (Grime 1979; Keddy 1990; Tilman *et al.* 1994; Gaudet & Keddy 1995; Leps 1999). Another aspect of competitive ability in productive habitats is the ability to grow rapidly in order to be able to preempt space and light (Grime 1979). Plants that are good competitors in fertile habitats have been shown to have faster growth rates than species that are good competitors in infertile habitats (Grime & Hunt 1975; Chapin 1980; Tilman & Wedin 1991a).

Thus, tall broad-leaved grasses are generally more competitive than tall narrow-leaved grasses because they have higher growth rates (Grime & Hunt 1975), and broad-leaves are more effective at intercepting and preempting light. A requirement of rapid growth rates is not only high rates of photosynthesis but also an ability to extract nutrients and water rapidly from the soil (Grime 1979). Species characteristic of fertile habitats have been shown to be able to absorb nutrients more rapidly per unit root mass than species characteristic of infertile habitats when grown with the same availability of nutrients (Chapin 1980). It should be noted, however, that growth rate is only important in short-term competitive ability, whereas the long-term outcome of competition is determined more by height and shade-tolerance (Tilman 1985; Huston & Smith 1987). Fast growing species usually dominate initially in secondary successions (Clements 1916; Grime 1979; Tilman 1985; Huston & Smith 1987) but are eventually replaced by slower growing (Grime & Hunt 1975) shade-tolerant trees (Clements 1916; Tilman 1988).

Finally, the ability to produce large amounts of litter has been shown to be a trait of competitive species that allows them to exclude other species (Al-Mufti et al. 1977). Seeds of many species may not germinate beneath litter (Foster & Gross 1998; Jutila & Grace 2002) and their seedlings are unable to grow through a dense litter layer. Although, high allocation to above-ground biomass and height may confer a competitive advantage in productive habitats, it may reduce competitive ability in unproductive

habitats (Tilman 1988). A strong competitive effect or response in unproductive habitats should not be related to the ability to preempt space above-ground or avoid being shaded because light is generally not limiting, owing to low above-ground production. Rather, the ability to take up nutrients and maintain physiological, physical and reproductive processes with limited nutrient supply should favour plants in unproductive habitats. One of the major differences between plants growing in fertile productive habitats and plants growing in infertile unproductive habitats is the rate at which they can extract nutrients. Surprisingly when plants characteristic of fertile and those of infertile habitats are grown in fertile soils, it is the species characteristic of fertile habitats that are able to exctract nutrients from the soil system at a greater rate per unit root mass than the species characteristic of infertile habitats (Chapin 1980).

One would expect that an importation adaptation to growing in infertile habitats would be a greater ability to extract nutrients per unit root mass than species characteristic of environments, where nutrients are less limiting. It has been shown that in infertile habitats, however, soil processes are the primary control over nutrient absorption by each unit of root (Chapin 1980). In other words, the diffusion rate of nutrients to the root surface is much slower than the absorption rate necessary for optimal plant growth. Thus, under these conditions the kinetic properties of nutrient absorption by roots exert only a minor influence over nutrient acquisition by plants (Chapin 1980). Consequently, there is no advantage for a plant to have the ability to extract nutrients at a rapid rate in infertile habitats, because the diffusion rate in the soil limits uptake rates by the plant rather than a plants inherent nutrient extraction rate capacity per unit root mass. Therefore, the only way that a plant can maximize its extraction rate of nutrients in infertile habitats is to have a very large root biomass and large root surface area.

Further, rapid nutrient absorption capacity declines with age but the accumulation of large root biomass requires high root longevity. Consequently, rapid nutrient absorption capacity per unit root mass and large root biomass may be incompatible (Chapin 1980). High allocation to roots has been observed to result in strong competitive ability in unproductive environments (Austin et al. 1985; Gleeson & Tilman 1990). If nutrients are costly and difficult to extract, it is in a plants best interest to hold on to those nutrients for as long as possible (i.e. large tissue longevity/nutrient retention). Hand

in hand with the cost of extracting limiting nutrients and the importance of nutrient retention is the ability to produce more biomass per unit limiting nutrient (i.e. nutrient use efficiency). Under conditions of low nutrient availability and low tissue nutrient concentration it is important for a plant to be able to maintain metabolic effectiveness. Many species not adapted to infertile habitats are incapable of maintaining metabolic effectiveness under these conditions (Chapin 1980).

Craine et al. (2002) found that plants able to produce large biomass in infertile habitats had wide C:N ratio tissues (roots and shoots), tough dense roots and leaves and long leaf and fine root longevity. Further, these species had low photosynthetic rates and low respiration rates indicating that they had high metabolic efficiency. Leaf width and leaf mass per area are strongly correlated with leaf life span (Wright et al. 2002). In addition, leaf mass per area tends to increase with decreasing soil fertility (Wright et al. 2002; Craine & Lee 2003). Leaf life span should be correlated with nutrient retention and, therefore, nutrient loss rates. High nutrient loss rates have been shown empirically (Berendse & Elberse 1990) and mathematically (Tilman 1990) to result in lower competitive ability in infertile habitats, explaining the observed relationships between leaf mass per area and soil fertility (Wright et al. 2002).

Narrow leaves appear to be an adaptation to habitats where soil resources are limiting, whereas broad-leaves appear to be an adaptation to habitats where light is limiting. Indeed, species successful on infertile soils have low specific leaf area (Craine et al. 2002). Narrow-leaved species performed relatively better (in terms of competitive effect) than broad-leaved species in nutrient stressed treatments compared with high-nutrient treatments (Keddy et al. 2002). It would appear, therefore, that leaf width and leaf mass per area have much potential for understanding relationships between species and their environment. Craine et al. (2002) note that there are two strategies for being able to produce large biomass in low fertility habitats. The first is to avoid nutrient limitation by fixing nitrogen (i.e. legumes). The second strategy was not necessarily to acquire more of a limiting nutrient but rather to have high nutrient use efficiency and low loss rates of those nutrients through long root and leaf longevity.

Under regular disturbance, traits that minimize loss of biomass and prevent damage of meristems should confer a competitive advantage over species with higher

loss rates. A short or creeping growth form is likely to reduce loss of biomass under grazing or mowing. Tall-grass species were shown to have greater nutrient loss rates than short grasses under a mowing regime which resulted in the shorter grasses being more competitive (Berendse & Elberse 1990). Basal meristems are less likely to be damaged by grazing or mowing than apical meristems, which should give species with basal meristems and advantage over species with apical meristems in regularly grazed or mown systems.

In summary, plant traits represent specific adaptations to various environmental influences and constraints. Consequently, developing an understanding of relationship between plant traits and species response to various environmental influences has much potential for predicting species response to these influences.

A mechanistic theory of plant competition

Tilman (1982) has developed a theory of competition for limiting resources based on earlier work on competition for limiting nutrients among algae species (Tilman 1976). A population of algae with a specific mortality rate and loss rate of nutrients (through metabolic processes and leaching) requires a specific supply rate of nutrients to allow growth rate to balance mortality and loss rates. This level of resource supply rate at which the population is at equilibrium is known as the R^* of a species. For a population to grow the resource supply rate must be above the level of R^* for that species. If the resource supply rate drops below the level of R^* for that species, the population will decline. When the resource level is above the level of R^* of a species, its consumption rate of that resource will increase as its population increases, which will cause the level of the resource to drop down to the equilibrium levels (R^*). Species differ in their ability to reduce the concentration of a limiting resource to the lowest level at which the supply rate of that resource balances their mortality and loss rates. Thus, species differ in their R^* value, which allows prediction of the outcome of competition for a limiting nutrient among species with different values of R^*. The species with the lowest R^* will competitively displace all other species, irrespective of its initial abundance, because so

long as it has the lowest R* of all the species, the concentration of the limiting nutrient will always be above its R* if it has a much lower abundance than its competitors (because the concentration of the limiting nutrient will be determined by the R* of the most abundant species). This will cause the population of the species with the lowest R* to increase, resulting in a reduction of the concentration of the limiting nutrient below the R* values of the other species. A rigorous mathematical proof of this concept has been developed by Hsu et al. (1977).

Although this theory was developed using competition for nutrients amongst algae the possibility exists that it can be extended to understanding competition for nutrients amongst multi-cellular plants. This is not an unreasonable assumption because it is well recognized that: 1) plant species differ in their response to limiting nutrients (Parrish & Bazzaz 1982; Austin et al. 1985; Wilson & Keddy 1985; Austin 1990), and 2) plant species differ in their effect on nutrient cycling and nutrient availability (McClaugherty et al. 1985; Tilman & Wedin 1991b; Sirotnak & Huntly 2000; Van der Krift & Berendse 2001; Craine et al. 2002; Knops et al. 2002).

What evidence is there in support of the R* concept of nutrient competition? Wedin & Tilman (1993) found that a species that reduced NO_3^- and NH_4^+ to the lowest levels in the soil in monoculture (*Schizachyrium scoparium*), was able to competitively displace on low N soils, species with higher NO_3^- and NH_4^+ levels in the soil in monoculture (*Poa pratensis* and *Agropyron repens*). However, when extra nitrogen was added *Poa pratensis* and *Agropyron repens* competitively excluded *Schizachyrium scoparium*. Similarly *Agropyron repens,* which had lower NO_3^- and NH_4^+ levels in monoculture than *Poa pratensis*, displaced *Poa pratensis* on the lower N soils.

This is exactly what is predicted by R* nutrient competition theory: with low nutrient supply rates the species with the lowest R* will win, but if the nutrient supply rate is increased above the level of R* of the species with a higher R*, the species with the higher level of R* will win because it has higher growth rates. Moreover, the prediction of R* nutrient competition theory that the species with the lowest R* will competitively displace species with a higher R* irrespective of the initial abundance of that species was also observed. When *Schizachyrium scoparium* was sown or planted into existing monocultures of *Poa pratensis* and *Agropyron repens* it eventually displaced

these species in spite of its lower initial abundance. Other evidence for the R* mechanism of nutrient competition is seen in the demonstration that large plant species do not have a competitive advantage over small plant species in below-ground competition (Cahill & Casper 2000). This is predicted by the R* hypothesis because the mechanism of competition for nutrients is determined by effects of species on the concentration of the limiting nutrient. If a small plant has a lower R* than the concentration of the limiting nutrient it will increase in size irrespective of the size of its competitors (so long as below-ground competition is dominant over above-ground competition with the larger competitors).

R* is strongly influenced by nutrient loss rate (Tilman 1982; 1990) because increased loss rates of a limiting nutrient demand increased supply rates of that nutrient if the species is to be able to maintain a population at equilibrium. This can be proven mathematically (Tilman 1990). Thus, the R* of a species will increase with increasing loss rates. The implications of this are that a particular form of disturbance such as mowing, grazing or burning that causes a greater loss rate of nutrients in one species compared with another may result in the R* of one of the species exceeding the nutrient supply rate. This will result in competitive exclusion of that species by the species with the lower loss rate, provided its R* is still below the nutrient supply rate. This has been demonstrated empirically in a competition experiment using *Festuca rubra* and *Arrhenatherum elatius* (Berendse & Elberse 1990). With clipping, the taller *Arrhenatherum elatius* lost 64% of the nitrogen that it absorbed, whereas the shorter *Festuca rubra* lost only 29% of its absorbed nitrogen. *Arrhenatherum elatius* dominated in the high nutrient treatments under cutting but was replaced by *Festuca rubra* in the low fertility treatments. This demonstrates that *Arrhenatherum elatius* was able to remain competitive in spite of high nutrient loss rates if the nutrient supply rate was above its R*.

In another example, *Eragrostis curvula* was strongly decreased in abundance by mowing infertile grassland in summer (Fynn et al. in review) but dominated adjacent fertilized grassland despite being mown as frequently (Le Roux & Mentis 1986). *Eragrostis curvula* is known to have a relatively high nitrogen requirement (Roux 1954).

Tilman (1982) developed a graphical (mathematical) approach for understanding competition for two limiting resources known as the Zero Net Growth Isocline (ZNGI)

approach. The ZNGI approach uses the R* concept where two or more competing species differ in their level of R* for two limiting resources. For resource 1 (R1) species A may have the lowest R* but for resource 2 (R2) species B may have a lower R*. Consequently, the ratio of the availability of two resources (R1/R2) or the total pool (S) of two resources (S1/S2) will determine the outcome of competition amongst two species. The ZNGI model can accommodate cases where species A has the lowest R* for R1 and R2 in which case Species A excludes Species B at any level or ratio of R1 and R2. If the species differ in their R* for R1 and R2, a species will exclude the other if the level of the resource that limits the other species more than itself (say R1) is below the R* for R1 of the other species but above its own R * for R1. Likewise, it will be excluded when the level of R2 is below its R* for R2 but above the R* for the other species.

Further, there will be a stable equilibrium where the isoclines cross provided that each species consumes relatively more of the resource that limits itself to a greater degree than the other species. If, however, they consume relatively more of the resource that most limits the other species, there will be an unstable equilibrium at that ratio of resources where the outcome of competition will be determined by initial density. The latter option is likely to be the case in most plant communities because a species that is a good competitor for nutrients is likely to consume more of the nutrient that limits a good competitor for light, whereas the good light competitor is likely to preempt more light than the nutrient competitor. Thus, the outcome of competition at this nutrient/light ratio where both species can survive in the absence of competition, will depend on the initial densities of the nutrient or light competitor. If the nutrient competitor is initially abundant it will reduce nutrient levels below the R* of the light competitor, whereas if the light competitor is initially abundant it will reduce light levels below the R* of the nutrient competitor. Tilman (1984) tried to test whether the ratio of two limiting soil resources may influence the outcome of competition amongst species. Although, there was some evidence to suggest that the ratio of nitrogen/magnesium influenced composition, this effect could have been caused by nitrogen alone rather than the nitrogen/magnesium ratio. There was no way to verify that it was the ratio that was important because treatments were not applied in all combinations. The fact that *Aristida basiramea* was dominant only in sites that did not receive nitrogen, suggests that it was competitively

excluded when even the lowest level of nitrogen was applied. Further, this species dominated in sites of widely different nitrogen/magnesium ratios. It is unlikely that it is the ratio of two limiting soil resources that is important but rather their absolute amounts because two soil resources are generally not limiting at the same time (Fynn & O'Connor in review).

However, the ratio of a limiting soil resource to light as proposed in the resource ratio hypothesis (Tilman 1985) appears to be a very useful predictive model of succession. This is because the availability of a limiting soil resource influences productivity, which is inversely correlated with light. Species abilities to compete for a limiting soil resource and light are generally inversely correlated. Clearly, both light and a soil resource can be limiting (to varying degrees) at the same time, implying that the various ratios of a limiting soil resource to light may result in marked differences in composition. Tilman (1985) showed that simulation models using this approach could generate a classic successional sequence with different species dominating at various points along the gradient of soil resource/light ratios. Thus, varying abilities to tolerate shade and compete for a limiting soil resource may be the cause of many successional sequences. The assumption is that the change in the availability and ratio of resources is slower than the rate of competitive displacement, thereby allowing competitive equilibrium to be established at various points along the resource ratio gradient. It is a population-based approach encompassing population mortality, recruitment and effects of the population on resources.

Huston & Smith (1987) have used a non-equilibrium model based on competition amongst individuals rather than populations. Their criticism of population-based models is that succession is driven by interactions amongst individuals with context relevant competitive ability rather than an abstract concept of the average trait of a species that may not be context relevant. An individual of a species may vary greatly in competitive ability depending upon its age and size. Their model has been able to generate successional sequences by varying growth rates, sapling establishment, plant height and shade tolerance. It is useful in that it is able to show what combination of life history traits confers a competitive advantage on a species. In their model, growth rate has a major influence on competitive ability early in succession with plant height and shade

tolerance having an important influence later in succession. Sapling establishment is important with specific combinations of traits, especially shade tolerance. They fail to acknowledge, however, that growth rate early in succession may be determined by the ability to compete for a limiting soil resource, especially during primary succession or during secondary succession on extremely infertile soils. In contrast to the resource ratio hypothesis (Tilman 1985), which considers competition for soil resources and light, this model considers only competition for light. Thus, they have assumed that stress tolerance and not competition is important in infertile habitats (e.g. Grime 1979). As reviewed in an earlier section, there is good evidence that plants do compete in infertile habitats. This model is more likely to be applicable to secondary succession on fertile soils. Succession on an infertile sandplain in Minnesota was shown to be driven by increasing allocation to roots, a trait conferring competitive success for nutrients, not light (Gleeson & Tilman 1990). Thus, the model of Huston & Smith (1987) appears to have less power and general predictive ability than the resource ratio hypothesis. Clements (1916) noted that the relative importance of soil resource limitation to light limitation changed over time with competition for a limiting soil resource being most important in early succession and competition for light being most important in late succession. Therefore, the resource ratio hypothesis (Tilman 1985) is a mathematical representation of a process recognized by some of the earliest ecologists. However, Tilman (1985) does note that in late succession, competition for a limiting soil resource may still be important rather than just competition for light. Tilman emphasizes that it is the ratio of a soil resource to light that is important rather than their absolute amounts.

Plant competition and diversity

Plant competition intensity has been proposed to be an important determinant of diversity (Grime 1973). Grime has proposed that humpbacked productivity-diversity relationships (Al-Mufti et al. 1977; Moore & Keddy 1989) represent inversely correlated gradients of stress and competitive exclusion. Diversity is low in the most infertile sites because only a few stress-tolerant species are able to survive there. Diversity is also low

in the most fertile and productive sites because competition is most intense in these sites and only a few highly competitive species are able to survive there. At intermediate levels of fertility, competition intensity is less intense and fertility levels are generally tolerable for most species, allowing the greatest coexistence of species. The same relationship can also be expected along disturbance gradients with highest diversity being found at intermediate levels of disturbance because only the most competitive species survive in undisturbed habitats and the most tolerant species in highly disturbed habitats. This is clearly based on Grime's CSR model (Grime 1977, 1979) and some alternative explanations of low diversity in infertile sites may be offered by the models of Tilman (Tilman 1982, 1985, 1988) and Cahill (Cahill 1999).

Grime's model only predicts competitive exclusion in fertile habitats, whereas the models of Tilman (Tilman 1982, 1985, 1988) and Cahill (Cahill 1999) predict competitive exclusion in infertile habitats through intense root competition (see section on theories of community organization). Thus, it is possible that low diversity at the infertile end of the gradient represents competitive dominance of a few species that are the best competitors for soil nutrients, whereas dominance at the fertile end of the gradient represents competitive dominance of a few species that are the best competitors for space and light. Numerous studies have found that only root competition is present in infertile habitats (Wilson & Tilman 1991, 1993; Twolan-Strutt & Keddy 1996; Cahill 1999), suggesting that competitive exclusion, owing to intense root competition, may be an important determinant of low diversity in infertile habitats. While competition may be an important determinant of diversity in infertile sites, stress has been shown to have overriding effects on the productivity-diversity relationship (Gough et al. 1994). Only when sites of extreme stress (salinity) were removed was productivity an important predictor of species richness.

Although shoot competition is undoubtedly important in fertile habitats (Wilson & Tilman 1991, 1993; Gaudet & Keddy 1995; Twolan-Strutt & Keddy 1996; Cahill 1999), the effect of competition for light as the only cause of reduced diversity in fertile habitats has been questioned. Experiments have shown that reducing light availability by increasing productivity through watering (Goldberg & Miller 1990), or through the use of shadecloth (Rajaniemi 2002) had no effect on diversity, whereas nitrogen fertilization had

a strong effect. Further, root competition may reduce a species ability to compete in fertile habitats (Cahill 1999) and root but not shoot competition has been shown to reduce diversity in fertilized treatments (Rajaniemi et al. 2003).

Disturbance may influence productivity-diversity relationships by preventing competitive species from preempting space and resources (Grime 1973, 1979; Huston 1979). Thus, disturbance may reduce competition intensity (Wilson & Tilman 1993), thereby allowing greater coexistence of species. These predictions have been verified by studies showing that species diversity can be improved by mowing (Milton 1940; Armesto & Pickett 1985; Collins et al. 1998; Leps 1999; Jacequemyn et al. 2003) and removal of the dominant species (Gurevitch & Unnasch 1989; Leps 1999). Disturbance may also influence composition and diversity through indirect effects on soil resources. Protection from disturbance has been shown to result in an increase in total soil nitrogen and increased rates of nitrogen mineralization (Ojima et al. 1994; Turner et al. 1997; Fynn et al. 2003). The effect of burning on nitrogen availability is emphasized by the small productivity response observed in infrequently burnt grassland (9%) compared with the large response in annually burnt grassland (68%) (Seastedt et al. 1991). Further, burning has been shown to result in reduced soil moisture (Redmann 1978; Knapp & Seastedt 1986; Knapp et al. 1998; Snyman 2002) and an associated reduction in productivity (Redmann 1978; Tainton et al. 1977; Tainton et al. 1978). This reduction in soil resource availability and productivity is likely to reduce the competitive vigor of large highly competitive species. Thus, disturbance may have an indirect effect on species diversity. Further, an accumulation of litter in the absence of disturbance (Dix 1960; Knapp & Seastedt 1986; Fynn et al. 2003) may affect recruitment of many species by reducing seed germination (Foster & Gross 1998; Jutila & Grace 2002) and preventing seedling establishment (Sydes & Grime 1981) resulting in a few litter-tolerant species being able to persist.

Important questions in contemporary plant ecology

The importance of competition as a determinant of community organization and structure is a topic that has received much attention in plant ecological theory but despite 30 years of research has not yet been satisfactorily resolved. Would most species grow in any habitat in the absence of competition or is there a strong correlation between a species physiological optima and its realized niche? Further, what is the importance of root, shoot and total competition intensity in structuring plant communities along productivity gradients? This is probably one of the most debated and poorly understood areas of plant ecological theory. Resolving this question has important implications for developing a predictive understanding of plant competition along productivity gradients, because it enables a better understanding of which plant traits are related to competitive ability at different regions along these gradients.

Another poorly resolved question is the influence that multiple limiting resources exert over time as a determinant of community composition. Is there a dominant limiting resource (e.g. nitrogen) that ultimately shapes plant communities or does the relative importance of limiting resources (e.g. nitrogen, phosphorus, water, light) change in space and time (*sensu* Knapp et al. 1998)? If nitrogen is not always the dominant limiting resource, what implications does this have for our abilty to understand and predict the out come of competition overtime amongst a range of species?

Perhaps the area of greatest potential for the development of plant ecology as a predictive science is developing an understanding of the relationship between plant traits and different forms of resource limitation (moisture, nutrients, light), different types of disturbance (burning, grazing, mowing and the frequency and timing thereof) and with different types of stress (salinity, pH, temperature etc.). Detailed knowledge of how specific traits (physiological, root, leaf, position of meristems and tiller initiation, life cycles, mutulisms, effect on nitrogen cycling, effect on light availability etc.) enable a species to react to specific environmental influences, will enable a greater understanding of plant species-environment relationships and the ability to predict how specific environmental changes (climate change, disturbance) may influence plant species. In

addition, it will allow greater success in the choice of species for restoration of grasslands and the management of specific species (rare or invasive) in grasslands.

The potential of the Ukulinga long-term experiments for furthering knowledge of mesic grassland dynamics

Two of the longest running ecological experiments in the world are located at the University of Natal's research farm at Ukulinga. These experiments were started in 1950 and consist of the long-term grassland fertilization experiment and the long-term burning and mowing experiment. The fertilization experiment has manipulated nitrogen (four levels and two types), phosphorus (two levels) and lime (two levels) in a factorial design with three replications of each treatment. The burning and mowing experiment is a split-plot design with four summer mowing treatments as whole-plots (none, early, late and both early and late summer mow), whereas the sub-plot treatments consist of burning frequency (annual, biennial, triennial) and time of burning (autumn, winter or spring) as well as mowing (winter or spring) with three replications of each treatment. Thus, these two experiments allow testing of hypotheses related to two of the major axes of ecological theory, habitat fertility and disturbance. In addition, their long-term nature (50 years) is extremely useful because it allows for stabilization of vegetation processes as well as for the long-term effects of different forms of disturbance or fertilization on soil characteristics and resources to become manifest. This is critical because it may be the effects of treatments on soil resources rather than direct effects of treatments on the plants (e.g. defoliation) that may have important influences on vegetation processes.

Thus, the aims of this study were to: 1) examine the effects of long-term burning of grassland on soil organic matter content because of its potential impact on nitrogen cycling and community composition, 2) examine patterns of community composition and species richness in response to different type, timing and frequency of disturbance (burning and mowing) in a long-term grassland burning and mowing experiment and to different type and amounts of fertilizer application in a long-term grassland fertilization experiment, 3) develop hypotheses concerning the response of different species to

disturbance and fertilization, and test these hypotheses using pot and plot competition experiments, and 4) provide a general synthesis of the results of the various field, pot and plot experiments that may be used to develop a predictive theoretical framework for mesic grassland dynamics.

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CHAPTER 2

EFFECT OF LONG-TERM BURNING ON THE SOIL ORGANIC MATTER CONTENT OF A SOUTH AFRICAN GRASSLAND

Abstract

The effects of burning a native grassland on soil organic matter status was investigated on a long-term (50 years) field experiment where different times and frequencies of burning were compared. Significant decreases in organic C were observed only in the surface 0-2 cm layer and only under annual and biennial winter burning and biennial and triennial autumn burning. Burning in spring did not significantly affect organic C content presumably because substantial amounts of litter decomposed and / or were incorporated into the soil by faunal activity prior to burning. Total N content was decreased substantially to a depth of 6 cm by all burning treatments and as a result, the C:N ratio of soil organic matter was widened. In addition, the amount of potentially mineralizable N, as measured by either aerobic incubation or plant N uptake in a pot experiment, was much reduced. Burning also induced a decrease in light fraction and hot water-extractable C in the 0-2 cm layer but an increase in these parameters, and in microbial biomass C and root density, in the 4-10 cm layer. This was attributed to burning causing a decrease in above-ground litter inputs but increased turnover of root material below the surface. Despite the decrease in organic C and total N content with increasing soil depth, potentially mineralizable N showed the opposite trend. This unexpected finding was confirmed at a nearby site under native grassland and contrasted with decreasing potentially mineralizable N with depth which was measured under a fertilized kikuyu grass dairy pasture. The wide C:N ratio of litter from native grassland, in association with the decreasing size and activity of the microbial biomass with depth results in greater N immobilization (thus less net mineralization) occuring in soil samples taken from close to the soil surface.

Introduction

Fire is an important management tool in African savanna and grassland systems for both livestock farmers and wildlife managers who use it regularly to control bush encroachment and to remove dead and dying vegetation that has low forage quality and is unpalatable to animals (Tainton, 1999). Indeed, burning grassland often results in earlier grass growth at the beginning of the growing season and greater annual dry matter production (Ojima et al. 1994; Blair, 1997). This is attributable to the removal of dead surface litter, which results in greater light penetration and higher soil temperatures in spring.

However, during burning, large amounts of C, N, S held in herbage are lost via volatilization. Although regular burning has been reported to have no consistent long-term effect on organic C or total N content in the surface 15 cm of grassland soils, reductions in organic matter content and the size of the microbial biomass in the surface few cm are commonly recorded (Ojima et al. 1994; Blair, 1997; Turner et al. 1997). There is also often a decrease in the amount of potentially mineralizable N, the rate of net N mineralization and the quantity of extractable mineral N present (Blair, 1997; Turner et al. 1997). As a result, N becomes more limiting to plant production under burnt than unburnt conditions and typically grasses with a high N use efficiency become dominant (Schimel et al. 1991).

The size and activity of the soil microbial biomass in agricultural soils has been shown to be concentrated in the surface 2.5 cm and it declines rapidly with depth (Murphy et al. 1998). Because of this gradient in microbial activity, the potential for N mineralization also decreases greatly with depth (Purnomo et al. 2000; Paul et al. 2001). Indeed, Paul et al. (2001) reported that the surface 2.5 cm of soil contributes between 35-90% of net or gross N mineralization under pastures, crops and forests. Such gradients in microbial biomass and N mineralization potential under unfertilized native grassland are yet to be characterized.

Total soil N and mineralizable N are major determinants of community composition and diversity (Al-Mufti et al. 1977; Tilman & Wedin 1991, 1993; Gibson et al. 1993; Gaudet & Keddy 1995; Leps 1999; Wilson & Tilman 2002). For this reason we investigated the effects of burning on total soil organic matter content, labile organic C and N fractions and microbial biomass C and N within the surface 10 cm of soil under a long-term experiment at

Pietermaritzburg, South Africa. The experiment was started 52 years ago and compares different times and frequencies of burning and cutting under undisturbed native grassland vegetation.

Methods

Study area

The burning experiment is situated at Ukulinga, a research farm of the University of Natal, Pietermaritzburg (29° 24′ E, 30° 24′ S). The experiment is situated on top of a small plateau ranging in altitude from 847 m to 838 m. Soils at the site were classified as Westleigh forms (Soil Classification Working Group 1991) or Plinthic Acrisols (FAO).

The vegetation of the area is classified as southern tall grassveld (Acocks 1953) which is an open savanna of *Acacia sieberiana* DC with patches of *Hyparrhenia hirta* L. and other species. In the absence of fire, indigenous trees such as *Acacia karroo* Hayne., *Acacia nilotica* Wiltd. and *Celtis africana* Burm. and exotic trees such as *Acacia mearnsii* DeWild. and *Melia azedarach* L. and grasses such as *Aristida junciformis* Trin.& Rupr. are common while with regular burning trees are sparse and *Themeda triandra* Forssk. is the dominant grass. The native grass species in the locality all use the C4 photosynthetic pathway.

The mean annual precipitation in the locality is 790 mm and about 79% of this falls during summer (October to April). Mean monthly maximum and minimum temperatures range from 26.4°C in February to 8.8°C in July respectively.

Experimental design

A full description of the experiment, which was established in 1950 on virgin native grassland is given in chapter three (Table 3.1). For the purposes of this study only plots in whole-plot A (plots not mown in summer) were used because the objective was to investigate the effects of burning on soil organic matter. The treatments are replicated 3 times in a randomized block design and plots are 18.3 x 13.7 m in size and are separated by rows 4.5 m wide. The plots are left ungrazed and are not mown for hay. The treatments are listed in Table 2.1 and consist of

annual burning in winter or spring and biennial and triennial burning in winter, spring or autumn. For comparison, no burn and annual mown treatments are also included. Autumn burns are carried out in April, winter burns in the first week of August and spring burns are carried out immediately following the first spring rain (defined as the first rain of 12.5 mm in 24 hours in spring).

Total and potentially mineralizable C and N

Soil samples were collected in July 2000 in 2 cm layers down to a depth of 10 cm. Sampling was done along three transects in each plot with six samples per transect. Samples at each depth were bulked, air-dried, seived (< 2 mm) and a subsample was ground (< 0.5 mm). Ground subsamples were analysed for organic C and total N using a LECO CNS analyzer (LECO corporation, St Joseph, Michigan, USA).

Potentially mineralizable C and N were determined on the no burn and winter triennial, biennial and annual burn treatments using a closed aerobic incubation at $25°$ C for 12 days. Two replications of 20 g of air dried soil from each treatment at 0-2, 2-4 and 4-10 cm depths were weighed into 100 ml erlenmeyer flasks and moistened to field capacity and placed in 1 litre airtight jars. The CO_2 evolved during the incubation was trapped in a container of 10 ml of 0.25 M NaOH and determined by titration with 0.5 M HCl (Ohlinger, 1995). The nitrogen mineralized during incubation was determined by difference after measuring extractable inorganic soil N (NH_4^+ and NO_3^--N) at the commencement and end of the incubation using steam distillation after extraction of 20 g of soil with 50 ml 2 M KCl (Bremner, 1965).

Potentially mineralizable N was also estimated by plant uptake in a greenhouse experiment. Air-dried soil samples (500 g) from each treatment (treatments and depths as with the incubations) were weighed into polystyrene pots, wetted to field capacity with distilled water and planted with Oats (*Avena sativa*) at 5 seedlings per pot. Oats were chosen because of their marked response to increasing levels of N. A basal dressing containing major (P, K, Ca, Mg, K, S) and minor (Zn, Cu, Mn, Fe, B and Mo) nutrients was applied. The pots were arranged in a randomized complete block design in a greenhouse. After 9 weeks, above-ground biomass was harvested, oven dried at $60°$ C and weighed. The dried material was ground (< 0.5 mm) and the

N content determined using a LECO CNS analyser. Above-ground plant uptake of N was calculated and used as an index of the amount of N mineralized.

Labile C and N fractions

In order to further understand the effects of burning on soil organic matter quality, the no burn and annual winter burn treatments were resampled in the 0-2 and 4-10 cm layers. These depths were chosen because of burning-induced decreases in organic C noted in the 0-2 cm layer and a tendency for increases in organic C and mineralizable C content at lower depths. The same sampling procedure was used as outlined previously. Bulked, field-moist samples were sieved (< 2 mm), a subsample was air-dried and a subsample of that was ground (< 0.5 mm).

Light fraction organic matter was extracted from soil by the method of Gregorich and Ellert (1993) using NaI solution (SG = 1.7). Isolated light fraction material was oven dried (60° C), weighed, ground (< 0.5 mm) and analysed for organic C and total N as outlined above.

Hot water extractable organic matter was extracted from ground soil with hot water (80° C) using 1:5 ratio for 16 hours in a water bath (Haynes and Francis, 1993). Organic C in the centrifuged extracts (10000 rpm for 5 minutes) was analysed by dichromate oxidation (Walkley, 1947) and total N by Kjeldahl digestion and determination of the liberated NH_4^+ using a Technicon autoanalyser.

Microbial biomass C and N were determined by the fumigation-extraction method based on the difference between organic C and total N extracted with 0.5 M K_2SO_4 from chloroform-fumigated and unfumigated soil samples using a k_c factor of 0.38 (Vance et al. 1987) and a k_n factor of 0.45 (Brookes et al. 1985).

Surface litter and root biomass

The amount of surface litter and root biomass were determined from the no burn and annual winter burn treatments in order to help explain total and labile soil C and N results. Quadrats (0.25 m^2) were placed 4 m in from each corner and long boundary mid-points of each plot (6 quadrats per plot). Surface litter within each quadrat was collected, washed, dried at

60°C for 48 hours, weighed and milled and the C and N content determined as outlined previously. Eight soil cores (3 cm diam.) were randomly taken from each plot (0-2 and 4-10 cm layers), bulked and root material was extracted by washing in a 0.25 mm diam. sieve, dried and weighed. The C and N content of root material was determined as described previously.

Comparison of a rangeland and pasture site

Because this study revealed an increase in potentially mineralizable N with increasing soil depth while many other studies in agricultural soils have shown the opposite (Paul et al. 2001), a comparison was made between an adjacent unfertilized rangeland (i.e. native grassland) and a fertilized, improved pasture. The study site was situated on Carwin farm about 8 km south of the Ukulinga burning experiment. It consists of a pasture / rangeland contrast between a grazed, dryland fertilized (150 kg N ha^{-1} yr^{-1}) kikuyu grass (*Pennisetum clandestinum* Chiov.) pasture and an adjacent mown rangeland dominated by *T. triandra* and *Cymbopogon excavatus* Hochst. Soil at the site was classified as a Swartland form (Soil Classification Working Group, 1991) or Chromic Luvisol (FAO). Three paired sampling areas from rangeland and pasture (5 m out from the fenceline) were chosen 50 m apart down the fenceline. At each sampling site, 15-20 samples were collected from the 0-5 cm and 5-10 cm layers, bulked, air-dried, sieved (< 2 mm) and a subsample was ground (< 0.5 mm). Samples were analysed for organic C, total N, light fraction C and potentially mineralizable C and N by methods described previously.

Statistical analysis

Statistical analysis of data was carried out by ANOVA using GENSTAT (GENSTAT 1993). For analyses of surface litter, and root and surface litter C:N ratio, a one way ANOVA was used with burning treatment as the main effect. For all other analyses, a two way ANOVA was used with burning treatment and soil depth as main effects and their interactions (burning treatment x soil depth).

Results

Total C and N

As expected both organic C and total N declined with depth (Table 2.1). The only significant decreases in organic C occurred in the 0-2 cm layer under annual and biennial winter burning and biennial and triennial autumn burning. By contrast, total N was reduced in the surface 6 cm of soil in most burning treatments (Table 2.1). The 0-2 cm layer of all treatments, except the winter mow, had a lower total N content than the no burn treatment. Below 8 cm there was no difference in total N between treatments. The C:N ratio of soil organic matter was higher under burning than no burning although individual burning treatments had no clear effect (Table 2.1). The increased C:N ratio was statistically significant in the 0-6 cm layer and was still evident, although not always significant, in the 6-10 cm layer. In the 8-10, and to a lesser extent 6-8 cm layer, there was a tendency for there to be an increase in organic C content induced by burning although the effect was not statistically significant.

Potentially mineralizable C and N

Potentially mineralizable N, measured by aerobic incubation, was greatly decreased by burning although frequency of burning had no consistent effect (Fig. 2.1a). Mineralizable N increased with increasing depth (0-2 < 2-4 < 4-10). By contrast, the amount of C mineralized during aerobic incubation decreased with increasing depth (Fig. 2.1b). In the 0-2 cm layer, mineralizable C tended to be increased by triennial burning but decreased by biennial and more particularly annual burning. In the 2-4 cm layer, it tended to be increased by triennial and biennial burning and in the 4-10 cm layer it was significantly increased by all the burning treatments. The ratio of CO_2-C evolved to mineral N accumulated tended to be greater under burning than no burning in the 2-4 and 4-10 cm layers (Fig. 2.1c).

Potentially mineralizable N, as estimated by plant N uptake, was greatly decreased by burning although its frequency had little effect (Fig. 2.1d). As with mineralizable N, measured by incubation, when measured by plant uptake it tended to increase with increasing soil depth.

Table 2.1. Concentrations of organic C, total N and the C:N ratio of soil organic matter at increasing depths under long-term burning and mowing treatments

Treatment		Organic C (g kg^{-1})					Total N (g kg^{-1})					C:N ratio				
		0-2[a]	2-4	4-6	6-8	8-10	0-2	2-4	4-6	6-8	8-10	0-2	2-4	4-6	6-8	8-10
No burn		42.6	34.5	32.2	30.1	27.5	3.4	2.8	2.6	2.4	2.2	12.6	12.4	12.4	12.8	12.8
Annual burn	winter	35.5	33.5	31.3	31.2	29.6	2.4	2.3	2.2	2.2	2.1	14.7	14.4	14.3	13.9	13.9
Annual burn	spring	39.8	35.3	32.3	31.1	29.2	2.8	2.5	2.4	2.3	2.1	14.2	13.9	13.6	13.7	13.7
Biennial burn	winter	37.4	34.5	32.3	30.4	27.9	2.6	2.5	2.3	2.2	2.0	14.3	14.0	13.9	13.9	13.9
Biennial burn	spring	39.8	34.5	32.4	29.6	27.1	2.7	2.5	2.3	2.1	2.0	14.7	14.1	14.0	13.9	13.8
Biennial burn	autumn	36.0	33.9	31.8	30.8	28.2	2.5	2.4	2.3	2.2	2.0	14.2	14.0	14.0	14.2	14.2
Triennial burn	winter	41.6	35.4	32.8	30.4	27.4	2.9	2.5	2.3	2.1	1.9	14.4	14.0	14.5	14.7	14.6
Triennial burn	spring	40.3	35.8	32.8	30.9	28.5	2.9	2.6	2.4	2.2	2.0	14.1	13.8	13.7	13.8	14.3
Triennial burn	autumn	35.7	35.2	32.8	30.6	27.2	2.5	2.5	2.4	2.2	2.0	14.1	14.2	13.6	13.7	13.7
Annual mow	winter	42.4	34.7	32.1	30.4	28.4	3.1	2.6	2.4	2.2	2.0	13.9	13.5	13.7	13.8	14.0
Annual mow	spring	39.8	34.0	31.9	30.6	28.4	3.0	2.6	2.4	2.3	2.1	13.3	13.2	13.2	13.4	13.6
LSD (P≤0.05)		4.9	2.7	2.7	2.1	2.6	0.3	0.3	0.3	0.2	0.3	1.2	1.2	1.4	1.1	1.2

[a] soil depths shown in cm.
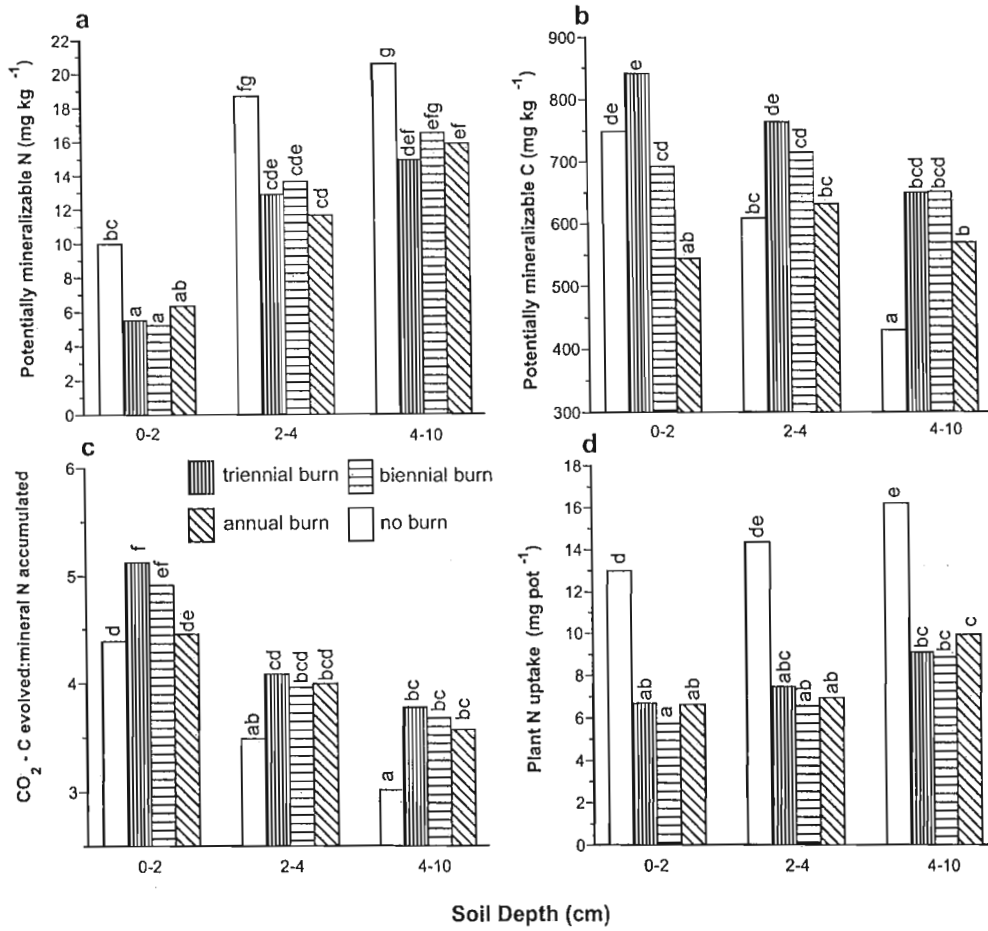
Fig. 2.1. Effect of frequency of long-term burning of native grassland on potentially mineralizable N (a), C (b), the ratio of CO_2-C evolved:mineral N accumulated (c) and uptake of N in a pot experiment (d) in three soil layers (0-2, 2-4 and 4-10 cm). Means associated with the same letter are not significantly different (P≤0.05).

Labile C and N fractions

Light fraction dry matter was not affected by burning in the 0-2 cm layer but tended to be higher in the annual winter burn treatment in the 4-10 cm layer. It was greater in the 0-2 than 4-10 cm layer. Both the C and N content of the light fraction organic matter tended to be lower in the annual burn than no burn treatments (Fig. 2.2b, c) although this effect was not significant for C in the 0-2 cm layer. The light fraction C:N ratio was wider in the annual than no burn treatments (Fig. 2.2d). Light fraction C and N were lower in the annual burn than no burn treatment in the 0-2 cm layer but in the 4-10 cm layer, amounts present were similar in the two treatments (Fig. 2.2e, f). More light fraction C and N was present in the 0-2 than 4-10 cm layer and this effect was more pronounced under the no burn treatment.

