ABOVE- AND BELOWGROUND COMPETITION IN SAVANNA SYSTEMS

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ABSTRACT

The structure and composition of savanna vegetation is influenced by resource availability and disturbance. Grasses, a major component of savannas, influence this resource availability by competing directly with trees for light, water and soil nutrient resources. The direct causes of bush encroachment are not always apparent, but are commonly ascribed to overgrazing and consequent decreased grass competition. The interaction, both above and belowground, between tree and grass seedlings and the surrounding grass sward is dependant on many factors, such as soil depth, seedling species and sward composition. These factors, as well as the presence or absence of defoliation, in the form of grazing or fire dictate whether the system will remain in a transition state as savanna or move towards a stable woodland state. The major competitive effects experienced by the tree seedlings were dependant on grass species and nutrient level. *A. nilotica* was affected by aboveground competition while *A. karroo* was affected by belowground competition. *E. capensis* caused the greatest decrease in *A. karroo* plant biomass. Both *E. capensis* and *H. hirta* had large competitive effects on the aboveground biomass of *A. nilotica*, while *S. africanus* had the greatest effect on belowground biomass. Increasing nutrient availability resulted in an increase in the competitive effect exerted on *A. karroo*, while little to no change was seen in the competitive effect exerted on *A. nilotica*. Soil depth constrained plant size in both tree species. The intensity of belowground interactions on tree biomass was unaffected by soil depth, while aboveground competition had a significant effect on shallow soils. Belowground competition was also of greater importance than aboveground competition in dictating tree seedling height. Grass seedlings growing on all three soil depths differed in mean mass, with *E. racemosa* having the least mass and *T. triandra* having the greatest. Simulated grazing by cutting the surrounding sward resulted in biomass increases in all three grass species. Changes in savanna composition and structure are thus likely to be influenced by initial species composition and soil depth and soil nutrient composition. While grazing creates niches for grass seedling establishment, heavy grazing has been observed to increase grass seedling mortality. Encroachment is thus more likely to occur on intensively grazed shallow and deep soils than on medium depth soils. This highlights the importance of ensuring the grass sward remains vigorous by resting and monitoring stocking rates to ensure veld is not over-utilized. It is then possible to maintain some form of tree-grass coexistence at a level where available grazing is not compromised.

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.

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CHAPTER ONE

LITERATURE REVIEW

1.1 INTRODUCTION

1.1.1 Savanna

Skarpe (1992) defines savanna as a 'tropical or near-tropical seasonal ecosystem with a continuous herbaceous layer, usually dominated by grass or sedges, and a discontinuous layer of trees and/or shrubs' while Sankaran *et al.* (2005) refer to savanna as a system where two contrasting plant life forms, namely trees and grasses, are co-dominant. These areas are similarly described under the term rangelands by Blench and Sommer (1999). The term savanna is generally used to describe the vegetation in its natural state while the term rangelands refers to areas which have resulted from, or been impacted upon by, some anthropogenic force such as controlled burning, livestock grazing and crop production. In Africa it is believed that humans have been deliberately burning savanna regions for some 2.5 million years (Scholes & Archer, 1997), originally to attract wildlife to the flush of new growth and improve hunting efficiency, and later to provide palatable grazing for livestock.

The savanna/rangeland vegetation type is estimated to cover between 16 and 23 percent (Blench & Sommer, 1999) or 1600 million hectares (Scholes & Archer, 1997) of the earth's surface and some 40 to 50 percent of Africa's land surface (Chirara, 2001). Savannas are found over a broad rainfall gradient ranging from 300 and 1800 mm per annum. As well as providing fodder for approximately 360 million cattle, 600 million sheep and goats (Blench & Sommer, 1999) and countless wild antelope, they also play a vital role in the lives of rural communities as a source of firewood and, in the higher rainfall areas, arable soil for crop production (Chirara, 2001).