Hot water extractable C and N concentrations were decreased by annual burning in the 0-2 cm layer but increased in the 4-10 cm layer (Fig. 2.3a, b). Microbial biomass C and N were unaffected by annual burning in the 0-2 cm layer but were increased in the 4-10 cm layer (Fig. 2.3c, d).
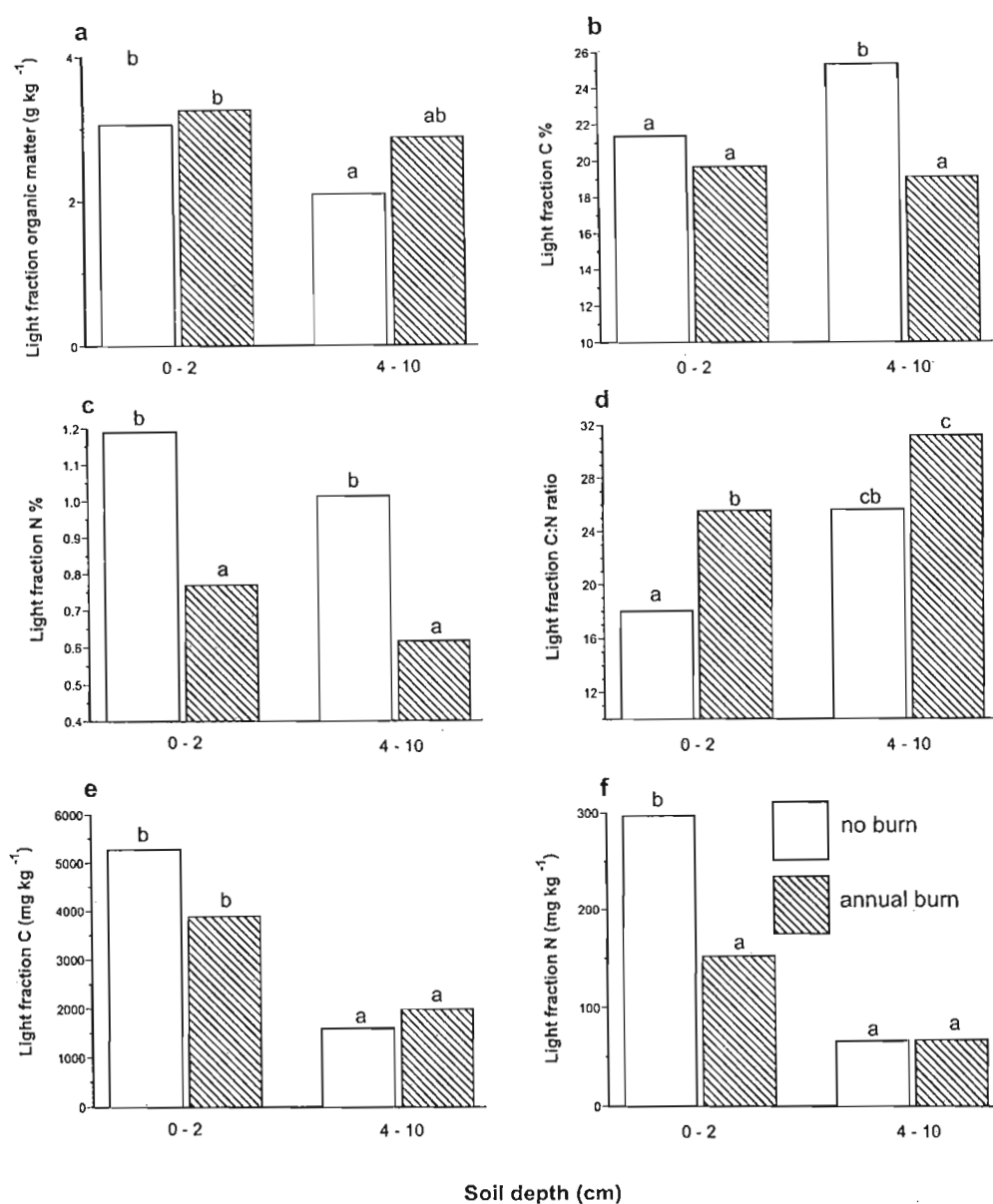
Fig. 2.2. Effect of long-term annual burning of native grassland in winter on light fraction dry matter (a), concentrations of C (b) and N (c) in the light fraction, its C:N ratio (d) and amounts of light fraction C (e) and N (f) held in two soil layers (0-2 and 4-10 cm). Means associated with the same letter are not significantly different (P≤0.05).
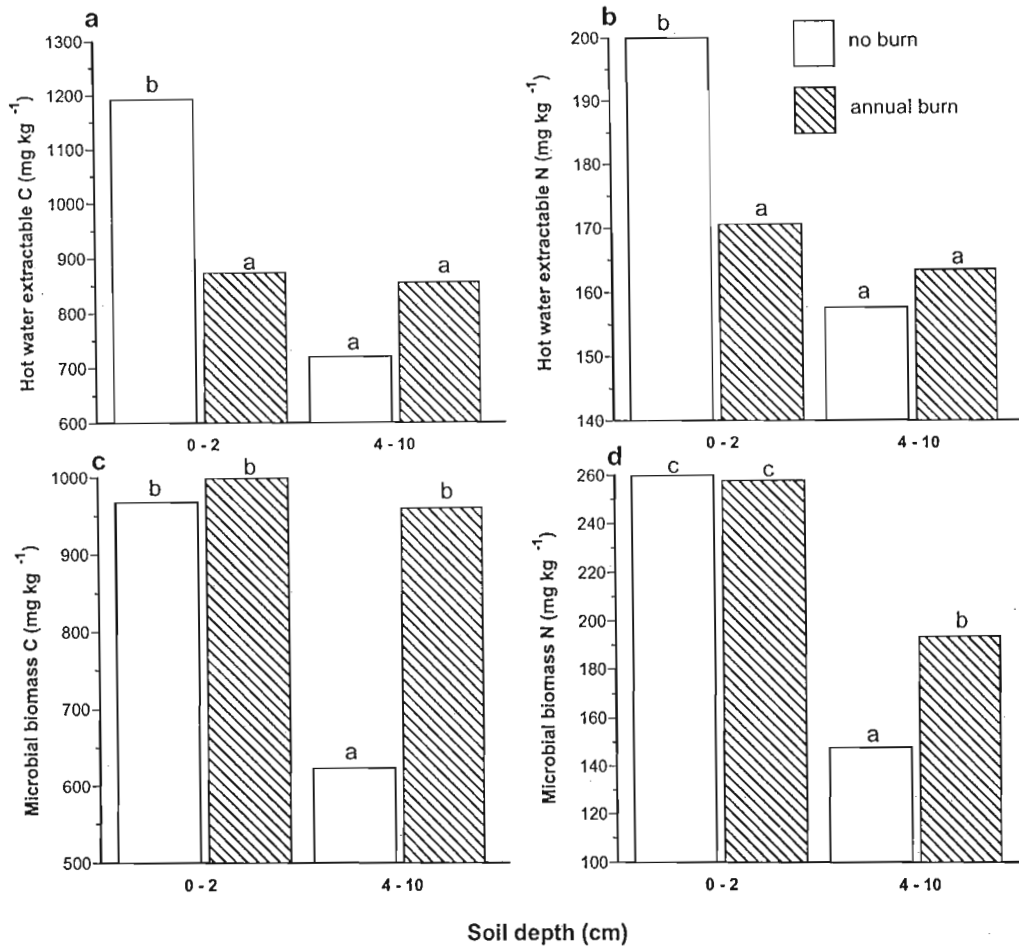
Fig. 2.3. Effect of long-term annual burning of native grassland in winter on hot water extractable C (a) and N (b), and microbial biomass C (c) and N (d) in two soil layers (0-2 and 4-10 cm). Means associated with the same letter are not significantly different (P≤0.05).

Surface litter and root biomass

There was more surface litter in the no burn than annual burn treatment (Fig. 2.4a) and the C:N ratio of the litter was narrower in the no burn (Fig. 2.4b). There was no difference in root biomass between the no burn and annual burn treatments in the 0-2 cm layer (Fig. 2.4c) but in the 4-10 cm layer it was markedly greater under annual burning. The C:N ratio of the root material also tended to be wider in the annual burn treatment (Fig. 2.4d).

Comparison of a rangeland and a pasture site

Whilst under rangeland, potentially mineralizable N increased with increasing depth, the reverse was the case under kikuyu pasture (Fig. 2.5a). Nevertheless, the amount of potentially mineralizable C (Fig. 2.5b) and the ratio of CO_2-C evolved to mineral N accumulated (Fig. 2.5c), decreased with increasing depth under both land uses. Soil organic C and total N content and light fraction C and N decreased with increasing depth under both treatments (Table 2.2). The C:N ratio of the light fraction was wider in the 5-10 than 0-5 cm layer and considerably wider under rangeland than pasture (Table 2.2).

Table 2.2. Concentrations of organic C, total N, light fraction C, N and C:N ratio under a fertilized pasture and an adjacent unfertilized native rangeland in the 0-5 and 5-10 cm layers

Land use and soil layer (cm)	Organic C (g kg^{-1})	Total N (g kg^{-1})	Light fraction C (mg kg^{-1})	Light fraction N (mg kg^{-1})	Light fraction C:N ratio
Pasture(0-5)	57	4.7	9795	728	13.5
Pasture(5-10)	33	2.6	953	59	16.2
Rangeland(0-5)	58	4.0	3359	117	28.6
Rangeland(5-10)	51	3.5	1494	37	41.2
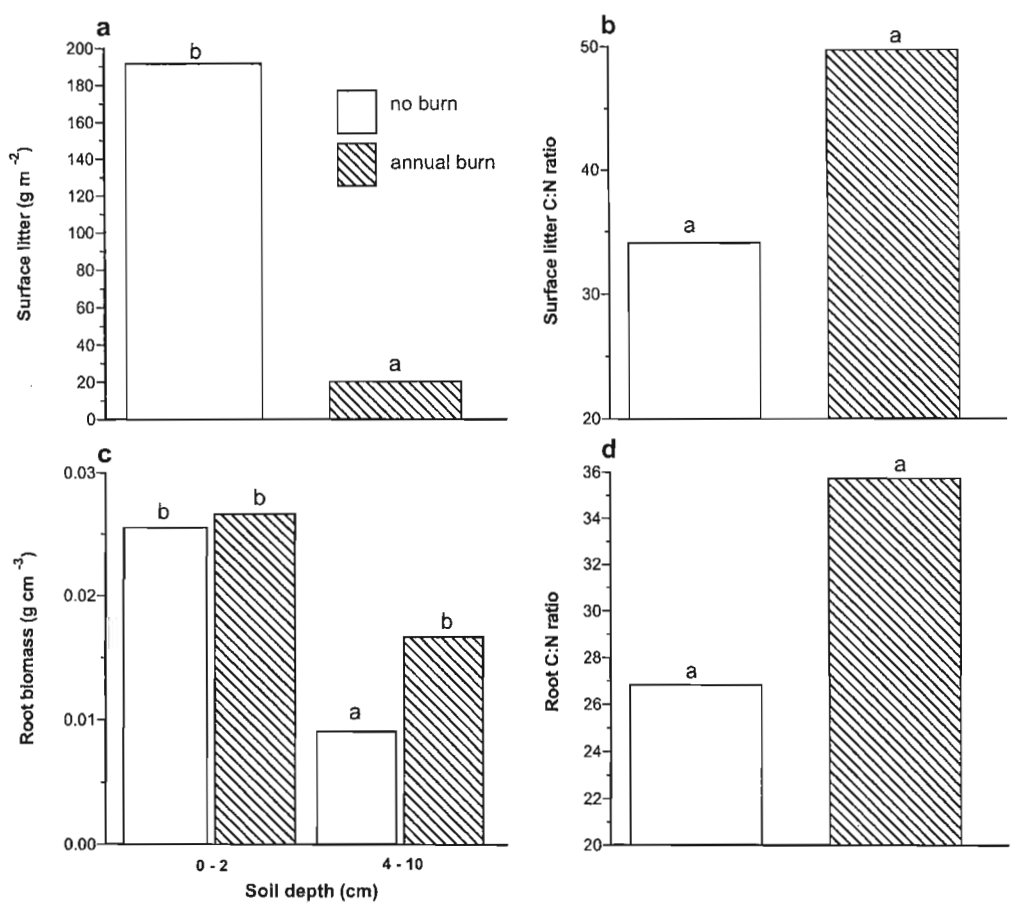
Fig. 2.4. Effect of long-term annual burning of native grassland in winter on surface litter mass (a) it's C:N ratio (b) and root mass in two soil layers (0-2 and 4-10 cm) (c) and the C:N ratio of bulk root samples. (d) Means associated with the same letter are not significantly different(P≤0.05).
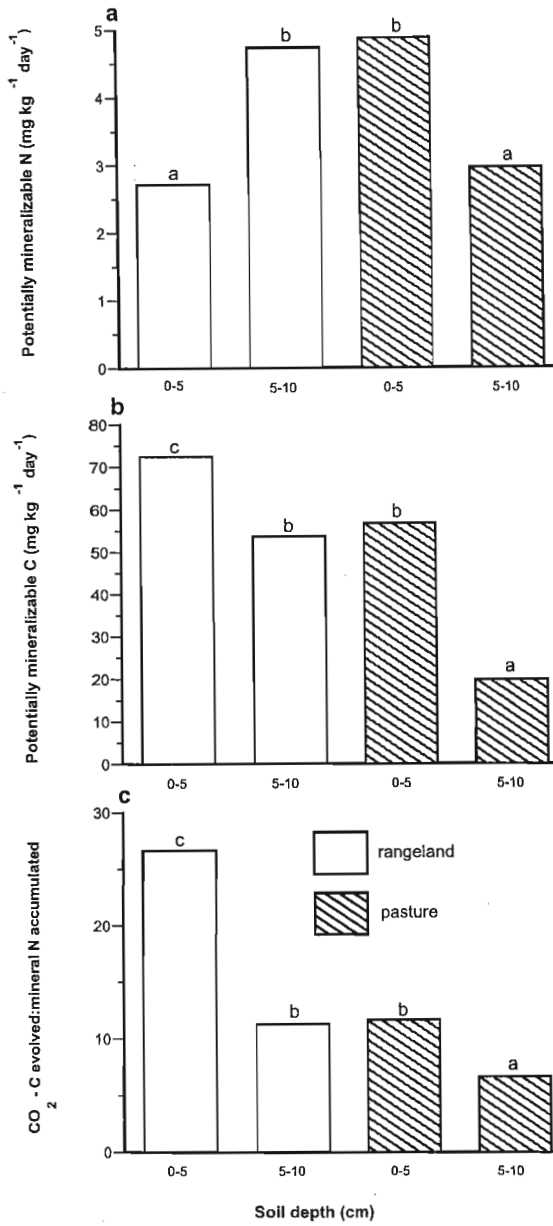
Fig. 2.5. Comparison of potentially mineralizable N (a), C (b) and ratio of CO_2-C evolved:mineral N accumulated (c) at a paired rangeland and improved pasture site in two soil layers (0-5 and 5-10 cm). Means associated with the same letter are not significantly different ($P \leq 0.05$).

Discussion

Organic C and total N

The bulk density of soils was unaffected by treatment (Tainton & Mentis 1984). Thus the changes in organic C and total N concentrations presented in Table 2.1 would be similar in magnitude if they were expressed on a per unit area basis. A reduction in organic C under long-term burning that is limited to the top few cm of soil has been reported in several other long-term burning experiments (Ojima et al. 1994; Materechera et al. 1998). Leaf litter input makes a significant contribution to soil organic matter in the top few cm of soil and therefore it's removal by fire reduces the organic matter content near the surface. The effect is negligible at deeper levels because most of the organic matter in grassland soils originates from root turnover. As noted below, the root mass may, in fact, be increased under burning.

That annual and biennial spring burning did not result in a decrease in organic C in the surface 2 cm, yet autumn and winter burning on an annual and biennial basis, and even autumn burning on a triennial basis, did cause a decrease demonstrates the importance of the timing of burning. When burning is practised in spring, the opportunity exists during the previous winter for litter to decompose and / or become incorporated into the soil through the activity of soil fauna. As a result, there is less loss of C during spring burning than would occur under winter, or more particularly, autumn burning. In addition, with autumn and winter burning, the soil surface is left partly exposed over the dry winter period and some loss of surface soil through wind erosion could occur. However, if the timing of burning had a large effect on fire intensity (cf. Trollope 1987), then more intense winter burns may also contribute to lower soil C and N than spring burning.

The reason for the greater decrease in soil N than organic C, and thus increase in C:N ratio, under burning is that C and N are lost via volatilization during burning but whilst large C inputs to the soil occur via photosynthesis, plant growth and litter decomposition, N inputs are small (i.e. mostly by wet and dry deposition). As a result, the vegetation becomes N-stressed and vegetation tolerant of a low N supply and having tissue containing a wide C:N ratio is selected for (Tilman and Wedin, 1991). Indeed, in this study the dominant grass in unburnt plots was *A*.

junciformis (58% of the biomass) while *T. triandra* was absent. Under annual winter burning *T. triandra*, a species adapted to low N fertility (Le Roux & Mentis, 1986), dominated (39% of the biomass) whilst *A. junciformis* contributed only 1% to the biomass. Thus, in this and other studies (Ojima et al. 1994; Benning and Seastedt, 1997), both above-ground and root material characteristically has a lower N content and a wider C:N ratio under burning. As a consequence, there are reduced inputs of N relative to C via litter deposition.

Labile pools of C and N

The light fraction consists of partially decomposed plant tissue and it is important because it serves as a readily decomposable substrate for soil microorganisms and a short-term reservoir of plant nutrients (Janzen et al. 1992; Gregorich and Ellert, 1993). It has been suggested that it is an early indicator of the effects of soil management on soil organic matter status (Gregorich et al. 1994). Similarly, hot water-extractable C represents a soluble, readily metabolizable C source in soils and it has also been used as an early indicator of changes in soil C status (Haynes and Francis, 1993). The fact that both light fraction C and soluble C (as well as potentially mineralizable C) were decreased by annual burning in the 0-2 cm layer confirms that burning decreases C inputs to the surface via litter. That the C:N ratio of the light fraction was increased by burning again reflects the N stress that occurs under burning and the wider C:N ratio of plant tissue growing under a burning regime.

It is important to note here that the composition of the light fraction may well differ between burnt and unburnt treatments. That is, in the burnt treatments a significant part of the organic C (including light fraction C) may consist of inert charcoal (Golchin et al. 1997). Thus, the reduction in active C in the surface 2 cm under burning is likely to have been more pronounced than that suggested by the measured decrease in organic C and light fraction C.

In comparison with the unburnt control, mean annual standing dry matter over the first 24 years of the experiment on the annual winter and spring burn treatments were 62 and 70 % whilst the equivalent values for biennial and triennial burning were 71 and 72% and 94 and 76% respectively (Tainton et al. 1978). However, these values are the result of one, two or three year's growth and are being compared with a large amount of old, moribund vegetation which dominates on the unburnt treatments. In fact, annual dry matter production, both above- and

below ground is usually greater under regular burning in mesic grasslands (Rice et al. 1998). There is a characteristic increase in root biomass as plants compensate for N limitation by exploring a greater volume of soil (Johnson and Matchett, 2001). In addition, regular defoliation, caused by burning, will result in death and deposition of root material because of a decrease in photosynthate production and a reallocation of C resources to regrow photosynthetic tissue (Barnes, 1989). Turnover of the larger root biomass under burning helps explain the greater labile C in the 4-10 cm layer. Increased deposition of root material in response to regular burning was observed by Ojima et al. (1994) to result in relative increases in organic C content below the surface. That significant effects have not yet been detected at this study site presumably reflects the high background concentrations of organic C (i.e. 27-31 g kg^{-1}) already present in the 4-10 cm layer.

Although most labile C pools were decreased by annual burning in the 0-2 cm layer, surprisingly, the size of the microbial biomass remained unaffected. However as expected, the microbial biomass was larger under annual burning in the 4-10 cm layer. It is possible that factors other than C-supply (e.g. lack of water and a tendency for dessication) may have been limiting the size of the microbial biomass in the 0-2 cm layer.

Potentially mineralizable N

Whether measured by laboratory incubation or by plant uptake in a pot experiment, potentially mineralizable N was markedly decreased by burning. This reflects the shortage of N under a burning regime and the substantially wider C:N ratio of the bulk soil, the light fraction organic matter and deposited above-ground and below-ground plant litter under burning. Reductions in mineralizable N in soils under long-term burning regimes in North American grasslands have been noted previously by a number of workers (Ojima et al. 1994; Turner et al. 1997; Blair, 1997).

A surprising finding was, however, that mineralizable N increased with increasing soil depth (i.e. 0-2 cm < 2-4 cm < 4-10 cm) for both unburnt and burnt treatments while total N, organic C and mineralizable C all decreased. This occurred in both the incubation and pot experiments clearly indicating that net N mineralization increased with depth. Furthermore, the same trend was observed under rangeland in the subsidiary experiment. We are not aware of

other studies that have reported a similar-finding. Indeed, much recent research in agricultural soils has demonstrated that microbial activity and both net and gross mineralization of N decrease markedly with increasing soil depth as do organic C and total N contents (Murphy et al. 1998; Paul et al. 2001). Similarly, at the agricultural site used in the subsidary experiment (an improved kikuyu pasture) both CO_2 evolution and net N mineralization decreased with depth (i.e. 0-5 cm > 5-10 cm).

A major difference between native grassland and an agricultural pasture is that the latter receives substantial inputs of fertilizer N (about 150 kg N ha^{-1} yr^{-1}) in order to produce high dry matter yields with a high protein content. Thus, a rangeland is N-limited (even more so under burning) while a pasture is not. This will be reflected in the C:N ratio of the deposited above-ground and below-ground litter and thus in the light fraction. For example, the C:N ratios of the light fraction were 13 and 16 under pasture in the 0-5 cm and 5-10 cm layers respectively while corresponding values under rangeland were 29 and 41. Similarly, in the main experiment the C:N ratio of the light fraction ranged from 18-31 (mean = 25). The wide C:N ratio of the decomposing plant material under native grassland means that N immobilization is favoured, while N mineralization is favoured under fertilized pasture where the C:N ratio of the decomposing plant material is narrower. Since the size (microbial biomass C) and activity (CO_2-C evolution rate) of the soil microbial community is highest in the surface layer, and decreases with depth, the tendency for N immobilization is also greatest near the surface. As a result, in rangeland soils the accumulation of mineral N increased with increasing depth down to 10 cm.

The current findings occurred where soil was removed from the field, sieved and the native vegetation removed. It was therefore under conditions which favoured net degradation of organic matter. Under equilibrium conditions in the field, soil organic matter content (organic C and total N) will have stabilized to a more-or-less constant level (Schimel et al. 1985). Under such conditions the flows of N through the soil organic matter pool will still be greatest near the surface and decrease with depth because the N content and N inputs are greatest near the surface.

Nevertheless, the relatively wide C:N ratio of the deposited residues will mean that temporary N immobilization occurs during the initial stages of their decomposition. As C is lost as CO_2-C and N is accumulated into the decomposing residues, their C:N ratio will narrow and net mineralization will then occur. This will mean that mineral N is conserved within the soil-plant system (Hayes and Seastedt, 1989) since any excess mineral N not taken up by plants will

be rapidly immobilized and released later. This cycle of N immobilization and subsequent mineralization will occur predominantly in the rhizosphere since most of the litter deposition will be in the form of root turnover. For the above reasons, concentrations of exchangeable mineral N in soils under grasslands are characteristically low (i.e. < 5 mg kg^{-1}) (Seastedt et al. 1991). The wider C:N ratio of residues from grasses that are dominant under burning will result in an even greater tendency for N immobilization. As suggested by Wedin and Tilman (1990) this may be a useful adaptation of those plants that are good competitors for N since greater N immobilization will reduce N availability and give them an even greater advantage over other species.

Conclusions

The fact that potentially mineralizable N increased with increasing soil depth in both unburnt and burnt treatments is a consequence of the shortage of N that exists under rangeland conditions. Indeed, as expected, under the fertilized Kikuyu pasture the opposite trend was observed. The greater N immobilization in the surface soil, where microbial activity was greatest, reflects the wide C:N ratio of deposited plant residues and of the resulting light fraction organic matter. This can be viewed as an adaptation of the ecosystem to conserve N and minimize N losses (e.g. by nitrate leaching). That is, any mineral N that is not absorbed by plant roots will be rapidly immobilized by the soil microbial biomass which is involved in degradation of litter inputs.

In agreement with North American studies, regular burning of the grasslands caused a proportionately greater loss of N than C from the plant-soil system and an even greater N-limitation. As a result, grassland species adapted to low N fertility dominated and the C:N ratios of litter inputs, light fraction matter and, indeed, the bulk soil organic matter were widened and the amount of potentially mineralizable N present was much reduced. Burning also apparently altered the distribution of organic matter inputs to the soil causing a general decrease in litter inputs to the surface 0-2 cm but an increase in the 4-10 cm layer due to greater turnover of root material.

Acknowledgements

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CHAPTER 3

INTERACTIVE EFFECTS OF DIFFERENT SEASONS OF BURNING AND MOWING ON GRASS AND FORB DIVERSITY IN A LONG-TERM GRASSLAND EXPERIMENT, SOUTH AFRICA

Abstract

Disturbance has been recognized as an important determinant of plant community organization and diversity. Short-term experiments may result in misleading information on the relationship between diversity and disturbance, because short- and long-term responses to disturbance may not be correlated. The effect of type, timing and frequency of disturbance on grass and forb species richness was examined using data from a long-term (> 50 year) grassland burning and mowing experiment in KwaZulu-Natal, South Africa.

Grass species richness declined dramatically (> 50%) in the absence of disturbance, whereas forb species richness was unaffected. Annual burning in sites not mown in summer tended to increase grass species richness relative to triennial burning (22% increase) with the reverse being true in sites mown twice in summer (37% decline). Forb species richness declined by 25% in sites mown twice in summer relative to sites only mown in early summer. Disturbance was necessary to achieve maximum grass species richness presumably by removing litter, increasing the availability of light and maintaining the system at disequilibrium. The interaction of time of mowing in summer and time of burning during the dormant period had the most dramatic effect on species richness. Time of burning had no effect on richness in sites mown in early summer, but winter burning resulted in a dramatic decline (27-42%) in richness in sites mown in late summer. This effect may be related to possible greater soil desiccation with this combination of disturbances than with other specific combinations.

Nomenclature: Arnold & De Wet (1993).

Introduction

Diversity has been proposed to play an important role in ecosystem function in terms of invasion resistance (Tilman 1997; Dukes 2001; Hector et al. 2001) and stability of production (Johnson et al. 1996; Naeem & Li 1997; Tilman et al. 1997). Thus, understanding the determinants of diversity and mechanisms by which many species competing for the same resources coexist, are key objectives of ecology.

Humpbacked productivity-diversity relationships (Al-Mufti et al. 1977; Moore & Keddy 1989) suggest that the availability of limiting resources may be an important determinant of diversity (Grime 1973). Habitats where resources such as nutrients or soil moisture are extremely limiting generally lie outside the fundamental niche of most species, whereas extreme competition for resources (especially light) in highly productive moist fertile habitats, allows only the most competitive species to persist. Consequently, the realized niche of most species and, therefore, highest diversity generally occurs somewhere between these extremes. Disturbance (e.g. burning, mowing or grazing) may be an important determinant of diversity by modifying resource availability and the abundance and vigour of competitive dominants (Huston 1979; Collins et al. 1998). Disturbance has been shown to reduce the intensity of competition for a limiting resource (Wilson & Tilman 1993). However, while disturbance may increase the availability of light (Knapp & Seastedt 1986; Collins et al. 1998), it may result in a concomitant decrease in the availability of other limiting resources such as soil moisture (Redmann 1978; Knapp & Seastedt 1986; Carson & Pickett 1990) and nitrogen (Ojima et al. 1994; Fynn et al. 2003). Moreover, disturbance may influence productivity (Tainton et al. 1978; Redmann 1978; Knapp & Seastedt 1986), an important determinant of diversity (Al-Mufti et al. 1977; Moore & Keddy 1989; Wheeler & Shaw 1991; Wilson & Tilman 2002). Consequently, in low productivity habitats, such as on infertile well-drained soils, disturbance may increase competition for a limiting soil resource. Thus, although disturbance may be an important requirement for species coexistence, the intensity of disturbance required for the coexistence of the maximum number of species should vary with habitat productivity (Huston 1979).

Furthermore, different types and timing of disturbance may have different or interactive effects on resource availability and competition intensity and diversity. For example, annual

burning in the prairies reduced diversity by favoring a dominant species but summer mowing negated that effect (Collins et al. 1998). Apart from the effects of disturbance on competition intensity, disturbance may also influence litter levels, a major determinant of diversity (Al-Mufti *et al.* 1977; Carson & Peterson 1990; Tilman 1993; Foster & Gross 1998), probably through negative effects on seedling germination and establishment in many species (Foster & Gross 1998; Jutila & Grace 2002).

Long-term experiments are valuable for examining the effect of disturbance on species richness because long-term disturbance may result in changes in the environment such as vegetation structure (Knapp & Seastedt 1986), soil organic matter and nitrogen availability (Fynn et al. 2003), which in turn, may affect species richness. In contrast, short-term experiments may result in spurious conclusions over the impact of disturbance on species richness because the initial response of species richness to disturbance may only be transient (Peet et al. 1983; Wilson & Tilman 2002).

The burning and mowing experiment of the University of Natal (KwaZulu-Natal, South Africa) provided an opportunity to examine the long-term (> 50 years) interactive effect of different types, seasons and frequencies of disturbance on the species richness of a subtropical mesic grassland. The aims of this study were to: 1) determine the long-term effect of type, season and frequency of disturbance on grass and forb diversity and richness, 2) examine relationships between richness and community factors, such as grass dominance, cover and productivity and 3) to gain insight into possible mechanisms through which disturbance affected diversity.

Methods

Study area

The burning and mowing experiment is located at Ukulinga (29° 24′ E, 30° 24′ S), the research and training farm of the University of Natal, which is in the south-eastern hinterland of the province of KwaZulu-Natal, South Africa. The experiment is situated on top of a gently sloping plateau ranging in altitude from 838 m to 847 m a.s.l.

The lithology consists of Ecca group shales of the Karroo sedimentary sequence. Soils at the site vary in depth from 50 mm to 600 mm. They are acidic and infertile and are classified as Westleigh (plinthic paleustalf) and Mispah forms (lithic ustorthent) (Soil Classification Working Group 1991).

The vegetation of the area has been classified as Southern Tall Grassveld (Acocks 1953) and is described as a dense closed grassland (0.5 - 0.75 m tall) with scattered trees of *Acacia sieberiana* and is dominated by grass species such as *Themeda triandra, Heteropogon contortus*, and *Tristachya leucothrix*.

The mean annual precipitation is 790 mm, mostly as convective storms during summer (September to April). Summers are warm to hot with a mean monthly maximum of 26.4 °C in February, and winters are mild with occasional frost and a mean monthly minimum of 8.8 °C in July. The growing period for grasses is mediated by temperature and rainfall, which are optimal for growth between October and April.

Experimental design

The Ukulinga experiment was established in 1950 with the general objectives being to establish a summer cutting (utilization) regime that would maximize hay production and the best dormant season treatment for removal of aftermath (which reduces quality). The experiment is a randomized blocks (three replicates) split-plot design with four whole-plot summer utilization treatments and eleven sub-plot dormant-season removal treatments (Table 3.1). Plot sizes are 13.7 x 18.3 m. Treatments range from sites defoliated three times per annum to sites completely protected from disturbance since 1950. Burning was initiated in each plot with a back burn for protection from runaway fires and closed out from the other end of the plot with a head burn. Mowing height was approximately seven centimeters. In the mowing treatments, grass residue was raked off the plots and removed. Prior to the establishment of the experiment, the site was mown annually in summer for hay (Rodel 1950). While a small number of antelope are occasionally observed on the experiment, their numbers are too low to have any major impact on plant dynamics.

Table 3.1. Description of the whole-plot and sub-plot treatments of the Ukulinga burning and mowing experiment

Whole-plot	Description of treatment
A	Control (not cut for hay)
B	One hay cut taken early in the summer when the grass is approximately 200 mm high
C	One hay cut taken late in the summer (end of February)
D	Two hay cuts taken, one early (B) and one late (C) in the summer
Sub-plot	
1	Control (no burn)
2	Annual burn in the first week of August
3	Annual burn after the first effective spring rains (12.5 mm in 24 hours)
4	Biennial burn in the first week of August
5	Biennial burn after the first effective spring rains (12.5 mm in 24 hours)
6	Biennial burn in autumn (mid May)
7	Triennial burn in the first week of August
8	Triennial burn after the first effective spring rains (12.5 mm in 24 hours)
9	Triennial burn in autumn (mid May)
10	Annual mow in the first week of August
11	Annual mow after the first effective spring rains (12.5 mm in 24 hours)

Note - treatments 6 and 9 do not receive any summer defoliation to allow sufficient fuel to accumulate to apply an early dormant season burn in autumn.

Sampling

In the 1999/2000 growing season, a survey of the composition of the whole experiment encompassing all grass, forb and sedge species was undertaken using a nested quadrat method (Morrison et al. 1995). A series of nested concentric sub-quadrats (1 m^2, 2 m^2, 5 m^2, 10 m^2, 20 m^2, 50 m^2 and 100 m^2 in size) was located in the centre of each plot. Species were given the maximum importance score of seven if they were encountered in the smallest sub-quadrat, which decreased successively to the lowest importance score of one if only encountered in the largest sub-quadrat.

In the 1996 growing season, a point sampling method (Mentis 1981) was used to determine grass species composition on the experiment to provide a precise measure of grass relative abundance in each plot. The nearest species to the point of a metal spike located systematically at one metre intervals was recorded, with 200 sample points taken per site. Non-graminoid monocotyledons and dicotyledons were grouped as forbs. Basal cover was determined using the method of Hardy & Tainton (1993) with 100 sample points per site.

For estimation of dry matter production at a site, a 2.8 m by 13.7 m strip was mown in late summer at each site and the biomass determined. A grab sample is taken for moisture content determination and used to adjust the fresh biomass value for dry matter determination. This is only done in all sites (except the undisturbed sites) every seven years when all treatments coincide and are suspended.

Data analysis

Species richness (number of species per plot), evenness and the Shannon-Weaver diversity indices were calculated for each plot. Analysis of variance was used to examine orthogonal contrasts between treatments using GENSTAT 5 (GENSTAT 1993) to determine the main and interactive effects of treatments on species richness, evenness and diversity. Once significant effects on species richness had been established using ANOVA, Chi-square tests were used (presence or absence) to determine which individual species had been favoured or reduced by those treatments.

To describe the main floristic gradients in the data, correspondence analysis (CA) was conducted on the grass species abundance data using CANOCO 4 (ter Braak 1988). Gradients in grass composition were determined because grasses make up 80 % of the biomass of this grassland and their composition, therefore, has the potential to influence species richness. CA was the method of choice because of the non-linear response of species along gradients (DCA gradient length of first axis > 3.5 turnover units for grass and forb data). Detrending was not required as no severe arch effect was evident. No transformations were used and species with only one occurrence in the data were removed. Rare species were not down weighted.

Regression analysis using GENSTAT 5 (GENSTAT 1993) was used to determine the relationship between various community attributes and species richness. The community attributes that were investigated were composition (CA axis 1 scores), basal cover %, grass species evenness and productivity at a site. Data were taken from the mean of dry matter production determined in each plot during the 1989/90 and 1997/98 test years (i.e. sum of dry matter in the 1989/90 and 1997/98 seasons divided by two). Linear and squared terms were fitted to test for quadratic relationships.

Results

Effects of disturbance on species richness

Long-term protection from disturbance (Fig. 3.1a; black bar) resulted in a 55% and 66% decrease in grass species richness relative to sites burnt in the dormant-period (Fig 1a) and mown in early summer (Fig. 3.1b) respectively (WP1 x SP1; Table 3.2). In contrast, protection from disturbance had no effect on forb species richness relative to disturbed sites (Fig. 3.1e).

Mowing in early- and late-summer resulted in 42% and 25% higher grass species richness respectively relative to sites not mown in summer, but had no effect on forb species richness (Fig. 3.1) (WP1; Table 3.2). Thus, in addition to summer mowing improving grass species richness an early-summer mow resulted in higher grass species richness than a late-summer mow (WP3; Table 3.2). The frequency of summer mowing (one versus two mows) had no effect on grass species richness, but mowing in both early- and late-summer resulted in a 25%

decline in forb species richness relative to sites mown in early-summer only (Fig. 3.1) (WP2; Table 3.2). Not burning in the dormant-period combined with a double summer mow (Fig. 3.1h; black bar) resulted in a 48% reduction in forb species richness relative to sites mown twice in summer and burnt in the dormant-period and a 65% reduction relative to sites mown once in summer (WP2 x SP1; Table 3.2).

A striking effect on grass and especially forb species richness was the interaction between the time of mowing in summer and the time of burning in the dormant-period (WP3 x SP4; Table 3.2). For example, the time of burning in the dormant period (spring vs. winter) had no effect on grass or forb species richness in sites that were not mown in summer or mown in early summer (Fig. 3.1a,b,e,f), but winter burning strongly reduced grass and forb species richness in sites mown in late summer (Fig. 3.1c,d,g,h). In sites mown in late summer, annual, biennial and triennial winter burning resulted in 42%, 30% and 27% lower forb species richness respectively than the associated spring burning treatments.

The effect of dormant-season burning frequency on grass species richness tended to interact with summer mowing frequency as indicated by a significant summer mowing regime (whole-plot) by dormant-period burning frequency (linear) effect on grass species richness (Table 3.2). Where sites were not mown in summer, grass species richness tended to be higher in sites burnt annually than in sites burnt triennially (Fig. 3.1a) with the reverse being true where sites were mown twice in summer (Fig. 3.1d). There was no clear effect of burning frequency (linear or quadratic) on forb species richness.
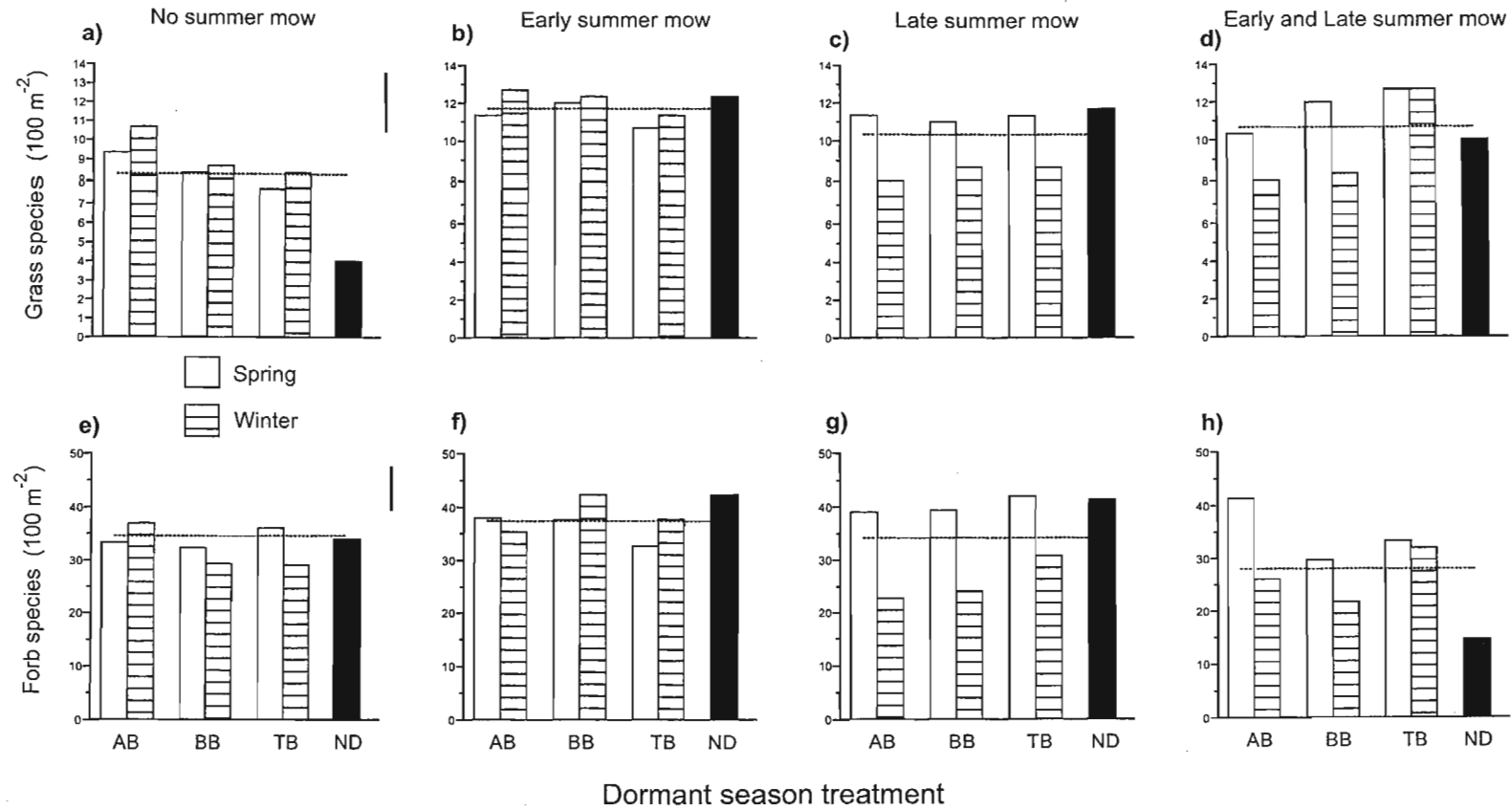
Fig. 3.1. The long-term interactive effect of different burning and mowing treatments on the grass and forb species richness of Tall grassveld at Ukulinga. AB, annual burn; BB, biennial burn; TB, triennial burn; ND, no dormant-season disturbance. Vertical bar = L.S.D. Horizontal dotted line = mean for species richness under a specific summer mowing regime, averaged across dormant-season treatment

Table 3.2. Analysis of variance, and orthogonal contrasts of grass and forb species richness in whole-plot and sub-plot treatments of the burning and mowing experiment in Tall grassveld at Ukulinga

Source of variation	d.f.	Forbs v.r.	Forbs F pr.	Grasses v.r.	Grasses F pr.
Rep stratum	2	0.49		3.92	
Whole-plots	3	10.23	**0.009**	30.06	**<.001**
No summer mow vs. summer mow (WP1)	1	0.93	0.373	75.45	**<.001**
One summer mow vs. two summer mows (WP2)	1	26.19	**0.002**	1.19	0.317
Early vs. late summer mow (WP3)	1	3.58	0.107	13.53	**0.01**
Residual	6	1.78		0.46	
Sub-plots	8	7.78	**<.001**	1.84	0.085
No dormant-period disturbance vs. dormant-period disturbance (SP1)	1	0.14	0.713	1.84	0.18
Dormant-period burn vs. dormant-period mow (SP2)	1	0.47	0.494	0.34	0.559
Winter vs. spring mow (SP3)	1	32.08	**<.001**	8.69	**0.004**
Spring vs. winter burn (SP4)	1	24.43	**<.001**	2.9	0.094
Linear effect of burning frequency	1	0	0.952	0.13	0.720
Quadratic effect of burning frequency	1	3.02	0.087	0.08	0.772
Spring vs. winter burn x linear effect of burning frequency	1	2.09	0.153	0.13	0.720
Spring vs. winter burn x quadratic effect of burning frequency	1	0.01	0.917	0.62	0.433
Whole-plot x Sub-plot interaction	24	4.9	**<.001**	1.96	**0.017**
WP1 x SP1	1	0	0.961	13.82	**<0.001**
WP1 x SP2	1	11.22	**0.001**	0.29	0.59
WP1 x SP3	1	1.83	0.181	0.03	0.861
WP1 x SP4	1	3.15	0.081	3.73	0.058
WP2 x SP1	1	37.03	**<0.001**	1.52	0.223
WP2 x SP2	1	1.5	0.225	0.01	0.905
WP2 x SP3	1	1.93	0.169	0.56	0.458
WP2 x SP4	1	0.64	0.425	0.74	0.392
WP3 x SP1	1	0.39	0.536	0.21	0.65
WP3 x SP2	1	0.88	0.351	1.65	0.203
WP3 x SP3	1	3.26	0.075	1.01	0.318
WP3 x SP4	1	27.21	**<0.001**	7.05	**0.01**
Whole-plot x linear effect of burning frequency	3	1.66	0.183	4.36	**0.007**
Whole-plot x quadratic effect of burning frequency	3	3.73	**0.015**	0.4	0.756
Whole-plot x spring vs. winter burn x linear effect of burning frequency	3	3.38	**0.023**	0.39	0.764
Whole-plot x spring vs. winter burn x quadratic effect of burning frequency	3	0.22	0.882	0.43	0.733
Residual	64				
Total	107				

Effects of community attributes on richness

Community attributes such as grass species composition (Fig. 3.2a,b), basal cover (Fig. 3.2c,d), grass species evenness (Fig. 3.2e,f) and productivity (Fig. 3.2g,h) had little or no effect on grass or forb species richness. Grass species richness was only related to productivity in sites not mown in summer where it tended to decline with increasing productivity (Fig. 3.3a). Forb species richness was only related to productivity in sites mown once in summer where it had a strong quadratic relationship with productivity (Fig. 3.3d). Neither grass nor forb species richness was related to productivity in sites mown twice in summer (Fig. 3.3g,h).
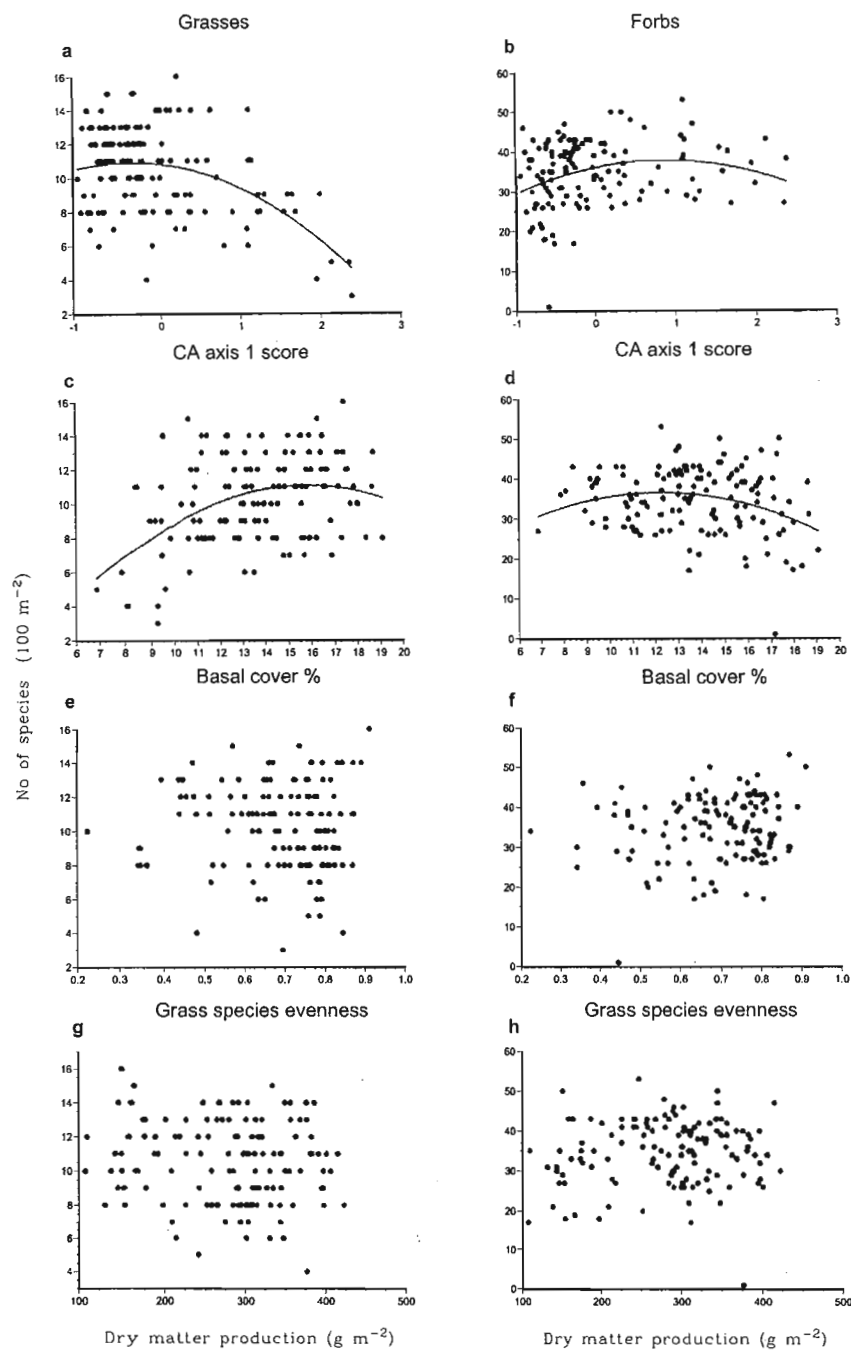
Fig. 3.2. The relation between various community attributes on the grass and forb species richness of Tall grassveld at Ukulinga.
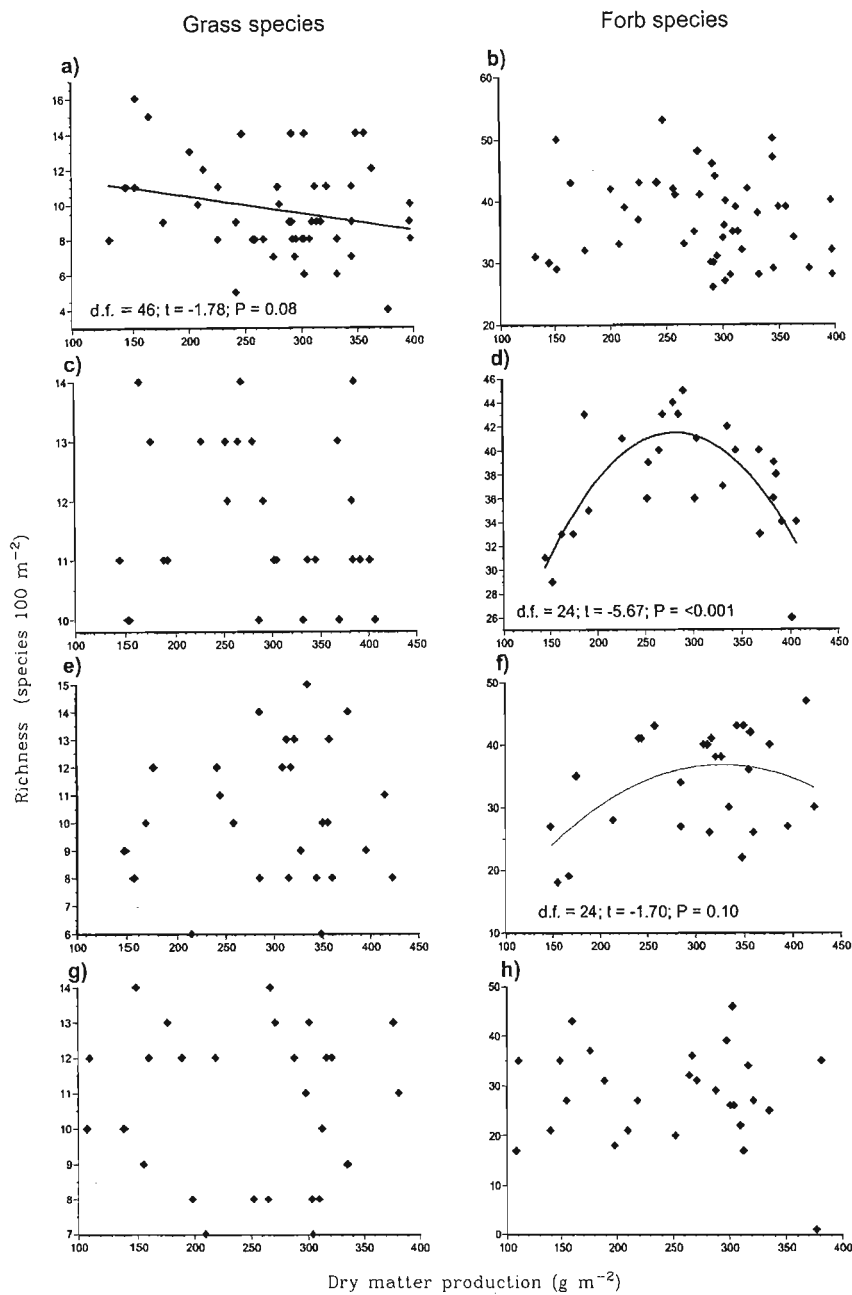
Fig. 3.3. The relation between productivity and grass and forb species richness under different summer mowing regimes in Tall grassveld at Ukulinga. a & b, no summer mow; c & d, early-summer mow; e & f, late-summer mow; g & h, early- and late-summer mow.