The vegetative structure of savanna is determined by four driving factors, namely soil moisture, soil nutrients, herbivory and fire. These factors interact to determine the palatability and nutritional value of the vegetative material and the species and structural composition of the landscape (Scholes & Archer, 1997; Chirara, 2001; Bond *et al.*, 2003; Sankaran *et al.*, 2005). It is believed that while soil moisture controls the length of the growing season, soil nutrients control the growth rate during that time (Scholes, 1990). As the southern hemisphere rainy season coincides with the summer growth period soil moisture cannot be regarded as a controlling factor in the development of savanna in these regions. Soil nutrients are a fairly consistent factor showing little fluctuation over the

seasons and act as a factor limiting the extent of plant growth and the plant species combinations that a system can support (Chirara, 2001). The interaction of these two factors also contributes to determining the number of trees a savanna system can support. In low rainfall regions the grass layer utilizes a large percentage of the soil moisture that is not lost to evaporation and as a result very little filters through into the deeper soil layers, while in areas with higher rainfall the greater infiltration rate results in a much greater volume of water becoming available to the tree layer. This increased infiltration is accompanied by leaching of soil nutrients in deeper soil layers (Chirara, 2001) increasing their availability to the tree layer and thus increasing growth rates and nutritional value of the woody foliage (Skarpe, 1992).

Although resource partitioning is a major driving force in terms of tree-grass interactions it must be stated that this only applies after the trees have broken through the grass layer and are essentially occupying different above- and belowground niches. In the seedling stage the trees interact within the same above- and belowground niches as the grass and thus will compete directly for resources. In this case soil moisture becomes more of a limiting factor than soil nutrients as many savanna trees are part of the legume family and have the ability to fix air-borne nitrogen which provides sufficient nutrients for growth in the seedling stage (Mopipi, 2005).

The theory that herbivory may impact on the structure and composition of vegetation began to develop in the mid 1950's. It was suggested that ecosystems were affected by the regulation of herbivores by predator populations. Without predators the herbivore populations would increase and thus their impact on the vegetative layer would increase. In response to this the plants would begin to focus development on mechanisms for defence against herbivory rather than on competitive ability (Bond & Keeley, 2005). In a multi species wildlife system browsers and grazers coexist, thus impacting on both the tree and grass layers (Chirara, 2001). In Africa agro-pastoralists have been herding cattle, sheep and goats for the past 6000 years (Chirara, 2001). As these animals were herded in one group their impact on the vegetation was similar to that of wildlife, with both the tree and grass components being defoliated. The arrival of European settlers in Africa during the 18th and 19th centuries saw large areas of savanna being fenced off to form cattle farms. While these fences protected the cattle from theft and predators and prevented them from straying, they also restricted the movement of wildlife (Chirara, 2001; Cole, 1986) resulting in a switch

from what was essentially a multi species system to a single species system largely eliminating browsers.

In South Africa savanna ecosystems are kept away from the expected climatic equilibrium by the presence of fire. Areas of savanna in regions such as the Drakensberg often have small patches of forest present in unburnt areas within the larger matrix of savanna vegetation indicating that in the absence of fire it may be possible for these areas to support forest vegetation (Bond *et al.*, 2003). Fire serves a similar function to herbivory but behaves as a general defoliator, breaking down both living and dead material, while herbivory impacts only on the living parts palatable species (Bond & Keeley, 2005). Many grasses have evolved to become fire dependant and in the absence of regular burning become moribund and die. Fire also serves to regulate tree density as young saplings are sensitive to burning and many are killed before they are able to grow above the grass layer (Trollope, 1980). Fire intensity and its impact on the tree seedlings varies depending on the environmental conditions, namely air temperature, relative humidity, fuel load and fuel moisture (Trollope, 1980).