Discussion

Summer and dormant-period disturbance

Disturbance may be necessary to maintain species diversity in plant communities by preventing the system reaching competitive equilibrium (Huston 1979). In this experiment, burning in the dormant period or mowing in summer was necessary to maintain grass species richness, which declined dramatically when sites were completely protected from disturbance (Fig. 3.1). Protection from disturbance generally results in a loss of species richness (Bakker 1989). Summer mowing or clipping has been shown to maintain species richness in grasslands globally (Armesto & Pickett 1985; Collins *et al.* 1998; Leps 1999; Jutila & Grace 2002; Jacequemyn et al. 2003). Complete protection from disturbance resulted in high litter levels on the soil surface (Fynn et al. 2003), which may reduce germination and emergence of seedlings (Foster & Gross 1998; Leps 1999; Jutila & Grace 2002). In addition, tall-grass species and trees dominated protected sites, and may have shaded out and excluded the shorter grass species, which were rare or absent in undisturbed sites. Disturbance is likely to reduce the degree of asymmetric competition for light. Light availability has been shown to be an important determinant of species diversity (Collins *et al.* 1998; Henry et al. 2002). An early- summer mow resulted in higher grass species richness than a late-summer mow (Fig. 3.1) possibly because it would improve light availability over the main growing period for grasses whereas a late-summer mow would only improve light availability at the end of the growing period.

It is surprising, however, that protection from disturbance had no effect on forb species richness. It appears that although many species were lost from undisturbed sites they were replaced by other species (see chapter 4) that were possibly more shade- or litter-tolerant. Higher phylogenetic diversity for forbs than grasses (41 forb families versus 1 grass family) increases the probability of having forb taxa adapted to specific conditions. The size of the regional species pool (Partel et al. 1996; Zobel 1997) or the size of the pool of species adapted to the specific conditions of a site (Gough et al. 1994; Partel *et al.* 1996) will constrain species richness at that site. Thus, although the composition of forbs changed dramatically between disturbed and undisturbed sites (unpubl.), diversity remained unchanged because species that were possibly

excluded by disturbance or a lack of it, were replaced by others probably better adapted to those conditions.

The interactive effect of different types and seasons of disturbance

Season of burn and timing of mowing in summer interacted in their effect on species richness (WP3 x SP4; Table 3.2). Winter burning resulted in a dramatic reduction in grass and especially forb species richness in sites that were mown in late summer but had no effect on richness in sites mown in early summer or not mown at all (Fig. 3.1). It seems that many species were least vulnerable to disturbance in spring but, importantly, winter burning only reduced richness under specific conditions (i.e. in combination with a late summer mow). Winter and spring burning is executed before and after the first spring rains respectively, suggesting that the negative effect of winter disturbance on species richness may be related to soil moisture. For example, a late-summer mow is likely to result in greater evaporation and soil desiccation over the winter period than an early-summer mow because there is much more time during the growing period for establishment of cover before the onset of winter after an early-summer mow than after a late-summer mow. The combination of a late-summer mow with further exposure of the soil surface after winter burning is likely to result in a greater degree of soil desiccation than in sites having good cover over the winter period or sites only burnt after first good rains in spring. Indeed, removal of cover through disturbance has been shown to result in soil desiccation (Redmann 1978; Knapp & Seastedt 1986; Carson & Pickett 1990) and an associated reduction in species richness (Carson & Pickett 1990).

Support for soil desiccation as the cause of reduced species richness with this combination of disturbances is seen in the fact that moisture-sensitive species were eliminated by the late-summer mow and winter burn combination but not with other combinations. For example, the sedge *Schoenoxiphium sparteum,* a species characteristic of hygrophyllous grasslands, was common in sites mown in late-summer and burnt in spring but was absent from all sites burnt in winter. Soil desiccation may affect the seeds rather than the adults of some of these species. For example, the orchid *Habenaria dives,* which was also absent in all sites mown in late-summer and burnt in winter, has a fungal symbiont necessary for seed germination that may be vulnerable to desiccation. In addition, recalcitrant seeds are generally intolerant of desiccation (Tweddle et al.

2003). *Boophane disticha*, a species with recalcitrant seeds, was absent in the late-summer mow/winter burn combination but common in the late-summer mow/spring burn combination.

Another possibility for reduced species richness with the late-summer mow/winter burn combination is that a late-summer mow improves light penetration in the sward, which may stimulate seedling germination (Jutila & Grace 2002) before winter, while the removal of meristems may extend flowering and fruiting of many species into winter, rendering them vulnerable to a winter burn. Further studies, however, will be needed to confirm whether soil desiccation or altered phenological patterns are mechanisms responsible for reduced species richness in the late-summer mow/winter burn combination.

Another dramatic interactive effect was a 48% reduction in forb species richness in sites mown twice in summer and not burnt in the dormant period relative to sites mown twice in summer and burnt in the dormant period (Fig. 3.1h). It is difficult to explain why this particular combination resulted in lower forb species richness than other summer mow/dormant-period burn combinations. Further investigations will be needed to elucidate the mechanisms causing low species richness in these sites.

Frequency of disturbance

Mowing twice in summer had a far greater negative effect on forb than on grass species richness (Table 3.2; Fig. 3.1). Forbs may be more susceptible to disturbance than grasses, which have basal meristems that largely escape defoliation. Further, African grasses are adapted to defoliation having evolved under a long history of heavy grazing (Stuart-Hill & Mentis 1982) while many forbs, rather than being grazing-tolerant, avoid grazing through production of chemical compounds toxic or distasteful to herbivores.

In contrast to the prairies where annual burning without summer mowing reduced species richness (Collins et al. 1998), in Tall grassveld annual burning without a summer mow tended to increase grass species richness relative to a triennial burn, and had no effect on forb species richness (Fig. 3.1a). Annual burning increases productivity in mesic prairie grasslands (Knapp et al. 1998), while it reduced productivity in this experiment (Tainton et al. 1978). Increased productivity and abundance of C_4 grasses with annual burning in the prairies (Collins et al. 1998) may have resulted in exclusion of C_3 and annual grass species and certain forb species. C_3 grass

species are absent at Ukulinga, being only present in the highest altitude grasslands (> 2000 m) in the KwaZulu-Natal region. In addition, annual grass species are rare in this type of grassland, generally.

Effect of community attributes on species richness

Dominance by a few species (Al-Mufti *et al.* 1977; Hector *et al.* 2002) and high above-ground production (Al-Mufti *et al.* 1977; Moore & Keddy 1989; Wheeler & Shaw 1991) may result in low species richness, generally because of intense competition for resources. Other studies, however, have not shown any effect of above-ground production on species richness (Goldberg & Miller 1990; Tilman 1993; Rajaniemi 2002). Litter accumulation may have a greater effect on species richness than above-ground production (Tilman 1993). Many other studies have demonstrated the negative effect of litter on species richness (Al-Mufti *et al.* 1977; Carson & Peterson 1990; Facelli & Facelli 1993; Foster & Gross 1998). In this study, no relationship was observed between grass and forb species richness and grass species evenness (an index of dominance) (Fig. 3.2e & f), or site productivity when examined over the entire range of summer mowing treatments (Fig. 3.2g & h). This is possibly because the experiment is located on relatively shallow dry nitrogen-limited soils (Fynn et al. 2003) that do not have the potential for extremely high productivity. In addition, the effect of burning or mowing is likely to ameliorate the effect of productivity and dominant species on species richness by reducing the intensity of competition for resources (Huston 1979; Wilson & Tilman 1993). Furthermore, species richness has been found to be controlled primarily by environmental regulation of potential richness and secondarily by productivity. When extreme environmental conditions were eliminated productivity became the primary predictor of species richness (Gough et al. 1994). Indeed, in this experiment the productivity-species richness relationship was stronger when examined within specific summer mowing regimes. Grass species richness tended to decline with increasing productivity in sites not mown in summer (Fig. 3.3a) whereas forb species richness peaked at intermediate levels of productivity in sites mown once in summer (Fig. 3.3d,f).

Conclusion

Complete protection from disturbance resulted in a marked reduction in grass but not forb species richness. Therefore, grass species richness appears to be controlled by factors related to infrequent disturbance such as reduced light availability and increased litter levels. Disturbance was less important for maintaining forb than grass species richness probably because of a much larger species pool than grasses. Forb species that were lost with lack of disturbance were replaced by species possibly more tolerant of sward structural and microclimatic conditions associated with undisturbed sites. In more productive environments, however, disturbance may play a more important role in maintaining forb species richness. Thus, theoretical predictions that disturbance is necessary for maintaining species diversity (Huston 1979) were supported by the results of this experiment, but various groups of plants may respond differently. Numerous studies on species richness have examined only total species richness and have ignored possible different responses of grasses and forbs.

The interactive effects of type, timing and sequence of disturbance events on species richness were the salient features of the data. Only a specific sequence and combination of disturbance events impacted species richness and resulted in the most dramatic changes. This impact on species richness was possibly an indirect effect of a combination of disturbance events on soil desiccation, but further investigations are needed to test this. The results of this study may have general implications for the management of biodiversity. Contrary to what is generally assumed, this study shows that plants are vulnerable to disturbance during the dormant-period, especially when combined with specific growing-period disturbance regimes. Thus, the timing and combination of disturbance needs to be carefully considered when drafting management policy for specific regions.

Acknowledgements

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CHAPTER 4

EFFECT OF TYPE, TIMING AND FREQUENCY OF DISTURBANCE ON GRASS AND FORB COMPOSITION IN A 50 YEAR GRASSLAND BURNING AND MOWING EXPERIMENT, SOUTH AFRICA

Abstract

Disturbance has been recognized as an important determinant of plant community composition but a predictive understanding of its effects on the distribution and abundance of plants of different traits, growth form and phylogenies is incomplete. The ongoing long-term (> 50 years) grassland burning and mowing experiment of the University of Natal, South Africa was used to examine the effect of different type, timing and frequency of disturbance on grass and herbaceous forb (non-graminoid monocots and dicots) composition in a mesic grassland. An assessment of community composition indicated that grasses responded to the type, timing and frequency of disturbance, whereas the timing and frequency of disturbance had little effect on forb composition. Summer mowing and annual or biennial dormant-period burning maintained short-grass dominated communities, whereas tall-grass species dominated under annual dormant-period mowing, triennial burning or protection from disturbance. However, in the protected sites where litter levels were very high, species with below-ground tiller initiation and sharp erect shoots were more abundant than tall competitive species. Many species of herbaceous dicots and grasses were unable to persist in the protected sites.

Many erect herbaceous dicot species with aerial meristems were intolerant of summer mowing, whereas most small creeping herbaceous dicot species required summer mowing. Certain short-grass species became extremely competitive in productive sites under a mowing regime in summer, whereas they were restricted to the least productive sites in the absence of summer mowing. The smallest grass species appeared to be toleraters rather than competitors, and were restricted to the least

productive sites, irrespective of the disturbance regime. The effect of different type, timing and frequency of disturbance on habitat features such as total soil nitrogen, productivity, and litter levels appeared to be an important determinant of community composition and structure.

Nomenclature: Arnold & De Wet (1993)

Introduction

Much is known about patterns of grassland composition in relation to disturbances such as burning and mowing (Everson & Tainton 1984; Tainton & Mentis 1984; Knapp & Seastedt 1986; Gibson & Hulbert 1987; Peet et al. 1999) but knowledge of the mechanisms responsible for these relationships is incomplete. The interaction of disturbance and habitat productivity appears to provide a framework for understanding patterns of composition in relation to disturbance. For example, in the productive mesic grasslands of South Africa, regular burning is necessary for the maintenance of grassland dominanted by the short-grass species, *Themeda triandra*. Infrequent burning results in a decline in basal cover and dominance by taller less palatable late-successional grass and tree species (Tainton & Mentis 1984). In the less productive semi-arid grasslands of South Africa, however, *Themeda triandra* dominates in the absence of burning (Tainton & Mentis 1984).

Nutrient availability, productivity and disturbance have been recognized as the principal determinants of plant composition and diversity (Grime 1979; Huston 1979; Tilman 1988). Light availability generally declines with increasing productivity (Tilman 1988; Schimel et al. 1991; Peltzer et al. 1998; Cahill 1999). Consequently, species with high maximum growth rates (Grime 1979, Huston & Smith 1987; Wedin & Tilman 1993) and tall stature (Aerts & Berendse 1988; Tilman 1988; Wedin & Tilman 1993; Gaudet & Keddy 1995) tend to have a competitive advantage over shorter slower growing species in fertile productive habitats. This is because tall stature and faster growth rates allow the taller species to overgrow and shade the shorter species. By contrast, shorter species may

be better competitors than taller species in infertile habitats because of an ability to grow faster at lower levels of nutrient availability (Rice et al. 1960; Parrish & Bazzaz 1982; Tilman 1986), a lower demand for nutrients (Chapin 1980; Craine et al. 2002), an ability to maintain metabolic effectiveness at lower levels of nutrient availability (Chapin 1980) and lower loss rates of nutrients (Berendse & Elberse 1990; Craine et al. 2002).

Regular disturbance can alter the competitive balance between short and tall species by creating microclimatic and soil conditions where short species are most competitive. For example, disturbance improves light availability (Knapp & Seastedt 1986; Collins *et al.* 1998) and reduces above-ground competition intensity (Wilson & Tilman 1993). Further, disturbance reduces nutrient availability (Ojima et al.1994; Fynn et al. 2003), soil moisture (Redmann 1978; Knapp & Seastedt 1986), and productivity (Tainton et al. 1978; Redmann 1978), favouring shorter species (Aerts & Berendse 1988; Wedin & Tilman 1993; Gaudet & Keddy 1995).

The loss rate of nutrients is a factor proposed to have an important influence on competitive ability in low to moderate fertility habitats (Tilman 1990). Tall species may lose relatively greater amounts of nutrients than short species under a mowing regime (Berendse & Elberse 1990), which should favour the shorter species.

However, the type and timing of disturbance may result in markedly different effects on nutrient loss rates and soil fertility. Mowing during the dormant-period is likely to result in very little loss of nitrogen relative to mowing in summer because plants have transferred most of their nitrogen below-ground at during the dormant-period. Spring and winter burning may result in different effects on soil nitrogen (Fynn et al. 2003). Thus, an understanding of the effects of disturbance on composition is likely to require knowledge of the effect of type, timing and frequency of disturbance on soil fertility and nutrient loss rates.

Disturbance may not only influence community composition by altering the competitive balance among species but by directly affecting recruitment through interruption of life cycles of certain species, resulting in marked changes in composition (Hazell 1965; Howe 1994). Further, an accumulation of litter in the absence of disturbance (Dix 1960; Knapp & Seastedt 1986; Fynn et al. 2003) may affect recruitment by reducing seed germination (Foster & Gross 1998; Jutila & Grace 2002) and preventing

seedling establishment in species whose shoots are unable to penetrate a litter layer (Sydes & Grime 1981). Litter levels may have striking effects on composition (Sydes & Grime 1981). Thus, disturbance may alter the relative importance of above- and below-ground competition and the overall importance of competition as a determinant of community composition.

Long-term experiments have great value when studying the effects of disturbance or other factors on community composition and diversity because of the transient nature of the initial species responses (Tilman 1988). This makes the interpretation of the results of short-term experiments difficult because the traits of the initial dominants may be unrelated to the long-term outcome of competition (Tilman 1988). Further, it may take decades before the effect of disturbance or the lack of it on soil resources and litter accumulation and its associated effect on composition becomes strongly manifest. The long-term nature of the Ukulinga burning and mowing experiment with its different type, timing, frequency and interaction of disturbances provides a valuable opportunity to examine current conceptual and theoretical understanding of disturbance as a determinant of community composition. More specifically, the objectives of this study were to: 1) describe patterns of community response (grasses and forbs) to the type, timing, frequency and combination of disturbance at the University of Natal's long-term ongoing burning and mowing experiment; 2) link the response of species to specific traits and life cycles; and 3) examine some possible mechanisms of community response to disturbance.

Methods

Study area

The burning and mowing experiment is located at Ukulinga (29° 24′ E, 30° 24′ S), the research and training farm of the University of Natal, outside Pietermaritzburg in the south-eastern hinterland of the province of KwaZulu-Natal, South Africa. The experiment is situated on top of a gently sloping plateau ranging in altitude from 838 to

847 m a.s.l. The lithology consists of Ecca group shales of the Karroo sedimentary sequence. Soils at the site vary in depth from 50 to 600 mm. They are acidic and infertile and are classified as Westleigh (plinthic paleustalf) and Mispah forms (lithic ustorthent) (Soil Classification Working Group 1991). The mean annual precipitation is 790 mm, mostly as convective storms during summer (September to April). Summers are warm to hot with a mean monthly maximum of 26.4 °C in February, and winters are mild with occasional frost and a mean monthly minimum of 8.8 °C in July. The growing period for grasses is mediated by temperature and rainfall, which are optimal for growth between October and April (Rethman & Booysen 1969).

The vegetation of the area has been classified as Southern Tall Grassveld (Acocks 1953) and is described as a dense, closed grassland (0.5 - 0.75 m tall) with scattered trees of *Acacia sieberiana* and dominated by C_4 grass species such as *Themeda triandra, Heteropogon contortus*, and *Tristachya leucothrix*. In the absence of fire, indigenous trees such as *Acacia karroo, A. nilotica* and *Celtis africana*, exotic trees such as *A. mearnsii* and *Melia azedarach*, and grasses such as *Cymbopogon* spp., *Hyparrhenia spp.* and *Aristida junciformis* become common (Titshall et al. 2001). C_3 grass species are absent from the Ukulinga grasslands.

Experimental design

The Ukulinga burning and mowing experiment was established in 1950 (Rodel 1950) with the general purpose of identifying a summer cutting (utilization) regime to maximize hay production and the best dormant season treatment for removal of aftermath (which reduces quality). The experiment comprises a randomized blocks (three replicates) split-plot design with four whole-plot utilization treatments and eleven sub-plot removal treatments. The whole-plots were summer mowing treatments with a control and the sub-plots are dormant-period burning and mowing treatments with a control (Table 4.1). Thus, various combinations of dormant-period treatments (burning or mowing) and summer mowing treatments were achieved. Each experimental plot (e.g. annual burn, no-summer mow, replication 1 or triennial burn, early-summer mow, replication 3, etc.) was 13.7 x 18.3 m in size. Disturbance frequency ranged from sites

mown twice in summer and burnt or mown in the dormant period each year to sites completely protected from disturbance. Burning was initiated in each plot with a back burn for protection from runaway fires and closed out from the other end of the plot with a head burn. In the mowing treatments, grass residue was raked off the plots and removed. Mowing height was approximately seven centimeters. Prior to the establishment of the experiment, the site was mown annually in summer for hay (Rodel 1950). While a small number of antelope are occasionally observed on the experiment, their numbers are too low to have any major impact on composition.

Table 4.1. Description of the whole-plot and sub-plot treatments of the Ukulinga burning and mowing experiment

Whole-plot	Description of treatment
A	Control (not cut for hay)
B	One hay cut taken early in the summer when the grass is approximately 200 mm high
C	One hay cut taken late in the summer (end of February)
D	Two hay cuts taken, one early (B) and one late (C) in the summer
Sub-plot	
1	Control (no burn)
2	Annual burn in the first week of August
3	Annual burn after the first effective spring rains (12.5 mm in 24 hours)
4	Biennial burn in the first week of August
5	Biennial burn after the first effective spring rains (12.5 mm in 24 hours)
6	Biennial burn in autumn (mid May)
7	Triennial burn in the first week of August
8	Triennial burn after the first effective spring rains (12.5 mm in 24 hours)
9	Triennial burn in autumn (mid May)
10	Annual mow in the first week of August
11	Annual mow after the first effective spring rains (12.5 mm in 24 hours)

Note - treatments 6 and 9 do not receive any summer defoliation to allow sufficient fuel to accumulate to apply an early dormant season burn in autumn.

Sampling

Surveys of composition in the 1950/51, 1955/56 and 1960/61 seasons were conducted using the point strike method using 120 points per plot (Dix 1961). The nearest plant method (Mentis 1981) was used for all subsequent grass composition surveys (1975, 1988 and 1996 seasons). In the nearest plant method surveys, the species nearest to the point of a metal spike located systematically at one metre intervals was recorded, with 200 sample points taken per site. Grass species were identified and other herbaceous species were categorized as either forbs (non-graminoid monocots and dicots) or sedges. In the 1999/2000 growing season, a survey of the composition of the whole experiment encompassing all grass, forb (non-graminoid monocots and dicots) and sedge species, was undertaken using the importance score method (Morrison et al. 1995). A series of nested concentric sub-quadrats (1 m^2, 2 m^2, 5 m^2, 10 m^2, 20 m^2, 50 m^2 and 100 m^2 in size) was located in the centre of each plot. Species were given the maximum importance score of seven if they were encountered in the smallest sub-quadrat, scores decreasing successively to an importance score of one if encountered only in the largest sub-quadrat.

Above-ground phytomass production (AGP) is determined for all plots in the experiment (except the plots protected from disturbance) every seven years when all treatments coincided (for details see Tainton et al. 1978). For estimation of AGP, a 2.8 m by 13.7 m strip was mown in late summer at each site and the fresh biomass determined. For an estimate of moisture content, a grab sample was taken and dried at 60°C until constant mass and used to adjust the fresh biomass value for dry matter (AGP). Methods of determination of total soil nitrogen in plots have been described previously (Fynn et al. 2003).

Plant traits

Plants that are good light competitors generally allocate more carbon to stems and tall leaves while plants competing for nutrients allocate less carbon to these components and more to roots (Tilman 1988). Wide leaves are generally associated with shade-

tolerance. Therefore, maximum leaf height, maximum leaf width and stem diameter at 300 mm above the soil surface were measured on at least ten mature individuals of each of the most important grass species (in terms of response to disturbance) on the Ukulinga plateau.

Data analysis

To describe the main floristic gradients in the data, correspondence analysis (CA) was conducted on separate grass (1996 data) and forb species (1999 data) data sets using CANOCO 4 (ter Braak & Smilauer 1998). CA was the method of choice because of the non-linear response of species along gradients (gradient length of first axis > 3.5 turnover units for grass and forb data). No transformations or weighting of rare species were used. Species with only one occurrence in the data were excluded. Detrending was not required as no severe arch effect was evident. Grass and forb compositional data was analyzed separately in order to gain insight into the response of these two different functional groups to burning and mowing. All analyses of grass composition were done using the data from the point sampling method (Mentis 1981) and for non-grasses (forbs and sedges) using data from the importance score method (Morrison et al. 1995).

Analysis of variance was used, with GENSTAT 5 (GENSTAT 1993) to determine the main and interactive effects of treatments and to examine orthogonal contrasts between treatments on grass and forb composition and the abundance of individual key grass species. The response to disturbance of those species with at least 20% of their variance accounted for by CA axis 1, was examined further. CA axis 1 scores from the correspondence analysis of the grass and forb composition data were used as the response variate to examine the effects of treatments on the main pattern of variation in grass and forb composition. The effect of autumn burning was not included in the main ANOVA because autumn burns were not applied in whole-plots that received a summer mow to allow fuel to accumulate, but were compared separately with spring and winter burns using paired t-tests. In order to determine which forb species responded to treatment contrasts that were found to have a significant effect in the ANOVA on forb composition, paired t-tests were done on the abundance of each forb species in those treatments. Paired

samples consisted of the average abundance of a forb species in the two treatments under examination (i.e. disturbed sites versus protected sites; sites mown in summer versus sites not mown in summer; etc.) for a specific replication, resulting in three paired samples for each analysis.

Total soil nitrogen is known to have a strong influence on community composition (Aerts & Berendse 1988; Wedin & Tilman 1993); burning treatments were found to have a large influence on total soil nitrogen in this experiment (Fynn et al. 2003). In order to establish whether burning treatments may influence composition through their effect on total soil nitrogen and productivity (AGP), multiple linear regression analysis including linear and quadratic terms was used to examine the response (relative abundance) of selected grass species to these two variables. The relationship between species abundance and total soil nitrogen could only be examined for sites not mown in summer because data for total soil nitrogen is available for these sites only. The relationship between species abundance and site productivity (AGP) was examined separately for sites that were not mown in summer and for sites that were mown in summer in order to be able to determine if summer mowing modified this relationship.

Results

Traits of key grass species

Key species at Ukulinga can be separated into short (0-500mm), medium (500-1000mm) and tall (> 1000mm) height classes based on their maximum leaf height. Short-grass species were: *Eragrostis racemosa, Eragrostis capensis, Heteropogon contortus, Diheteropogon amplectens, Themeda triandra* and *Tristachya leucothrix* (Fig. 4.1). Species of intermediate height were: *Aristida junciformis, Eragrostis curvula, Hyparrhenia hirta* and *Cymbopogon excavatus,* whereas the tall-grass species were *Cymbopogon validus* and *Panicum maximum* (Fig. 4.1).

Temporal patterns of grass composition in relation to disturbance

Themeda triandra, a short-grass species (Fig. 4.1), was dominant at the commencement of the experiment but declined rapidly in abundance in sites protected from burning and mowing, whereas another short-grass species, *Tristachya leucothrix,* increased to a period of transient dominance by 1961 (Fig. 4.2a). This species was eventually replaced by taller species such as *Aristida junciformis, Eragrostis curvula* and *Cymbopogon* spp., which rose rapidly to dominance between 1975 and 1988 (Fig. 4.2a). In contrast, *Themeda triandra,* maintained its dominance of annually burned sites over the entire duration of the experiment, with relatively little fluctuation in abundance (Fig. 4.2b).
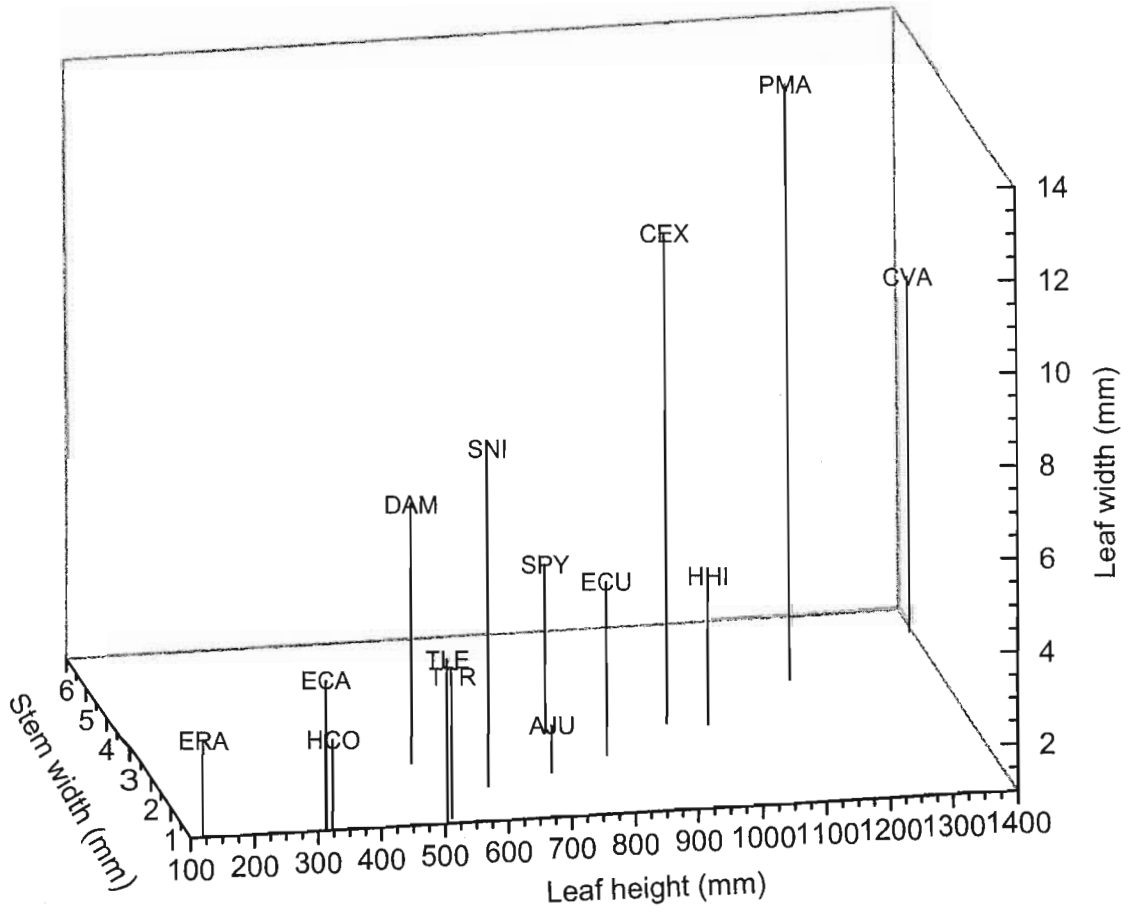
Fig. 4.1. Traits of key-grass species at the Ukulinga long-term grassland burning and mowing experiment. AJU, *Aristida junciformis*; CEX, *Cymbopogon excavatus*; CVA, *Cymbopogon validus*; DAM, *Diheteropogon amplectens*; ECA, *Eragrostis capensis*; ECU, *Eragrostis curvula*; ERA, *Eragrostis racemosa*; HCO, *Heteropogon contortus*; HHI, *Hyparrhenia hirta*; PMA, *Panicum maximum*; SNI, *Setaria nigrirostris*; SPY, *Sporobolus pyramidalis*; TLE, *Tristachya leucothrix*; TTR, *Themeda triandra*.
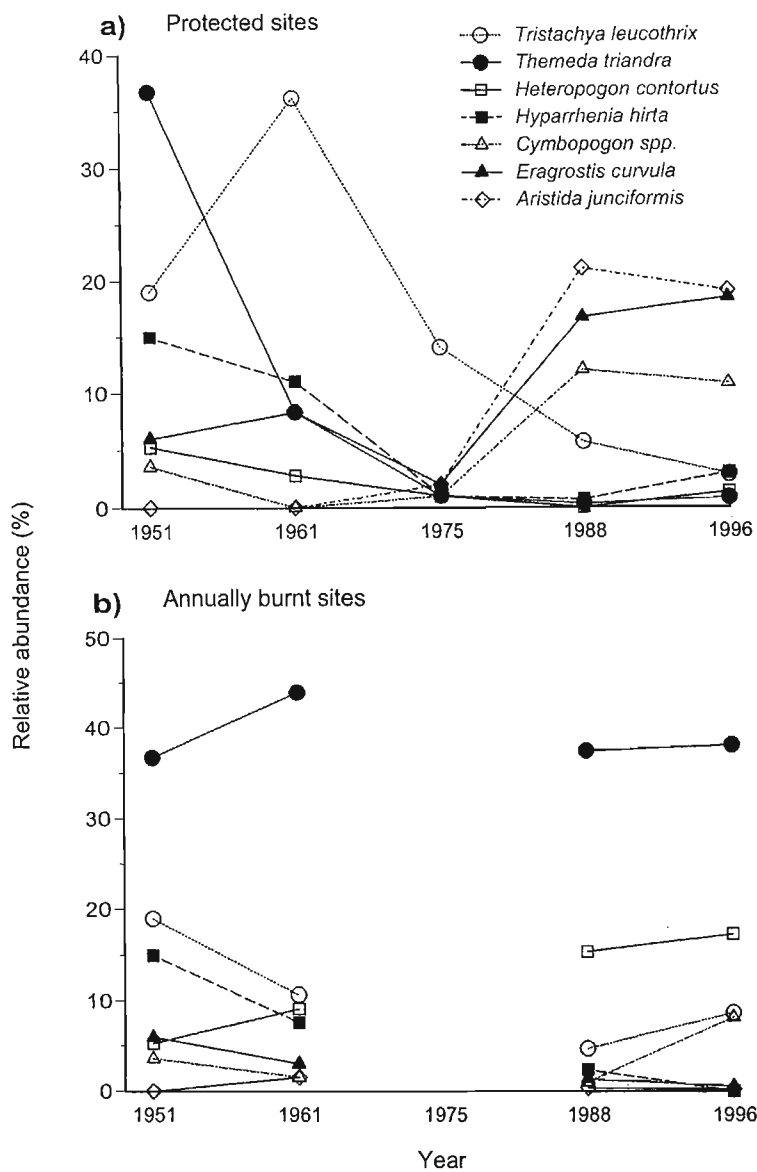
Fig. 4.2. Changes in relative abundance of key grass species between 1951 and 1996 in sites protected from disturbance (a) and sites burned annually in winter but not mown in summer (b) at the Ukulinga long-term grassland burning and mowing experiment. 1975 annual burn data missing.

Effect of type, timing and frequency of disturbance on grass composition

The correspondence analysis (CA) of the data collected after approximately 50 years of treatment application (1996 grass data and 1999 forb data) identified clear patterns of change in both grass and forb composition that were strongly related to treatments (Table 4.2; Fig. 4.3). Sites mown in summer (whole-plots B, C, D) and especially those mown twice in summer (whole-plot D) were located at the extreme left hand side of CA axis 1, whereas sites completely protected from disturbance (A1) were located at the extreme right of CA axis 1 (Fig. 4.3). There was a clear burning frequency gradient for sites not mown in summer. Sites burnt annually in the dormant-period (winter or spring) were similar in composition to sites mown in summer while triennially burnt sites were similar in composition to protected sites with biennially burnt sites at an intermediate position. Burning frequency appeared to have had very little effect on composition if sites were mown in summer (Fig. 4.3). Importantly, sites mown annually during the dormant-period had similar CA axis 1 scores to sites burnt triennially during this period (Fig. 4.3a).

Table 4.2. Summary of the overall performance of the correspondence analysis (CA) of the grass and forb composition of the Ukulinga burning and mowing experiment, in terms of the variance accounted for by each axis and species environment relations

Axes	1	2	3	4	Total inertia	
Grass species						
Eigenvalue	0.339	0.136	0.096	0.083	1.298	
Species-environment correlation	0.817	0.265	0.33	0.225		
Cumulative percentage variance						
of species data	27.6	38.7	46.5	53.3		
of species-environment relation	79.9	83.3	87	88.5		
Sum of all unconstrained eigenvalues						1.229
Sum of all canonical eigenvalues						0.283
Forb species						
Eigenvalue	0.317	0.163	0.14	0.12	3.497	
Species-environment correlation	0.807	0.133	0.493	0.303		
Cumulative percentage variance						
of species data	9.5	14.4	18.6	22.2		
of species-environment relation	58.8	59.6	69.3	72.5		
Sum of all unconstrained eigenvalues						3.331
Sum of all canonical eigenvalues						0.351
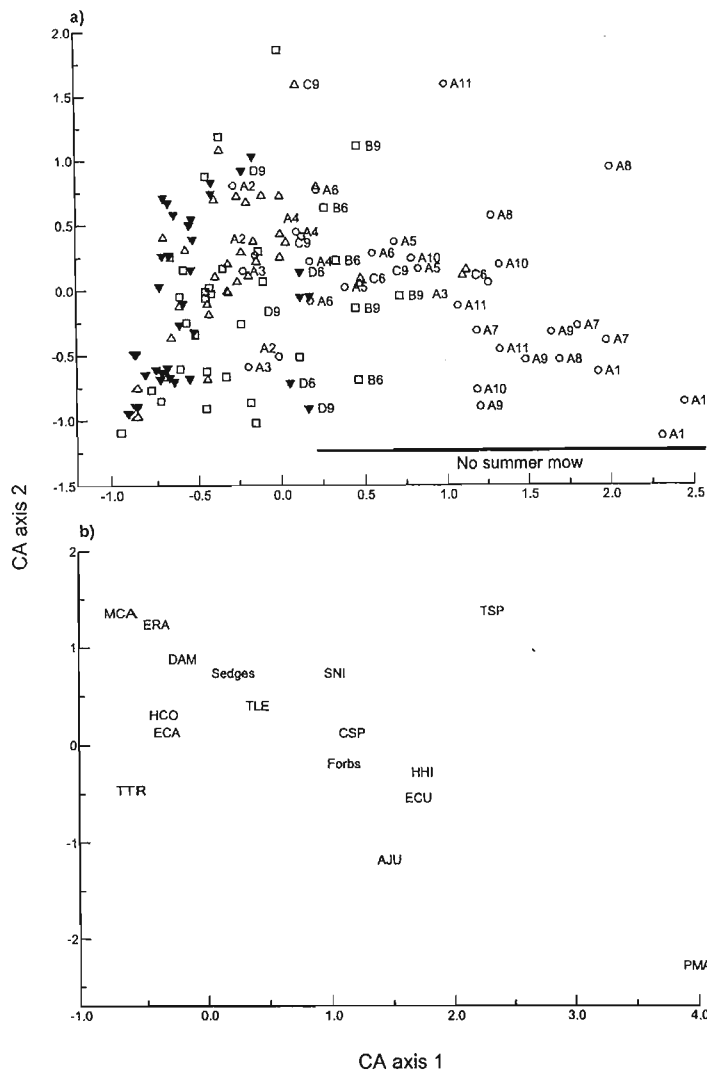
Fig. 4.3. Correspondence analysis (CA) of the grass species in all sites at the Ukulinga burning and mowing trial showing the distribution of sites (a) and species (b) on axis 1 and 2. Circle, whole-plot A; square, whole-plot B; open triangle, whole-plot C; solid triangle, whole-plot D. Letter = whole plot treatment; number = subplot treatment (Table 4.1). AJU, *Aristida junciformis*; CSP, *Cymbopogon* spp.; DAM, *Diheteropogon amplectens*; ECA, *Eragrostis capensis*; ECU, *Eragrostis curvula*; ERA, *Eragrostis racemosa*; HCO, *Heteropogon contortus*; HHI, *Hyparrhenia hirta*; MCA, *Microchloa caffra*; PMA, *Panicum maximum*; SNI, *Setaria nigrirostis*; TLE, *Tristachya leucothrix*; TSP, *Trachypogon spicatus*; TTR, *Themeda triandra*. Only species with > 10 % of their variance accounted for by axis 1 and 2 are plotted.

The principal gradient in grass composition (CA axis 1) was significantly related to a number of summer and dormant-period treatments of which summer mowing, burning frequency and the type of disturbance in the dormant period (burning versus mowing) were most important (P < 0.001) (Table 4.3). Summer mowing had an important effect on all key grass species except *Tristachya leucothrix* (Table 4.4). The salient feature of this response is that the abundance of all the taller species such as *Cymbopogon* spp, *Eragrostis curvula*, *Hyparrhenia hirta* and *Aristida junciformis* were decreased while shorter species such as *Heteropogon contortus* and *Themeda triandra* were increased in abundance by summer mowing (Fig. 4.4).

The effect of burning frequency was only pronounced in sites not mown in summer (significant whole-plot by linear effect of burning frequency interaction; Table 4.3). In sites not mown in summer, short-grass dominated communities were only maintained by annual or biennial burning, whereas tall-grass species dominated in sites burnt only every three years (Fig. 4.4). In sites mown in summer, however, short-grass species dominated irrespective of burning frequency (Fig. 4.4). Annual burning during the dormant period favoured short-grass species such as *Themeda triandra* and *Heteropogon contortus*, whereas annual mowing during this period favoured *Tristachya leucothrix* and tall-grass species such as *Eragrostis curvula* and *Aristida junciformis* (Table 4.4; Fig. 4.4). Importantly, winter burning resulted in a more of *Heteropogon contortus,* and less of *Hyparrhenia hirta* than did spring burning (Table 4.4; Fig. 4.4). Autumn burning resulted in different composition to spring (t_{11} = 3.04; P = 0.01) or winter (t_{11} = 4.26; P = 0.001) burning. *Themeda triandra* had a relative abundance of 3.3% in sites burnt triennially in spring or winter, whereas it had a relative abundance of 19.6% in sites burnt triennially in autumn.