1.1.2 Bush encroachment

Bush encroachment 'is the phenomenon whereby trees and shrubs invade into open grassland or thicken up in already wooded areas' (Trollope, 1980). This problem has been developing since the early 1900's and its severity was recognized early as seen in a statement made by West (1947). In a paper published in *The Rhodesia Agricultural Journal* outlining methods of thorn bush removal and veld management techniques he stated 'there can be no future for the cattle industry in these parts unless the invading thorn can be controlled' (West, 1947). Bush encroachment is not only a problem in cattle farming areas. It has been observed in many game reserves and national parks (Prins & van der Jagd, 1993, Van der Vijver, Foley & Olff, 1999) resulting in a loss of grazing and declines in the populations of grazing species (Ben-Shaher, 1992) and a loss of biodiversity due to the loss of palatable grass species and changes in sward species composition (Trollope, 1983). In addition bush encroachment may have played a role in the increasing numbers of Tsetse flies associated with the rinderpest by providing bush refuges for the flies (McNaughton, 1992). It is estimated that 13 million hectares of South Africa's savanna regions are in various stages of bush encroachment (Mopipi, 2004; Trollope, 1983) resulting in a loss of approximately fifty percent of available grazing (Smit, 2004).

There is much debate over the cause of this problem. Originally it was thought to result from overgrazing. This decreases the competitive ability of the grass, allowing water to infiltrate deeper into the soil profile (Skarpe, 1992: Stuart-Hill, 1985; Tobler *et al.*, 2003) and decreases the available grass biomass greatly reducing fire intensity. In addition to this livestock may serve as seed dispersal agents by ingesting protein rich seed pods but failing to fully digest the seeds. They also displace indigenous browsers which control seedling numbers (Tobler *et al.*, 2003). While overgrazing appears to be the major driving factor behind the bush encroachment problem it may also occur as a result of low grazing pressure. As large herbivores accelerate the nutrient cycle in savanna regions, the exclusion of these animals allows nutrients to infiltrate to deeper soil layers thus promoting woody plant growth (Skarpe, 1992). Incorrect management may also exacerbate the problem, for example burning during the dry season may result in an increase in woody plant density due to the fact that the grasses cannot maintain their initial post-fire growth spurt. The new shoots either wilt and die through lack of water or are grazed and the plant's nutrient reserves are insufficient to replace them (Skarpe, 1992).

Scholes & Archer (1997) suggest that savanna structure results from disturbances such as fire, bush clearing and livestock utilization. These disturbances maintain the vegetation in a transition state between grassland and woodland and if removed the vegetation would naturally progress toward a stable woodland state (Scholes & Archer, 1997). Ward (2003) supports this statement, noting that young trees utilize the same soil layer as grasses and cannot escape competition by niche differentiation until later growth stages. Bush encroachment has also been observed in regions where the soil depth is not sufficient to allow for this differentiation (Ward, 2003).

While it appears to be a widely accepted fact that an increase in bush density results in a decrease in available grass biomass, there are some contradicting opinions on the severity of the situation with regard to livestock farming. During the growing season the grass contains sufficient nutrient content to sustain livestock, however during the dry season it loses much of this nutritional value. Over this period browse may play an important role by providing an additional nutrient source. At the beginning of the growing season most woody plants develop new shoots before the grasses and this assists browsing animals to maintain condition before the flush of new grass (Plowes, 1956). This opinion is supported

by Friedel (1987) who emphasizes the need for the inclusion of browse assessment in standard veld assessment techniques even though the veld is mainly utilized by grazers (Friedel, 1987). This may be more relevant to sheep production than cattle production as sheep are known to utilize a higher proportion of forbs and small shrubs in their diet than cattle, who rarely ingest more than 5 % browse in their diet. Availability of short shrubby bushes may therefore allow sheep to supplement their diet during times when the grass has little nutritional value but will have little value in a cattle farming system (Owen-Smith, 1999).

Trials run at Nyamandhlovu in Zimbabwe showed a contrasting result. The steers in the camps which had been cleared of all bush showed consistently higher liveweights than those in the uncleared camps. It is likely that this is due to an increase in available grass, as the cleared plots yielded 59.9 % more grass material than the uncleared plots. This is however a specific case in a high rainfall region and results may differ in the drier regions (Plowes, 1956).

In addition the increasing atmospheric CO_2 levels are aggravating the bush encroachment problem (Meadows, 2006). Levels of atmospheric CO_2 are predicted to double, from 350 ppm to 700 ppm, by the middle of the 21st century (Bazzaz & Williams, 1991. Leishman *et al.*, 1992, Bazzaz & Miao, 1993, Lotz, 2001). South Africa produces a significantly large amount of this CO_2 and as a developing country this level is unlikely to decrease (Scholes & Bailey, 1996). This increase will be coupled with an ambient temperature rise of between 3 and 5°C, significantly affecting the distribution of many plant species and thus altering land use patterns accordingly (Paterson & Flint, 1980, Bolin *et al.*, 1986 cited by Lotz, 2001, Coleman & Bazzaz, 1992, Lindroth *et al.*, 1993, Schlesinger, 1993).

Rising CO_2 levels will result in an increase in net photosynthesis, water use efficiency, the occurrence of symbiosis, reproductive potential, rooting ability, branching, tiller production and overall plant growth (Hatton & Smart, 1984, Bolin *et al.*, 1986 cited by Lotz, 2001, Norby, 1987, Bazzaz, 1990, Garbutt *et al.*, 1990, Coleman & Bazzaz, 1992, Poorter, 1993, LeTheic & Dixon, 1996, Mjwara *et al.*, 1996, Schaffer *et al.*, 1996, Drennan & Nobel, 2000, Lotz, 2001) and a decrease in stomatal conductance and the concentrations of nitrogen in various plant parts (Garbutt *et al.*, 1990 Tyree & Alexander, 1993, Roden & Ball, 1996, Lotz, 2001).

Plant responses to this are very species dependant and vary from decreases of up to 58% to increases of up to 468% (Rawson, 1992). Plants with a C_4 photosynthetic system, such as most grasses, photosynthesise at a rate 50% higher than that of C_3 plants, such as trees, and thus their photosynthetic ability becomes saturated at much lower CO_2 levels (Johnson *et al.*, 1993, Rogers & Dahlman, 1993, Polley, 1997). The increasing levels of atmospheric CO_2 will have a large effect on C_3 plants, fast growing plants and plants with the ability to fix atmospheric nitrogen (Poorter, 1993, Roumet & Roy, 1996). This 'CO_2 fertilization effect' would allow the trees to grow bigger, more quickly and would further increase the competitive ability of woody plants in areas where the grass layer has already been impacted (Scholes & Bailey, 1996, Lotz, 2001).

1.1.3 Management

As previously mentioned soil moisture plays an important role in determining savanna structure. Research done at Matapos Research Station in Zimbabwe showed that the roots of one Marula tree cover approximately one acre and in a season yielding 16 inches of rain the moisture did not infiltrate further than 132 cm into the soil. In such a case the removal of trees would greatly increase the volume of available water and result in a much denser grass sward (Plowes, 1956). This competition for moisture, as well as for light, nutrients and growing space (Plowes, 1956) is the major reason that tree removal is regarded as vital in obtaining maximum livestock liveweight yield from the veld, particularly in regions where soil moisture is limited.

Successful savanna management requires an understanding of system stability, resilience and the system's domain of attraction. This principle is illustrated in Figure 1. Position 1 (Figure 1) represents a system which has little to no bush encroachment, has a high grass production and is moderately stable. If pressures, such as drought or grazing, exerted on the system are within it's domain of attraction then the system will return to its original state following the removal of those pressures. If the pressure is too intense for the system to endure or persists for an extended period of time the system will be pushed beyond its domain of attraction and move toward position 2 (Figure 1). In this state the woody plant density increases and the grass production decreases (Smit, 2004). The final woody plant density and thus the severity of bush encroachment which occurs is determined by the level of inter-tree competition. In areas with a high rainfall, greater than 650 mm per annum, a

dense stand with little to no grass layer will develop, while in drier regions, less than 650 mm per annum, a more open stand with a fairly continuous grass layer results (Sankeran *et al.*, 2005, Scholes & Archer, 1997).