Table 4.3. Analysis of variance of the effect of type, season and frequency of disturbance on grass and forb composition at the Ukulinga long-term burning and mowing experiment

Source of variation	d.f.	Grasses		Forbs	
		F ratio	F prob.	F ratio	F prob.
Rep stratum	2	2.62		0.48	
Whole-plots	3	76.22	<.001	10.74	0.008
No summer mow vs. summer mow	1	220.17	<.001	31.76	0.001
One summer mow vs. two summer mows	1	7.36	0.035	0	0.996
Early- vs. late-summer mow	1	1.13	0.328	0.45	0.527
Residual	6	3.5		0.7	
Sub-plots	8	16.89	<.001	4.59	<.001
No dormant-period disturbance vs. dormant-period disturbance	1	47.39	<.001	35.41	<.001
Dormant-period burn vs. dormant-period mow	1	19.29	<.001	0	0.962
Winter vs. spring mow	1	2.56	0.115	0.03	0.864
Winter vs. spring burn	1	2.36	0.129	0.53	0.469
Linear effect of burning frequency	1	61.15	<.001	0.18	0.67
Quadratic effect of burning frequency	1	0.71	0.402	0.13	0.72
Winter vs. spring burn x linear effect of burning frequency	1	0.3	0.586	0.39	0.535
Winter vs. spring burn x quadratic effect of burning frequency	1	1.33	0.254	0.02	0.898
Whole-plot x sub-plot interaction	24	7.74	<.001	3.56	<.001
WP x no dormant-period disturbance vs. dormant-period disturbance	3	19.49	<.001	28.13	<.001
WP x dormant-period burn vs. dormant-period mow	3	1.52	0.217	0.02	0.995
WP x winter vs. spring mow	3	0.79	0.503	0.05	0.987
WP x winter vs. spring burn	3	2.11	0.108	0.11	0.955
WP x linear effect of burning frequency	3	29.03	<.001	0.04	0.991
WP x quadratic effect of burning frequency	3	6.36	<.001	0.02	0.996
WP x winter vs. spring burn x linear effect of burning frequency	3	0.88	0.457	0.1	0.961
WP x winter vs. spring burn x quadratic effect of burning frequency	3	1.75	0.166	0.01	0.998
Residual	64				
Total	107				

Table 4.4. Analysis of variance of the effect of type, season and frequency of disturbance on the abundance of key grass species at the Ukulinga long-term burning and mowing experiment

Source of variation	d.f.	TTR[1] F ratio	AJU F ratio	TLE F ratio	CSP F ratio	HHI F ratio	ECU F ratio	HCO F ratio
Whole-plots	3	5.54*	6.05*	2.54	9.28*	3.13	31.86***	9.7***
No summer mow vs. summer mow	1	13.89*	16.86**	4.4	24.03**	8.31*	90.58***	16.82***
One summer mow vs. two summer mows	1	0.87	1.22	1.27	3.48	1.06	4.94	3.95
Early- vs. late-summer mow	1	1.87	0.07	1.96	0.33	0.01	0.06	8.33**
Residual	6	12.9	2.07	6.49	4.02	4.92	1.08	
Sub-plots	8	7.26***	2.59*	2.68*	0.42	2.55*	3.25**	2.54*
No dormant-period disturbance vs. dormant-period disturbance	1	4.61*	11.99***	0	1.92	2.02	5.83*	4.47*
Dormant-period burn vs. dormant-period mow	1	17.17***	4.72*	18.26***	1.08	1.44	3.36	3.77
Winter vs. spring mow	1	2.1	0	0.06	0	2.73	0.04	0.7
Winter vs. spring burn	1	0.02	0.3	0.12	0.21	0.73	0.81	7.74**
Linear effect of burning frequency	1	26.42***	3.4	1.38	0.1	1.89	13.04***	2.06
Quadratic effect of burning frequency	1	4.3*	0.01	1.4	0	3.24	0.05	1.07
Winter vs. spring burn x linear effect of burning frequency	1	2.67	0.11	0.26	0.05	8.14**	1.34	0.51
Winter vs. spring burn x quadratic effect of burning frequency	1	0.77	0.15	0	0.02	0.18	1.55	0
Whole-plot x sub-plot interaction	24	1.53	1.35	1.85*	0.58	1.8*	1.98*	1.02
WP x no dormant-period disturbance vs. dormant-period disturbance	3	1.48	6.36***	6.92***	1.34	1.07	0.79	1.69
WP x dormant-period burn vs. dormant-period mow	3	0.42	1.07	3.58*	0.87	1.13	0.5	0.44
WP x winter vs. spring mow	3	0.39	0.41	0.82	0.19	1.36	0.87	0.7
WP x winter vs. spring burn	3	0.18	0.04	1.05	0.06	3.79*	0.44	0.45
WP x linear effect of burning frequency	3	4.78**	1.67	0.6	0.84	0.12	7.67***	2.09
WP x quadratic effect of burning frequency	3	2.01	0.95	0.86	0.29	2.83*	1.73	1.91
WP x winter vs. spring burn x linear effect of burning frequency	3	2.17	0.05	0.9	0.76	2.42	1.79	0.75
WP x winter vs. spring burn x quadratic effect of burning frequency	3	0.83	0.2	0.07	0.26	1.67	2.07	0.16
Residual	64							
Total	107							

[1]AJU, Aristida junciformis; CSP, Cymbopogon spp.; ECU, Eragrostis curvula; HHI, Hyparrhenia hirta; HCO, Heteropogon contortus; TLE, Tristachya leucothrix; TTR, Themeda triandra. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
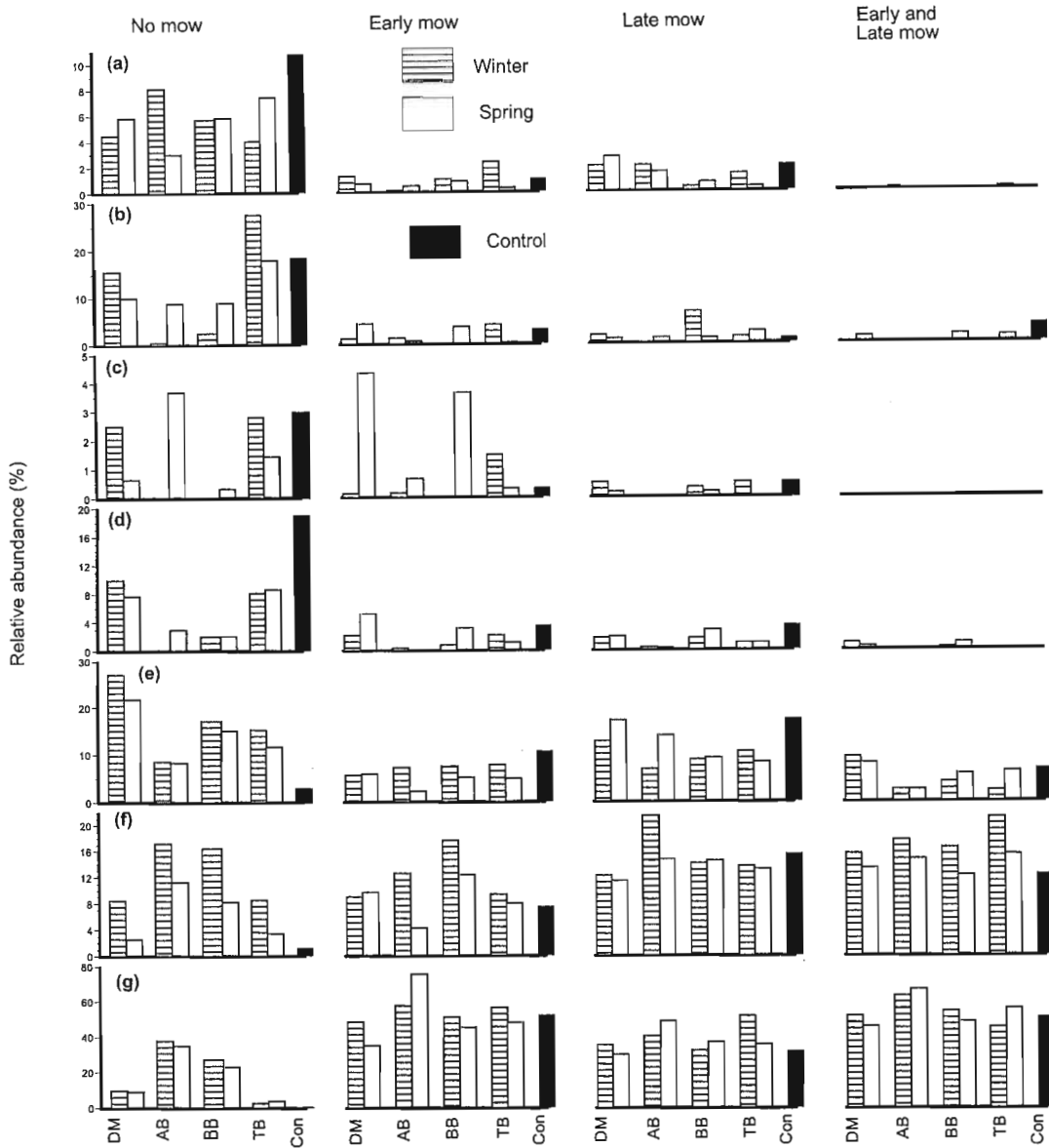
Fig. 4.4. Effect of various summer mowing and dormant-season burning and mowing treatments on the abundance of selected key grass species at the Ukulinga burning and mowing trial. a, *Cymbopogon* spp.; b, *Eragrostis curvula*; c, *Hyparrhenia hirta*; d, *Aristida junciformis*; e, *Tristachya leucothrix*; f, *Heteropogon contortus*; g, *Themeda triandra*. Each species is plotted on its own scale. DM, dormant-period mow; AB, annual burn; BB, biennial burn; TB, triennial burn; Con, control (no burn or mow in winter or spring). Only species with > 20 % of their variance accounted for by CA axis 1 were examined.

Short grasses such as *Eragrostis racemosa, Eragrostis capensis, Heteropogon contortus, Diheteropogon amplectens* and *Themeda triandra* had significant negative relationships with total soil nitrogen in sites not mown in summer (Table 4.5). None of the tall grasses had a significant relationship with total soil nitrogen but some (e.g. *Eragrostis curvula*) tended to increase in abundance with increasing total soil nitrogen (Table 4.5).

Similar to their relationship with total soil nitrogen, all short grasses tended to decline in abundance with increasing productivity in sites not mown in summer, whereas a species of intermediate height, *Aristida junciformis*, increased with increasing productivity (Table 4.5; Fig. 4.5). Summer mowing modified the relationship between the abundance of certain species and productivity. The shortest species, *Eragrostis racemosa*, declined strongly in abundance with increasing productivity, whether or not it was mown in summer (Table 4.5; Fig. 4.5 & 4.6). However, where *Themeda triandra* and *Eragrostis capensis* had tended to decline in abundance with increasing productivity in sites not mown in summer, (Table 4.5; Fig. 4.5) they increased strongly in abundance with increasing productivity in sites mown in summer (Table 4.5; Fig. 4.6). *Themeda triandra* attained a relative abundance of up to 90% in sites of high productivity that were mown in summer (Fig. 4.6).

Table 4.5. Linear regression analysis of the relationship between various grass species and total soil nitrogen and productivity in sites not mown in summer in the Ukuling burning and mowing experiment

Species	d.f.	Slope	*t*. value	*t*.prob	R^2
Total soil nitrogen (no summer mow)					
Eragrostis racemosa	31	-13.22	-2.63	0.013	15.6
Eragrostis capensis	31	-7.23	-2.59	0.014	15.2
Heteropogon contortus	31	-14.87	-4.42	<0.001	36.4
Diheteropogon amplectens	31	-9.09	-3.05	0.005	20.6
Themeda triandra	31	-15.07	-3.18	0.003	22.2
Tristachya leucothrix (linear)	30	82.5	1.79	0.084	1.9
Tristachya leucothrix (quadratic)	30	-154.2	-1.9	0.068	9.4
Aristida junciformis	31	8.39	1.48	0.15	3.6
Eragrostis curvula	31	9.32	1.77	0.086	6.3
Hyparrhenia hirta	31	0.2	0.05	0.96	0
Cymbopogon spp.	31	4.35	1.15	0.26	1
Productivity (no summer mow)					
Species	d.f.	Slope	*t*. value	*t*.prob	R^2
Eragrostis racemosa (linear)	27	-0.1308	-4.69	<0.001	27.3
Eragrostis racemosa (quadratic)	27	0.000175	4.01	<0.001	52.8
Eragrostis capensis	28	-0.01064	-2.67	0.013	17.4
Heteropogon contortus	28	-0.0094	-0.66	0.512	0
Diheteropogon amplectens	28	-0.00838	-2.1	0.045	10.6
Themeda triandra	28	-0.0073	-0.23	0.823	0
Tristachya leucothrix (linear)	26	0.0219	1.29	0.17	2.2
Tristachya leucothrix (cubic)	26	0.000003	2.04	0.05	17.3
Aristida junciformis	28	0.0389	2.88	0.008	20.1
Eragrostis curvula	28	0.0076	0.34	0.737	0
Hyparrhenia hirta	28	-0.00201	-0.42	0.681	0
Cymbopogon spp.	28	-0.0029	-0.31	0.756	0
Productivity (summer mow)					
Species	d.f.	Slope	*t*. value	*t*.prob	R^2
Eragrostis racemosa (linear)	96	-0.0907	-3.24	0.002	18
Eragrostis racemosa (quadratic)	96	0.000114	2.43	0.017	22
Eragrostis capensis	97	0.02085	3.92	<0.001	12.8
Heteropogon contortus	97	-0.01489	-2.22	0.029	3.9
Diheteropogon amplectens	97	-0.02008	-4.47	<0.001	16.2
Themeda triandra	97	0.0858	4.92	<0.001	19.2
Tristachya leucothrix (linear)	96	0.0886	2.07	0.041	4.5
Tristachya leucothrix (quadratic)	96	-0.00018	-2.53	0.013	9.6
Aristida junciformis	97	0.01207	4.17	<0.001	14.3
Eragrostis curvula	97	-0.00097	-0.26	0.799	0
Hyparrhenia hirta	97	-0.00197	-1.16	0.247	0.4
Cymbopogon spp. (linear)	96	0.00782	1.77	0.08	4.9
Cymbopogon spp. (quadratic)	96	-0.000015	-2.15	0.034	6.3
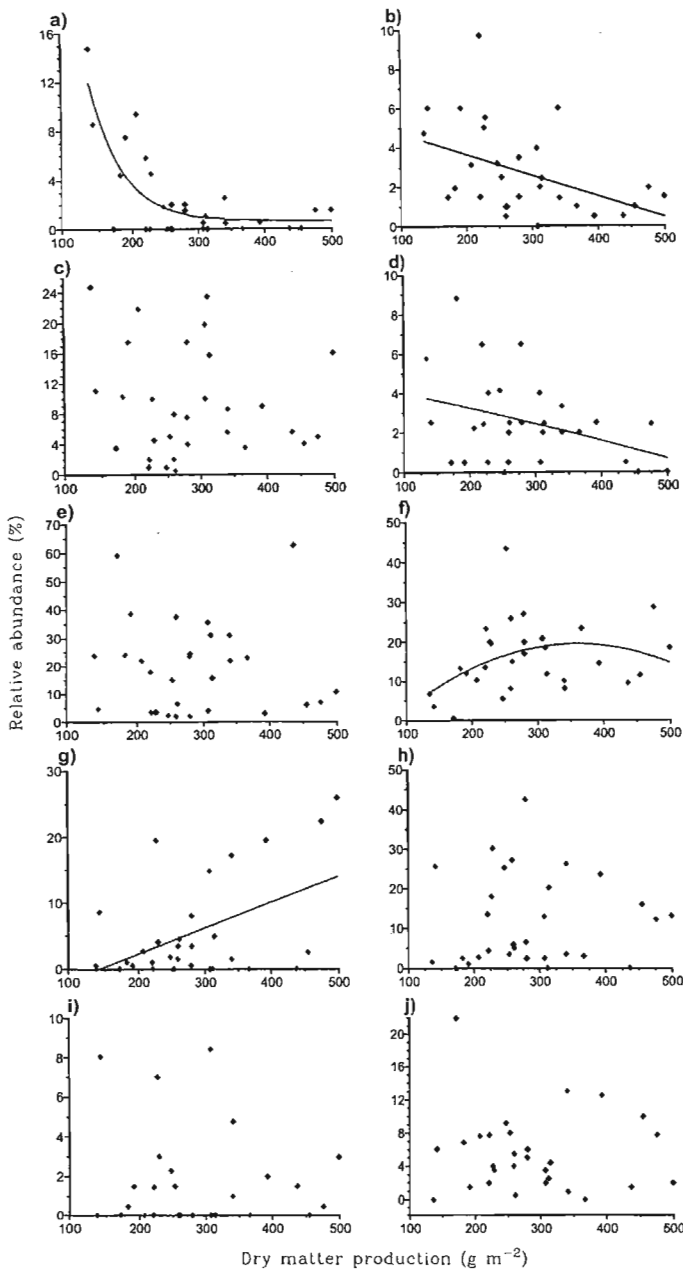
Fig. 4.5. Relationship between productivity and the relative abundance of various grass species in sites not mown in summer in the Ukulinga burning and mowing experiment. *Eragrostis racemosa*, a; *Eragrostis capensis*, b; *Heteropogon contortus*, c; *Diheteropogon amplectens*, d; *Themeda triandra*, e; *Tristachya leucothrix*, f; *Aristida junciformis*, g; *Eragrostis curvula*, h; *Hyparrhenia hirta*, i; *Cymbopogon* spp, j. Best models and *P* values for the response of each species given in Table 4.5.
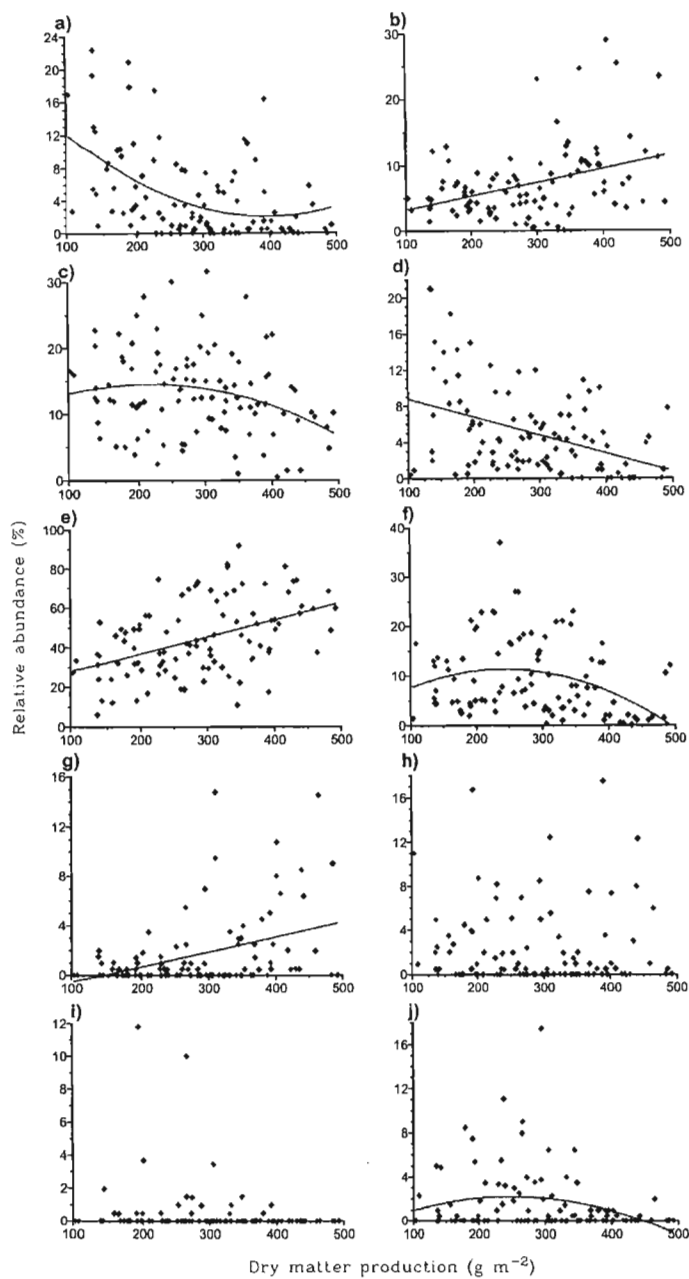
Fig. 4.6. Relationship between productivity and the relative abundance of various grass species in sites mown in summer in the Ukulinga burning and mowing experiment. *Eragrostis racemosa*, a; *Eragrostis capensis*, b; *Heteropogon contortus*, c; *Diheteropogon amplectens*, d; *Themeda triandra*, e; *Tristachya leucothrix*, f; *Aristida junciformis*, g; *Eragrostis curvula*, h; *Hyparrhenia hirta*, i; *Cymbopogon* spp, j. Best models and P values for the response of each species given in Table 4.5.

Effect of type, timing and frequency of disturbance on forb composition

In contrast to grasses, the frequency of summer mowing (one summer mow versus two summer mows) or dormant-period burning (linear or quadratic effect of burning frequency) or dormant-period mowing versus dormant-period burning had no effect on forb composition (Table 4.3). The principal gradient in forb composition (CA axis 1) was significantly related to two main factors: protection from disturbance, and summer mowing (Table 4.3). The time of mowing in summer (early or late) did not have an important influence on the principal gradient in forb composition (Table 4.3). Although some species of forbs were equally as common in protected and disturbed sites (Table 4.6), complete protection from disturbance resulted in a dramatic change in forb composition as indicated by a highly significant whole-plot by dormant-period disturbance interaction (Table 4.3).

Numerous species were unable to persist in sites protected from disturbance (Table 4.6), whereas other species were favoured by complete protection from disturbance (Table 4.6). Species intolerant of disturbance generally had small below-ground storage organs, whereas most of the species that required disturbance had strong root systems or tubers. In addition to below-ground storage capacity, life history appeared to be linked to tolerance of disturbance, where annuals such as *Conyza floribunda* and *Tagetes minuta* and weak perennials such as *Conyza chilensis* were far more abundant in undisturbed sites. No annual species were favoured by disturbance. Alien invasive herbaceous and woody species such as *Tagetes minuta, Passiflora suberosa, Lantana camara, Acacia mearnsii* and *Melia azadarach* were far more abundant in protected sites with most of these species being completely absent from disturbed sites.

Certain species were favoured while others were disadvantaged by summer mowing (Table 4.6). The general trend that emerges is that the species disadvantaged by summer mowing such as *Acalypha puncata, Becium grandiflorum, Thunbergia atriplicifolia, Conyza floribunda* and *Polygala hotentotta* are erect species with aerial meristems, whereas the species advantaged by summer mowing were small creeping or prostrate species such as *Rhyncosia totta, Aeschynomene micrantha, Zornia capensis* and

Alysicarpus rugosus or species with flat rosettes such as *Helichrysum pilosellum* and hemicryptophytes such as the sedge *Abuldgardia ovata* (Table 4.6).

Although, the time of mowing in summer did not have a large overall influence on forb composition (Table 4.3) a few species were influenced by the time of mowing. For example, *Boophane disticha* was absent from sites mown in early summer but common in sites mown in late summer. *Tragia meyeriana* was absent from sites mown in late summer but present in sites mown in early summer.

Table 4.6. Effect of disturbance on certain forb species at the Ukulinga burning and mowing experiment

| Species | d.f. | Protected from disturbance | | | Summer mowing | | |
		t value	P value	response	t value	P value	response
Abuldgardia ovata	2	7.04	0.02	-	3.35	0.08	+
Acalypha punctata	2				5.45	0.03	-
Aeschynomene micrantha	2				3.25	0.08	+
Alysicarpus rugosus	2	4.07	0.06	-	3.49	0.07	+
Aster bakerianus	2	4.98	0.04	-			
Becium grandiflorum	2				17.4	0.003	-
Boophane disticha	2	6.22	0.02	-			
Chaetacanthus sp.	2	8.59	0.01	-			
Cheilanthes viridis	2	20.41	0.002	+			
Commelina africana	2	0.65	0.58	none			
Conyza chilensis	2	3.83	0.06	+			
Conyza floribunda	2	5.89	0.03	+	13.38	0.006	-
Corchorus asplenifolius	2	4.22	0.05	-			
Crabbea hirsuta	2	0.57	0.63	none	5.08	0.04	-
Eriosema cordatum	2	9.27	0.01	-			
Eriospermum abyssinicum	2	26	0.001	-	5.37	0.03	+
Eulophia sp.	2	3.98	0.06	-			
Gerbera kraussii	2	5.48	0.03	-			
Helichrysum miconiifolium	2	3.25	0.08	+			
Helichrysum pilosellum	2	21.07	0.002	-	21.42	0.002	+
Hibiscus aethiopicus	2	0.48	0.68	none			
Hypoxis colchicifolia	2	10.81	0.008	-			
Pachycarpus sp.	2	7.91	0.02	-			
Pelargonium luridum	2				5.44	0.03	-
Pentanisia angustifolia	2	0.56	0.63	none			
Polygala hottentotta	2	23.8	0.002	-	3.49	0.07	-
Rhynchosia cooperi	2	3.67	0.07	-			
Rhynchosia totta	2	7.15	0.02	-	2.92	0.10	+
Scenecio coronatus	2	14.49	0.005	-			
Schoenoxiphium sparteum	2	5.71	0.03	-			
Tagetes minuta	2	3.77	0.06	+			
Thesium sp.	2	5.93	0.03	-			
Thunbergia atriplicifolia	2	1.96	0.2	none	3.88	0.06	-
Tragia meyeriana	2	3.07	0.09	+			
Vernonia natalensis	2	15.5	0.004	-			
Zornia capensis	2				5.56	0.03	+

None, no response; (-) responded negatively; (+) responded positively

Discussion

Effect type, timing and frequency of disturbance on grass composition

Grass species constitute over 80% of the biomass of the grassland at Ukulinga (Fynn unpubl.) and, therefore, have the major influence on community composition and structure. The principal gradient in grass composition (CA axis 1) was clearly correlated with the frequency of disturbance (Fig. 4.3). Mesic grassland communities globally have been shown to respond strongly to the interval of disturbance (Everson & Tainton 1984; Gibson & Hulbert 1987; Peet et al. 1999). Regular disturbance in the form of annual or biennial burning or summer mowing appears to prevent succession from short-grass dominated communities to tall-grass dominated communities (Fig. 4.3 & 4.4). Infrequent disturbance (e.g. triennial burning), or certain types of annual disturbance (e.g. mowing during the dormant period) were unable to arrest succession and maintain a *Themeda triandra* dominated community (Fig. 4.3 & 4.4). The initial phase of succession following protection from disturbance appears to be the replacement of *Themeda triandra* and *Heteropogon contortus* by another short species, *Tristachya leucothrix* (Fig. 4.2). This transition has been observed following protection from burning in other mesic grasslands in KwaZulu-Natal (Everson and Tainton 1984). With long-term protection from disturbance, however, shorter species were replaced by taller species such as *Eragrostis curvula, Cymbopogon* spp. and *Aristida junciformis* (Fig. 4.2). Protection from grazing or only moderate intensity grazing in a 45year grazing experiment in Texas resulted in a tall-grass dominated community, whereas short-grass species dominated under heavy grazing (Fuhlendorf & Smeins 1997). Likewise, short-grass species were shown to decrease in abundance with protection from grazing in the Serengeti (Belsky 1992). Other studies also show that grazing favours short-grass dominated communities (Morris et al. 1992; Cingolani et al. 2003). However, selective grazing of short grasses may favour tall grasses over the short grasses (Morris et al. 1992). Therefore, it appears that for mesic grasslands globally, frequent non-selective disturbance, whether it is in the form of burning, mowing or grazing, is necessary to prevent the replacement of short-

grass species by taller species. Infrequent grazing or burning appears to be insufficient to prevent the replacement of shorter species by taller species.

In ecological theory, several factors have been proposed to have an important influence on community composition and the competitive balance among species with different traits and strategies: 1) Habitat fertility/productivity is likely to influence the relative importance of above- and below-ground competition in interspecific interactions. Infertile habitats are likely to favour shorter species that have made a tradeoff for below-ground competition (Gleeson & Tilman 1990; Wedin & Tilman 1993) or species with long tissue longevity, and lower nutrient loss rates (Chapin 1980; Berendse & Elberse 1990; Tilman 1990; Craine et al. 2002). These tradeoffs are a disadvantage in fertile habitats, however, where rapid growth rates (Grime 1979; Huston 1979; Huston & Smith 1987; Tilman 1988) and tall stature (Grime 1979; Huston & Smith 1987; Tilman 1988; Gaudet & Keddy 1995) are essential for preemption of space and light. 2) Litter accumulation may have a large influence on community composition through effects on seed germination and seedling emergence (Knapp & Seastedt 1986; Foster & Gross 1998; Jutila & Grace 2002). Shoot morphology is an important adaptation in sites with a large amount of litter accumulation because the shoots of many species are unable to penetrate a litter layer (Sydes & Grime 1981). 3) Disturbance may influence nitrogen availability (Seastedt et al. 1991; Ojima et al. 1994; Fynn et al. 2003), habitat productivity (Redman 1978; Tainton et al. 1978; Knapp & Seastedt 1986), litter accumulation (Knapp & Seastedt 1986; Fynn et al. 2003); soil moisture (Knapp & Seastedt 1986; Snyman 2002) and recruitment (Hazell 1965; Howe 1994). In the following sections the long-term role of the type, timing and frequency of disturbance as a determinant of community composition are examined in relation to the above three points.

Influence of disturbance on composition through effects on nitrogen availability and productivity

The effect of fire and other disturbances on litter accumulation, soil organic matter and nitrogen availability has been recognised as the principal mechanism determining the composition of Dutch wet heathlands (Aerts & Berendse 1988) and may

be responsible for the disturbance-composition relationships in this experiment. All short-grass species in this experiment declined with increasing total soil nitrogen and productivity in sites not mown in summer (Table 4.5; Fig. 4.5). Total soil nitrogen and productivity was able to account for different effects that various type, frequency and timing of disturbance had on grass composition. For example, one of the shortest species, *Heteropogon contortus,* was always more abundant in winter burnt sites than spring burnt sites (Fig. 4.4f; Table 4.4). Winter burnt sites had lower total soil nitrogen (Fynn et al. 2003) and lower productivity (Tainton et al. 1978) than spring burnt sites. Moreover, dominance of tall-grass species under annual dormant-period mowing and triennial burning and short-grass species under annual dormant-period burning (Fig. 4.3 and 4.4) was associated with higher productivity (Tainton et al. 1977; 1978) and total soil nitrogen (Fynn et al. 2003) in the sites mown in the dormant-period or burnt triennially compared with sites burnt during the dormant-period. However, triennial burning in autumn resulted in a much higher abundance of *Themeda triandra* than triennial burning in spring and winter (19.6% in autumn burnt sites versus 3.3% in winter and spring burnt sites). This can again be explained by effects on soil nitrogen because triennial burning in autumn results in much lower soil nitrogen than triennial burning in spring or winter (Table 2.1).

The notion that this effect of time of burning (winter versus spring) may be related to negative effects of the hotter winter burn on the recovery of various species rather than its effects on soil nitrogen is not creadible, because winter burning actually favours better recovery of grassland than spring burning (Trollope 1987), suggesting that it has less negative direct effects on grass species. It is difficult to imagine why taller species should be less tolerant of winter burning than shorter species because they are all dormant during this period. The weight of evidence of how different burning and mowing treatments (winter versus spring burning, autumn versus winter and spring burning, annual versus triennial burning, summer versus dormant-period mowing) affected soil nitrogen is a far more parsimonious explanation of the effects of disturbance on grass composition. It is predicted by ecological theory (Tilman 1990) and strongly supported by empirical studies (Aerts & Berendse 1988; Wedin & Tilman 1993). Arguments for differential tolerance of disturbance amongst species with the same phylogenetic history

and phenotypic classification (hemicryptophytes) are, at best, weak. There is no logical reason why a tall-grass species should be less tolerant of burning than a short-grass because they both have basal meristems. Differential tolerance only holds creadibility for species of different phenotypic classication (e.g. species with basal meristems, hemicryptophytes versus species with aerial meristems, phanerophytes). Besides, tall grasses dominate under annual burning on deep fertile soils in the KwaZulu-Natal region, showing that they are most certainly not intolerant of burning (Platt et al. in prep).

In prairie grasslands, infrequently burned sites showed only a nine % increase in production following fertilization with nitrogen, whereas annually burned sites showed a 68% increase (Seastedt et al. 1991), indicating that nitrogen was much less limiting in infrequently burnt sites. The fact that in an adjacent long-term experiment, the taller *Eragrostis curvula* replaced *Themeda triandra* in grassland fertilized with nitrogen (Le Roux & Mentis 1986), suggests that it replaced *Themeda triandra* in protected and infrequently burnt sites in this experiment because of an increase in total soil nitrogen with infrequent disturbance (Fynn et al. 2003).

Pot experiments have shown that when nutrients are limiting, *Themeda triandra*, grows better than taller species such as *Eragrostis curvula* and *Hyparrhenia hirta*, with the reverse being true in high nutrient treatments (Ghebriwot unpubl.). Thus, disturbance is likely to favour *Themeda triandra* and other short-grass species by reducing nitrogen availability, soil moisture and productivity, whereas a lack of disturbance will favour taller species. Increased nitrogen availability and productivity generally favour taller species (Aerts & Berendse 1988; Gaudet & Keddy 1995).

It is important to recognise that tall-grass species are not less tolerant of summer mowing than short-grass species. Monoculture plots of tall grasses that were cut intensely (every two weeks during summer) were always much more productive than monoculture plots of a short-grass species, whereas the tall species were much less productive when in competition against a short species under cutting (see Chapter 7). Mowing changes the competitive relationships between short and tall grassses favouring short grasses. This is possibly because summer mowing reduces productivity (Tainton et al. 1978) and is likely to result in low soil nitrogen because of the loss of plant nitrogen after mowing. In addition, a higher loss rate of nutrients of tall- compared with short-grass species under

summer mowing (Berendse & Elberse 1990) may give shorter species a competitive advantage (Berendse & Elberse 1990; Tilman 1990). This is supported by the observation that *Eragrostis curvula* was strongly reduced by summer mowing of unfertilised grassland (Fig. 4.4), whereas in an adjacent long-term experiment it dominated grassland mown twice in summer but fertilized with nitrogen (Le Roux & Mentis 1986). Furthermore, this clearly demonstrates that *Eragrostis curvula* was reduced by summer mowing through effects on its nitrogen balance and not because of intolerance of mowing. This is exellent support for Tilmans R* theory of competition for limiting soil nutrients (Tilman 1988; Tilman 1990), where it is shown mathematically that losses of nutrients by a plant/species (whether through herbivory, mowing, burning, disease etc.) affect a species R*.

Influence of disturbance on composition through effects on litter levels

Sites protected from disturbance or with infrequent disturbance generally have higher litter levels than frequently disturbed sites (Knapp & Seastedt 1986; Fynn et al. 2003). This results in a reduction in light availability (Knapp & Seastedt 1986). *Themeda triandra* and many other short-grass species are vulnerable to litter accumulation and self-shading (Belsky 1992) and tiller initiation is strongly reduced relative to other species if shaded (Everson et al. 1988). In the absence of disturbance or with infrequent disturbance, another short-grass species, *Tristachya leucothrix* replaced *Themeda triandra* and *Heteropogon contortus* (Fig. 4.2a & 4.4e). Likewise, *Aristida junciformis*, a species of intermediate height, dominated the protected sites, which have the highest litter levels (Fynn et al. 2003). Numerous forb species were unable to persist in the protected sites (Table 4.6), most likely as a result of the high litter levels. *Tristachya leucothrix* and *Aristida junciformis* initiate tillers below ground, whereas other short-grass species in this experiment initiate tillers above ground. Consequently, they are not as dependent upon light as a cue for tiller initiation (Everson et al. 1988). Thus, in the absence of disturbance, below-ground tiller initiation appears to be a trait that has given these species an advantage over short-grass species that initiate tillers above-ground. Further, they have sharp rigid erect shoots that appear to be an adaptation for penetrating litter.

Sharp erect shoots have been shown to be necessary for penetration of litter (Sydes & Grime 1981). Species without these adaptations were unable to persist in sites with high litter levels (Sydes & Grime 1981). In addition, *Aristida junciformis* has extremely rigid erect leaves that are able to grow through aerial litter, which has accumulated to a large degree in the protected sites. Thus, it appears that *Tristachya leucothrix* and *Aristida junciformis* were successful in infrequently disturbed sites because of their shoot and leaf morphology, which enables them to cope with accumulated litter. As a consequence of the high litter levels in the protected sites, larger more competitive species such as *Cymbopogon* spp., *Eragrostis curvula* and *Panicum maximum*, which generally dominate sites fertilized with nitrogen in an adjacent experiment (le Roux & Mentis 1986), were unable to dominate the protected sites, despite them having the highest soil nitrogen levels (Fynn et al. 2003). This is supported by the fact that *Eragrostis curvula* was by far the most abundant species in the infrequently burnt sites (Fig. 4.4b), where litter accumulation is less severe but where total soil nitrogen is higher than in the annually burnt sites.

Certain species may have benefited from high litter levels in sites protected from disturbance because such sites provide shaded habitat that is protected against extremes of temperature and soil desiccation (Knapp & Seastedt 1986). This may have favoured the fern *Cheilanthes viridis* (Table 4.6), which is most vulnerable to desiccation in the gametophyte stage.

Species abundance along productivity gradients in relation to summer mowing

The shortest species, *Eragrostis racemosa,* declined in abundance with increasing productivity, whether or not it was mown in summer (Fig. 4.5 & 4.6). However, its average relative abundance was increased by summer mowing. Thus, the abundance of very small species may be increased by summer mowing but their optima, appears to be restricted to the least productive sites irrespective of the disturbance regime. This may appear to be circular reasoning because it is obvious that short species will produce less biomass than tall species, hence the relationship between species height and plot productivity (Fig. 4.5). Thus, is the mechanism leading to low productivity may be

dominance by short species rather than low productivity leading to dominance by short species? However, it is clearly shown that increasing productivity through fertilization (chapter 5) or irrigation (chapter 7) resulted in dominance by tall species. Furthermore, in KwaZulu-Natal grasslands the shortest species (*Sporobolus stapfianus, Microcloa caffra* and *Eragrostis racemosa* predictably only dominate sites with extremely shallow-dry soils (0-50 mm deep) (Platt et al. in prep). They are unable to compete with taller grasses on even slightly deeper soils (100-300 mm deep).

However, summer mowing may alter the relationship between inherent site productivity and the abundance of short and tall species. For example, in this experiment the optima of *Themeda triandra* and *Eragrostis capensis* were restricted to the least productive sites in the absence of summer mowing, but shifted to the most productive sites with summer mowing (Fig. 4.5 & 4.6). Summer mowing may alter this relationship between inherent site productivity and the abundance of short and tall species by reducing above-ground competition intensity (Wilson & Tilman 1993) and by directly improving light availability during the growing period. Summer mowing has been shown to prevent exclusion of small species in the prairies (Collins et al. 1998). Disturbance is predicted to be necessary to prevent small species being excluded by large species, which are able to pre-empt resources, especially light (Huston 1979). In the absence of disturbance, competitive exclusion is most likely to occur in productive sites where growth rates of the large species are highest (Huston 1979; Huston & Smith 1987).

Different response of grasses and forbs to disturbance

There were some conspicuous differences in the response of grasses and forbs to disturbance. Different grass species responded very differently to type of disturbance (dormant-period burn versus dormant-period mow) but forbs showed a consistent response to these different types of disturbance (Table 4.3). Further, grasses responded very strongly to burning frequency but forbs showed no response (Table 4.3). Both of these factors appeared to affect grasses through their effect on total soil nitrogen, which suggests that the effect of disturbance on soil nitrogen is not as important a determinant of forb composition.

No grass species were intolerant of summer mowing, whereas a number of forb species (herbaceous dicots) were intolerant of summer mowing. Grasses (whether short or tall) have basal meristems, whereas herbaceous dicots have apical meristems. Erect herbaceous dicots such as *Thunbergia atriplicifolia*, *Becium grandiflorum* and *Polygala hottentotta* appeared to be vulnerable to summer mowing probably because they have aerial meristems, which are easily removed by mowing (Table 4.6). For example, *Acalypha punctata* is dioecious; the male flowers are produced on lateral inflorescences on male plants, whereas the female flowers are produced terminally on stems of female plants. For successful pollination to occur male and female anthesis must be synchronised. The lateral inflorescences can be replaced quickly by the removal of apical dominance but the replacement of complex terminal female inflorescences is likely to be slower. Thus mowing may affect synchrony. *Becium grandiflorum* flowers in spring and fruits mature during early summer. Summer mowing will probably prevent fruit maturation, thereby preventing recruitment. Further, some species that were intolerant of disturbance were annuals or weak perennials (e.g. *Conyza floribunda* and *Tagetes minuta*) that invest most of their energy into rapid aerial growth, rendering them vulnerable to being defoliated.

In contrast, short creeping herbaceous dictots such as *Aeschynomene micrantha, Rhynchosia totta* and *Zornia capensis* were favoured by summer mowing probably because their meristems are below the cutting height of the mower. The short height, however, would render them vulnerable to being shaded by neighbours in unmown sites, hence their higher abundances in mown sites.

The fact that the time of mowing in summer (early or late) had very little influence on forb composition (Table 4.3) contrasts with other studies that demonstrated marked effects of time of mowing on forb composition (Hazell 1965). However, a few species were influenced by the time of mowing and this appeared to be linked to their flowering time. For example, *Boophane disticha* is phenologically limited to spring flowering because it produces recalcitrant seeds, which need to establish during the growing season. This species flowers between August and October while its fruits mature between September and December. Thus, there was an overlap of the time of fruiting and the timing of the early-summer mow but not the late summer mow. This may account for

this species being absent in sites mown in early summer but common in sites mown in late summer.

Woody and alien invasive species

Woody species, many of which were alien invasive species, were only common in undisturbed sites (Titshall et al. 2001). Woody species only began to dominate in the protected sites after 1980. An increase in woody species with protection from disturbance appears to be a general response of mesic grasslands (Bragg & Hulbert 1976; Titshall et al. 2001; Briggs et al. 2002). Various models (Huston & Smith 1987; Tilman 1988) suggest that secondary succession is controlled initially by growth rate with fast growing competitive species (tall grasses) dominating initially and slower growing tree species (Grime & Hunt 1975) becoming important much later in succession. Phanerophytes (woody species) may be less tolerant of disturbance than geophytes (certain forbs) and hemicryptophytes (grasses) because dormant buds are aerial and susceptible to damage in phanerophytes but are protected by the substrate in geophytes and hemicryptophytes. Thus, disturbance may favour a higher proportion of geophytes and hemicryptophytes than phanerophytes. Further, lower soil moisture, nitrogen and productivity in disturbed sites may give grasses a competitive advantage over woody and alien invasive species. Woody alien species such as *Acacia mearnsii, Melia azadarach* and *Lantana camara* and herbaceous alien species such as *Passiflora suberosa* and *Tagetes minuta* were only common in the undisturbed sites, which have the highest levels of total soil nitrogen and nitrogen mineralization (Fynn et al. 2003). No alien species were common in regularly disturbed sites. Alien invasive species globally are generally more successful in sites with higher nitrogen availability (Baruch & Goldstein 1999; Craine & Lee 2003; Seabloom et al. 2003).

Conclusions

Similar to tallgrass prairie (Collins & Steinauer 1998), disturbance was a major determinant of species distribution, community organization and structure in South

African tall grassland. Some form of regular disturbance was necessary to prevent succession from a short-grass dominated community to a tall-grass and woody species dominated community but this depended on the type, timing and frequency of disturbance. Disturbance appeared to influence composition through its effects on total soil nitrogen and site productivity, litter levels, light availability and life cycles of certain species. The different effects of various type, timing and frequency of disturbance on total soil nitrogen and productivity appears to be able to account for their different effects on community composition. Disturbances that resulted in low total soil nitrogen (e.g. annual burning) favoured short-grass species, whereas disturbances that resulted in higher total soil nitrogen (e.g. dormant-period mowing or triennial burning) favoured tall-grass species. Thus, the effect of disturbance on soil nitrogen and productivity appears to be a unifying concept able to account for the effects of very different disturbance regimes on grass composition. However, the major determinant of composition in sites protected from disturbance appeared to be the extremely high litter levels. Only species with below-ground tiller initition (e.g. *Tristachya leucothrix* and *Aristida junciformis*) and sharp rigid erect shoots were able to dominate the protected sites. Thus, in sites where the type or frequency of disturbance allowed total soil nitrogen to accumulate but prevented excessive litter accumulation, a tall growth form was most important, whereas shoot morphology and position of tiller initiation rather than plant height became the most important factor with complete protection from disturbance. Height of meristems was an important determinant of the response of many species to summer mowing. Many erect herbaceous dicots and woody species, which have aerial meristems were intolerant of summer mowing, whereas hemicryptophytes or creeping herbaceous dicots were tolerant of or favoured by summer mowing. Summer mowing, probably through its effect on light availability and tiller initiation (cf. Everson et al. 1988), appeared to allow certain short-grass species (e.g. *Themeda triandra*) to become more competitive and dominate productive sites. Without summer mowing these species were restricted to less productive sites. This study emphasizes the importance of long-term experiments for identifying important functional traits determining the structure and organization of plant communities at various temporal scales.

Acknowledgements

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CHAPTER 5

EFFECTS OF NUTRIENT AVAILABILITY, PRODUCTIVITY AND SOIL PH ON
MESIC GRASSLAND DYNAMICS IN A LONG-TERM FERTILIZATION
EXPERIMENT, SOUTH AFRICA

Abstract

The influence of soil fertility and habitat productivity on grassland community
organization was examined with a 50 year fertilization experiment in KwaZulu-Natal,
South Africa. The influence of fertilization on the availability of nitrogen (N) and
phosphorus (P) and soil pH (through liming and type of N fertilizer) on variation in plant
traits, community composition and species richness were examined. Averaged over 30
years, above-ground phytomass production (AGP) was 337, 428 and 518 (g m^{-2}) in sites
not fertilized, fertilized with N and fertilized with both N and P respectively. AGP
depended directly on N fertilization but not on P fertilization or liming, and responded
positively to the interaction of N (first limiting nutrient) and P (second limiting nutrient).
Short narrow-leaved grass species (*Themeda triandra* and *Heteropogon contortus*)
dominated sites of lowest AGP where N was low and limiting (unfertilized, P fertilized or
limed sites). A tall narrow-leaved species (*Eragrostis curvula*) dominated sites of
intermediate AGP where P was limiting (N fertilized sites). By contrast, a tall broad-leaved
species (*Panicum maximum*) dominated the most productive sites where neither N nor P
were limiting (N and P fertilized sites). Certain species responded to liming and type of N
fertilizer because of their effects on soil pH. N fertilization reduced the density of
herbaceous dicots (forbs) from 14 species m^{-2} (unfertilized) to two species m^{-2} (high N, no
P, no lime) and five species m^{-2} (high N, no P, limed). This effect was attributed not only
to increased AGP but also an increase in soil acidity from pH 4.94 (KCl) in unfertilized
sites to 4.29 (high N, no lime) and 4.71 (high N and lime). Soil acidification had no effect
on grass species richness but influenced the abundance of certain species. This long-term
experiment has revealed that grassland community organization is determined not only by

the influence of N availability, but also by the interaction of N and P availability, in part through their compounded effect on AGP, and by individualistic species responses to soil pH.

Nomenclature: Arnold & De Wet (1993)

Introduction

Nutrient availability and productivity have been recognized as important determinants of plant community organization and structure (Grime 1979; Tilman 1988; Gibson et al. 1993; Gaudet & Keddy 1995). Competition has been invoked as an important mechanism structuring plant communities along productivity gradients (Austin 1990; Gaudet & Keddy 1995) but the importance of competition in low fertility habitats has been disputed (Grime 1979). While it is agreed that above-ground competition intensity generally increases with increasing habitat fertility/productivity there is little general agreement as to the trends in below-ground and total competition intensity along productivity gradients (Grime 1979; Tilman 1988; Twolan-Strutt & Keddy 1996; Cahill 1999; Rajaniemi 2002; Rajaniemi et al. 2003).

Certain general patterns of plant-trait variation are evident along productivity gradients. Species that dominate infertile habitats are small (Gaudet & Keddy 1995; Berendse & Elberse 1990), slow-growing (Chapin 1980), have leaves with low specific leaf area (Wright et al. 2002; Craine & Lee 2003), long root and leaf life spans (Chapin 1980; Berendse & Elberse 1990; Craine et al. 2002; Wright et al. 2002) and allocate a high proportion of biomass to roots (Gleeson & Tilman 1990; Craine et al. 2002). In contrast, species that dominate fertile habitats are generally fast growing (Chapin 1980), tall and broad-leaved (Gaudet & Keddy 1995; Leps 1999). Plant size, height and leaf width are well correlated with competitive ability in fertile habitats (Keddy et al. 2002). Specific leaf area appears to vary predictably with nutrient availability (Wright et al. 2002; Craine & Lee 2003). Consequently, plant traits offer great potential for predicting plant competitive ability and response in various environments (Goldberg 1996). Although much progress has been made in identifying and linking important plant traits with species response to the

environment (Craine et al. 2002; Lavorel & Garnier 2002; Pywell et al. 2003; Suding et al. 2003), little is known about the relationship between traits and different types of limiting nutrients, soil pH etc. Do traits that enable a species to be a good competitor for nitrogen also enable a species to compete well for phosphorus or some other nutrient? Further, the observation that specific limiting resources may vary in importance in time and space (Knapp et al. 1998), suggests that the relative competitive balance amongst plants of different traits should also vary in time and space. The strength of limitation of specific limiting nutrients may vary with rainfall. An understanding of factors that determine shifts in resource limitation may, therefore, be necessary for predicting community response over time.

Fertilization of grassland generally results in a decline in species diversity (see Rajaniemi 2002), which may be more pronounced for forbs than grasses (Gibson et al. 1993). This decline has been attributed to decreasing light availability resulting from increasing productivity with increasing levels of fertilization, but studies that have manipulated productivity without the use of fertilizer have not shown a comparable decline in diversity (Goldberg & Miller 1990; Rajaniemi 2002). Recent studies have shown that below-ground competition may contribute to a decline in diversity following fertilization (Rajaniemi et al. 2003). Current thinking on this matter focuses on the influence of below, above and total competition intensity as influenced by the effects of fertilization on productivity (Rajaniemi 2002; Rajaniemi et al. 2003), but has yet to consider the influence of fertilization on soil pH, which may in turn determine competitive interactions amongst species (Tilman et al. 1994). Thus, the use of fertilizer experiments for examining the influence of productivity on competitive interactions amongst species and diversity may be partially confounded if a proportion of the species are sensitive to changes in soil pH.

It is difficult to know whether the relationship between plant traits, competitive ability and composition and diversity in short-term studies is relevant to vegetation processes in the long-term, because traits of the initial dominants may be unrelated to the long-term outcome of competition. For example, the final dominants in the 140 year old Park Grass experiment at Rothamsted often declined in abundance in the first 20 years of the experiment but eventually rose to dominance, sometimes as late as 80 years after treatments began (Tilman 1988). Spurious conclusions on the relationship between traits of

the various grass species and competitive ability in specific treatments in the Park Grass Experiment would have been drawn even when the experiment was 20-30 years old. Long-term experiments of rigorous statistical design that have manipulated many of the major nutrients known to be most limiting to plants are rare. Thus, data on the long-term response of species of differing traits and growth form in long-term experiments (> 50 years) should provide a valuable opportunity for testing current understanding.

The Ukulinga long-term fertilization experiment (1950 - present) was established to examine the effect of N and P fertilization and liming on the botanical composition and yield of a grassland on the research farm of the University of Natal. This experiment therefore offered an invaluable opportunity to examine the long-term influence of nutrient availability, productivity and soil acidity on grassland community organization.

Specifically we sought to: 1) Examine relationships between fertilization treatments and above-ground phytomass production (AGP) in order to determine which nutrients are limiting; 2) examine the abundance of key grass species and species richness in relation to the effects of fertilization on AGP, different forms of nutrient limitation (nitrogen or phosphorus) and soil pH; 3) identify whether morphological traits of key grass species were related to AGP or nutrient availability; 4) examine whether soil pH, independently of productivity, influenced species richness; 5) examine whether the duration of the experiment may have influenced the interpretation.

Methods

Study area

A long-term fertilization experiment was established in 1951 (Booysen 1954) with the objective of assessing the effects of fertilization with nitrogen (N), phosphorus (P) and Lime (L) on the production and botanical composition of grassland. The experiment is located at Ukulinga Research Farm (29° 24' E, 30° 24' S) of the University of Natal, Pietermaritzburg, South Africa. Mean annual precipitation is 690 mm, occurring mostly as convective storms during summer (September to April). The CV% of rainfall is 22%.

Summers are warm to hot with a mean monthly maximum of 26.4 °C in February, and winters are mild with occasional frost and a mean monthly minimum of 8.8 °C in July. The growing period for grasses is mediated by temperature and rainfall, which are optimal for growth between October and April.

The experiment is situated on top of a gently sloping plateau ranging in altitude from 838 m to 847 m a.s.l., whose lithology consists of Ecca group shales of the Karroo sedimentary sequence. Soil depth varies from 600 mm to over 1000 mm. Soils are acidic and relatively infertile, and are classified as Westleigh form (plinthic paleustalf) (Soil Classification Working Group 1991). The vegetation is classified as Southern Tall Grassveld (Acocks 1953), which is a dense closed grassland (0.75 m tall) dominated by *Themeda triandra, Heteropogon contortus*, and *Tristachya leucothrix*.

Experimental design

The experiment consisted of 96 plots, each of 9 x 2.7 m in size with 1 m walkways between plots. Treatments consisted of lime applied every five years at two levels (0 and 225 g m^{-2}), P applied annually as superphosphate at two levels (0 and 33.6 g m^{-2}) and two forms of N (ammonium nitrate and ammonium sulphate) each applied annually at four levels. Half the annual application of N was applied in spring and the other half in mid-summer. The application rate of each ensured that the ammonium nitrate dressings (0, 21, 42.1 and 63.2 g m^{-2}) and the ammonium sulphate dressings (0, 33.6, 67.2 and 100.8 g m^{-2}) provided the same amount of N per plot (0, 7.1, 14.1, 21.2 g m^{-2}). Each type of N was never applied in combination with the other, only with P and lime, resulting in a 4 x 2^3 factorial design with certain second and third order interactions being partially confounded. Treatments were arranged randomly in three blocks (replications).

Sampling

Botanical composition was sampled as absolute abundance (in g m^{-2}) of grass and forb species in mid-summer of 1999. Each plot was sampled in four randomly placed 0.25 m^2 quadrats, allowing for an edge effect. Each species in a quadrat was clipped separately, bagged, oven-dried to constant mass, and weighed. Species richness was determined as the number of species found in the four quadrats.

Above-ground phytomass (AGP) was estimated in each plot each year by mowing a 2.13 m wide strip in December and at the end of February. Wet material was weighed, and this weight was converted to dry mass using a grab sample that was dried to constant mass. AGP of the December and February cuts were summed as an index of a season's productivity.

Simple plant traits such as plant height and leaf width have been shown to be well correlated with competitive ability (Gaudet & Keddy 1988; Keddy *et al*. 2002). Therefore, maximum leaf height (whether originating from stems or crowns), maximum leaf width and stem diameter at 300 mm above the soil surface were measured on at least ten mature individuals of each of the 12 most important grass species.

The effect of the grass canopy on attenuation of photosynthetically active radiation (PAR) was determined between 12pm and 1pm over two days at the end of summer in 2003. PAR reduction in the canopy was determined using a Decagon Sunfleck Ceptometer (Decagon, Pullman, Washington, USA) by calculating the percentage of PAR at 300 mm above the soil surface relative to PAR above the vegetation canopy. The average of six equally-spaced measurements along each plot was used as a measure of light penetration. Light penetration to 300 mm above the soil surface rather than to the soil surface was considered a more meaningful measure because most leaves of short-grass species are generally located below this height.

Soil pH was determined from soil samples taken from the surface 100mm layer and the 550-650mm layer at two locations in each plot (opposite ends of each plot but 1m in from the edge of the plot to avoid edge effects). The values of pH (using KCl for extraction and hydrogen ion probe for measurement of pH) obtained from the two sample locations in

the plot and the two soil layers were averaged to give an average value of pH through the soil profile in a plot.

Statistical analysis

Analysis of variance of the effect of fertilization on AGP, abundance of key grass species and grass or forb richness was undertaken using GENSTAT (GENSTAT 1993). The treatments comprised a factorial treatment set with added controls, the factors under consideration being two forms of N, ammonium sulphate or ammonium nitrate (N-Type), each measured over 4 levels (N-Level); the zero level of N for the two forms of N were considered as controls. This enabled the analysis to be performed as "Control vs. the Remainder" and "Remainder among Themselves", the latter being in effect the subdivision of (N-Type x N-Level) into its components of main effects and interactions. In order to meet assumptions, no transformations were necessary for analyses of AGP or diversity, but $\log_e$ transformation was necessary for analysis of the abundance of key species.

Multiple linear regression was used, to examine if the relationship between AGP or level of N fertilization and the abundance of key species and grass or forb species richness was linear or quadratic. AGP or level of N fertilization was fitted first and the square of AGP or the square of the level of N fertilization fitted to the residuals. For species richness, this analysis was performed separately for limed and unlimed sites in order to determine if liming may alter the nature of the relationship (linear or quadratic) between AGP or level of N fertilization and grass and forb species richness. A change from linear to quadratic or vice versa would indicate that the intensity of the relationship had changed. Multiple linear regression was also used to determine if any residual variation in grass and forb species richness, not accounted for by AGP or the level of N fertilization, could be accounted for by liming. This was done by fitting AGP or level of N fertilization first and by fitting liming to the residuals.

Anova could not be used to analyze soil pH data because it was available for replication 1 only. The 32 plots of block 1 allowed for the testing of the effect on soil pH of 1) N fertilization versus no fertilization, 2) type of N, and 3) liming of N fertilized plots,

using paired t-tests, in which the paired units were the same except for the value under consideration.

Results

Effect of fertilization on soil pH

Fertilization with ammonium nitrate or ammonium sulphate resulted in lower soil pH than sites that were not fertilized with N or sites fertilized with P alone (Table 5.1). Ammonium sulphate resulted in lower soil pH than ammonium nitrate. Sites fertilized with N and lime had higher soil pH than sites fertilized with N but not limed.

Table 5.1. Paired t tests of the effect of nitrogen fertilization treatments on soil pH (KCl) in the Ukulinga long-term grassland fertilization experiment.

	Means		Paired *t* tests		
Paired contrasts	Control	N added	d.f.	*t.*	*P.*
Control versus ammonium nitrate (AN)	4.94[a]	4.37	3	13.27	<0.001
Control versus ammonium sulphate (AS)	4.94	4.27	3	10.40	0.002
	No Lime	Lime			
Ammonium nitrate versus ammonium nitrate +Lime	4.53	5.76	5	9.33	<0.001
Ammonium sulphate versus ammonium sulphate +Lime	4.28	4.88	5	2.44	0.059
	AS	AN			
Ammonium sulphate versus ammonium nitrate	4.28	4.53	5	2.59	0.049
Ammonium sulphate +Lime versus ammonium nitrate +Lime	4.88	5.76	5	4.32	0.007

[a]values of pH represent an average across the 0-100mm layer and 550mm-650mm layer

Effect of fertilization on above-ground phytomass production and light availability

Effects of fertilization on above-ground phytomass production (AGP) in the 1951/52 season were well correlated with the effect of fertilization on AGP averaged over 30 years and AGP in the 1999/2000 season (Table 5.2; Fig. 5.1a). Thus, AGP responded to fertilization in the first season of the experiment and the pattern of differences endured thereafter. Averaged over 30 years, fertilization with ammonium nitrate or ammonium sulphate, but not P, resulted in a 29% and 37 % increase in AGP, respectively, relative to sites not fertilized with N (Table 5.2; Fig. 5.1). Highest AGP was obtained by fertilization with ammonium nitrate and P or ammonium sulphate and P, which resulted in a 68% and 74 % increase in AGP, respectively, relative to sites not fertilized with N (Table 5.2; Fig.5.1). Fertilization had very little effect on AGP in very dry years (Fig.5.1b), indicating that soil moisture was the most limiting resource in dry years, whereas N and P were most limiting in wet years. Although ammonium sulphate generally resulted in a significantly greater increase in AGP relative to ammonium nitrate (Table 5.2) it was small (8 %) relative to the effect of N itself. Fertilization with P or lime alone had little effect on AGP (Fig.5.1). Lime (L) interacted negatively with the N and P treatments (Control.P.L; Table 5.2), where potential maximum AGP normally attained in sites fertilized with both N and P was not realized (Fig. 5.1). However, this effect was not observed in the 1999/2000 season (Table 5.2).

The level of N fertilization and the interaction of N and P had a significant effect on the percentage of PAR above the canopy that reaches 300 mm above the soil surface (Table 5.2). Linear regression indicated that there was a strong negative relationship between AGP and the percentage of PAR reaching 300 mm above the soil surface (PAR = -0.0943AGP + 98.82; t_{94} = -4.34; $P < 0.001$; R^2 = 15.8).

Table 5.2. F ratios and probabilities for analyses of variance of the effect of fertilization treatments on above-ground phytomass production and photosynthetically available radiation (PAR) at the Ukulinga long-term grassland fertilization experiment

Source of variation	d.f.	Above-ground phytomass production			PAR
		1951/1952 season	Average 1951-1980	1999/2000 season	2002/2003 season
Control (N versus no N)	1	263.7***	88.5***	23.06***	126.1***
Control.Ntype	1	1.1	10.2**	3.03	0.01
Control.Nlevel	2	10.8***	0.4	7.14**	37.2***
Control.P (NxP)	2	71.9***	12.7***	45.48***	4.8*
Control.L	2	1.2	1.4	2.93	1.5
Control.Ntype.Nlevel	2	2.1	0.8	1.66	0.2
Control.Ntype.P	1	1.9	1.4	0.02	0.8
Control.Nlevel.P	2	10.5***	1	7.28**	4.1*
Control.Ntype.L	1	0.8	2.2	5.01*	5.9*
Control.Nlevel.L	2	1.2	1.5	0.81	0.7
Control.P.L	2	5.5*	8.6***	0.6	0.2
Control.Ntype.Nlevel.P	2	0.6	0.6	0.59	1.1
Control.Ntype.Nlevel.L	2	1.7	0.03	2.55	2.6
Control.Ntype.P.L	1	0.3	2.3	4.33*	1.6
Control.Nlevel.P.L	2	0.6	1.8	1.97	2.4
Control.Ntype.Nlevel.P.L	2	0.3	0.9	0.35	0.4
Residual	66				
Total	95				

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$
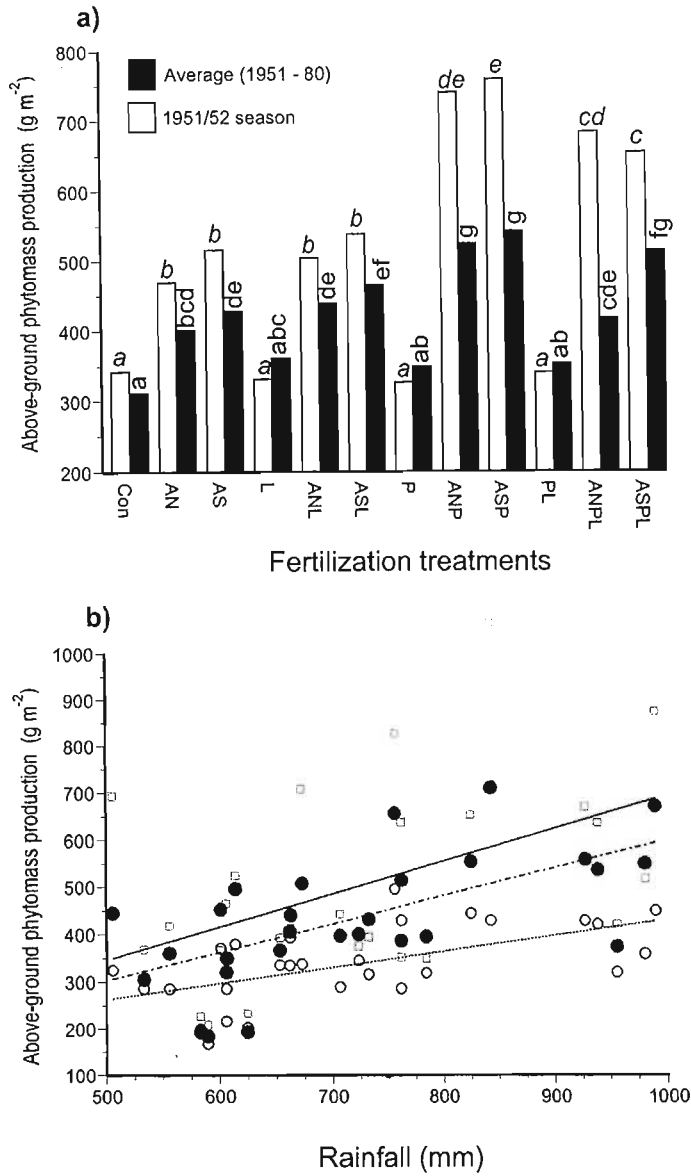
Fig 5.1. Above-ground phytomass production in the Ukulinga long-term grassland fertilization experiment in relation to: a) fertilization treatments in different seasons, and b) the interaction of N and P with rainfall. Key to fertilization treatments: Con, control; AN, ammonium nitrate; AS, ammonium sulphate; L, lime; P, phosphorus. Means associated with the same letter did not differ ($P < 0.05$). Means compared within seasons only. Open circles and dotted line, no fertilization with N or P; closed cirles and intermittently dotted line, fertilization with N only; open squares and solid line, fertilization with both N and P.

Traits of key grass species

Heteropogon contortus, Themeda triandra, Diheteropogon amplectens and *Tristachya leucothrix* are narrow-leaved species of low maximum leaf height (Table 5.3). *Panicum maximum* has the greatest maximum leaf height and the broadest leaves of the species in the fertilization experiment. In contrast, species such as *Eragrostis curvula* and *Hyparrhenia hirta* are tall but have relatively narrow leaves. *Paspalum dilitatum* has a low maximum leaf height but has amongst the broadest leaves of all the species.

Table 5.3. Traits of key grass species at Ukulinga

Species	Leaf height	Leaf width	Stem width
Diheteropogon amplectens	510.00	6.60	2.00
Heteropogon contortus	323.00	2.94	0.00
Paspalum dilatatum	462.00	13.76	2.13
Tristachya leucothrix	504.00	4.55	0.00
Themeda triandra	517.00	4.05	0.18
Setaria nigrirostris	603.64	8.29	1.12
Eragrostis curvula	814.00	4.75	1.89
Cymbopogon excavatus	937.00	11.58	2.80
Hyparrhenia hirta	999.00	4.20	2.68
Panicum maximum	1165.45	13.84	3.97

Effect of fertilization on composition

Fertilization of natural grassland resulted in dramatic changes in composition (Table 5.4; Fig. 5.2). Averaged across all levels, N fertilization reduced the abundance of all species except for *Eragrostis curvula* and *Panicum maximum* (Fig. 5.2i,j). *Eragrostis curvula* came to dominate sites fertilized with N only, whereas *Panicum maximum* dominated sites fertilized with both N and P (Fig. 5.2i,j); note N x P interaction in Table 5.4. *Cymbopogon excavatus* also tended to be most abundant in sites fertilized with both N and P but provided they were also limed. The general trend was for the shorter species to decline in abundance with increasing levels of N fertilization and AGP, whereas most tall species peaked at some level of N fertilization or AGP (Table 5.5; Fig. 5.3 & 5.4). *Panicum maximum* was the only species to show no tendency to decline at the highest levels of N and P fertilization and AGP. The only short species not to decline markedly with increasing level of N fertilization or AGP were *Tristachya leucothrix* and *Setaria sphacelata* (Fig. 5.3 & 5.4).

The type of N had a significant influence on the abundance of several species (Table 5.4). *Eragrostis curvula* and *Tristachya leucothrix* were more abundant in sites fertilized with ammonium sulphate compared with ammonium nitrate, whereas the opposite was true for *Cymbopogon excavatus* (Fig. 5.2). Certain species appeared to be sensitive to soil pH (Table 5.4). *Tristachya leucothrix* and *Eragrostis curvula* were strongly reduced in abundance, whereas *Heteropogon contortus*, *Setaria nigrirostris*, *Hyparrhenia hirta* and *Cymbopogon excavatus* were increased in abundance through fertilization with lime (Fig. 5.2).

Table 5.4. Anova of the effect of fertilization treatments on the abundance (g m^{-2}) of key grass species (1999 data) at the Ukulinga long-term grassland fertilization experiment

	d.f.	HCO	DAM	TTR	TLE	SNI	SSP	HHI	CEX	ECU	PMA
						F probability value					
Control (N versus no N)	1	<.001	0.007	<.001	<.001	<.001	0.844	<.001	<.001	<.001	<.001
Control.Ntype	1	0.64	1.000	0.09	0.02	0.54	0.278	0.90	0.01	0.01	0.52
Control.Nlevel	2	0.81	1.000	<.001	<.001	<.001	0.807	0.02	<.001	0.79	0.02
Control.P	2	0.004	0.840	<.001	<.001	0.01	0.186	0.33	0.46	0.45	<.001
Control.L	2	0.25	0.840	0.01	<.001	<.001	0.629	<.001	<.001	0.03	0.53
Control.Ntype.Nlevel	2	0.81	1.000	0.26	0.06	0.19	0.701	0.25	0.97	0.93	0.19
Control.Ntype.P	1	0.64	1.000	0.05	0.19	0.04	0.033	0.14	0.49	0.87	0.47
Control.Nlevel.P	2	0.81	1.000	0.21	<.001	0.80	0.925	0.56	0.10	0.29	0.08
Control.Ntype.L	1	0.64	1.000	0.03	0.22	0.89	0.72	0.36	0.98	0.38	0.72
Control.Nlevel.L	2	0.81	1.000	0.01	<.001	0.41	0.344	0.59	0.01	0.97	0.94
Control.P.L	2	0.56	0.009	0.20	0.10	0.80	0.337	0.91	0.30	0.75	0.26
Control.Ntype.Nlevel.P	2	0.81	1.000	0.13	0.06	0.60	0.447	0.58	0.10	0.41	0.02
Control.Ntype.Nlevel.L	2	0.81	1.000	0.06	0.43	0.26	0.014	0.77	0.19	0.49	0.70
Control.Ntype.P.L	1	0.64	1.000	0.31	0.07	0.02	0.244	0.17	0.03	0.34	0.33
Control.Nlevel.P.L	2	0.81	1.000	0.10	0.51	0.10	0.101	0.89	0.35	0.29	0.69
Control.Ntype.Nlevel.P.L	2	0.81	1.000	0.79	0.47	0.66	0.225	0.41	0.34	0.82	0.33
Residual	66										
Total	95										

HCO, *Heteropogon contortus*; DAM, Diheteropogon amplectens; TTR, *Themeda triandra*; TLE, Tristachya leucothrix; SNI, *Setaria nigrirostris*; SSP, *Setaria sphacelata*; HHI, *Hyparrhenia hirta*; CEX, *Cymbopogon excavatus*; ERA, *Eragrostis curvula*; PMA, *Panicum maximum*
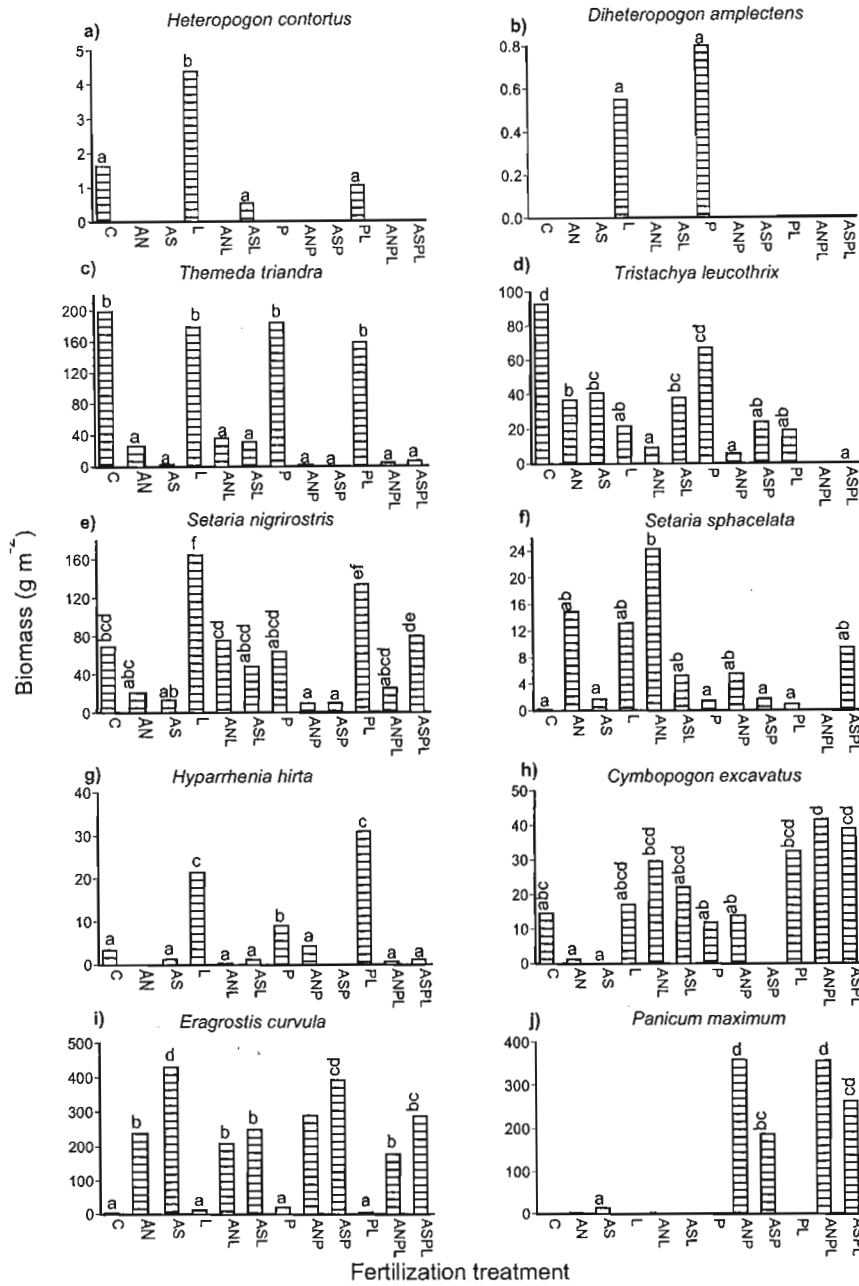
Fig 5.2. Effect of fertilization treatments on relative abundance of key grass species (1999 data) at the Ukulinga long-term grassland fertilization experiment. C, control; AN, ammonium nitrate; AS, ammonium sulphate; L, lime; P, phosphorus. Means associated with the same letter are not significantly different ($P < 0.05$). Note that scale varies.

Table 5.5. Multiple linear regression of the relationship between levels of N fertilization (with and without P) or AGP and the abundance of key grass species (1999 data) in the Ukulinga long-term fertilization experiment

Species	Best Model	Slope	t value	t prob.
N fertilization only				
Heteropogon contortus	Nitrogen level	-0.572	-1.74	0.087
Diheteropogon amplectens	Nitrogen level	-0.1012	-2.28	0.025
Themeda triandra	Nitrogen level	-149.6	-7.45	<.001
	Nitrogen level squared	31.04	4.54	<.001
Tristachya leucothrix	Nitrogen level	14.2	0.87	0.391
	Nitrogen level squared	-11.56	-2.08	0.042
Setaria nigrirostris	Nitrogen level	-36.05	-5.28	<.001
Setaria sphacelata	Nitrogen level	4.03	1.55	0.126
Hyparrhenia hirta	Nitrogen level	-15.98	-3.14	0.003
	Nitrogen level squared	3.61	2.08	0.042
Cymbopogon excavatus	Nitrogen level	-4.52	-1.66	0.101
Eragrostis curvula	Nitrogen level	115.8	7.96	<.001
Panicum maximum	Nitrogen level	1.89	1.07	0.287
N and P fertilization				
Heteropogon contortus	Nitrogen level	-0.619	-1.92	0.06
Diheteropogon amplectens	Nitrogen level	-0.119	-1.75	0.085
Themeda triandra	Nitrogen level	-187.2	-9.87	<.001
	Nitrogen level squared	43.72	6.77	<.001
Tristachya leucothrix	Nitrogen level	-18.34	-5.08	<.001
Setaria nigrirostris	Nitrogen level	-39.56	-5.24	<.001
Setaria sphacelata	Nitrogen level	-0.42	-0.27	0.787
Hyparrhenia hirta	Nitrogen level	-5.65	-3.8	<.001
Cymbopogon excavatus	Nitrogen level	30.4	2.32	0.024
	Nitrogen level squared	-13.2	-2.97	0.004
Eragrostis curvula	Nitrogen level	303.5	5.64	<.001
	Nitrogen level squared	-73.6	-4.02	<.001
Panicum maximum	Nitrogen level	148.2	6.35	<.001
AGP				
Heteropogon contortus	AGP	-0.00458	-1.68	0.097
Diheteropogon amplectens	AGP	-0.000652	-1.15	0.252
Themeda triandra	AGP	-3.808	-5.93	<.001
	AGP squared	0.003535	5.18	<.001
Tristachya leucothrix	AGP	-0.95	-2.24	0.027
	AGP squared	0.000881	1.96	0.053
Setaria nigrirostris	AGP	-0.1718	-1.99	0.05
Setaria sphacelata	AGP	0.0425	1.79	0.076
Hyparrhenia hirta	AGP	-0.0388	-2.88	0.005
Cymbopogon excavatus	AGP	-0.0333	-0.87	0.389
Eragrostis curvula	AGP	5.41	3.22	0.002
	AGP squared	-0.00482	-2.7	0.008
Panicum maximum	AGP	0.989	4.05	<.001
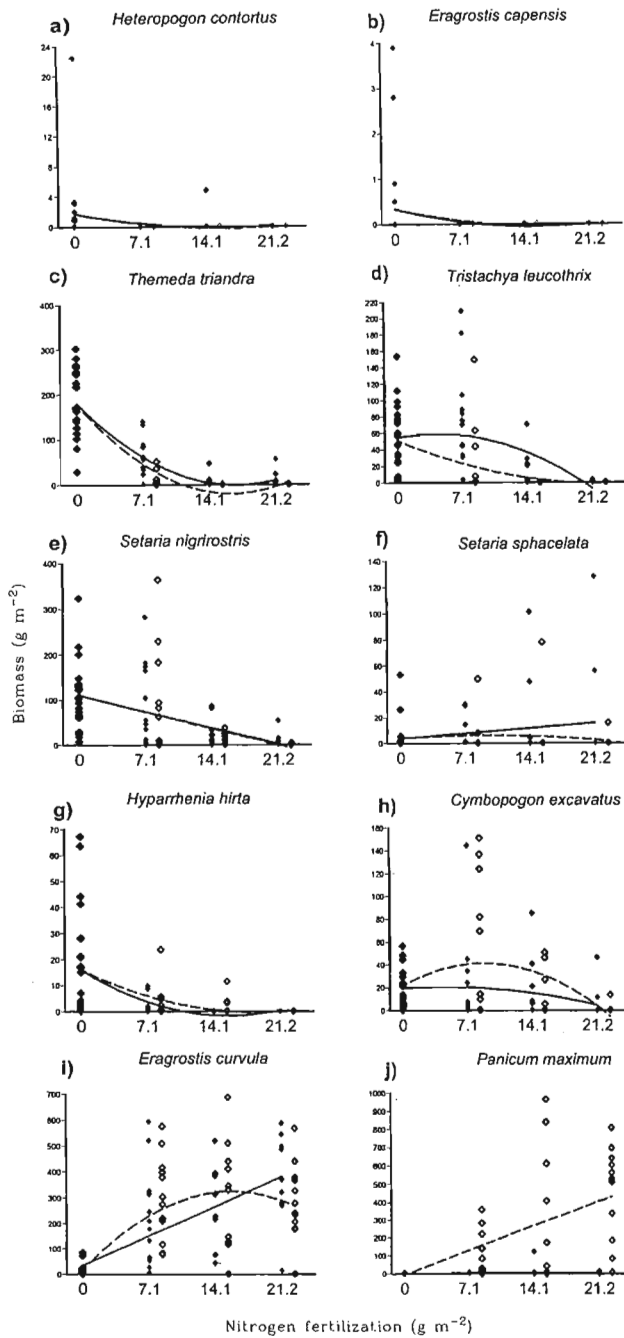
Fig 5.3. Relationship between the level of N fertilization and the biomass (g m^{-2}) of key grass species (1999 data) in the Ukulinga long-term grassland fertilization experiment. Filled stars, fertilization with N only; Open stars, fertilization with both N and P. Note that scale varies.
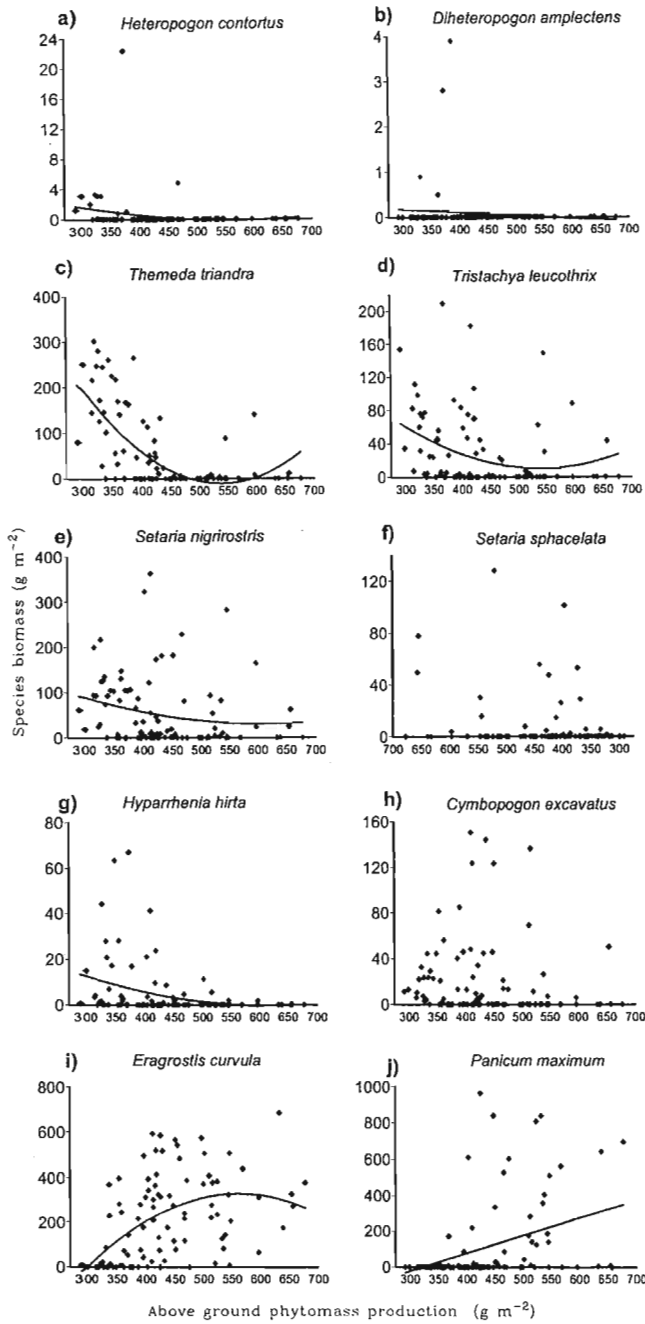
Fig 5.4. Relationship between above-ground phytomass production and the biomass (g m^{-2}) of key grass species (1999 data) in the Ukulinga long-term grassland fertilization experiment. Note that scale varies.

Effect of fertilization on species richness

Fertilization with N resulted in a decrease of both grass and forb species richness, whereas fertilization with lime or P only, had very little effect (Table 5.6; Fig. 5.5). Averaged across all levels of N fertilization, ammonium nitrate and ammonium sulphate resulted in a 30% and 32% decline in grass species richness, respectively (Table 5.6, Fig. 5.5a), whereas they resulted in a 69% and 94% decline in forb species richness, respectively (Table 5.6; Fig. 5.5b). Thus, the type of N did not have an effect on grass species richness but had a strong effect on forb species richness. Liming had no effect on grass species richness but strongly ameliorated the negative effect of N fertilization on forb species richness (Table 5.6). For example, there was only a 35% and 55% decline in forb species richness with fertilization by ammonium nitrate and ammonium sulphate respectively in limed sites, compared with the 69% and 94% decline for these N types in unlimed sites (Table 5.6; Fig. 5.5b). This is clearly displayed in the relationship between AGP or level of N fertilization and grass and forb species richness (Fig. 5.6). There was no difference in this relationship in limed and unlimed sites for grass species richness (Fig. 5.6a,c). The decline in forb species richness with increasing AGP or N fertilization was linear in limed sites but was exponential in unlimed sites (Fig. 5.6b,d). Multiple linear regression revealed that liming accounted for a significant amount of the variance in forb species richness after the effect of AGP ($F_{92} = 6.82$; $P < 0.05$) or N fertilization ($F_{92} = 11.79$; $P < 0.001$) had been accounted for. Liming did not account for a significant amount of the variance in grass species richness after the effect of AGP ($F_{92} = 1.03$; $P > 0.05$) or N fertilization ($F_{92} = 1.8$; $P > 0.05$) had been accounted for.

Table 5.6. Analysis of variance of the effect of fertilization treatments on grass and forb species richness (1999 data) at the Ukulinga long-term grassland fertilization experiment

	d.f.	Grass richness			Forb richness		
		% variance	F ratio	F prob	% variance	Fratio	F prob
Control (N versus no N)	1	18.4	35.0	<.001	39.4	123.5	<.001
Control.Ntype	1	1.0	1.9	0.17	8.0	25.0	<.001
Control.Nlevel	2	22.7	21.6	<.001	10.7	16.8	<.001
Control.P	2	10.5	10.0	<.001	1.7	2.7	0.08
Control.L	2	2.0	1.9	0.17	10.2	16.1	<.001
Control.Ntype.Nlevel	2	2.2	2.1	0.13	0.8	1.2	0.30
Control.Ntype.P	1	0.1	0.1	0.71	0.0	0.0	0.85
Control.Nlevel.P	2	0.3	0.3	0.74	0.1	0.2	0.84
Control.Ntype.L	1	0.1	0.1	0.71	0.2	0.6	0.46
Control.Nlevel.L	2	0.4	0.3	0.72	0.2	0.3	0.72
Control.P.L	2	0.4	0.4	0.71	3.8	6.0	0.001
Control.Ntype.Nlevel.P	2	0.8	0.8	0.47	0.3	0.4	0.66
Control.Ntype.Nlevel.L	2	1.4	1.3	0.27	2.6	4.1	0.02
Control.Ntype.P.L	1	1.4	2.7	0.11	0.0	0.0	0.85
Control.Nlevel.P.L	2	0.9	0.8	0.44	0.6	1.0	0.37
Control.Ntype.Nlevel.P.L	2	0.4	0.4	0.67	0.1	0.1	0.90
Residual	66	34.7			21.1		
Total	95						
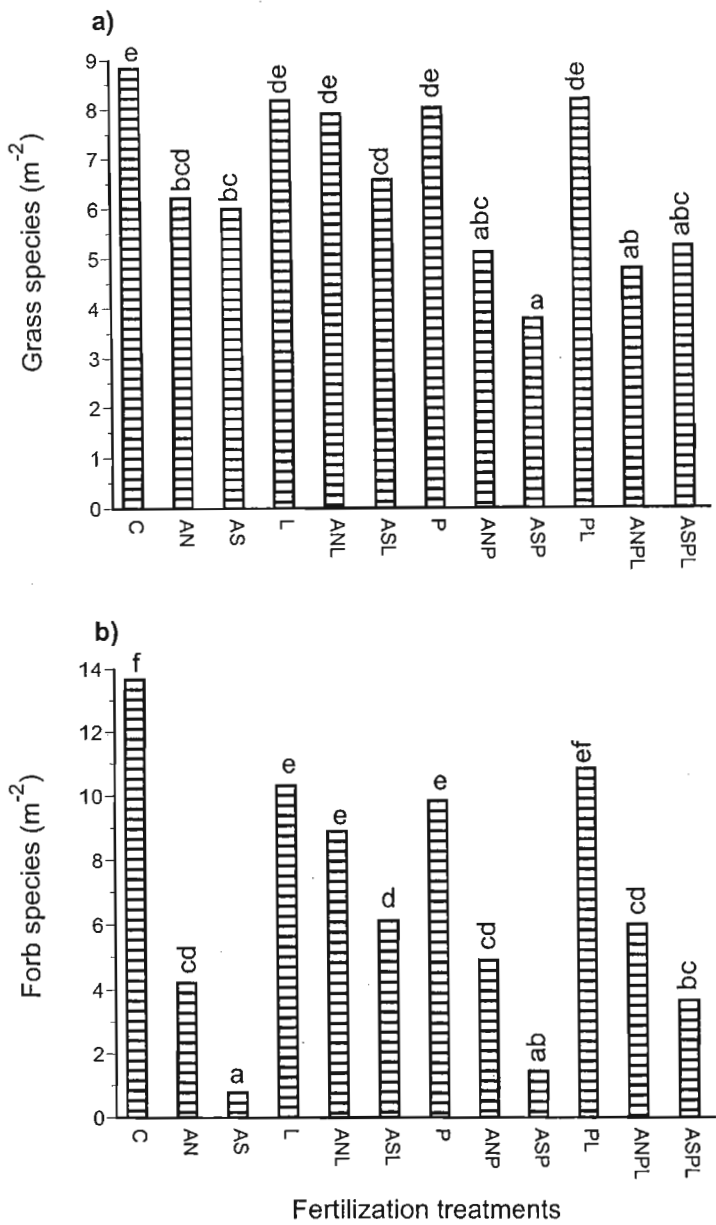
Fig 5.5. Effect of fertilization treatments on grass and forb species richness (1999 data) in the Ukulinga long-term grassland fertilization. C, control; AN, ammonium nitrate; AS, ammonium sulphate; L, lime; P, phosphorus. Means associated with the same letter are not significantly different ($P < 0.05$).
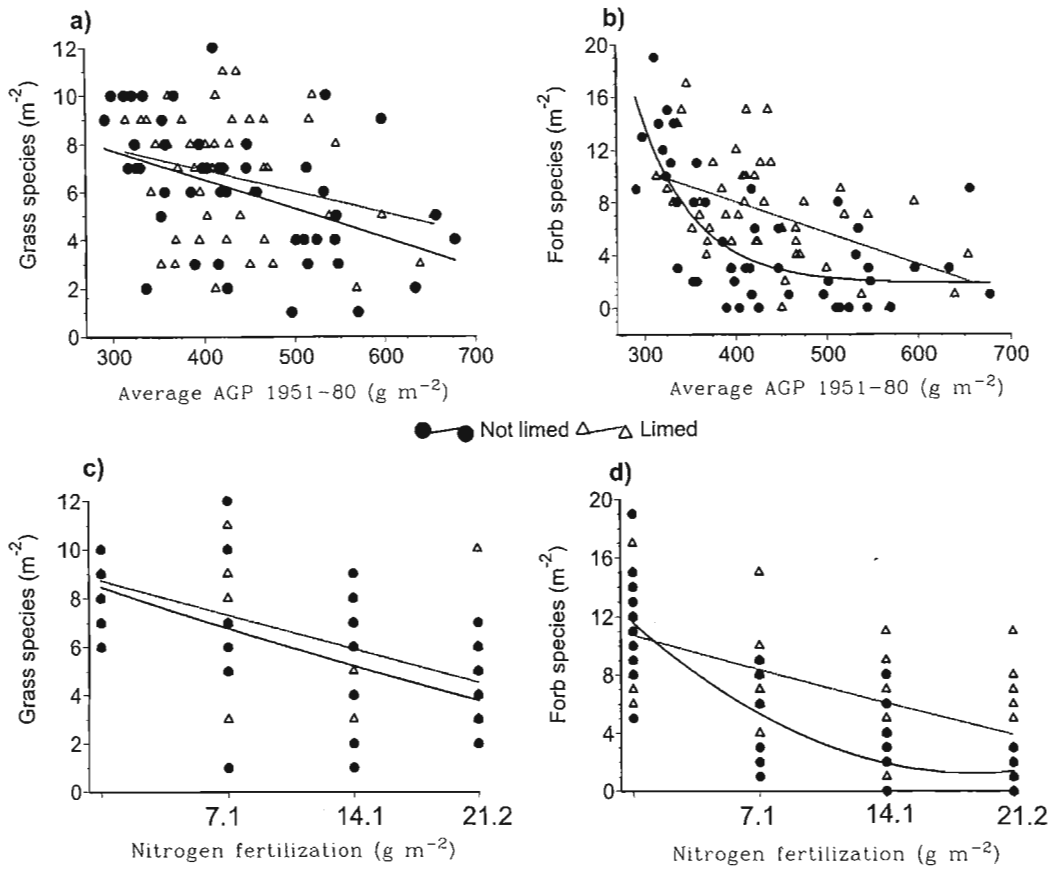
Fig 5.6. Effect of above-ground phytomass production (a, b) and nitrogen fertilization (c, d) on grass and forb species richness (1999 data) in the Ukulinga long-term grassland fertilization experiment. a) unlimed, $F_{46} = 11.1$; $P = 0.002$; limed, $F_{46} = 4.0$; $P = 0.05$; b) unlimed, $F_{45} = 25.8$; $P < 0.001$; limed, $F_{46} = 12.4$; $P < 0.001$; c) unlimed, $F_{46} = 31.2$; $P < 0.001$; limed, $F_{46} = 31.2$; $P < 0.001$; d) unlimed, $F_{45} = 49.7$; $P < 0.001$; limed, $F_{46} = 31.3$; $P < 0.001$.