The aim of bush control techniques is, in the case of a degraded or encroached system, to return the system to the position 1 (Figure 1) stable, productive state. Depending on the techniques used the system will return to one of two states. The first and more desirable state (position 1a, Figure 1) is that of structured savanna. This state has a higher productivity than state 1b (Figure 1) and is more stable as it has a larger domain of attraction. State 1b (Figure 1) is that of unstructured savanna. While it has a higher productivity than state 2 (Figure 1) is not as stable and as a result is prone to fairly rapid re-encroachment. This state results from the removal of large trees, rapidly increasing the grass yield but creating available niches for woody seedlings to grow and possibly worsening the encroachment problem. It is therefore preferable to remove some trees, but keep the large developed plants, encouraging them to create larger shading zones thus preventing woody seedlings from growing but allowing a shade tolerant sward to develop. This would result in a stable, productive, structured savanna (position 1a, Figure 1) (Smit, 2004).
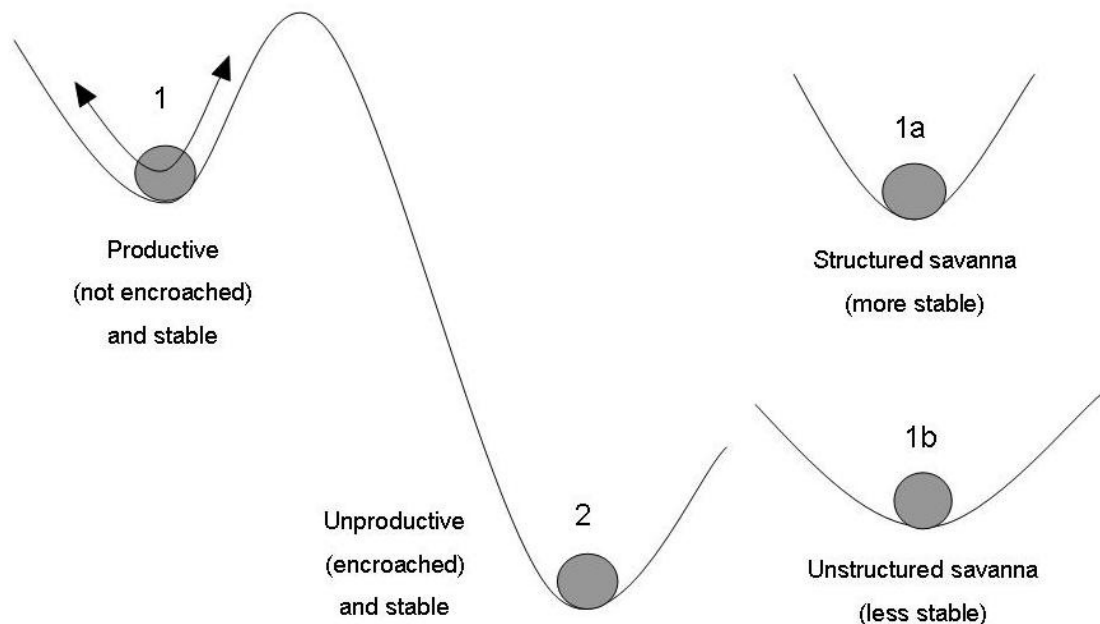
Figure 1.1: Stability, resilience and domain of attraction with reference to savanna systems (Smit, 2004)

The concept of veld management has long been a part of livestock farming. West (1947) in his paper published in The Rhodesia Agricultural Journal outlines the four main factors required for maintaining a productive grass sward and controlling woody plant density. He recommends a rotational grazing system incorporating the following; a stocking rate slightly below the carrying capacity of the veld, regular burning or mowing of the veld, rest periods to allow the grasses to replenish depleted root reserves and a burn following the rest period (West, 1947) to remove moribund grass material, encourage new growth and kill woody plant seedlings. This pre-burn rest is important as it allows sufficient fuel load to accumulate, resulting in a high intensity fire which is the most effective for controlling bush encroachment (Trollope, 1974). The conditions required for such a burn to take place are as follows; air temperature >25°C, relative humidity <30%, fuel load >3000kg/ha and fuel moisture <40% (Trollope, 1980).