Discussion

Hierarchical nutrient limitation

N was the primary limiting nutrient in this experiment, as demonstrated in many other studies (see Tilman 1988). When applied in isolation, N was the only nutrient to result in an increase in AGP over that of the control (Fig. 5.1). Where both N and P were applied together, however, AGP was greatly increased. Addition of P alone did not result in an increase in AGP because P only becomes limiting when the demand for it is increased owing to accelerated plant growth following fertilization with N. This indicates that N and P are both limiting but in a hierarchical and interactive fashion. Similar results have been demonstrated for N and magnesium in Minnesota grasslands (Tilman 1984). Sulphur also appeared to be limiting (ammonium sulphate resulted in an increase in AGP relative to ammonium nitrate) but this effect was small relative to that of P (Table 5.2; Fig. 5.1).

The fact the liming had no affect on AGP in sites fertilized with N only, but reduced AGP in sites fertilized with both N and P indicates that it induced some form of nutrient limitation only where growth rates and nutrient demands are greatest. Liming through its effects on competition with Ca^{2+} for root uptake or its effect on soil pH may reduce the uptake or availability of certain nutrients such as potassium, magnesium, zinc, copper, manganese and boron (Tisdale et al. 1993). There was a marked difference in response to fertilization in seasons of very different rainfall (Fig. 5.1b). Thus, it appears that nutrient and moisture limitation is determined by potential growth rate as influenced by another limiting resource that may influence growth rate. For example, N was most limiting in good rainfall seasons, P became limiting following N fertilization, an unknown nutrient became limiting in limed sites, following fertilization with both N and P and soil moisture was most limiting in fertilized sites (Fig. 5.1). In the Tallgrass prairie, the responses to N fertilization were greater in burned lowland sites than burned upland sites because soil moisture was less limiting in lowland sites (Turner et al. 1997). Reducing light limitation through burning normally improves AGP in Tallgrass prairie,

but in years of below-average rainfall burning may reduce AGP in upland sites only because moisture becomes limiting following burning only in the upland sites (Knapp et al. 1998). In this experiment, however, the relative importance of N, P and soil moisture as determinants of AGP may have varied between wet and dry seasons and fertilized and unfertilized sites (*sensu* Knapp et al. 1998), but the general pattern of nutrient limitation was consistent between wet and dry seasons (Fig. 5.1). It is expected, therefore, that there were no changes in the hierarchy of importance of N, P and soil moisture as determinants of community organization between seasons.

Influence of nutrient limitation on composition: links to plant traits

In this experiment, most short-grass species tended to decline in abundance with increasing levels of N fertilization and AGP, whereas most tall-grass species showed some form of positive response to fertilization (Fig. 5.3 & 5.4). This was attributed to short-grass species being vulnerable to shading by taller species as fertility/productivity increased. Toxic effects of N on the short species (cf. Grossman & Cresswell 1974) is discounted because they grew much better in N fertilized sites following N fertilization in the first year of the experiment (Fig. 5.1 and see Booysen 1954), remembering that these sites were dominated by short species in 1951. *Themeda triandra* grew extremely well at a high concentration of ammonium nitrate (200 ppm) but died at double this concentration (Grossman & Cresswell 1974). The point is that *Themeda triandra* grows much better at some level of N fertilization than without fertilization but dies very rapidly at toxic levels of N. If N fertilization was toxic to *Themeda triandra*, why did it not die, but instead grew larger in fertilized sites compared with unfertilized sites (Booysen 1954)?

Height is a trait that conveys a strong competitive effect (shade competitors) and response (avoid being shaded) in productive habitats (Goldberg 1996). Plant biomass, plant height and leaf width are usually well correlated with competitive effect in productive habitats (Goldberg 1987; Gaudet & Keddy 1988; Gaudet & Keddy 1995; Freckleton & Watkinson 2001; Keddy et al. 2002). These traits would all contribute to a species ability to preempt space and light (strong competitive effect). Broad-leaves are

also associated with shade-tolerance (competitive response), a trait that is critical for seedling survival in productive, shaded habitats (Huston & Smith 1987; Tilman 1988).

Panicum maximum, the tallest species with the broadest leaves, was the only species whose abundance increased linearly with increasing levels of fertilization with N (Fig. 5.3) and increasing AGP (Fig. 5.4). *Panicum virgatum* was the only grass to respond positively to fertilization at Konza prairie (Gibson et al. 1993). *Eragrostis curvula*, although a reasonably tall species, has relatively narrow leaves, and tended to decline in abundance at the highest levels of N fertilization and AGP only in sites fertilized with P where *Panicum maximum* was most abundant (Fig. 5.3), possibly owing to increasing competition intensity from *Panicum maximum*. Light availability declined strongly with increasing AGP ($P < 0.001$), which should result in tall broad-leaved species gaining an advantage over the tall narrow-leaved species in the most productive sites. *Cymbopogon excavatus*, tended to peak at intermediate levels of N fertilization and AGP, probably owing to intense competition at higher levels of N fertilization and AGP.

The tall narrow-leaved *Eragrostis curvula*, dominated sites fertilized with N alone, where P was strongly limiting (Fig. 5.1). It is a general observation that specific leaf area decreases as nutrient limitation increases (Chapin 1980; Craine et al. 2002; Wright et al. 2002; Craine & Lee 2003). This may explain why the tall broad-leaved species, *Panicum maximum*, was unable to dominate sites fertilized with N only (Fig. 5.2).

Tall species were unable to dominate sites not fertilized with N (Fig. 5.2), where N was strongly limiting (Fig. 5.1). This is consistent with predictions of theories that large above-ground allocation represents a tradeoff for an ability to compete for light at the expense of an ability to compete for soil resources (Tilman 1988). In a pot experiment, *Themeda triandra* allocated far more to roots than taller species such as *Eragrostis curvula* and *Hyparrhenia hirta*, and grew and competed better than the taller species in low nutrient treatments (Ghebrihwot unpubl.). Certain species are able to grow faster than others at low levels of fertility (Rice *et al.* 1960; Parrish & Bazzaz 1982; Tilman 1986; Austin *et al.* 1985). High root allocation may favour species in infertile habitats (Chapin 1980; Gleeson & Tilman 1990; Craine et al. 2002), because the

diffusion rate of nutrients and not the extraction rate per unit root mass is the process limiting nutrient uptake (Chapin 1980).

The only short species to show any degree of increasing abundance with increasing N fertilization were *Tristachya leucothrix* and *Setaria sphacelata* (Fig. 5.3). *Tristachya leucothrix* initiates tillers below ground, whereas *Themeda triandra* and *Heteropogon contortus* initiate tillers above-ground (Everson et al. 1988). Tiller initiation in *Tristachya leucothrix* was less sensitive to shading treatments than *Themeda triandra* and *Heteropogon contortus* (Everson et al. 1988). Position of tiller initiation is a trait that has received little attention (e.g. Goldberg 1996; Crain et al. 2003), but has potential for understanding responses of species to factors that may affect light availability. *Setaria sphacelata* has broad leaves, which may allow it to be tolerant of shading in fertilized productive sites. Models predict that both height and shade tolerance are necessary for long-term dominance (Huston & Smith 1987; Tilman 1988). Another short broad-leaved species, *Paspalum dilitatum*, invaded sites fertilized with N in the first 30 years of the experiment (Le Roux & Mentis 1986). As predicted, *Paspalum dilatatum,* was replaced in the long-term by the tall broad-leaved species, *Panicum maximum.* The fact that it took more than 30 years for this replacement to occur, underscores the importance of long-term experiments when investigating the relationships between plant traits and the long-term response of species.

Effect of soil pH and AGP on composition and species richness

Although the major compositional responses were determined by fertilization treatments that had the greatest effect on AGP (N and its interaction with P), many species were affected by liming, which had very little effect on AGP (Fig. 5.1) but a large influence on soil pH (Table 5.1). The effect of the type of N on species appeared to be related to its effects on soil pH. For example, all the species that responded to the type of N also responded to liming (Table 5.4). *Eragrostis curvula* and *Tristachya leucothrix* were strongly reduced in abundance in sites fertilized with lime and had higher abundances in sites fertilized with the soil acidifying ammonium sulphate compared with the less acidifying ammonium nitrate, whereas *Cymbopogon excavatus* was favoured by

liming and by ammonium nitrate (i.e. if a species was favoured by liming it was also favoured by the type of N fertilizer that was less acidifying and vice versa). Consequently, *Eragrostis curvula*, which is extremely tolerant of low soil pH, was dominant over *Panicum maximum* in sites fertilized with the acidfying ammonium sulphate, whereas the reverse was true in sites fertilized with ammonium nitrate (Fig. 5.2). Different types of N fertilizer influenced soil pH in the Park Grass Experiment at Rothamsted. *Arrhenatherum elatius* dominated the higher soil pH sites fertilized with NO_3^- or N fertilized limed sites, whereas *Holcus lanatus* dominated the lower soil pH sites fertilized with NH_4^+ or N fertilized unlimed sites (Tilman 1988; Tilman et al. 1994). Soil pH may influence species tolerance or competitive ability through effects on the availability of certain nutrients or aluminum toxicity (Tisdale et al. 1993).

Many studies have used N fertilization to examine the influence of productivity on root, shoot and total competition intensity (Wilson & Tilman 1993; Cahill 1999; Rajaniemi et al. 2003) and diversity (see Rajaniemi 2002). None of these studies considered the possibility that fertilization may not entirely influence these processes through effects on productivity but rather through effects on soil pH. This experiment shows that soil pH may have an important influence on species richness. The fact that the type of N, which has very little effect on AGP (Fig. 5.1), but has a strong effect on soil pH (Table 5.1), had an effect on forb species richness, and that liming ameliorated the negative effect of both forms of N on forb species richness (Table 5.6, Fig 5 & 6), suggests that the effect of N fertilization on forb species richness is not only related to its effect on AGP but also to its effects on soil pH. Thus, forb species richness declined strongly with increasing AGP or N fertilization in sites that were limed or unlimed, but liming reduced the rate of decline (Fig. 5.6). The fact that grass species richness was unaffected by the type of N or liming (Table 5.6, Fig. 5.5 & 5.6), shows that the effect of N fertilization on AGP rather than soil pH, impacted grass species richness. The impact of N fertilization on species richness partly through its affect on soil pH, appears to be a general phenomenon because liming was shown to ameliorate the negative effect of N fertilization on species richness in the Park Grass Experiment (Tilman et al. 1994). Other experiments have shown that reducing light availability by increasing productivity through watering (Goldberg & Miller 1990), or through the use of shadecloth (Rajaniemi

2002) had no effect on diversity whereas N fertilization had a strong effect, suggesting that the effect of fertilization on species richness was weakly related its effects on AGP and light availability in those experiments. Rather, N fertilization was shown to affect diversity through effects on root competition and not above-ground competition (Rajaniemi et al. 2003), which may, in part, be caused by changes in soil pH.

Conclusions

The effect of hierarchical nutrient limitation on AGP had the major influence on composition with soil pH having an additional effect. Plant traits such as height and leaf width appear to be important determinants of competitive ability under different forms of nutrient limitation and at different temporal scales. Owing to the hierarchical nature of nutrient limitation, limitation by N results in different composition than under limitation by P because of differences in AGP under these two forms of nutrient limitation. Lowest AGP under N limitation favoured short-grass species, whereas higher AGP under P limitation favoured tall narrow-leaved species. Tall broad-leaved species dominated where neither N nor P were strongly limiting. Thus, narrow leaves appear to be an advantageous trait under any form of nutrient limitation, whereas broad leaves appear to be an advantageous trait in highly productive sites with minimal nutrient limitation. Position of tiller initiation (above- or below-ground) may also influence species response along productivity gradients. Species that initiate tillers below ground are less vulnerable to the effects of shading on tiller initiation in more productive sites. A combination of the effects of N fertilization on soil acidification and AGP was shown to determine forb species richness. Consequently, using N fertilization as a means of examining the effect of productivity on community organization and diversity may be problematic if species are sensitive to changes in soil pH.

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CHAPTER 6

PLANT STRATEGIES AND COMPETITIVE ABILITY IN FERTILE AND INFERTILE HABITATS: A POT EXPERIMENT

Abstract

Grass species of contrasting strategies and habitat types were grown in a pot-experiment to test the hypothesis that short-grass species characteristic of low to medium fertility habitats are not more productive or competitive in low nutrient treatments than tall-grass species characteristic of higher fertility habitats. In addition, we tested the hypothesis that short-grass species are not less shade-tolerant than tall-grass species. Species were grown in an individual plant and a competition experiment in sand culture under low (tap water) and high (50 % Hoaglands solution) nutrients. A shading treatment was included to test the hypothesis that tall-grass species are not more shade-tolerant than short-grass species. The hypothesis that short-grass species are not more productive or competitive in low nutrient treatments was rejected. Short-grass species produced approximately double the biomass of tall-grass species in the low nutrient treatments with the reverse being true in the high nutrient treatments. Moreover, the competitive hierarchy was contingent upon nutrient treatments. The hypothesis that tall-grass species were not more shade-tolerant than short-grass species was accepted. Tall-grass species did not produce relatively more biomass under shade than short-grasses.

Nomenclature: Arnold & De Wet (1993)

Introduction

Plant strategies generally differ between species common in infertile and those common in fertile habitats (Grime 1979; Tilman 1988). Species common in infertile habitats generally have shorter stature, inherently slower growth rates, long-lived tissues, large allocation to roots and smaller shoot to root ratios than species common in fertile habitats (Chapin 1980; Berendse & Elberse 1990; Gleeson & Tilman 1990; Craine et al. 2002). Species common in productive habitats generally have a tall growth form, broad leaves and shade-tolerance (Goldberg 1996, Gaudet & Keddy 1995, Leps 1999).

The ability to reduce the loss rates of nutrients through investment of nutrients into long-lived non-photosynthetic tissues rather than into short-lived photosynthetic tissue combined with the ability to effectively forage for limiting soil resources through large allocation to roots and large root absorbtive surfaces may result in a competitive advantage in infertile environments (Berendse & Elberse 1990; Gleeson & Tilman 1990). By contrast, the ability to capture light and avoid being shaded by other species through tall growth form and the ability to photosynthesize efficiently in shade (especially as seedlings) through broad leaves and investment of nutrients and energy into photosynthetic mechanisms, may result in a competitive advantage in fertile light-limited environments (Grime 1979; Tilman 1988; Bazzaz 1996). Productivity generally increases with increasing soil resource availability (moisture and nutrients) resulting in an inverse correlation between light availability and habitat fertility/productivity (Tilman 1988). Consequently, traits that confer an advantage to certain species in infertile habitats may be a disadvantage to those species in fertile habitats and vice-versa because of unavoidable tradeoffs between traits and strategies. For example, high allocation of available energy to producing above-ground structures and photosynthetic mechanisms results in less available energy to allocate to producing below-ground structures and mechanisms concerned with uptake of soil resources. Thus, Tilman proposed that plants have made a tradeoff for the ability to compete for soil resources in infertile habitats and the ability to compete for light in fertile habitats (Tilman 1988).

Others, however, have argued for a unified concept of competitive ability where plants do not make tradeoffs for above- or below-ground competition but rather adopt a

competitive strategy in productive habitats and a stress-tolerant strategy in unproductive habitats (Grime 1977; 1979). Grime has contended that there is very little evidence that plants that have made a tradeoff for traits assumed to confer a competitive advantage in infertile habitats (small shoot/root ratios, low nutrient loss rates) are able to perform better (in terms of biomass produced) than plants that have made a tradeoff for the ability to compete for light (Grime 1979). Grime has proposed that total competition intensity (sum of root and shoot competition) declines with decreasing soil fertility and productivity, whereas Tilman has contended that shoot competition declines and root competition increases with decreasing habitat fertility resulting in no change in total competition intensity along productivity gradients (Tilman 1988).

If plants do compete for nutrients in infertile environments, then species that have made a tradeoff for the ability to compete for nutrients should have the highest rankings in a competitive hierarchy of species in infertile habitats whereas species that have made a tradeoff for the ability to compete for light should have the highest rankings in fertile environments. In other words, the competitive hierarchy should be contingent upon the habitat. The evidence is equivocal, with examples of competitive hierarchies being contingent upon the fertility of the habitat and other examples of a consistent competitive hierarchy irrespective of the fertility of the habitat (Goldberg 1996; Keddy *et al.* 2000).

Fertilization with nitrogen favoured tall-grass species in the long-term fertilizer experiment, whereas annual burning, which generally reduces soil nitrogen (Ojima et al. 1994; Fynn et al. 2003), soil moisture (Knapp & Seastedt 1986; Snyman 2002), and productivity (Tainton et al. 1978) favoured short-grass species in the burning and mowing experiment. Protection from burning has been shown to favour tall-grass species in other regions (Everson & Tainton 1984; Titshall et al. 2001). Therefore, it was hypothesized that regular burning allows short-grass species to be more competitive than tall-grass species by reducing soil nitrogen availability.

Thus, the specific objectives of this experiment were to test whether: 1) species of widely contrasting traits (short versus tall growth form) differed in their ability to grow in high and low nutrient treatments, 2) the competitive hierarchy of various short and tall species was consistent across or contingent upon high and low nutrient treatments, 3) tall

species are more shade-tolerant than short species because this may give them a competitive advantage in productive light limited habitats.

Methods

Species

Species were selected that were common in the KwaZulu-Natal mesic grasslands and that had contrasting responses to management (burning, mowing and fertilization) and of contrasting strategies (short versus tall). *Themeda triandra* is a short-grass species dominant on well-drained dystrophic soils in the KwaZulu-Natal region. It is replaced by later succession species in the absence of disturbances such as burning and mowing (Everson & Tainton 1984). *Aristida junciformis* is a species of medium height common in the higher rainfall coastal and mistbelt grasslands of KwaZulu-Natal. It is adapted to well-drained extremely dystrophic soils. It often replaces *Themeda triandra* with overgrazing because it is extremely unpalatable resulting in animals selecting other species to its advantage. It also produces a prolific amount of seed allowing it to rapidly colonize overgrazed areas. *Eragrostis curvula* is a species of medium height and occurs over a wide range of soil types. It tends to replace *Themeda triandra* in the absence of burning or mowing or with nitrogen fertilization (le Roux & Mentis 1986). *Hyparrhenia hirta* is a tall robust species common in relatively productive habitats such as along stream banks and road verges.

Measurement of species traits

In order to obtain a measure of certain traits known to be correlated with competitive ability in various habitats (e.g. Goldberg 1996), ten of the largest individuals of each species at a site were selected and their maximum leaf height, maximum leaf width and stem diameter were measured.

Experiment

The species were grown from seed and planted in composted Pine bark growth medium in seedling trays. Approximately one month after germination they were sufficiently large to be transplanted into 500 ml volume polystyrene pots (with drainage holes) filled with fine river sand. The experimental treatments consisted of *Themeda triandra* as a phytometer species grown against the other three species (mixtures) as well as each species grown in monoculture. The mixtures consisted of one plant of *Themeda triandra* in a pot with one of the other species in the pot (i.e. two plants per pot). The monoculture treatments consisted of two plants of a species in a pot to ensure that the density of plants was consistent across treatments for comparative purposes (i.e. two plants per pot).

Treatments consisted of a high and low nutrient treatment and a shaded and unshaded treatment in a split-plot design with shaded and unshaded treatments as whole-plots and nutrient treatments as sub-plots with four replications. The high-nutrient treatment consisted of watering the pots each day with a 50% Hoaglands nutrient solution (107 ppm N), whereas in the low-nutrient treatment the pots were just given tap water. In addition, all pots received tap water each day to prevent dessication and were flushed thoroughly with water every few weeks to prevent the accumulation of salts. The shading treatment consisted of an 80 % green shadecloth tent (1 m high) over the pots. The shading treatment was included to examine whether competitive relationships would be consistent in shaded and unshaded conditions (i.e. are certain species more shade tolerant). The experiment was conducted in a greenhouse from mid November to late January (2002/2003 season).

At the termination of the experiment each species in a pot was cut at the base, bagged separately in brown paper bags, dried in an oven until constant mass at 80° C and weighed. In order to obtain the average mass of a species in monoculture the sum of the mass of the two plants of that species in a pot was divided by two.

Data analysis

The intensity of the competitive effect of each species on the phytometer species, *Themeda triandra*, was calculated as an absolute and a relative measure. Absolute competition intensity (Abs. CI) was calculated as the monoculture biomass of *Themeda triandra* minus the biomass of *Themeda triandra* in competition against a specific species. Relative competition intensity (Rel. CI) was calculated as the monoculture biomass of *Themeda triandra* minus the biomass of *Themeda triandra* in competition against a specific species over the monoculture biomass of *Themeda triandra*.

The effect of the nutrient and shading treatments on the monoculture biomass of each species was analyzed using ANOVA (split-plot design with shading treatments as whole-plots) using GENSTAT 5 (GENSTAT 1993). A species by nutrient treatment two-way ANOVA on the absolute (Abs. CI) and relative (Rel. CI) competitive effect of each species on the phytometer, *Themeda triandra*, was used to determine whether the hierarchy of competitive effect of each species was consistent across nutrient treatments or contingent upon nutrient treatments. Paired t tests were used to test whether a specific species grew differently (in terms of biomass accumulated) in monoculture than in competition against another species. Paired samples consisted of the biomass of a species in monoculture versus its biomass in competition against another species in a specific replication. This enabled four paired samples (four replications) for each analysis.

Results

Species traits

   Themeda triandra and *Aristida junciformis* are relatively short species with narrow leaves and very little allocation to stems, whereas *Eragrostis curvula* and *Hyparrhenia hirta* are tall species also with relatively narrow leaves but with greater allocation to stems (Table 6.1).

Table 6.1. Selected traits of the species used in the pot experiment. Values are means of at least ten individuals in the field

Species	Sample size	Maximum leaf height (mm)	S.E.	Maximum leaf width (mm)	S.E.	Stem diameter (mm)	S.E.
Themeda triandra	10	517.00	17.83	4.05	0.19	0.18	0.18
Aristida junciformis	10	713.64	19.5	2.00	0.07	1.45	0.09
Eragrostis curvula	15	814.00	29.66	4.75	0.18	1.89	0.18
Hyparrhenia hirta	10	999	29.19	4.2	1.27	2.68	0.14

Biomass of monocultures

   Light, nutrients and species all had highly significant effects on monoculture biomass (Table 6.2). An important result was a highly significant species x nutrient interaction (Table 6.2). In high nutrient treatments, *Hyparrhenia hirta* produced double the biomass of *Themeda triandra* and *Aristida junciformis* with the reverse being true under low nutrients (Fig. 6.1). A non-significant species x light interaction (Table 6.2) indicates that species did not grow better or worse relative to each other under shade than in full sunlight.

Table 6.2. Analysis of variance of the effect of light and nutrients on the shoot biomass of *Hyparrhenia hirta, Eragrostis curvula, Aristida junciformis* and *Themeda triandra* in monoculture in a pot experiment

| Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	3	58.723	19.574	2.84	
Rep.Light stratum					
Light	1	1483.02	1483.02	215.54	<.001
Residual	3	20.641	6.88	0.61	
Rep.Light.Nutrients stratum					
Nutrients	1	3101.655	3101.655	273.14	<.001
Light.Nutrients	1	1188.526	1188.526	104.67	<.001
Residual	6	68.132	11.355	2.01	
Rep.Light.Nutrients.*Units stratum					
Species	3	275.611	91.87	16.29	<.001
Light.Species	3	5.86	1.953	0.35	0.792
Nutrients.Species	3	450.979	150.326	26.66	<.001
Light.Nutrients.Species	3	44.167	14.722	2.61	0.066
Residual	36	202.968	5.638		
Total	63	6900.282			
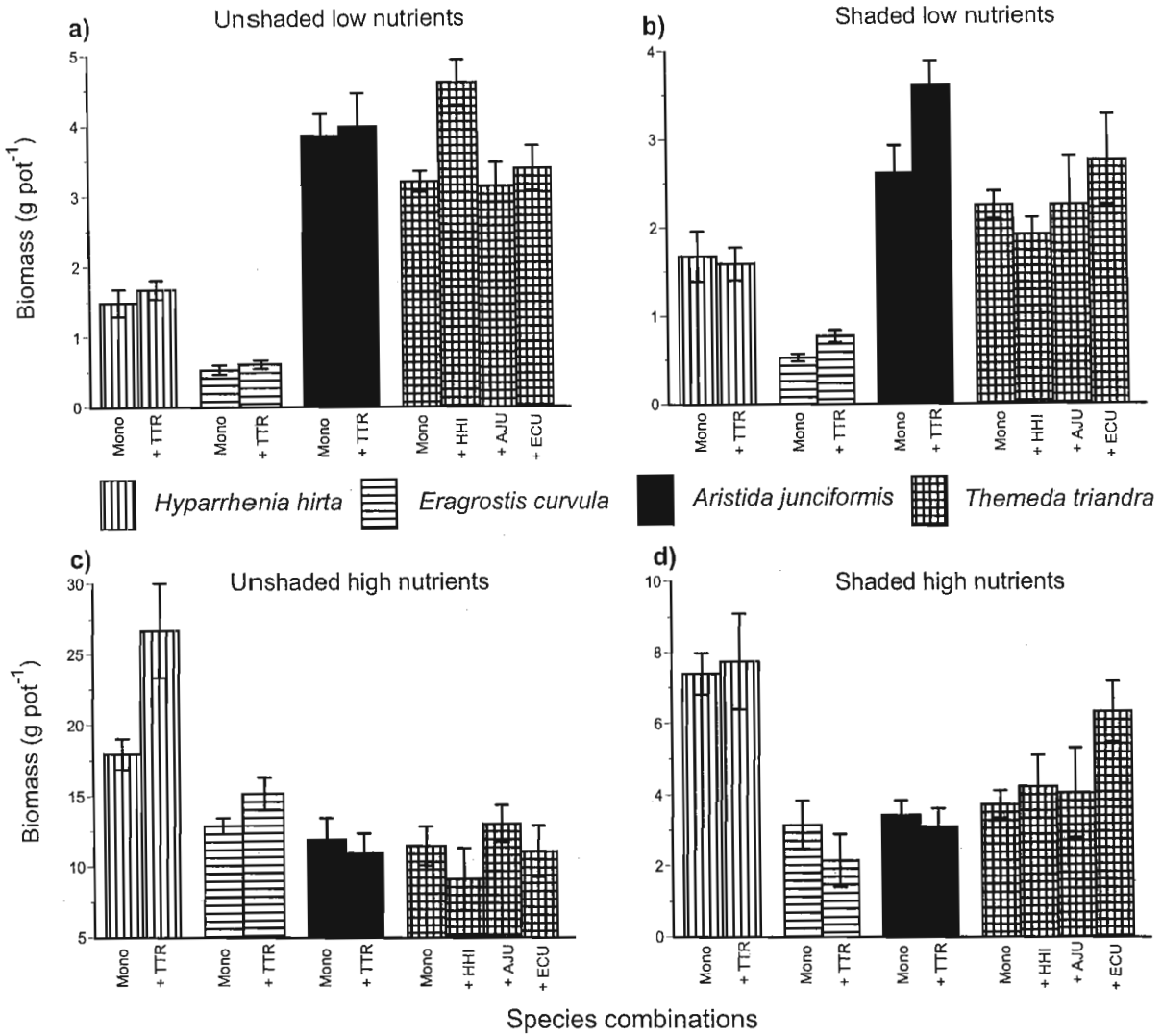
Fig. 6.1. Performance of four successional grass species grown in monoculture and combination in sand culture at high (50 % Hoaglands nutrient solution) and low (tap water) nutrient levels and shaded and unshaded conditions. AJU, *Aristida junciformis*; ECU, *Eragrostis curvula*; HHI, *Hyparrhenia hirta*; TTR, *Themeda triandra*. Bar = ±1 s.e.

Competition intensity and competitive hierarchies

In high nutrient treatments without shading, *Hyparrhenia hirta* grew better (d.f. = 3; t = 2.35; P = 0.10) in competition with *Themeda triandra* than it did against itself (Fig. 6.1c). A similar trend was observed for *Eragrostis curvula*. By contrast, *Themeda triandra* tended to grow better against itself or *Aristida junciformis* (d.f. = 3; t = 1.15; P = 0.33) than *Hyparrhenia hirta*. In low nutrient treatments without shading, few competitive effects were observed except that *Themeda triandra* grew better (d.f. = 3; t = 4.54; P = 0.02) when grown in competition with *Hyparrhenia hirta* than when grown in monoculture (Fig. 6.1a) suggesting that the intensity of competition was lower against the tall species than against itself. Shading tended to nullify these competitive effects (Fig. 6.1d), however, when shaded, *Themeda triandra,* tended to do better growing with *Eragrostis curvula* than in monoculture.

There was a significant species x nutrient level interaction for the relative competitive effect (Rel. CI) of *Hyparrhenia hirta, Eragrostis curvula* and *Aristida junciformis* on *Themeda triandra* (Table 6.3). In other words, the competitive hierarchy was contingent upon the nutrient treatment. For example, in the high nutrient treatment *Hyparrhenia hirta* had the greatest competitive effect on *Themeda triandra*, followed by *Eragrostis curvula* and *Aristida junciformis,* whereas in the low nutrient treatment the hierarchy was reversed (Fig. 6.2). This reversal was also observed for absolute competition intensity (Fig. 6.2a) but was not significant (Table 6.3).

Table 6.3. Analysis of variance of consistency of hierarchies of competitive effect of *Hyparrhenia hirta, Eragrostis curvula* and *Aristida junciformis* on a phytometer species, *Themeda triandra*, at high and low nutrients in unshaded treatments

| Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Absolute competition intensity (Abs. CI)					
Rep stratum	3	40.305	13.435	1.55	
Rep.*Units* stratum					
Nutrient level	1	4.833	4.833	0.56	0.466
Species	2	6.231	3.116	0.36	0.703
Nutrient level x Species	2	29.201	14.601	1.69	0.218
Residual	15	129.727	8.648		
Total	23	210.298			
Relative competition intensity (Rel. CI)					
Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	3	0.54041	0.18014	1.92	
Rep.*Units* stratum					
Nutrient level	1	0.1552	0.1552	1.66	0.218
Species	2	0.05396	0.02698	0.29	0.754
Nutrient level x Species	2	0.75326	0.37663	4.02	0.04
Residual	15	1.40496	0.09366		
Total	23	2.9078			
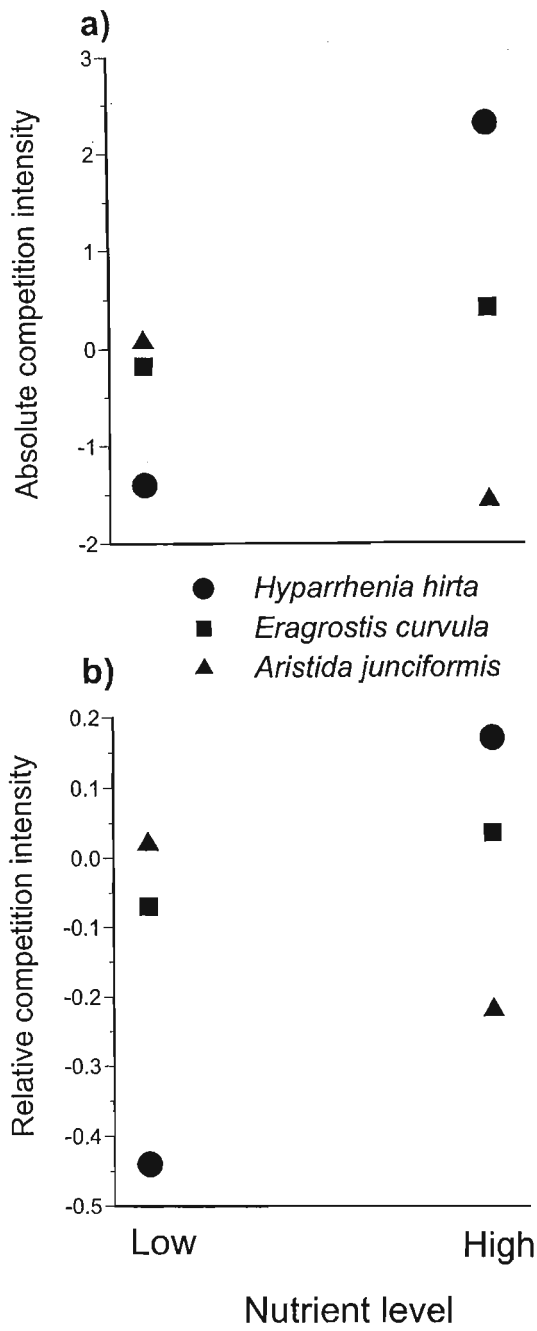
Fig. 6. 2. Hierarchy of competitive effect of *Hyparrhenia hirta, Eragrostis curvula* and *Aristida junciformis* on a phytometer species, *Themeda triandra,* grown in sand culture at high (50 % Hoaglands solution) and low (tap water) nutrient levels.

Discussion

Competitive ability in low and high nutrient treatments

If the unified concept of competitive ability (Grime 1977; 1979) is correct, species of contrasting traits should: 1) have a consistent ranking in the hierarchy of biomass production in high and low nutrient treatments, 2) have a consistent ranking in the hierarchy of competitive effect on a phytometer species in low and high nutrient treatments. If the tradeoff concept of competitive ability (Tilman 1988) is correct violations of one or more of the above two predictions would be expected.

In this experiment, the two shorter species, *Themeda triandra* and *Aristida junciformis,* characteristic of low to medium fertility habitats in the KwaZulu-Natal region were able to produce double the biomass of the tall *Hyparrhenia hirta* and *Eragrostis curvula* in low nutrient treatments with the reverse being true in high nutrient treatments (Table 6.2; Fig. 6.1). *Themeda triandra* and *Aristida junciformis* allocate relatively more to roots that shoots (Ghebrihiwot et al. in prep), which may allow them to grow better than the taller species in the low nutrient treatments. The fact that the diffusion rate of nutrients and not the extraction rate per unit root mass is the process limiting nutrient uptake by plants in infertile habitats (Chapin 1980) suggests that species with extensive root systems and wide root/shoot ratios should be able to extract more nutrients in the low nutrient treatments. Other studies have shown that shorter early successional species were able to grow faster than larger late successional species at low levels of fertility (Rice et al. 1960; Tilman 1986).

Moreover, the competitive hierarchy was completely reversed between low and high nutrient treatments with *Aristida junciformis* having the greatest and *Hyparrhenia hirta* the least competitive effect on *Themeda triandra* in low nutrient treatments and the reverse being true in high nutrient treatments (Table 6.3; Fig. 6.2). Other studies have found certain species are superior competitors in infertile habitats (Parrish & Bazzaz 1982; Austin et al. 1985) and that the competitive hierarchy may be contingent upon fertility (Goldberg 1996). Gleeson & Tilman (1990) showed that species that allocated a

large proportion of their biomass to roots were the most successful species in an infertile Minnesota sandplain.

Below-ground competition was evident in the low nutrient treatments because *Themeda triandra* grew much better against the taller *Hyparrhenia hirta* than against itself or *Aristida junciformis* (Fig. 6.1a). This is probably a result of the much higher root allocation of *Themeda triandra* than *Hyparrhenia hirta* (Ghebriwot *et al.* in prep) resulting in more intense competition below-ground against itself than against *Hyparrhenia hirta*. However, the fact that *Themeda triandra* did not respond in a similar fashion against *Eragrostis curvula*, which also has very low allocation to roots (Ghebriwot *et al.* in prep), raises the possibility that there was a positive interaction between *Hyparrhenia hirta* and *Themeda triandra* at low nutrient levels.

Although the potential for above-ground competition and shading was relatively small because target plants were not surrounded by neighbors, above-ground competitive effects were clearly present. For example, the tall species, *Hyparrhenia hirta*, was able to grow better against the shorter species, *Themeda triandra*, in high nutrient treatments. This would probably have been a result of the greater degree of shading and shoot interference that *Hyparrhenia hirta* would have experienced when growing against itself than against a shorter less productive species. Tall productive species have been shown to be most competitive in productive habitats (Goldberg 1987; Gaudet & Keddy 1988; Gaudet & Keddy 1995; Freckleton & Watkinson 2001; Keddy et al. 2002). Consequently, *Themeda triandra* grew better in monoculture than against the taller species in the high treatments probably because there would be less potential for shading and shoot interference when growing against itself than against the taller species. Further, when the supply rate of nutrients is high, large competitive species characteristic of fertile habitats, are able to extract nutrients more rapidly per unit root mass than species characteristic of infertile habitats (Chapin 1980). This may have resulted in more intense competition for nutrients for *Themeda triandra* when growing against *Hyparrhenia hirta* than when growing against itself in the high nutrient treatments.

Shade-tolerance as a competitive trait

A tall growth form is an important trait in productive habitats because it allows a species to have a strong competitive effect (shade other species) and response (avoid being shaded). It is only an advantage, however, as an adult where competition for light is likely to be symmetric, whereas during the seedling stage (especially in infrequently disturbed productive habitats), when competition is likely to be asymmetric, survival will be determined by the ability to mature in the shade of adult neighbors (Huston & Smith 1987; Tilman 1988). In monoculture, *Hyparrhenia hirta* was able to produce in the shaded treatments, double the biomass of the other species (Fig. 6.1d). However, the difference in biomass accrued between *Hyparrhenia hirta* and the other species in the shaded treatments was not greater than the difference in biomass between *Hyparrhenia hirta* and the other species in full sunlight, as indicated by a non significant species x light interaction (Table 6.2). Thus, *Hyparrhenia hirta* was not more shade-tolerant than the shorter species. This raises an important question as to why species like *Hyparrhenia hirta* grow big and tall but have relatively narrow leaves compared with other species of productive habitats in this region, which have extremely broad leaves (up to 80 mm wide)? The answer may lie in the frequency of disturbance and productivity of a habitat. In frequently disturbed productive habitats the degree of asymmetric competition between seedlings and adults will be lower than in infrequently disturbed productive habitats because disturbance (fire or mowing) reduces all individuals to ground level. In general, tall narrow-leafed species such as, *Hyparrhenia hirta* and *Cymbopogon validus*, dominate grassland habitats of intermediate fertility, whereas tall broad-leafed species such as *Setaria megaphylla* and *Panicum maximum* dominate the most productive habitats or protected habitas such as forest margins or shaded woodland habitats where light availability (especially during the seedling stage) is strongly reduced. The narrower leaf of *Hyparrhenia hirta* and *Cymbopogon validus* probably has greater leaf mass per area than the broader-leaved species, which has been shown to result in longer leaf life span and, therefore, nutrient retention (Craine et al. 2002; Wright *et al.* 2002). Greater nutrient retention may be an advantage to these narrower leaved species in intermediate fertility habitats (Berendse & Elberse 1990; Tilman 1990), and where periodic disturbance will provide windows of opportunity for seedling establishment in the absence of the previous seasons standing biomass.

Conclusions

Short species were able to grow better in low nutrient treatments with the reverse being true of tall species (Fig. 6.1). The growth advantage of the short and tall species in the low and high nutrient treatments respectively, appeared to translate into a reversal of the competitive hierarchy in low and high nutrient treatments. Thus, short species that allocate most of their biomass below-ground appear to have made a tradeoff for below-ground competition, whereas species that allocate most of their biomass above-ground appear to have made a tradeoff for above-ground competition. Thus, the hypothesis that above- and below-ground competitive ability is positively correlated (Grime 1977; 1979) was contradicted, whereas the hypothesis that plants have made tradeoffs for above- or below-ground competitive ability (Tilman 1988) was supported. Consequently, regular burning may favour short-grass species over tall-grass species in KwaZulu-Natal mesic grasslands (Everson & Tainton 1984) because it reduces soil nitrogen availability (Ojima *et al.* 1994; Fynn *et al.* 2003), soil moisture availability (Redmann 1978; Knapp & Seastedt 1986; Snyman 2002) and habitat productivity (Tainton et al. 1978; Redmann 1978), which should give the short-grass species a competitive advantage over tall-grass species. Conversly, protection from burning will allow nitrogen and soil moisture availability to increase, which should give the taller species the competitive edge. Both short and tall grasses should be equally tolerant of burning or mowing because they have basal meristems. Thus, differential tolerance of burning or mowing is an unlikely explanation of their responses to burning or mowing.

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CHAPTER 7

COMPETITIVE ABILITY AT VARIOUS LEVELS OF PRODUCTIVITY AND DISTURBANCE: LINKS TO PLANT TRAITS

Abstract

Grass species of contrasting traits and strategies were grown in an outdoor competition experiment in order to gain a better understanding of the mechanisms determining their various response patterns under burning, mowing and fertilization in natural grassland. It was hypothesized that the outcome of competition between short and tall species and broad- and narrow-leaved species was determined by site productivity and disturbance. Species were grown in competition and monoculture in a split-plot experiment with various fertilizer, irrigation and cutting treatments. The tall broad-leaved species, *Panicum maximum*, followed by the tall narrow-leaved species, *Hyparrhenia hirta*, were most competitive, especially when resource availability and productivity was high. Shorter species were much less competitive in these high productivity sites. Under a cutting regime, however, the short-grass species *Themeda triandra* became extremely competitive, strongly reducing the biomass of most other species relative to their monoculture biomass in cutting treatments. Under cutting, tall-grass species lost the competitive advantage that they had held over *Themeda triandra* in the uncut treatments. The superior competitive ability of the tall broad-leaved species, *Panicum maximum*, in productive sites explains why tall broad-leaved species dominate sites of deep moist fertile soils or grassland fertilized with nitrogen and phosphorus in this region. The superior competitive ability of *Themeda triandra* under cutting explains its dominance of regularly mown grasslands in this region.

Nomenclature: Arnold & De Wet (1993)

Introduction

A predictive understanding of patterns of plant species distribution along gradients of soil depth, fertility, moisture, productivity and disturbance is a general goal of plant ecology. Plant traits and their links to plant competitive ability in different environments and at various levels of disturbance may form part of a framework for predicting and understanding patterns of plant species distribution and response (Leishman & Westoby 1992; Westoby 1998; Craine *et al.* 2002; Lavorel & Garnier 2002). Traits that confer competitive ability may differ at various levels of fertility and disturbance. Plants associated with infertile habitats are generally short and slow growing (Chapin 1980), have low specific leaf area (Wright et al. 2002; Craine et al. 2002; Craine & Lee 2003) and allocate proportionally more to roots than shoots (Gleeson & Tilman 1990; Craine et al. 2002) whereas plants associated with fertile habitats are generally tall (Gaudet & Keddy 1995; Leps 1999) and fast growing and allocate proportionally more to shoots than roots (Chapin 1980). In addition, they have high tissue nitrogen content (Craine et al. 2002; Craine & Lee 2003) and high specific leaf area (Wright et al. 2002).

Leaf width may be a very important trait in productive light limited habitats because it may improve shade-tolerance, especially during the seedling stage when competition for light will likely be asymmetric. This important point has been recognized by others: *the competitive response of seedlings or juveniles to established vegetation should reflect the long-term response of populations at equilibrium, because in a population at equilibrium, seedlings must be able to tolerate depleted resource levels imposed by surrounding adults* (Goldberg 1996). Furthermore, tall broad-leaved species may be more effective in preempting light than tall narrow leaved species allowing them to have a greater competitive effect on other species in productive habitats. However, the cost of broad–leaves with high specific leaf area is a shorter life span and higher nutrient loss rates (Craine et al. 2002; Wright *et al.* 2002). High nutrient loss rates in infertile habitats may reduce the competitive ability of a species (Berendse & Elberse 1990; Tilman 1990). Thus, specific leaf area and leaf width may be very useful traits for understanding species distribution and competitive ability along fertility gradients.

Disturbances such as grazing and mowing may also influence nutrient loss rate. Tall species with a greater proportion of their nutrients in elevated structures than short

species are likely to experience greater nutrient loss rates under grazing and mowing than short species, which may give the short species a competitive advantage (Berendse & Elberse 1990; Tilman 1990). In the absence of disturbance, short species are vulnerable to shading by taller species, which may greatly reduce their ability to initiate tillers (Everson et al. 1988). Consequently, improved light availability at the soil surface following regular disturbance, may improve the competitive ability of many short species.

The fact that a tall broad-leaved species dominated sites of highest productivity and a tall narrow-leaved species dominated sites of intermediate productivity in the fertilizer experiment and that short-grass species dominated sites of lowest productivity and mown sites in the burning and mowing and fertilizer experiments, led us to hypothesize that the outcome of competition between short and tall species and broad- and narrow-leaved species was determined by site productivity and mowing. Thus, the aim of this experiment was to grow species of contrasting traits (short versus tall growth form and narrow versus broad leaved) in competition at various levels of cutting, moisture and nutrient availability. More specifically we intended to test whether 1) a tall broad-leaved growth form would be most competitive in highly productive, where there was no moisture or nutrient limitation, whereas a tall narrow-leafed species would be most competitive in sites of intermediate productivity, 2) a short species would be more tolerant of cutting than a tall species, 3) a short species would have a competitive advantage over a tall species in frequently cut sites with the reverse being true of uncut sites.

Methods

Species

Species common in the KwaZulu-Natal mesic grasslands of contrasting response to management (burning, mowing and fertilization) and of contrasting strategies (short versus tall) were selected for the experiment. In order to obtain a measure of certain traits assumed to confer a competitive advantage in various habitats (e.g. Goldberg 1996), ten of the largest individuals of each species at a site (Ukulinga) were selected and their maximum leaf height, maximum leaf width and stem diameter were measured. The characteristics of each of the species is presented in Table 7.1.

Themeda triandra is a short-grass species dominant on well-drained dystrophic soils in the KwaZulu-Natal region. It is replaced by later succession species in the absence of disturbances such as burning and mowing in the higher rainfall KwaZulu-Natal region (Everson & Tainton 1984) but dominates less productive habitats in the semi-arid regions of the country in the absence of disturbance.

Aristida junciformis is a species of medium height common in the higher rainfall coastal and mistbelt grasslands of KwaZulu-Natal. It is adapted to well-drained extremely dystrophic soils. It often replaces *Themeda triandra* with overgrazing because it is extremely unpalatable resulting in animals preferentially selecting other species, thereby giving it an advantage. It also produces a prolific amount of seed allowing it to rapidly colonize overgrazed areas.

Eragrostis curvula is a species of medium height and occurs over a wide range of soil types. It tends to replace *Themeda triandra* in the absence of burning or mowing or with nitrogen fertilization (le Roux & Mentis 1986).

Hyparrhenia hirta is a tall robust relatively narrow-leafed species common on deep soils along streams, hillsides and road sides. It has the ability to produce high biomass and form near monospecifc stands under favourable conditions.

Panicum maximum is a tall robust broad-leaved species found under trees or in open grassland in extremely fertile and productive habitats such as on deep moist soils along streams or where grassland has been fertilized with both nitrogen and phosphorus (le Roux & Mentis 1986).

Table 7.1. Selected traits of the species used in the competition experiment. Values are means of ten individuals in the field

Species	Sample size	Maximum leaf height (mm)	S.E.	Maximum leaf width (mm)	S.E.	Stem diameter (mm)	S.E.
Themeda triandra	10	517.00	17.83	4.05	0.19	0.18	0.18
Aristida junciformis	10	713.64	19.5	2.00	0.07	1.45	0.09
Eragrostis curvula	15	814.00	29.66	4.75	0.18	1.89	0.18
Hyparrhenia hirta	10	999	29.19	4.2	1.27	2.68	0.14
Panicum maximum	11	1165.47	30.1	13.84	0.49	3.97	0.23

Experimental design

The experiment was designed to manipulate disturbance, nutrients and moisture independently in order to examine the relationship of specific traits with competitive ability in habitats of varying levels of soil moisture availability, soil nutrient availability and disturbance. The experiment was established in December 2002 at the Neil Tainton arboretum and set up as a split-plot design with irrigation as whole-plots and fertilization as sub-plots with three blocks or replications (Fig. 7.1a). Before establishment the site was ploughed using a tractor and ripper to kill the lawn grasses. To maintain treatment integrity, irrigated sub-plots were separated from non-irrigated subplots by 4 meter walkways and fertilized sub-plots from non-fertilized sub-plots by 2 meter walkways (Fig. 7.1a). The various species mixture, monoculture and cutting treatments were randomly allocated to one of 25 experimental plots per sub-plot (there were 25 possible mixture and monoculture by cutting combinations) (Fig. 7.1b). The species combinations were: 1) all species in combination with *Themeda triandra* and, 2) *Hyparrhenia hirta* in combination with *Eragrostis curvula* or *Panicum maximum*. Disturbance treatments consisted of non-selective and selective cutting. A selective cutting treatment was included to simulate selective grazing by herbivores. With selective cutting, *Themeda triandra* was selectively cut leaving the other species uncut, whereas in non-selective cutting treatments, all species were cut. The selective cutting treatment was done only for *Themeda triandra* versus *Hyparrhenia hirta*, *Eragrostis curvula* or *Aristida junciformis*. The cutting height was 50 mm above the soil surface at an interval of two weeks during

the growing season (December to April) resulting in a total of six cuts. In the irrigated treatments, plots were watered with a mist spray irrigation system once a day for half an hour. In the fertilized treatments, fertilizer was applied once a month at a rate of 94 g m^{-2} of 2:3:2 NPK fertilizer. Species were grown from seed and established as plugs in speedling trays. Species were planted in plots of 16 plants comprising four rows of four plants spaced 50 mm apart (Fig. 7.1c). Plots consisted of monocultures of each species and mixtures of two species. In the mixtures, each species was planted in alternating positions in a row to ensure that interspecific competition was symmetric with respect to location of a competing species (Fig. 7.1c). In monoculture plots, the same layout as with the mixture plots was used but with only one species (i.e. 16 instead of 8 individuals of a species). Plots were regularly weeded to maintain only the planted species. The four individuals in the center of the plot were sampled as target individuals for determination of competitive effect and response (Fig. 7.1c). Thus, response of a species consisted of the mean of the biomass of two target individuals if it was a mixture plot, and the mean of four target individuals if it was a monoculture plot. Biomass attained by target species in the cut plots consisted of one months regrowth after the last cutting treatment in mid March 2003. Harvesting commenced in mid April 2003.

a) Experimental layout

N 1 = fertilized   W 1 = irrigated
N 0 = not fertilized W 0 = not irrigated

b) Mixture plots within sub-plots

5 meters

c) Species arrangement in mixture plots

50 mm

Target individuals
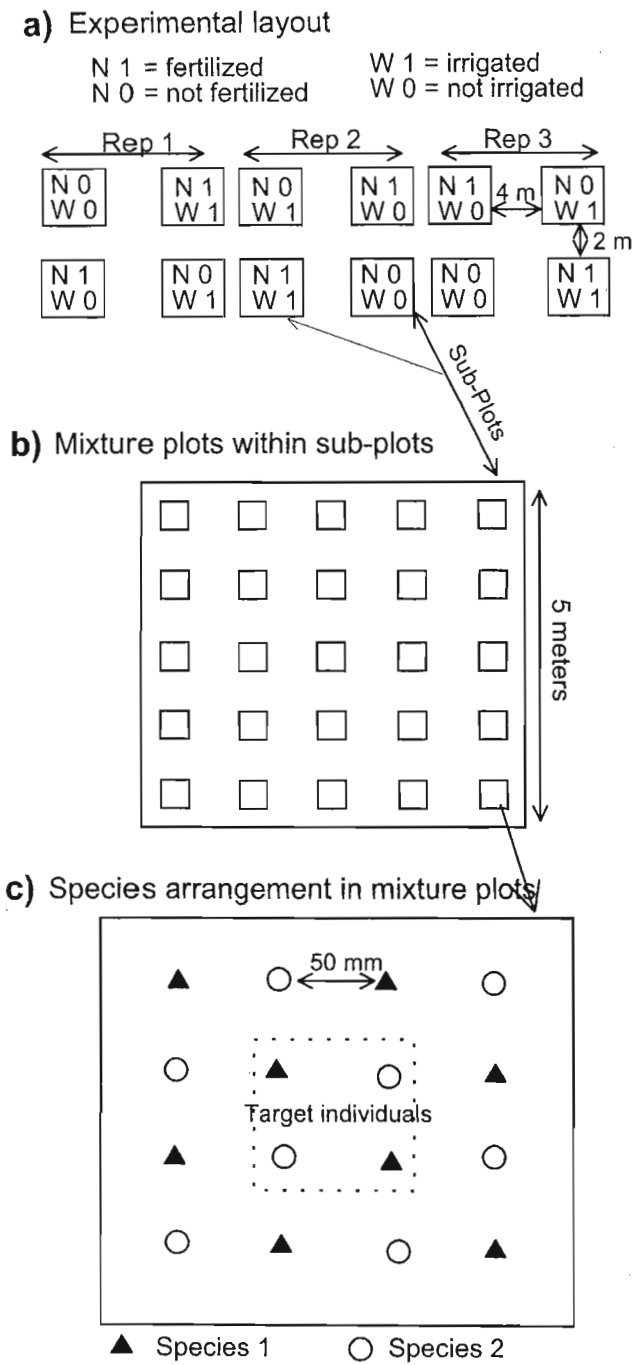
▲ Species 1   ○ Species 2

Fig. 7.1. Experimental design and layout of the competition experiment at various scales.

Productivity of sub-plots

Owing to large differences in inherent soil fertility over the experiment, productivity of the various sub-plots varied greatly, which had large influences on the outcome of competition in the various mixtures. To quantify the productivity (habitat productivity or inherent productivity potential) of each sub-plot, the mass attained by all target individuals in the various species mixtures and monoculture plots (uncut and cut treatments) in each sub-plot was summed (25 plots per sub-plot) to give an index of the inherent potential for plant production for that sub-plot (i.e. sub-plots with shallow-infertile soils that are not fertilized or irrigated will produce less plant biomass than sub-plots with the same soils but are fertilized and irrigated, whereas sub-plots with the deepest and most fertile soils in the experiment will produce the greatest amount of plant biomass). It was not possible to express this mass on an area basis because the target plants were sampled from particular positions in the competition mixture rather than on an area basis.

Effect of species on photosynthetic available radiation

The ability of a species to reduce PAR at various levels may provide insight into its competitive effect on other species. Thus, photosynthetic available radiation (PAR) was measured in each monoculture plot (cut and uncut treatments) using a Decagon PAR ceptometer (Decagon, Pullman, Washington, USA). Readings were taken above the canopy, at 600 mm above the soil surface and at 50 mm above the soil surface. The percentage of PAR above the canopy penetrating to the 600 mm and 50 mm level above the soil surface was calculated for each monoculture plot.

Statistical analyses

Analysis of variance was used to examine the effect of irrigation and fertilization on biomass production in each sub-plot using GENSTAT (GENSTAT 1993). Owing to the strong productivity gradient across the experiment, it was considered more useful to

analyze the species effect and response data using a multiple regression approach, which is better suited to analysis of trends along environmental gradients. Variation in productivity as a result of soil variation rather than treatment variation would have made it difficult to obtain useful results using Anova. Thus, multiple linear regression analysis was used to determine whether a species responded differently in competition with other species along productivity gradients. A different Y intercept or slope of the line of biomass produced by a species along a productivity gradient, when in competition with one species in comparison with competition with other species, would suggest that species differed in their competitive ability along a productivity gradient.

For an analysis of general competitive ability over the entire productivity gradient, paired *t* tests were used to test whether a species performed better when grown in monoculture than when grown in competition against another species. To test if a species biomass in mixture plots was different to its biomass in monoculture, pairs consisted of the biomass of the species in monoculture versus its biomass in competition against a specific species in a particular sub-plot. To test if one species reduced the biomass of *Themeda triandra* more than another was able to, pairs consisted of the biomass of *Themeda triandra* against species A versus the biomass of *Themeda triandra* against species B in a sub-plot. Thus, for each analysis there were 12 paired samples (12 sub-plots).

To determine if other grass species were less tolerant of cutting than *Themeda triandra*, the ratio of their monoculture biomass to monoculture biomass of *Themeda triandra* in uncut treatments, was compared with the same ratio in cut treatments using paired *t* tests. Thus, if the ratio for a species was lower in cut than uncut treatments, then it was less tolerant of cutting than *Themeda triandra*.

Results

Effect of treatments on productivity

An unforeseen consequence of soil disturbance through ploughing and planting during preparation of the experiment was higher than expected rates of mineralization of nutrients. Consequently, irrigation was the only factor that influenced overall productivity in sub-plots (Table 7.2).

Table 7.2. Analysis of variance of the effect of irrigation and fertilization on the productivity of sites in the competition experiment

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
Rep stratum	2	1017455	508728	58.42	
Rep x irrigation stratum					
Irrigation	1	1782783	1782783	204.74	0.005
Residual	2	17415	8708	0.1	
Rep x irrigation x fertilization stratum					
Fertilization	1	83710	83710	0.94	0.387
Irrigation x fertilization	1	39494	39494	0.44	0.542
Residual	4	355830	88958		
Total	11	3296688			

Effect of species on photosynthetic available radiation (PAR)

Only *Panicum maximum* and *Hyparrhenia hirta* were able to reduce PAR to any degree at 600 mm above the soil surface (Fig. 7.2a). The leaves of the shorter species did not reach this height above the soil surface. *Hyparrhenia hirta* appeared to be able to reduce PAR to a greater degree than *Panicum maximum* at very low levels of productivity, whereas *Panicum maximum* appeared most effective at reducing PAR at higher levels of productivity (Fig. 7.2a). This is indicative of the greater ability of *Hyparrhenia hirta* to grow and produce biomass at lower levels of habitat fertility/productivity than *Panicum maximum*. *Aristida junciformis* was least able to reduce PAR at the soil surface (Fig. 7.2b). Surprisingly, *Themeda triandra* reduced PAR at the soil surface to a greater degree than the tall species, especially at lower levels of productivity (Fig. 7.2b). Thus, the ability to reduce PAR at levels above the leaf height of shorter species is probably a better indication of a species competitive ability in productive environments.

Both *Eragrostis curvula* and *Aristida junciformis* were much less effective at reducing light availability at the soil surface than the other species in the cut treatments (Fig. 7.2c). *Panicum maximum, Hyparrhenia hirta* and *Themeda triandra* were all able to reduce PAR at the soil surface in cut treatments to a similar degree (Fig. 7.2c).

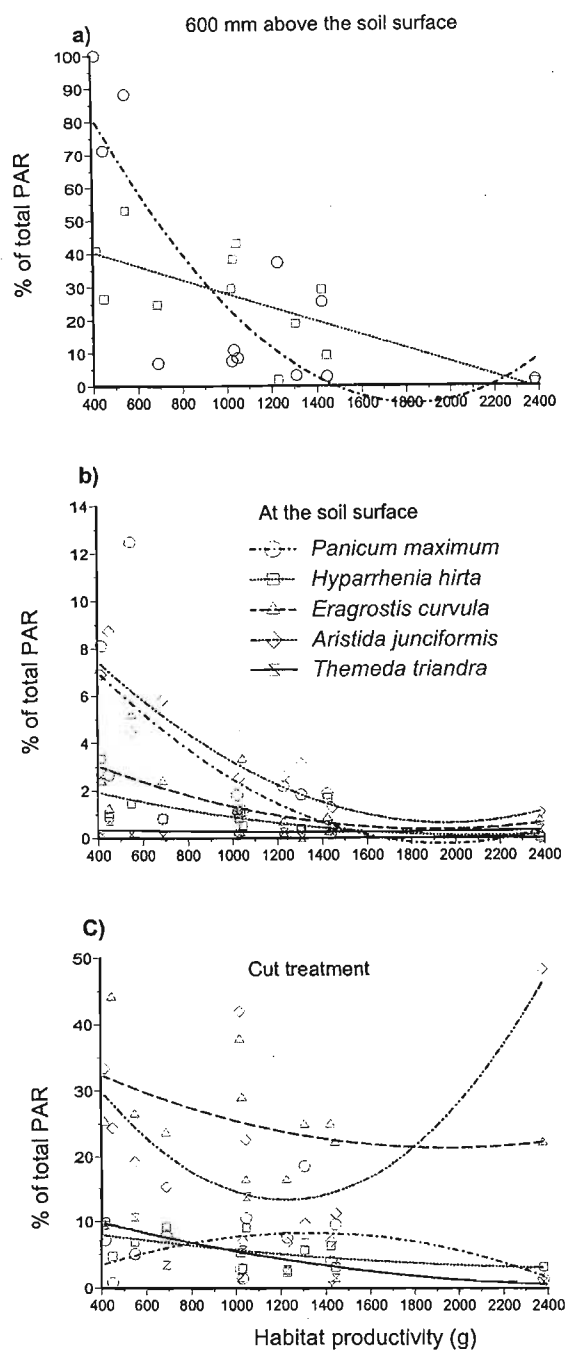**Fig. 7.2.** Effect of species and productivity on attenuation of photosynthetic available radiation (PAR) in monoculture plots in the competition experiment.

General competitive ability

The tall broad-leaved species, *Panicum maximum*, had the greatest competitive effect and response in the absence of disturbance. No species were able to reduce the biomass of *Panicum maximum* in competition below that of its monoculture biomass (Fig. 7.3a). *Panicum maximum* reduced the biomass of the tall narrow-leaved species, *Hyparrhenia hirta*, well below that of its monoculture biomass (Fig. 7.3a). In addition, *Panicum maximum* reduced the biomass of *Themeda triandra* by 58% of its monoculture biomass, whereas *Hyparrhenia hirta* was only able to reduce the biomass of *Themeda triandra* by 34% of its monoculture biomass (Fig. 7.3a). *Eragrostis curvula* and *Aristida junciformis* had no effect on *Themeda triandra* (Fig. 7.3a). Thus, the hierarchy in order of most to least competitive, in terms of their effect on *Themeda triandra*, was: *Panicum maximum* > *Hyparrhenia hirta* > *Aristida junciformis* = *Themeda triandra* = *Eragrostis curvula* (Fig. 7.3a). The shortest species, *Themeda triandra*, was unable to reduce the biomass of the other species relative to their monoculture biomass (Fig. 7.3a). *Hyparrhenia hirta* tended to grow better against *Themeda triandra* than against itself (Fig. 7.3 a). *Eragrostis curvula*, a species of intermediate height, had very little competitive effect on any other species.

Panicum maximum did not appear to be less tolerant of cutting than *Themeda triandra*. The ratio of the monoculture biomass of *Panicum maximum* to that of *Themeda triandra*, was not significantly different between uncut and cut treatments. However, the ratio of the monoculture biomass of *Hyparrhenia hirta* to that of *Themeda triandra* was significantly lower in cut compared with uncut treatments indicating that *Hyparrhenia hirta* was relatively less tolerant of cutting than *Themeda triandra*. Nonetheless, both tall species produced more biomass than *Themeda triandra* under cutting.
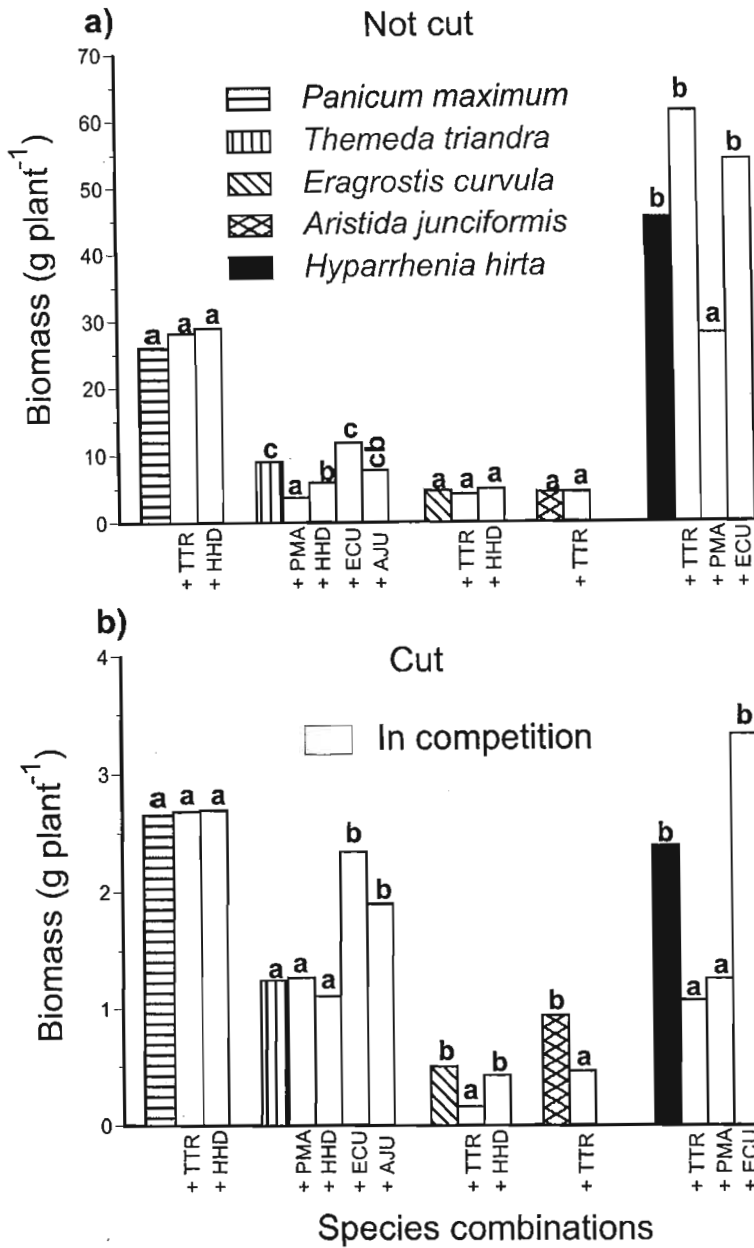
Fig. 7.3. Average competitive effect and response of species in the competition experiment. AJU, *Aristida junciformis*; ECU, *Eragrostis curvula*; HHD, *Hyparrhenia hirta*; PMA, *Panicum maximum*; TTR, *Themeda triandra*. Monocultures, patterned bars; mixtures, clear bars. + PMA (for example) is the biomass a species attained when in competition against PMA. Means associated with the same letter within each group on the graph are not significantly different; $P < 0.05$.

Disturbance in the form of regular cutting tended to change competitive relationships. Where the two taller species (*Panicum maximum* and *Hyparrhenia hirta*) had competitively suppressed *Themeda triandra* relative to its monoculture biomass with no cutting, they were unable to do so under cutting (Fig. 7.3b). *Themeda triandra* became extremely competitive under cutting reducing the biomass of *Eragrostis curvula* by 68 %, *Aristida junciformis* by 51 % and *Hyparrhenia hirta* by 53 %, relative to their respective monoculture biomass under cutting (Fig. 7.3b). Of great significance, *Themeda triandra* had a major competitive effect on *Eragrostis curvula*, but the tall narrow-leaved species *Hyparrhenia hirta,* had very little competitive effect on *Eragrostis curvula* (Fig. 7.3b). Surprisingly, *Themeda triandra* had no competitive effect on *Panicum maximum*, which remained extremely competitive under cutting, reducing the biomass of *Hyparrhenia hirta* by 48 % relative to its monoculture biomass (Fig. 7.3b).

Competitive effect of each species on Themeda triandra at various levels of productivity

Themeda triandra in competition with itself (monoculture) had a significantly different Y intercept in its response to productivity when compared against its Y intercept in its response to productivity in competition with other species (Table 7.3; Fig. 7.4a) (*Panicum maximum* = constant). Thus, at low levels of productivity it grew better against itself than other species. However, *Themeda triandra* tended to increase in biomass more rapidly with increasing productivity when growing against *Eragrostis curvula* ($P < 0.001$) and to some extent *Aristida junciformis* ($P = 0.13$) than when in competition with the other species (Table 7.3; Fig. 7.4a). Both the tall species had the greatest competitive effect on *Themeda triandra* at higher levels of productivity.

Cutting did not change the response of *Themeda triandra* to productivity when in competition against the various species. There were no significant differences in Y intercepts amongst the various combinations under cutting (Table 7.3). In a similar vein to its response without cutting, it tended to increase its biomass with increasing productivity to a greater degree against *Eragrostis curvula* ($P = 0.002$) and to a lesser degree, *Aristida junciformis* ($P = 0.17$), than the other species (Table 7.3; Fig 4b).

Table 7.3. Multiple regression analysis of the effect of *Panicum maximum, Hyparrhenia hirta, Eragrostis curvula* and *Aristida junciformis* on the biomass of *Themeda triandra* at various levels of productivity in a competition experiment

Uncut	estimate	t value	t prob.
Constant	1.57	0.62	0.537
Productivity	0.00202	0.96	0.34
Hyparrhenia hirta	3.02	0.85	0.402
Eragrostis curvula	-3.72	-1.04	0.302
Aristida junciformis	-1.46	-0.39	0.701
Themeda triandra	4.36	1.22	0.228
Productivity x *Hyparrhenia hirta*	-0.00077	-0.26	0.795
Productivity x *Eragrostis curvula*	0.01085	3.66	<.001
Productivity x *Aristida junciformis*	0.0047	1.53	0.133
Productivity x *Themeda triandra*	0.00087	0.29	0.77
Cut			
Constant	1.371	2.96	0.005
Productivity	-9.6E-05	-0.25	0.804
Hyparrhenia hirta	-0.102	-0.15	0.878
Eragrostis curvula	-0.904	-1.38	0.174
Aristida junciformis	-0.192	-0.29	0.771
Themeda triandra	-0.334	-0.48	0.633
Productivity x *Hyparrhenia hirta*	-5.4E-05	-0.1	0.922
Productivity x *Eragrostis curvula*	0.001827	3.35	0.002
Productivity x *Aristida junciformis*	0.00076	1.39	0.17
Productivity x *Themeda triandra*	0.000278	0.49	0.625

Competitive effect of each species on *Themeda triandra* compared against competitive effect of *Panicum maximum* on *Themeda triandra*
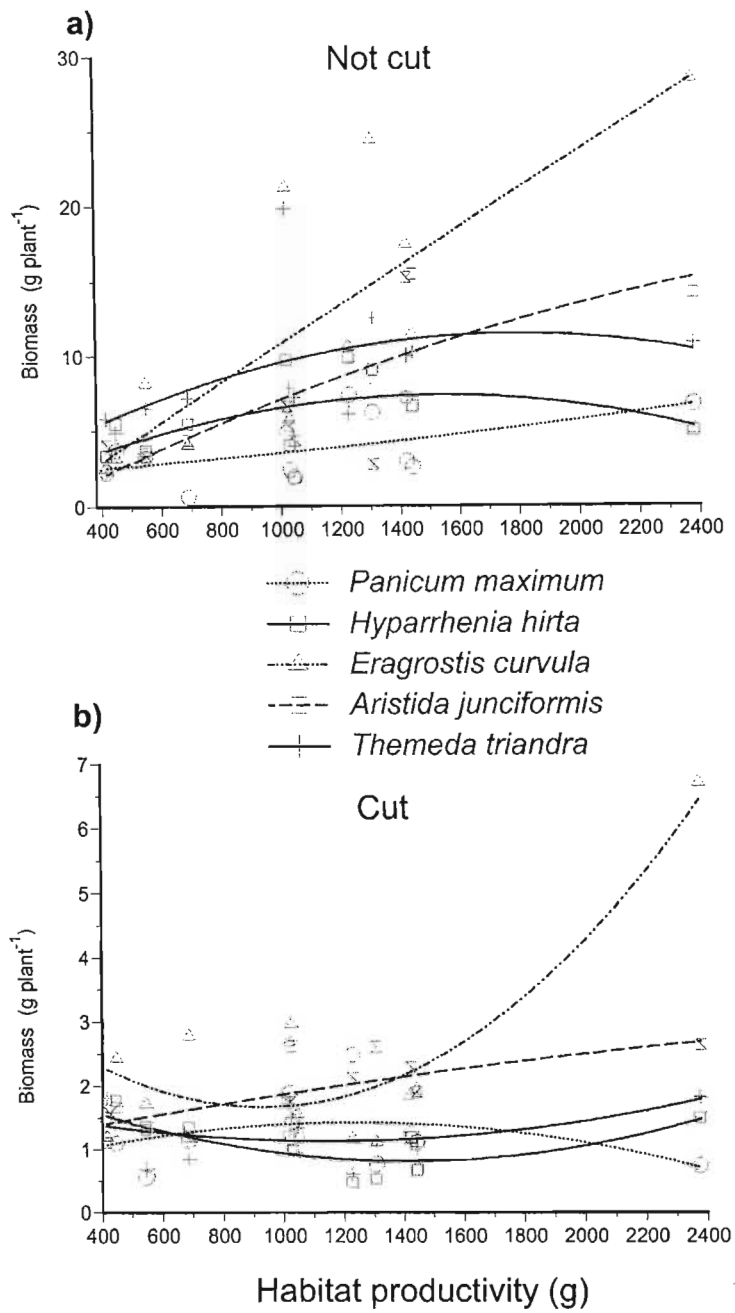
Fig. 7.4. Biomass attained by *Themeda triandra* when in competition against different species at various levels of productivity in cut and uncut treatments in the competition experiment.

Competitive response of each species at various levels of productivity

Eragrostis curvula (Fig. 7.5a), *Aristida junciformis* (Fig. 7.5b) and *Panicum maximum* (Fig. 7.5c) did not respond any differently in their ability to increase their biomass with increasing productivity, when growing in monoculture, than when competing against *Themeda triandra* (Table 7.4). *Hyparrhenia hirta*, however, grew better at higher levels of productivity when competing against *Themeda triandra* than when competing against *Panicum maximum* (Table 7.4; Fig. 7.5d).

Decreasing biomass of most species at the highest levels of productivity with cutting (Fig. 7.6) possibly reflects increasing inter and intra specific competition intensity and perhaps competition against forbs, which tended to establish to a greater degree in more productive sites, owing to higher soil moisture and nutrient levels. The broad-leaved species, *Panicum maximum*, was the only species to increase in biomass with increasing productivity, showing that it was not as susceptible to competition.

It is clear that with cutting, competition against *Themeda triandra* resulted in lower biomass of *Eragrostis curvula*, *Aristida junciformis* and *Hyparrhenia hirta* at most levels of productivity in comparison with their monoculture biomass. *Eragrostis curvula* (Fig. 7.6a) had a lower intercept growing against *Themeda triandra* (P = 0.006; Table 7.5) than when growing in monoculture. It is important to note that *Themeda triandra* was unable to competitively exclude *Eragrostis curvula* at low levels of productivity, but was able to do so at high levels of productivity (Fig. 7.6a). *Hyparrhenia hirta* had a lower intercept in competition with *Themeda triandra* than when growing in monoculture (P = 0.076). *Aristida junciformis* had a different slope of the line growing against *Themeda triandra* than when growing in monoculture (P = 0.081).

Table 7.4. Multiple linear regression analysis of the response of various species to competition with other species without cutting

	estimate	*t* value	*t* prob.
Eragrostis curvula			
Constant	2.46	1.75	0.096
Productivity	0.00162	1.38	0.182
Monoculture (*Eragrostis curvula*)	-1.22	0.61	0.548
Productivity x Monoculture	0.00064	-0.38	0.705
(comparison: competition versus *Themeda triandra*)			
Aristida junciformis			
Constant	1.95	1.62	0.121
Prod	0.002218	2.31	0.032
Monoculture (*Aristida junciformis*)	0.85	-0.53	0.603
Productivity x Monoculture	-0.00088	0.67	0.509
(comparison: competition versus *Themeda triandra*)			
Panicum maximum			
Constant	0	0	0.998
Prod	0.0268	2.01	0.053
Monoculture (*Panicum maximum*)	-34	-1.5	0.145
Themeda triandra	10.2	0.45	0.657
Productivity x Monoculture	0.0286	1.52	0.14
Productivity x *Themeda triandra*	-0.0101	-0.53	0.597
(comparison: competition versus *Hyparrhenia hirta*)			
Hyparrhenia hirta			
Constant	-3.7	-0.31	0.755
Prod	0.05995	6.16	<.001
Monoculture (*Hyparrhenia hirta*)	0.1	0.01	0.995
Themeda triandra	0.2	0.01	0.991
Productivity x Monoculture	-0.0148	-1.08	0.29
Productivity x *Themeda triandra*	-0.0309	-2.25	0.032
(comparison: competition versus *Panicum maximum*)			

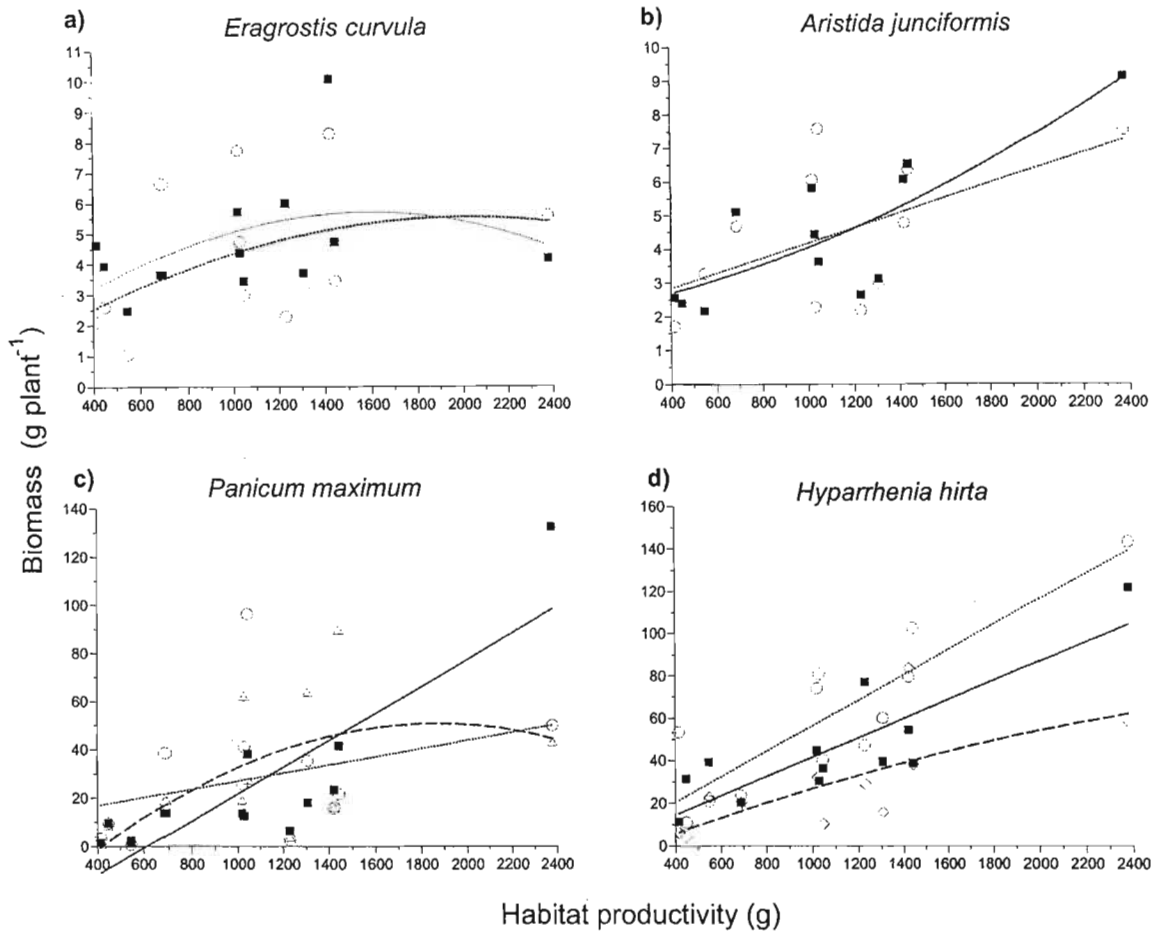**Fig. 7.5.** Competitive response of *Eragrostis curvula, Aristida junciformis, Panicum maximum* and *Hyparrhenia hirta* in competition with different species at various levels of productivity without cutting in the competition experiment. Monocultures, solid squares; competition with *Themeda triandra*, circles; competition with *Hyparrhenia hirta*, triangles; competition with *Panicum maximum*, diamonds.

Table 7.5. Multiple linear regression analysis of the response of various species to competition with *Themeda triandra* under cutting

|	estimate	*t* value	*t* prob.
Eragrostis curvula			
Constant	0.424	3.62	0.002
Prod	-0.00024	-2.47	0.022
Monoculture (*Eragrostis curvula*)	0.514	3.1	0.006
Productivity x Monoculture	-0.00017	-1.2	0.245
Aristida junciformis			
Constant	0.665	4.29	<.001
Prod	-0.00019	-1.48	0.154
Monoculture (*Aristida junciformis*)	0.116	0.53	0.601
Productivity x Monoculture	0.000335	1.84	0.081
Panicum maximum			
Constant	3.02	2.75	0.012
Prod	-0.00031	-0.34	0.736
Monoculture (*Panicum maximum*)	-1.68	-1.08	0.293
Productivity x Monoculture	0.00152	1.18	0.253
Hyparrhenia hirta			
Constant	0.664	0.92	0.368
Prod	0.000373	0.63	0.537
Monoculture (*Hyparrhenia hirta*)	1.9	1.88	0.076
Productivity x Monoculture	-0.00055	-0.65	0.523

All comparisons: competition versus *Themeda triandra*
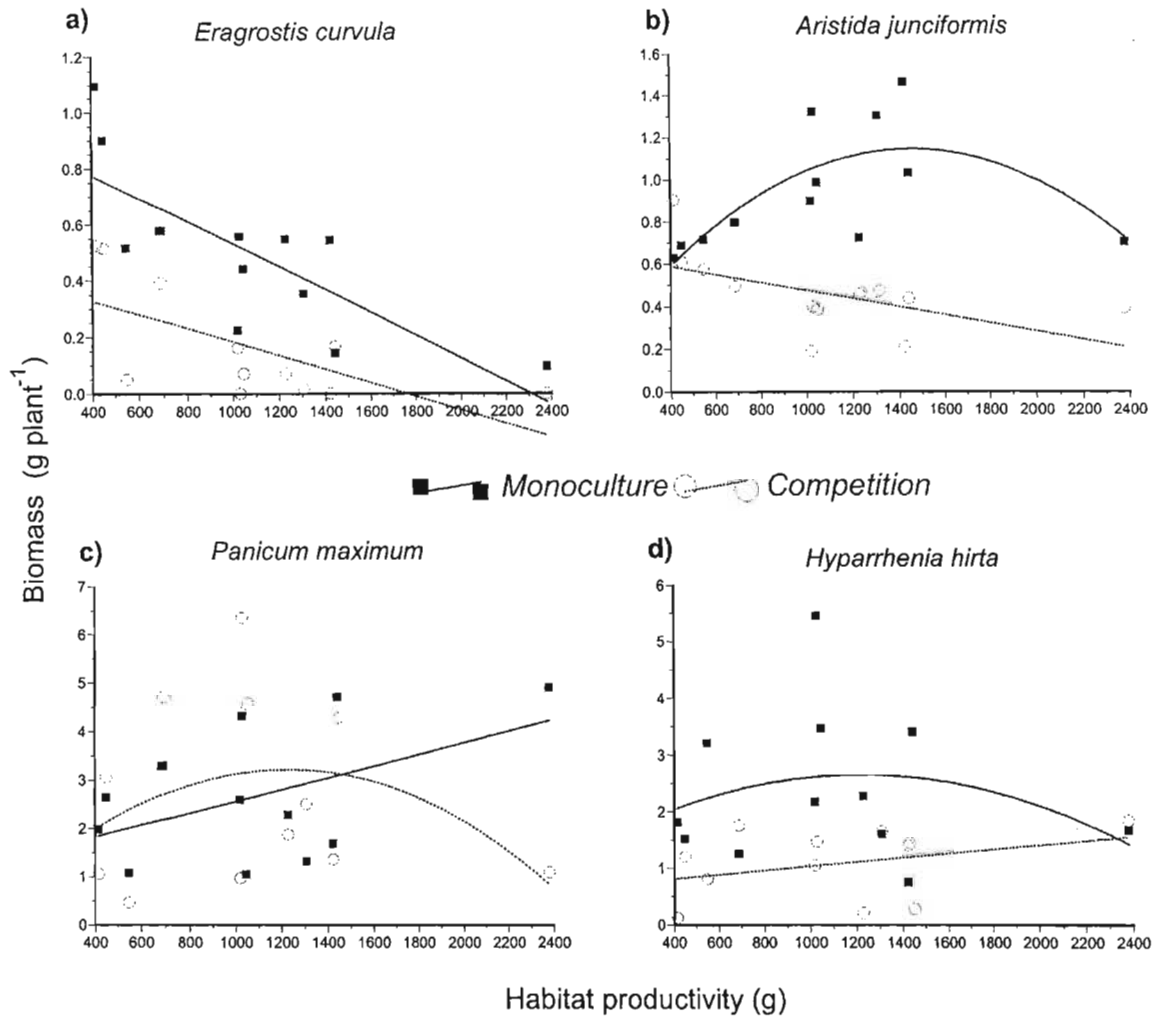
Fig. 7.6. Competitive response of *Eragrostis curvula, Aristida junciformis, Panicum maximum* and *Hyparrhenia hirta* in competition with *Themeda triandra* at various levels of productivity with cutting in the competition experiment. Monocultures, solid squares; competition with *Themeda triandra*, circles.

Effect of selective cutting on competitive ability

Both *Eragrostis curvula* and *Hyparrhenia hirta* resulted in rapidly decreasing regrowth of *Themeda triandra* with increasing productivity after selective cutting (Fig. 7.7). The taller species, *Hyparrhenia hirta*, resulted in mortality of *Themeda triandra* in all sites after a productivity level of 1200 g per plot, whereas *Eragrostis curvula* did not cause mortality of *Themeda triandra* in all sites at this level of productivity (Fig. 7.7). *Aristida junciformis* had much less of an effect on the regrowth of *Themeda triandra* with increasing productivity on the (Fig. 7.7). *Themeda triandra* did not suffer mortality at any level of productivity when selectively cut in the presence of *Aristida junciformis*, whereas it was unable to regrow at higher levels of productivity when selectively cut in the presence of the other species. This clearly demonstrates that *Aristida junciformis* has the weakest competitive effect of all the species.
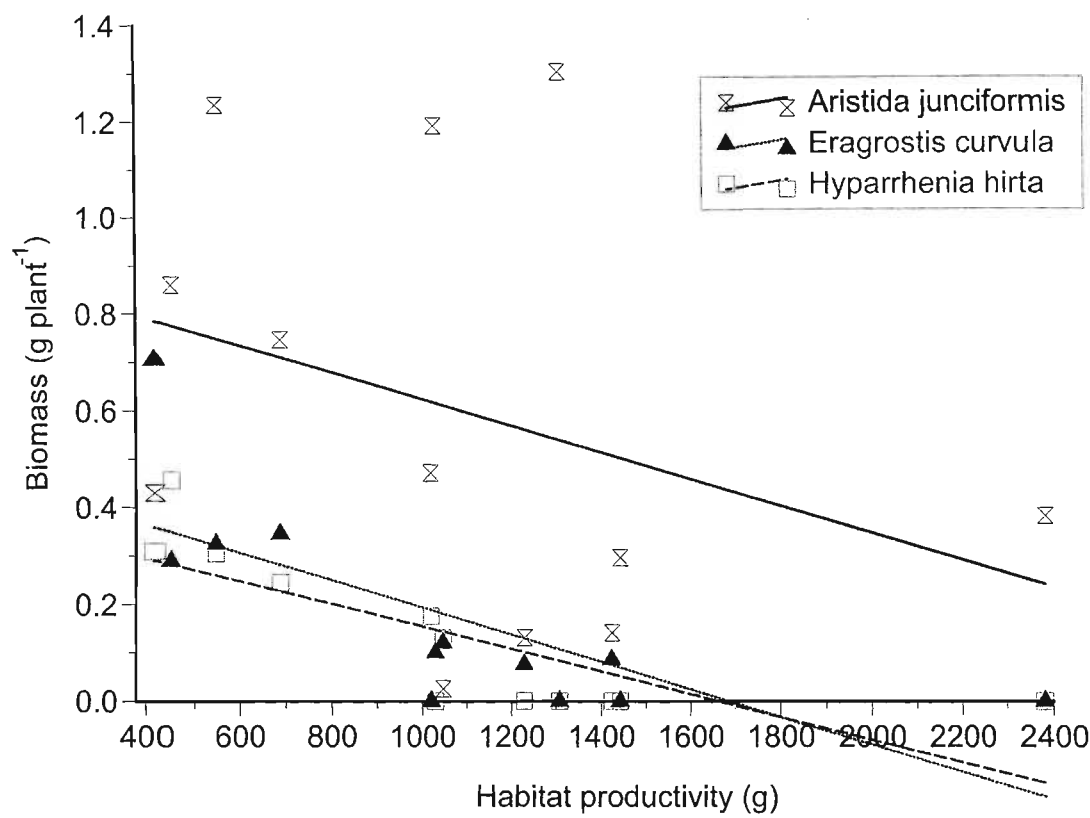
Fig. 7.7. Regrowth of *Themeda triandra* after selective cutting when in competition with certain species at various levels of productivity in the competition experiment.

Discussion

It is important to note that this is an ongoing experiment and that these results represent only the first seasons growth and competition effects. Numerous seasons may be needed for competitive equilibrium to be reached. Therefore, it would be prudent to recognize that the trends in competitive ability observed in the first season may not reflect the long-term outcome of competition. It should also be noted that the experiment lacked truly infertile soils, especially in the first season after soil disturbance, which tends to increase rates of mineralization of nutrients. Thus, competitive ability in infertile environments cannot be fully examined (at least not in the first season). Nevertheless, a wide range of levels of productivity were achieved (Fig. 7.4) which should provide some insight into the effect of productivity on competitive ability.

Traits conferring competitive ability in undisturbed habitats

Averaged across all environments two traits were associated with competitive ability in uncut sites. Tall species clearly had a competitive advantage over short species. For example, both *Panicum maximum* and *Hyparrhenia hirta* reduced the biomass of the shorter *Themeda triandra* relative to its monoculture biomass more than shorter species were able to (Fig. 7.3a). In contrast, *Hyparrhenia hirta* grew better against the shorter *Themeda triandra* than it did against itself. Both tall species appeared to have the greatest competitive effects at the highest levels of productivity (Fig. 7.4a). A tall growth form has been recognized as being an important competitive trait in productive environments (Goldberg 1987; Gaudet & Keddy 1988; Gaudet & Keddy 1995; Freckleton & Watkinson 2001; Keddy et al. 2002). It appears that the greater competitiveness of a tall species than a short species lies in its ability to reduce PAR at higher levels above the soil surface than a short-grass species can (Fig. 7.2a). This allows taller species to shade out the shorter species, which are unable to extend their leaves above the height of shading (Table 7.1; Fig. 7.2a). However, tall species may also be exteremly competitive below ground (Grime 1979), which may also account for their competitive effects in this

experiment). A broad-leaved growth form was another trait conferring competitive ability to a species. For example, *Panicum maximum*, which has broader leaves than *Hyparrhenia hirta* had a greater competitive effect on *Themeda triandra* than did *Hyparrhenia hirta* (Fig. 7.3a). Moreover, *Panicum maximum* greatly reduced the biomass of *Hyparrhenia hirta* relative to its monoculture biomass, whereas *Hyparrhenia hirta* had no effect on the biomass of *Panicum maximum* relative to its monoculture biomass. Leaf width has also been shown to have a good correlation with competitive ability in productive habitats (Keddy et al. 2002). A broad-leaved growth form probably results in more effective shading of competitors than a narrow-leaved growth form. For example, at higher levels of productivity, *Panicum maximum* resulted in greater PAR reduction at 600 mm above the soil surface than did *Hyparrhenia hirta* (Fig. 7.2a). The fact that *Eragrostis curvula* and *Aristida junciformis* were least able to reduce PAR (Fig. 7.2) indicates possible reasons why these species were the weakest competitors in the uncut treatments (Fig. 7.3a & 7.4a). *Aristida junciformis* has very narrow upright leaves that are probably least able to shade competitors. The weak competitive effect of *Eragrostis curvula* in this experiment was surprising because it generally dominates grasslands that are fertilized with nitrogen. It appears that the commercially available cultivar used in this experiment is very different from the wild type, which is taller and with tougher more erect leaves than the commercial cultivar.