Once an area is already encroached it becomes more difficult, expensive and time consuming to return it to an unencroached state. Originally the most effective method of bush clearing was thought to be the mechanical removal or poisoning of trees. In the clearing of seedlings cutting must be done as low to the ground as possible as plants cut above the point of cotyledon attachment tend to coppice and produce multiple stems (Brown & Booysen, 1967). West (1947) recommended using machinery such as bulldozers, power winches and chainsaws, followed by poisoning individual plants with paraffin or arsenic based solutions. Although these methods are effective, they can become very expensive as regular applications are required before the problem is under control (West, 1947).

In moist savanna regions (> 600 mm p.a) the use of fire alone is sufficient to keep bush encroachment under control, as the high rainfall results in sufficient grass production to sustain regular, hot fires (Trollope, 1980). In trials conducted by Trollope (1983) at the Fort Hare University Research Farm it was found that a combination of fire and browsing by goats proved to be an effective management tool in the control of bush encroachment in arid savanna regions. The encroached area was first burnt to bring the available browse height down to a suitable level and then goats were stocked at a rate of one animal per hectare. After five years the bush density was reduced by 90 percent, while in plots that were only burnt the bush density only decreased by 32 percent (Trollope, 1980). Goats are

an appropriate livestock species to use for this purpose as they have a very wide browse palatability range and will favour browse over grass if the former is available. As the bush density decreases it becomes necessary to decrease the stocking rate as they begin to impact on the grass sward (Trollope, 1983).

1.2 TREE-GRASS INTERACTIONS

Competition is defined as the effect that one plant or species has on the availability or quality of a shared resource to the detriment of neighbouring individuals (Bazzaz & McConnaughay, 1992)

1.2.1 Interactions between mature plants

1.2.1.1 Effects of trees on the grass layer

The effects of individual trees on the surrounding grass layer may differ to those of a woody thicket. These effects may also be altered by environmental conditions, substrate and species composition.

The grass species composition under the tree canopy is often very different to that of the rest of the grassland. This difference tends to be more distinct in the high rainfall areas than in the low rainfall areas. This composition is also affected by the level of grass and tree layer utilization. When the grass sward is heavily grazed the difference becomes less distinct, while in a situation where browse material is more heavily utilized the effect on the sward can be either negative or positive, depending on the response of the trees. Browsing may either reduce the volume of foliage allowing more light to penetrate through to the grass layer or it may encourage leaf growth increasing the shading effect (Scholes & Archer, 1997; Belsky *et al.*, 1989).

It is generally assumed that the presence of trees within a grass sward will decrease the productivity of the grass layer as a result of competition (Scholes & Archer, 1997). For example, an increase in bush density from below 400 tree equivalents/ha to 2 500 tree equivalents/ha can cause a reduction in potential grazing capacity of between 331 and 58%, depending on the vegetation type (Richter, Snyman & Smit, 2001). However this may not always be the case, while a tree competes for light by shading the grass layer and may compete for belowground resources such as water and nutrients it is also possible that trees will increase available water and nutrients. Many grassland tree species are leguminous,