Where the tall broad-leaved species had the greatest competitive effect on other species (Fig. 7.4 & 7.5), it also had the greatest competitive response. No species was able to reduce its biomass relative to its monoculture biomass, without (Fig. 7.4 & 7.5) and with cutting (Fig. 7.6). Thus, a tall broad-leaved trait, which facilitates both shade avoidance and shade tolerance prevented other species from having a negative effect on it. Models have shown that height or shade tolerance are correlated with competitive ability and that possession of both these traits results in competitive dominance in the long-term (Huston & Smith 1987; Tilman 1988).

Hyparrhenia hirta had greater biomass in monoculture at the lowest levels of productivity than *Panicum maximum* (Fig. 7.5c,d) and reduced PAR to a much greater degree than *Panicum maximum* at low levels of productivity (Fig. 7.2a). Thus, a narrow-leaved trait may be an advantage to a species in lower productivity habitats. In extremely

moisture and nutrient-limited habitats on very shallow rocky soils, species tend to have very narrow leaves (e.g. *Sporobolus stapfianus* and *Microchloa caffra* in South African grasslands). This may be an adaptation to preventing moisture loss and allowing a long leaf lifespan for conservation of nutrients (Wright *et. al.* 2002), which translates into greater competitive ability in nutrient limited habitats (Berendse & Elberse 1990; Tilman 1990). Tall broad-leafed species such as *Panicum maximum* and *Setaria megaphylla* are generally limited to moist fertile soils on stream banks, under trees or regions of extremely high rainfall in combination with fertile soils. They have demonstrated an inability to colonize drier less fertile soils (intermediate fertility), whereas tall narrow-leafed species such as *Cymbopogon validus* and *Hyparrhenia hirta* regularly colonize these habitats when disturbance is infrequent (Personal observations). Fertilization of these soils of intermediate fertility with nitrogen and phosphorus has allowed *Panicum maximum* to colonize these sites (le Roux & Mentis 1986).

Traits conferring competitive ability in disturbed habitats

Under regular cutting a short-growth form conferred a competitive advantage on species. For example, the shortest species, *Themeda triandra*, reduced the biomass of *Eragrostis curvula*, *Aristida junciformis* and *Hyparrhenia dregiania* by 68, 51 and 53 % respectively relative to their monoculture biomass under cutting (Fig. 7.3b). The competitive effect of *Themeda triandra* on these species was evident over a wide range of levels of productivity (Fig. 7.6). The strong competitive ability of *Themeda triandra* under cutting is further emphasized by the fact that it reduced the biomass of *Eragrostis curvula* by 68% of its monoculture biomass, whereas the tall *Hyparrhenia dregiania* was unable to have a significant impact on the biomass of *Eragrostis curvula* (Fig. 7.3b). Moreover, regular cutting resulted in the tall species losing their competitive advantage that they had clearly held over *Themeda triandra* without cutting (Fig. 7.3b). Although in monoculture, *Hyparrhenia hirta* produced relatively less than *Themeda triandra* in cut compared with uncut treatments, it still produced nearly double the biomass of *Themeda triandra* under cutting (Fig. 7.3b). However, when in competition with *Themeda triandra* under a cutting regime it did not produce more biomass than *Themeda triandra* (Fig.

7.3b). *Themeda triandra* tends to be replaced by taller species in the absence of burning or mowing in KwaZulu-Natal grasslands (Everson & Tainton 1984). Thus, it appears that the mechanism by which *Themeda triandra* is able to dominate regularly disturbed systems is not through being more tolerant of disturbance but rather through becoming more competitive under mowing or burning.

Under cutting, *Themeda triandra* grew much better against *Eragrostis curvula* and *Aristida junciformis* than it did against *Hyparrhenia dregiania* and *Panicum maximum* (Fig. 7.3b). Likewise, *Hyparrhenia dregiania* grew much better against *Eragrostis curvula* than against itself (Fig. 7.3b). This appears to be related to the fact that *Eragrostis curvula* and *Aristida junciformis* caused much less PAR reduction at the soil surface than the other species (Fig. 7.2c). Thus, the ability to reduce PAR appears to be an important competitive trait even under a cutting regime. This is because these species use light as a cue for tiller initiation with shading strongly reducing tiller initiation (Everson et al. 1988). However, root competition also appears to play an important role. For example, *Hyparrhenia hirta* and *Themeda triandra* were equally capable of reducing PAR under a cutting regime, yet *Themeda triandra* had a much stronger competitive effect on *Hyparrhenia hirta* than *Hyparrhenia hirta* had on itself (Fig. 7.3b). Moreover, *Themeda triandra* strongly reduced the biomass of *Eragrostis curvula* under cutting but *Hyparrhenia hirta* had very little effect on *Eragrostis curvula* (Fig. 7.3b). This suggests that *Themeda triandra* may have very strong below-ground effects on other species under a cutting regime.

Importantly, lower Y intercept values for competition best fit lines compared with monoculture best-fit lines in the response of *Eragrostis curvula* and *Hyparrhenia hirta* to increasing productivity indicate that *Themeda triandra* had a relatively greater competitive effect on these species at low levels of productivity (Fig. 7.5 & 7.6). Species that allocate more biomass to roots and have wider shoot/root ratios have been observed to be better competitors in infertile environments than species allocating more biomass to shoots (Gleeson & Tilman 1990) as predicted in ecological theory (Tilman 1988). Similar Y intercepts of competition and monoculture best-fit line for *Aristida junciformis* and *Panicum maximum* indicate that *Themeda triandra* did not have a greater competitive effect against these species in low productivity habitats (Fig. 7.5 & 7.6). *Themeda*

triandra would not be expected to have much competitive effect on *Aristida junciformis* in low productivity sites because *Aristida junciformis* is adapted to infertile habitats, whereas *Eragrostis curvula* and *Hyparrhenia hirta* are adapted to more fertile habitats. Surprisingly, *Themeda triandra* did not have much competitive effect on *Panicum maximum* in low productivity habitats. Being a tall productive species, *Panicum maximum* is not expected to do well in competition in unproductive habitats against a short species that allocates a large amount to roots, such as *Themeda triandra* (Tilman 1988). This species appeared to have a high general competitive ability, yet is rarely found in soil resource limited habitats in nature. More time will be needed before any conclusions can be drawn over the competitive ability of this species in low productivity habitats.

Selective cutting

The effect of selective cutting on *Themeda triandra* at various levels of productivity provided insight into the mechanisms of competition and the competitive ability of different species at different levels of productivity. Declining regrowth of *Themeda triandra* with increasing productivity (Fig. 7.7) reflects reduced ability to regrow with decreasing light intensity as productivity increases (Fig. 7.2a,b). It is clear that *Aristida junciformis* had a much weaker competitive effect than the other species (Fig. 7.7). *Aristida junciformis* was least able to reduce PAR with increasing productivity (Fig. 7.2b), which is why it had less of an effect on the regrowth of *Themeda triandra* with increasing productivity. Tiller inititiation in *Themeda triandra* is negatively affected by shading (Everson et al. 1988). Both *Hyparrhenia hirta* and *Eragrostis curvula* were more effective in reducing PAR at the soil surface (Fig. 7.2b), hence their stronger effects on regrowth. Mortality of *Themeda triandra* in all sites at a specific level of productivity occurred first in competition with the taller *Hyparrhenia hirta* (Fig. 7.7).

Conclusions

Species differ in their ability to reduce PAR penetration in the canopy. Only tall-grass species had the ability to reduce PAR at 600 mm above the soil surface. Moreover, a tall broad-leaved species caused the greatest reduction in PAR at this height, which was clearly correlated with its superior competitive ability (competitive effect) in uncut treatments. *Aristida junciformis* and *Eragrostis curvula* were less effective at reducing PAR, which was correlated with their weak competitive effects on other species. Broad-leaves probably also conveyed greater shade-tolerance upon *Panicum maximum*, explaining why it was not negatively affected in competition with other species. In other words, broad-leaves appeared to facilitate a strong competitive effect and response by *Panicum maximum*. A broad-leaved trait appeared to result in greatest competive ability at high levels of productivity. However at low levels of productivity, a narrow-leaved trait resulted in better growth of *Hyparrhenia hirta* than *Panicum maximum* (Fig. 7.5c,d) and greater PAR reduction (Fig. 7.2a) than a broad-leaved trait.

Cutting resulted in *Themeda triandra* becoming much more competitive than it was without cutting. *Themeda triandra* was able to effectively reduce PAR at the soil surface, which may partially explain its strong competitive effect with cutting on other species. Species that had much less of an effect on PAR reduction, with or without cutting, were consistently weak competitors. However, tall-grasses were as effective in reducing PAR under a cutting regime suggesting that below-ground effects were also important. Thus, *Themeda triandra* should be able to dominate regularly mown areas owing to its very strong competitive effects on other species when non-selectively defoliated by cutting. Selective grazing should result in the replacement of *Themeda triandra* by the ungrazed neighbours shading the grazed tufts of *Themeda triandra*, thereby reducing tiller initiation and the regrowth of *Themeda triandra*.

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CHAPTER 8

A THEORETICAL PREDICTIVE FRAMEWORK FOR PLANT ECOLOGY

Introduction

Predictive ability is a fundamental goal of ecology. Key to achieving this goal is an understanding of the principal variables influencing the distribution and abundance of species. Some of the variables that have been recognized as having an important influence on species distribution and abundance are habitat fertility, productivity and disturbance (Huston 1979; Grime 1979; Tilman 1988; Bazzaz 1996). However, a major obstacle to building realistic general predictive models is the complexity of ecological systems. Species may be influenced by a myriad of factors including temperature, salinity, pH, soil depth, soil moisture, nutrient availability, light availability, predation, disease, different type, timing and frequency of disturbance and various interactions amongst these factors. Herein lies the problem; complete predictive models would be expected to include all the specific factors that influence a species, resulting in such models being extremely complex and unrealistic (Tilman 1990a). Hope may lie in the observation that inclusion in a model of certain basic mechanisms of interaction among species and their environment may abstract most of the complexity associated with more detailed mechanisms (Tilman 1990a). Plant traits (e.g. Goldberg 1996; Westoby 1998; Craine et al. 2002; Lavorel & Garnier 2002; Craine & Lee 2003) have been recognized as an important potential tool for understanding and predicting the response of species to environmental factors and competitors because they may represent specific functional adaptations to various constraints. Trait tradeoffs that species may make in dealing with specific constraints may influence a species ability to compete under different conditions (Tilman 1988; Goldberg 1996; Suding et al. 2003). Thus, an understanding of the relationship between specific traits and environmental factors and knowledge of the tradeoffs that species have made for specific traits should enable greater general

predictive ability, while reducing the number of parameters needed to describe a species response to its environment (Tilman 1990a).

The objective of this final chapter is to provide a general synthesis of the patterns in species composition and species richness in the long-term burning and mowing experiment and fertilization experiment as well as on a nearby natural gradient of soil depth and productivity at the Hayfields conservency, and relate these patterns to the chapters dealing with the effect of disturbance on resources and the two plant competition experiments. Thus, is it possible to find a common thread or factor that is the underlying cause of vegetation response to widely different environmental influences such as fertilization, type, timing and frequency of disturbance, soil depth etc? In other words, is it possible to find a unifying principle that explains vegetation response to widely different environmental factors and influences?

Patterns of plant trait variation across gradients of soil depth, soil fertility and disturbance

A clear pattern that emerges from the burning and mowing experiment and the fertilization experiment, as well as on natural soil depth gradients in the region, is the relationship between plant growth form and site productivity. The shortest species tend to decline in absolute or relative abundance with increasing annual dry matter production, whereas the taller species tend to increase in abundance with increasing annual dry matter production (Fig. 4.5 & 5.4). The shortest species, *Eragrostis racemosa* was particularly restricted to the least productive soils (Fig. 4.5), whereas species of short to intermediate height such as *Themeda triandra* had a broader range along productivity gradients but were generally absent from the most productive sites. In sites of highest productivity, taller species such as *Aristida junciformis, Eragrostis curvula, Cymbopogon* spp. and *Panicum maximum* dominated (Fig. 4.5 & 5.4). This was evident on a natural soil depth gradient at the Hayfields conservancy, where *Eragrostis racemosa* was only abundant on extremely shallow soils (50 mm deep), which support very low annual dry matter production (150 g m^{-2}) (Platt et al. in prep). On deeper soils (100 – 500 mm deep) with

higher productivity (300-400 g m^{-2}), *Themeda triandra* dominated, whereas on the deepest soils (> 1000 mm deep) with the highest productivity (> 700 g m^{-2}), tall broad-leaved species such as *Panicum maximum* and *Sorghum bicolor* dominated (Platt et al. in prep). It is interesting to note that the tall broad-leaved species, *Panicum maximum*, dominated the most productive sites on the deep bottomland soils at Hayfields (Platt et al. in prep) and in sites where productivity had been artificially increased by fertilization (Fig. 5.4). In the burning and mowing experiment, it was only found in sites of highest nitrogen availability (Fig. 4.3). The shortest species, *Eragrostis racemosa*, has a maximum leaf height of 100 – 150 mm, which renders it vulnerable to shading, even by short to medium height species such as *Themeda triandra*. Consequently, *Eragrostis racemosa* is only abundant in sites where productivity is so low (150 g m^{-2}) that there is no potential for shading by other species. These sites are characterized by an open canopy, whereas *Themeda triandra* dominated sites have a closed canopy where there is very little light penetration to levels below the maximum leaf height of the shortest species. Likewise in sites on very deep soils, or fertilized sites or infrequently burnt sites, productivity is so high (500-1000 g m^{-2}) that light availability at levels below the maximum leaf height of species of intermediate height is very low (Chapter 5), resulting in domination by species that are tall enough to elevate their leaves above the region of intense shade. Thus, for a species to dominate productive habitats it must have a strong competitive effect (ability to suppress neighbours) and competitive response (ability to avoid being suppressed by neighbours).

At this point it would be prudent to note that these plant growth form/productivity relationships have a mechanistic origin and are not purely a logical sequitur of the shorter species being less productive (i.e. there is no tautological reasoning involved). For example, in the fertilization experiment, the plant growth form/productivity relationships (Fig. 5.4) developed as a result of modification of productivity through fertilization in an originally short-grass species dominated grassland. The first year of the experiment (1951) resulted in large increases in productivity in fertilized sites (Fig. 5.1a) despite the composition being identical. Increased productivity in the fertilized sites resulted in compositional change within a couple of years because short species were unable to compete with tall species in productive fertilized sites. Likewise sites at the Hayfields

conservancy, which are dominated by the shortest species, have the lowest productivity because the soils are extremely shallow and moisture limited (Platt et al. in prep). Obviously their low productivity is compounded by the fact that the shortest species have low productivity but the fact is their shallow-dry soils result in these sites being inherently less productive than sites dominated by larger species, which have deeper soils. This is the very reason why soil surveys are done for crop suitability surveys.

Furthermore, the notion that *Themeda triandra* was replaced by taller species such as *Eragrostis curvula* following nitrogen fertilization because it is intolerant of nitrogen is spurious. *Themeda triandra,* when grown in monoculture in the plot experiment (i.e. without competition), grew extremely well following heavy fertilization with nitrogen and continues to do so in the second season of the experiment. In contrast, it has been nearly eliminated in these sites when grown in competition with a taller species (Fig. 7.3 & & 7.4). Thus, this is clearly an effect of competition and not a consequence of intolerance of nitrogen. This is supported by the study of Grossman & Cresswell (1974), which shows that when grown in nutrient solution with an NH_4^+ concentration of 200 ppm, *Themeda triandra* produced more than double the biomass compared with its growth when the NH_4^+ concentration was 10 ppm. An NH_4^+ concentration of 400 ppm was toxic to it but this is beyond any realistic concentration that can be expected in the field. If nitrogen fertilization had been toxic to *Themeda triandra* it would have died in the first season of the fertilization experiment (Chapter 5) and the pot and plot experiments (chapters 6 & 7), but in reality grew much better under nitrogen fertilization than in unfertilized sites (Booysen 1954). The point is that *Themeda triandra* responds very well to realistic levels of nitrogen fertilization as demonstrated in this study (Fig. 6.1) and that of Grossman & Cresswell (1974), but there are other species (e.g. *Eragrostis curvula, Hyparrhenia hirta* and *Panicum maximum*) that are much more competitive than *Themeda triandra* under nitrogen fertilization (Fig. 6.1 & Fig. 7.3), resulting in it being competitively eliminated. The experiments in chapters 6 & 7 have clearly disproved the notion that *Themeda triandra* disappears from grassland fertilized with nitrogen because nitrogen is toxic to it. When grown without competition *Themeda triandra* produced very high biomass under nitrogen fertilization, but has been strongly reduced in abundance when grown in competition with more competitive species (Fig. 6.1 & Fig. 7.3).

This discussion is now well placed to allow informed comment on some misconceptions of the successional status of various grassland seres and South African grass species. Numerous studies refer to the replacement of *Themeda triandra* dominated grassland by *Eragrostis curvula* following increased soil fertility as successional retrogression (Roux 1954; Altona 1972; Grossman & Cresswell 1974). This is spurious and originates from an incomplete understanding of ecological theory. Successional advance involves an increase in total soil nitrogen (Crocker & Major 1955; Crocker & Dickson 1957; Olson 1958; Rice et al. 1960; Inouye et al. 1987; Tilman 1988; Olff 1993), and a change in plant strategies from small early-successional species that are better competitors for limiting soil resources or, at least, better able to tolerate limiting soil resources, to large late-successional species that have higher growth rates and are better competitors for light and space (Clements 1916; Rice et al. 1960; Grime 1979, Huston 1979, Inouye et al. 1987; Tilman 1988; Olff 1993; Gaudet & Keddy 1995). The mechanism of successional replacement, therefore, is a switch from competition for limiting soil resources to competition for light (Tilman 1988). This favours larger, more robust, faster growing species that are able to preempt space and light as nitrogen availability and productivity increase with organic matter accumulation over time. Consequently, losses of soil nitrogen very late in succession result in replacement of large late-successional species by smaller earlier-successional species (Crocker & Major 1955; Crocker & Dickson 1957; Wardle & Ghani 1995). *Eragrostis curvula* and other species such as *Panicum maximum,* are taller more robust and faster growing than *Themeda triandra* and are more competitive than *Themeda triandra* under high levels of nitrogen availability (Fig. 6.1 and Fig. 7.3). They have, therefore, the attributes of later-successional species than *Themeda triandra* and their replacement of *Themeda triandra* following nitrogen fertilization (chapter 5) represents successonal advance. If nitrogen fertilization was stopped and soil fertility declined over time and *Themeda triandra* was eventually able to replace these species, successional retrogression would have occurred. Therefore, *Themeda triandra* is a mid-successional species and *Eragrostis curvula* and especially *Panicum maximum* are late-successional species.

Effect of litter accumulation on composition

Another very interesting and insightful trend was the similar response of *Tristachya leucothrix* to the frequency of disturbance (Fig. 4.3 & 4.4) and nitrogen fertilization (Fig. 5.3). It generally peaked at some intermediate level of either disturbance or nitrogen fertilization. Other short species generally declined with increasing levels of nitrogen fertilization or decreasing disturbance frequency. This response again appears to be related to light availability, which generally declines, whereas litter levels and plant production increase with decreasing frequency of disturbance or increasing level of nitrogen fertilization. *Tristachya leucothrix* initiates tillers below-ground and, therefore, is not as dependent upon light as a cue for tiller initiation, whereas other short species initiate tillers above-ground and are reliant on light for tiller initiation (Everson et al. 1988). This is further evidence to show that a major factor determining composition along fertilization and disturbance gradients is light availability. However, the inability of the shoots of many species to penetrate litter may also account for this respose (e.g. Sydes & Grime 1981). Both *Tristachya leucothrix* and *Aristida junciformis* tiller below-ground and have short rigid erect shoots that are probably better able to penetrate a litter layer than many of the other species. A tall growth form will be of no advantage to a species in sites where litter levels are high if its shoots are unable to penetrate a litter layer. This may explain why the tallest species did not dominate the protected sites in the burning and mowing experiment despite these sites having the highest nitrogen levels.

Nitrogen availability and productivity as unifying factors in plant ecology

It is not surprising that various species showed similar responses to the level of nitrogen fertilization and disturbance because they both influence nitrogen availability. Nitrogen fertilization, through its influence on nitrogen availability, increases productivity (Fig. 5.1), whereas burning reduces total soil nitrogen (Seastedt et al. 1991; Ojima et al. 1994; Fynn et al. 2003) and soil moisture (Redman 1978; Knapp & Seastedt

1986; Snyman 2002), which reduces productivity in these grasslands (Tainton et al. 1977; Tainton et al. 1978; but see Knapp et al. 1998). The different effects of frequency, timing and type of disturbance on composition could clearly be explained by their effects on soil nitrogen. For example, annual burning resulted in lower levels of soil nitrogen than triennial burning (Table 2.1), which was associated with dominance of short-grass species under annual burning and domination by tall-grass species under triennial burning (Fig. 4.4). With regards the timing of disturbance, winter burning resulted in lower levels of soil nitrogen than spring burning (Table 2.1), which was associated with a higher abundance of one of the shortest species, *Heteropogon contortus,* under winter compared with spring burning (Fig. 4.4). Further, triennial burning in autumn, resulted in much lower soil nitrogen levels than triennial burning in spring or winter (Table 2.1), which was associated with a much higher abundance of *Themeda triandra* under triennial burning in autumn than under triennial burning in spring or winter. With regards the type of disturbance, annual mowing during the dormant-period and protection from disturbance resulted in the highest levels of soil nitrogen (Table 2.1), which favoured taller species (Fig. 4.4). Thus, annual burning and annual mowing during the dormant period appeared to result in very different composition (Fig. 4.3 & 4.4) because of their very different effects on soil nitrogen. Fertilization with nitrogen would obviously increase nitrogen availability, which resulted in domination by tall-grass species (Fig. 5.3). Thus, nitrogen availability, as influenced by fertilization or disturbance, was able to account for the effects of the season of mow, season of burn and frequency of burning on composition. Thus, nitrogen availability appears to be a common thread or unifying factor that is able to explain the effect of very different factors on plant composition. For example, *Eragrostis curvula* is a tall species that increased under nitrogen fertilization in the fertilizer experiment (Fig. 5.3) and increased with decreasing frequency of disturbance in the burning and mowing experiment (Fig. 4.4). The same trends were observed for the tall broad-leaved species, *Panicum maximum* (Fig. 4.3).

Nitrogen is known globally to affect plant composition (Aerts & Berendse 1988; Wedin & Tilman 1993; Tilman et al. 1994; Leps 1999). Thus, any factor that has a different effect on nitrogen availability (e.g. different type, timing or frequency of disturbance or soil depth or nitrogen fertilization etc.), would be expected to cause

different compositional responses. Pot experiments in chapter 6 showed that short species such as *Themeda triandra* are able to grow faster at low levels of nitrogen availability than taller species, and are better competitors than the taller species at these low levels of nitrogen availability, with the reverse being true with high nitrogen availability (Fig. 6.1 & 6.2). Consequently, any factor that reduces nitrogen availability, such as regular burning in winter, is likely to favour short-grass species over tall-grass species. Factors that result in the greatest reduction in nitrogen availability should result in higher abundances of short-grass species than factors that cause less of a reduction in nitrogen availability. For example, annual dormant-period mowing was not able to reduce nitrogen availability relative to undisturbed sites and, therefore, resulted in the lowest abundance of short-grass species of all the disturbance treatments. Therefore, the potential exists to develop a predictive understanding of the relationship between plant composition and different forms and intensities of disturbance or any other factor, simply through knowledge of their effect on nitrogen availability. There will undoubtedly be other influences to take into account, such as effects on litter levels and tolerances of certain plant forms, but effects of disturbance on nitrogen availability should form the basis of any theoretical predictive framework.

Other factors influencing plant composition

Summer mowing resulted in amongst the highest abundance and dominance of *Themeda triandra* in the burning and mowing experiment (Fig. 4.4). It is not clear if this is related to effects on nitrogen availability because soil nitrogen data is not available for the summer-mown sites in the burning and mowing experiment. However, studies on productivity show that, in the long-term, sites mown in summer have lower productivity than sites not mown in summer (Tainton et al. 1978). Mowing in the dormant-period, which does not reduce soil nitrogen (Table 2.1), and favours tall-grass species (Fig. 4.4), is likely to have a different effect on soil nitrogen compared with summer mowing because grasses have withdrawn their leaf nitrogen during the dormant-period. Consequently, losses of nitrogen through dormant-period mowing should be considerably

lower than under summer mowing where leaf nitrogen is high for purposes of photosynthesis. Thus, part of the beneficial effect of summer mowing on *Themeda triandra* may be related to a reduction of soil nitrogen and a reduction of productivity (Tainton et al. 1978).

However, there also appear to be other mechanisms leading to dominance of *Themeda triandra* under summer mowing. For example, *Themeda triandra* and *Eragrostis capensis* declined with increasing productivity in sites not mown in summer but increased with increasing productivity in sites that were mown in summer (Fig. 4.5 & 4.6). This effect of mowing on these species appears to be related to something other than effects of mowing on nitrogen availability, because these short grass species are generally vulnerable to shading by taller species as productivity increases. Thus, mowing may have changed the relationship between these short species and productivity by improving light availability. It was observed in the pot experiment that the rate of tiller initiation of *Themeda triandra* increases at higher levels of nitrogen availability. It has been shown that high light availability is essential for tiller initiation in this species (Everson et al. 1988). With this evidence in mind, rates of tiller initiation would be expected to increase with increasing productivity if light availability is maintained by mowing. This may result in *Themeda triandra* and *Eragrostis capensis* becoming more competitive with increasing productivity under a mowing regime. Evidence from the plot experiment would support this because *Themeda triandra* was able to eliminate *Eragrostis curvula* at high but not low levels of productivity (Fig. 7.6). *Themeda triandra* initiated a prolific amount of tillers in these high productivity plots that enabled it to spread laterally and preempt space. Thus, it was able to interfere aggressively with *Eragrostis curvula* in the high productivity plots but not to the same degree in the low productivity plots (Fig. 7.6). Without cutting, *Themeda triandra* was unable to exert a strong competitive effect on *Eragrostis curvula* at any level of productivity (Fig. 7.5).

Tall species grew very well with cutting in monoculture in the competition experiment but produced much less biomass under cutting, relative to their monoculture biomass, when grown in competition with *Themeda triandra* (Fig. 7.3). Thus, the dominance of *Themeda triandra* in sites mown in summer in the burning and mowing experiment (Fig. 4.4) is a result of it being more competitive than the tall species under a

mowing regime and not a consequence of the tall species being intolerant of summer mowing. The plot experiment and the fertilizer experiment reveal that tall-grass species are actually extremely tolerant of cutting and may be very competitive under a mowing regime when fertilized. This should not be surprising because both short- and tall-grass species have basal meristems. The only factor that differs between them is the greater loss rate of nutrients of the tall-grass species under mowing (see Berendse & Elberse 1990), which gives short-grass species a competitive advantage in nutrient-limited sites (Berendse & Elberse 1990; Tilman 1990b). For example, tall species such as *Eragrostis curvula* were rare under a mowing regime in the burning and mowing experiment (Fig. 4.4), where nitrogen is limiting, but dominated sites fertilized with nitrogen in the fertilizer experiment (Fig. 5.2) despite being mown twice in summer for 50 years. This clearly disproves any notion that tall-grass species do not dominate regulary mown sites because they are less tolerant of mowing than short grasses. These results provide strong support for mathematical predictions that the loss rate of nutrients has a major effect on competitive ability in nutrient-limited environments (Tilman 1990b).

In sites of high productivity and fertility, *Eragrostis curvula* and *Panicum maximum* dominate despite summer mowing (Fig. 5.2 & 5.3), because rates of regrowth of tall-grass species in high fertility sites are probably sufficiently high to ensure that short-grass species are quickly shaded after mowing. This phenomenon has been proposed as the reason for dominance of tall-grass species on productive roadsides in Britian (Grime 1979). In the plot experiment (chapter 7) the tall-grass species, *Panicum maximum* and *Hyparrhenia hirta* were observed to overgrow and shade *Themeda triandra* within two weeks after cutting in the most productive sites. This is because species characteristic of fertile habitats have inherently faster growth rates than species characteristic of infertile habitats, providing that nutrients are not limiting (Grime & Hunt 1975; Chapin 1980).

Although competition was clearly involved in determining the abundance of short- and tall- grass species in mown and unmown sites in the burning and mowing experiment, other plant types may have been intolerant of different forms and timing of disturbance. The burning and mowing experiment revealed that many erect herbaceous dicots and woody species, which have elevated meristems, were vulnerable to summer

mowing, probably because of removal of apical dominance and interruptions of life cycles (Table 4.6). Species whose flowering or fruiting period coincided with the timing of disturbance were especially vulnerable to disturbance. Thus, species with aerial meristems may be affected by mowing through effects on their ability to regrow or reproduce rather than on competitive effects. Importantly, these species were unaffected by burning during the dormant-period probably because this would not interrupt their flowering and fruiting. Thus, the type and timing of disturbance had important influences on the composition of herbaceous dicots. The improvement in light availability with mowing may be important for the persistence of many short herbaceous dicot species, which will also be vulnerable to shading. A number of very short or creeping herbaceous dicot species (e.g. *Aeschynomene micrantha, Zornia capensis* and *Rhynchosia totta*) were much more abundant in sites mown in summer compared with sites not mown in summer (Table 4.6). This is probably because they were easily shaded in the unmown sites, owing to their short stature. Thus, tradeoffs for short stature may give herbaceous dicots an advantage in environments where there is regular disturbance during the growing period because their meristems are less easiliy removed, but are a disadvantage where there is insufficient disturbance to maintain good light availability during the growing period.

Influences of disturbance and fertilization on species richness

The influence of fertilization on species richness was shown to be related to its effects mainly on productivity but also to its effects on soil pH (Fig. 5.5 & 5.6). It was originally thought that the decline in richness with increasing productivity was related to increasing competition for light with increasing productivity (see Rajaniemi 2002). However, recent studies suggest that root competition may make an important contribution to decreasing species richness with increasing productivity (Rajaniemi et al. 2003). Root competition during the development of a plant may slow its growth resulting in it being shaded by competitors later in the season (Cahill 1999). Whatever the mechanism (above- or below-ground competition), the decline in species richness with increasing productivity represents competitive exclusion of less competitive species

(generally shorter species) as productivity increases (see Grime 1973). Sites heavily fertilized have high productivity that results in only a few competitive species such as *Panicum maximum* and *Eragrostis curvula* dominating. These species are most competitive under these fertile productive conditions and are able to exclude most of the other species. Species richness is higher in unfertilized sites because competition will mainly be below-ground in these sites (see Cahill 1999). Below-ground competition is generally symmetric with respect to plant size, which may allow a wider diversity of growth forms to coexist. Thus, as with composition, the availability of nitrogen was a major determinant of species richness. The weaker relationship between species richness and productivity in sites not mown in summer in the burning and mowing experiment (Fig. 3.3a,b), is probably because much lower levels of productivity are attained in this experiment (maximum 425 g m^{-2}) compared with the fertilizer experiment (maximum 700 g m^{-2}). The same weak relationships between productivity and species richness are also observed in the fertilization experiment if sites of greater productivity than 425 g m^{-2} are excluded (Fig. 5.6). Nonetheless, grass species richness did tend to decline with increasing productivity in the burning and mowing experiment (Fig. 3.3a), because some short-grass species were unable to persist in the most productive sites (Fig. 4.5).

The large decline in grass species richness in the protected sites (Fig. 3.1a) is most likely a result of the high levels of litter that have accumulated with over 50 years of protection from disturbance (Fig. 2.4a). The shoots of many grass species may not be able to penetrate this litter resulting in their elimination. Thus, disturbance may not only improve species richness by reducing competition intensity (c.f. Huston 1979), but also by reducing stress in the form of high litter levels. However, certain forms and combinations of disturbances may increase stress by creating dry infertile soil conditions. For example, the strong interactive effects of summer mowing and time of burning on both grass and forb species richness, where richness was decreased by winter burning in sites mown in late summer (Fig 3.1), appear to be related to effects of disturbance on soil moisture and perhaps nitrogen. Winter burning resulted in the lowest levels of soil carbon and nitrogen (Table 2.1) and probably also result in greater soil dessication and moisture stress than spring burning, because spring burning is carried out only after good rains. Thus, low species richness in these treatments may be related to an inability of many

species to persist in extreme conditions, as shown in many humpbacked productivity-diversity relationships (Al-Mufti et al. 1977; Moore & Keddy 1989). Whether this is the result of competitive exclusion of many species by a strong below-ground competitor in these extreme conditions (low soil resource availability) or intolerance of these conditions is unknown.

The plot competition experiment showed that in cutting treatments, *Themeda triandra* was able to competitively exclude *Eragrostis curvula* in the higher productivity plots but not the lower productivity plots (Fig. 7.6). Thus, under a mowing regime, *Themeda triandra,* is likely to be most competitive in more productive sites. Thus, the decline in forb species richness at the highest levels of productivity in sites mown in summer in the burning and mowing experiment (Fig. 3.3d,f), appears to be related to the strong linear increase in the abundance of *Themeda triandra* and *Eragrostis capensis* with increasing productivity (Fig. 4.6). *Themeda triandra* reached a relative abundance of over 90% in the more productive sites mown in summer (Fig. 4.6e). A decrease in species richness as a result of the increase in abundance of competitive grass species with regular burning has been demonstrated in tallgrass prairie (Collins et al. 1998).

In summary, the major effects of disturbance on species richness appear to have been through removal of litter, which improved grass species richness (Fig. 3.1a), reduction of soil resources with winter burning, which decreased both grass and forb species richness (Fig. 3.1), and increased competitive ability of *Themeda triandra* with mowing, which reduced forb species richness in the higher productivity plots (Fig. 3.3d). The decline in species richness with increasing productivity and fertility (Fig. 3.3a & 5.6) suggests that in sites with high potential productivity (greater productivity than the sites in the burning and mowing experiment), burning should improve species richness because it reduces productivity and soil nitrogen. Thus, as with composition, it is clear that it is important to take habitat productivity into account when attempting to understand disturbance-diversity relationships.

Predictive plant traits

One of the goals of this study was to gain a greater predictive and mechanistic understanding of plant performance under different environmental influences. Many useful insights have been obtained that have helped to understand most of the patterns in plant composition observed in the burning and mowing experiment and the fertilizer experiment.

The pot experiment showed that short-species are able to grow and compete better than tall species when nutrients are strongly limiting (*sensu* Gleeson & Tilman 1990). The reverse is true in more fertile conditions where taller species grow faster and compete better than the short species (Fig. 6.1 & 6.2). The pot experiment helped to confirm that regular burning favours short-grass species by reducing nitrogen availability or rather by preventing a build up of nitrogen. This experiment also explains why *Themeda triandra* dominates the unfertilized sites in the fertilizer experiment, where nitrogen is strongly limiting and why taller species dominate the fertilized sites.

In agreement with recent studies (e.g. Keddy et al. 2002), the plot experiment showed that a tall broad-leaved growth form results in the greatest competitive ability in productive habitats (Fig. 7.3). The tall broad-leaved species, *Panicum maximum*, was able to reduce the biomass of *Themeda triandra* more than any other species, including the tall narrow-leaved species, *Hyparrhenia hirta*. No species was observed to have a competitive effect on *Panicum maximum* but it had a competitive effect on all species with which it grew in competition. Tall narrow-leaved species were shown to be second in the competitive hierarchy but tend to perform better than tall broad-leaved species at lower levels of fertility/productivity. This helped to explain why a tall broad-leaved species, *Panicum maximum*, dominated the most productive sites in the fertilizer experiment (800-1000 g m^{-2}), which were fertilized with the highest level of nitrogen and phosphorus. It also explained why a tall narrow-leaved species, *Eragrostis curvula*, dominated sites of medium to high productivity fertilized with nitrogen but where

phosphorus is limiting. Narrow-leaved species tend to become more common as fertility decreases (Wright et al. 2002).

The plot experiment also revealed how mowing may change the competitive hierarchy amongst species. In the absence of cutting tall species were much more competitive than the shorter *Themeda triandra*. However, cutting resulted in *Themeda triandra* becoming extremely competitive, probably by improving light availability, which stimulated tiller initiation and promoted lateral spread. Thus, short species may be more competitive in regularly disturbed environments. These results helped to explain the dominance of short species in mown sites in the burning and mowing experiment. However, mowing did not alter the response of the smallest species (100 mm maximum leaf height) in the burning and mowing experiment (Fig. 4.5 & 4.6), suggesting that they may be stress tolerators rather than competitors.

Below-ground tiller initiation and sharp, rigid and erect shoot morphology may be an adaptation to penetrating litter, that conveys an advantatge to species in sites with high litter levels. *Tristachya leucothrix* and *Aristida junciformis,* which initiate tillers below-ground and have sharp erect shoots were both able to tolerate high litter levels in the protected sites. However, *Tristachya leucothrix* was eventually replaced by *Aristida junciformis* in these sites. This may be related to the fact that the leaves of *Tristachya leucothrix* are soft and are not erect in stature, whereas those of *Aristida junciformis* are rigid, sharply pointed and grow absolutely erect. This appears to enable its leaves to pierce and shed accumulating aerial litter (personal observation), whereas the stature and strength of the leaves of *Tristachya leucothrix* would not allow them to shed and pierce accumulating litter. Consequently, the position of tiller initiation and shoot morphology of *Tristachya leucothrix* allows it to replace above-ground tillering species following protection from disturbance but its leaf morphology does not allow it to persist after more than 20-30 years of protection from disturbance (Fig. 4.2) because litter levels become to high for it. In contrast, *Aristida junciformis,* which has both below-ground tiller initiation and sharp erect leaves, was able to tolerate the high levels of litter that have accumulated after 30 years of protection from disturbance (Fig. 4.2). Another short species that is able to do well in fertile habitats in this region is *Imperata cylindrica*, which also has sharply pointed erect leaves. Thus, position of tiller initition, shoot and leaf morphology may be

extremely useful traits for predicting species response to any factor that causes litter levels to accumulate. Rigid sharply pointed erect leaves are also less vulnerable to being overgrown by competitors because they are able to grow through the canopy of the competitors. It is interesting to note that *Aristida junciformis* was one of the least competitive species in the plot competition experiment (Fig. 7.3 & 7.7), yet eventually dominated the protected sites in the burning and mowing experiment. This suggests that it was not competition that allowed this species to dominate these sites but rather the greatest ability to tolerate high litter levels.

Several generalizations for these mesic grasslands are now possible, which may apply to grasslands worldwide but this needs to be tested. Regular burning in spring or winter or summer mowing favour short species but this will depend upon habitat productivity. In extremely productive habitats tall broad-leaved species are likely to dominate even with regular burning or mowing (Fig. 7.4). Grazing also favours short-grass dominated communities (Belsky 1992; Morris et al. 1992; Fuhlendorf & Smeins 1997; Cingolani et al. 2003), but grazing systems that allow selective grazing of short grasses will favour dominance by taller species (Morris et al. 1992). Extremely short species (100-150 mm tall) will only be abundant in habitats where annual dry matter production is below 300 g m^{-2} even under a mowing regime (Fig. 4.5 & 4.6). Mowing does not have much of an effect on the relationship between abundance and productivity for these very small species. They appear to fit into Grime's (Grime 1979) stress tolerator category. Slightly taller species (30-50cm tall) may become extremely competitive under a mowing regime and even dominate moderately productive sites (500 g m^{-2}) if mown in summer. These species appear to be good competitors when light is not limiting (i.e. under summer mowing) and were shown to be good competitors when nutrients are limiting (Fig. 6.1 & 6.2). Thus, they appear to fit into Tilman's below-ground competitor category (Tilman 1988). Only tall species are able to persist in the most productive sites (> 700 g m^{-2}), even under a mowing regime. If nitrogen availability is high, but another nutrient is strongly limiting (e.g. phosphorus), tall broad-leaved species will be unable to compete against tall narrow-leaved species. However, if no nutrients are limiting, tall broad-leaved species are most likely to dominate. These species best fit the competitor category of Grime (Grime 1979) and the above-ground competitor category of Tilman

(Tilman 1988). Finally, species with below-ground tiller initiation and rigid erect shoots and leaves are able to tolerate high litter levels. These species were shown not to be very competitive and, therefore, also appear to fall into Grime's stress tolerator category.

A theoretical predictive framework

There was clear evidence of an interaction between the level of habitat productivity or nitrogen availability and the degree of disturbance in their effect on community composition. In the absence of disturbance, short-grass species are unable to persist in the long-term, even in inherently infertile sites (shallow soils on shale) because total soil nitrogen is able to accumulate. Disturbance, especially regular burning, reduces nitrogen availability and productivity, thereby maintaining intense competition for nitrogen favouring short-grass species. The same seems to apply to short forb species. The effect of different type, timing and frequency of disturbance resulted in different effects on nitrogen availability, which in turn resulted in different abundances of short-grass species. However, short species are able to persist or even dominate more productive habitats providing these sites are mown during summer, which results in a direct improvement in light availability, thereby reducing competition for light and increasing the relative proportion of below-ground competition. At very high levels of productivity and fertility (> 600 g m^{-2}), disturbance is unable to maintain short-grass species because it probably does not have sufficient impact on habitat productivity itself. Annual burning was unable to maintain short-grass species on the extremely productive bottomland soils at Hayfields but was able to maintain them on the less productive soils at Ukulinga, whereas infrequent burning resulted in replacement of short-grasses by tall-grasses even on these relatively unproductive soils at Ukulinga. Mowing was able to maintain short-grass species in the burning and mowing experiment but not in sites fertilized with nitrogen in the fertilizer experiment. Thus, it appears that productivity and disturbance form the axes of an extremely useful ecological framework for understanding the response of plant species to various environmental factors.

This framework is able to account for patterns in plant composition even at regional scales. For example, in the less productive semi-arid regions of the country, short-grass species are able to dominate in the absence of disturbance, whereas in the more productive high rainfall regions of the country they are rapidly excluded by tall-grass species in the absence of disturbance (Tainton & Mentis 1984).

Another very good example is the distribution of the fynbos biome in South Africa. Fynbos species generally only occur in the Cape Floral Kingdom on extremely infertile soils but islands of fynbos are found further north on infertile sands of the Msikaba formation (Pondoland) and in high altitude cool montane environments (Carbutt & Edwards 2001). In the more fertile regions between these islands, grasses dominate. The interesting feature of fynbos outcrops in the high altitude regions of the KwaZulu-Natal Drakensberg, is that the soils have extremely high total nitrogen levels, in direct contrast to the extremely nitrogen poor soils of the lower altitude fynbos regions. Studies of soil nitrogen mineralization have shown, however, that less nitrogen is mineralised in the nitrogen rich Drakensberg soils, at the temperatures experienced at those high altitudes, than the amount of nitrogen mineralised in the nitrogen poor Pondoland soils at their local temperatures (Carbutt et al. in prep). Thus, nitrogen availability is actually extremely low in these high altitude grasslands, which combined with less favourable conditions for plant growth in the colder climate results in very low productivity. This allows fynbos species to compete against the more competitive grass species.

Finally, there is excellent evidence of the interaction of productivity and disturbance on a rainfall gradient in the Umfolozi-Hluhluwe game reserve. In sites where megaherbivores (rhino) were excluded, smaller herbivores were unable to prevent tall bunchgrasses from eliminating short-grass, which dominate grazing lawns in the more productive higher rainfall regions of the reserve, but more intense grazing by megaherbivores in unfenced sites allowed the persistence of grazing lawns (Bond et al. 2003). By contrast, in the less productive lower rainfall regions of the reserve, grazing lawns were maintained in sites where megaherbivores were excluded.

Models show that to prevent less competitive species from being excluded by more competitive species the intensity of disturbance must increase with increasing habitat productivity (Huston 1979). It is clear, therefore, that productivity and disturbance

provide a solid theoretically derived and empirically supported framework for understanding the distribution and abundance of plant species.

Conclusions

A solid predictive and theoretical framework for ecology is a necessity. Advances in ecological understanding and predictive ability have been hampered by the inability to establish such a framework, probably because of the difficulties involved with identifying a common unifying factor underlying plant-environment-disturbance relationships across a range of scales. By linking plant traits with the results of pot and plot experiments and their patterns in relation to productivity and disturbance, this study reveals that the effects on the outcome of plant competition by nitrogen availability, productivity and litter levels, as influenced by environmental factors and various disturbances, is the most parsimonious explanation of patterns of plant species abundance and distribution in relation to soil depth, fertilization and different type, timing and frequency of disturbance. Thus, this study provides a mechanistic basis for understanding patterns of plant species abundance and distribution along gradients of rainfall, soil fertility, litter and disturbance. It is shown both theoretically (e.g. Huston 1979) and empirically, across a wide range of scales and examples, that a plant trait-productivity-disturbance framework is the context upon which the major primary variation in plant community-environment relationships can be explained. Residual variation in community composition can be explained by interference of life cycles, selective disturbance, disease, stochastic events, successional age, frost, soil pH and salinity. This study of mesic grassland dynamics, using the long-term burning and mowing and fertilizer experiments, in association with pot and plot experiments, demonstrates that a unified predictive theory is possible for plant ecology. Productivity and disturbance must form the major axes of such a theoretical framework because they have been shown to abstract the essential processes underlying most plant community-environment relationships. With further refining of our understanding of the relationship between various plant traits

and litter levels, soil nitrogen, soil moisture, light availability and their interactions, this framework has the potential to have great predictive power.

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