having the ability to fix nitrogen into a plant-available form thus increasing the nutrient content of the soil (Scholes & Archer, 1997). Ludwig *et al*. (2004) found that the nitrogen: phosphorus ratio in open grassland was significantly lower than that below leguminous trees, indicating that nitrogen availability may be a factor limiting grass growth in the absence of trees. In addition to this the deep roots of woody plants may draw nutrients up from deeper soil layers which would be otherwise inaccessible to the grass layer and the leaves within the tree canopy trap atmospheric dust which is washed off into the soil when it rains further enriching soil fertility. The shade and shelter provided by woody plants also attracts birds and animals which deposit nutrient rich dung and may redistribute surface nutrients to deeper soil layers by burrowing (Archer, Boutton & Hibbard, 2000). This effect has long term benefits to the grass layer and increased production may be observed for as long as thirteen years after the trees have been removed, provided the area remains unencroached (Scholes & Archer, 1997). This theory is supported by Ludwig *et al*. (2004) who observed increased soil nutrient levels up to eight years after the death of a tree. A tree with a substantial canopy, while shading the grass layer below will also decrease the effects of solar radiation on the soil layer and as a result decrease evaporative water loss (Scholes & Archer, 1997).

These effects may be variable and may be outweighed by negative competition effects, as Stuart-Hill (1985) found that individual *A. karroo* plants have the ability to suppress grass growth within a radius of much as nine metres from the plant stem and Knoop & Walker (1985) found that the removal of trees from a plot in mixed bushveld in the Nylsvley Provincial Nature Reserve resulted in an increase in both mean grass height and basal cover. This increase in grass growth after tree removal leads to the conclusion that water may be the limiting resource which suppresses grass growth under tree canopies. Ludwig *et al*. (2004) observed that grass growth increased by some sixty percent following the death of the competing tree. Soil analysis found that nutrient levels did not change drastically, however soil moisture was observed to increase (Ludwig *et al*., 2004). This was correlated with Dye & Spear (1982) who found that trees utilize much the same amount of soil water regardless of the season and thus fluctuations in rainfall only affect the volume of water available to the grass layer. This impact is more clearly observed on soils with high clay content showing strong correlations between rainfall and grass biomass and showing distinct changes in plant species competition (Dye & Spear, 1982).

The density of trees within the grassland also affects productivity levels. A grassland with a few scattered trees will have a higher productivity than a grassland with no trees present. This only applies at low tree density. As tree density increases grass productivity begins to decrease, as a result of factors such as increased shading, root competition and accumulation of leaf litter (Scholes & Archer, 1997).

1.2.1.2 Effects of the grass layer on trees

The effect exerted by the grass layer on adult trees varies depending on the rainfall, soil type and density of the grass layer. The removal of grass in areas on the Patagonian steppe was followed by an increase in tree density as the available soil moisture increased (Scholes & Archer, 1997). Stuart-Hill (1985) found corresponding results working in the false thornveld region of the Eastern Cape. The areas in which the grass sward was totally removed showed an increase in *A. karroo* density of between 40 and 166 % (Stuart-Hill, 1985). In experiments conducted at Nylsvley Provincial Nature Reserve the grass layer was removed from both an *Acacia tortilis* dominated stand on a fertile, loam soil and a *Burkea africana* dominated sward on infertile, sandy soil. The *Acacia* trees responded by increasing in stem diameter and twig length, while the *Burkea* trees showed little to no effect. This may be due to the fact that trees on sandy soils tend to rely more strongly on deep soil water and thus do not compete as directly with the grass layer as trees on loam and clay soils (Knoop & Walker, 1985). Similar observations have been made on trials run in the Kruger National Park. The basal diameter of both *Acacia nigrescens* and *Terminalia sericea* was found to increase significantly as a result of removal of the surrounding grass sward (Swemmer *et al*., 2006).

1.2.1.3 Effects of trees on other trees

Mature trees create a zone of resource depletion the size of which is dependant on the size of the plant concerned. When these zones overlap the volume of available resources for both of the neighbouring plants decreases. As a result the growth rate is reduced or ceases depending on the upper limit of potential size for that distance. This zone overlap is generally as a result of root interaction, as roots may extend as far as seven times further than the canopy (Smith & Walker, 1983; Smith & Goodman, 1986). Although little research has been done to determine the level of niche differentiation between roots of different tree species it was observed that there appeared to be little competitive interaction between *Acacia* and broadleaf-evergreen species in the Pilanesburg Game Reserve (Smith

& Walker, 1983). Calvert (1974) made similar observations between *Baikiaea* and other species in northern Zimbabwe.

1.2.1.4 Effects of individual grass plants on other grass plants

Fargoine & Tilman (2005) found that *Schizachyrium scoparium*, a dominant C4 bunchgrass, reduced the density of those species utilizing similar resource niches, by having a shallow root system and mid-season growth, while it coexisted with deep rooted species exhibiting early season growth.

1.2.2 Interactions between mature plants and seedlings

1.2.2.1 Effects of the grass layer on tree seedlings

The grass layer exerts stronger competitive effects on trees during the seedling stage. At this stage they are competing with the grass layer for both light and water and are still in the hottest part of the potential fire zone (Scholes & Archer, 1997). Field trials based in California found that in a well established grass sward the fibrous grass roots absorb soil moisture more efficiently than the taproots of woody plant seedlings, such as *Quercus* sp and *Pinus* sp. Often this resource is depleted before the woody plant roots can penetrate deeper soil layers and as a result large numbers of these seedlings die (Shultz *et al.*, 1955). Conversely, O'Connor (1995) found that under similar rainfall conditions near Stutterheim in the eastern Cape grass competition had little effect on the establishment of *Acacia karroo* seedlings.

Seedling trials run by Brown & Booysen (1967) at Ukulinga Research Farm, Pietermaritzburg found that seedlings grown within a grass sward tended to be taller and more spindly than those seedlings grown in plots where the grass layer had been cleared. These seedlings also showed signs of water stress before those plants grown in the cleared area (Brown & Booysen, 1967), indicating that water is a major limiting resource in the establishment of woody plant seedlings. The converse was found with reference to seed germination. The seeds in the cleared plots swelled, but as soon as conditions became drier the seeds dried out and died, while the seeds sown in the grass sward were protected from the heat and showed higher germination rates (Brown & Booysen, 1967). De Steven (1991a) found similar results, in trials run in Piedmont, North Carolina. Seedling emergence of small seeded species was generally higher than that of large seeded species owing to the fact that large seeds suffered higher levels of seed predation, however large

seeded species showed a high emergence rate in vegetated areas as the soil moisture is higher and they are less visible to seed predators (De Steven, 1991a). As expected seeding mortality was highest in the first season and decreased over time. Four of the six study species showed small reductions in survival as a result of competition with surrounding vegetation while one was unable to survive in the presence of competition and the other showed poor survival rates regardless of competition level (De Steven, 1991b).

Smith & Taylor (unpublished) observed that a decrease in irradiance caused by shading led to decreased root and shoot biomass and carbon allocation. This results in a decrease in seedling establishment.

1.2.2.2 Effects of trees on tree seedlings

Smith & Walker (1983) classed woody species into two groups, 'those whose establishment is either associated with or unaffected by canopy cover and those whose establishment is limited to 'open' environments'. *Acacia* species fall into the second category. Very few *Acacia* seedlings were found under established tree canopies indicating that exclusion is not species specific. This is possibly due to high seedling mortality as a result of resource competition (Smith & Walker, 1983). Conversely seedlings of broadleaved species such as *Ehretia*, *Grewia*, *Maytenus* and *Ziziphus* are able to establish beneath *Acacia* canopies and fill the available niche when these trees die (Smith & Goodman, 1986).

Competition for light plays a major role in the establishment of *Acacia* seedlings. Smith & Shackleton (1988) examined growth rates and biomass allocation of *Acacia tortilis* seedlings grown under three different light intensity levels. Plants grown under high photon flux density (PFD) showed high levels of root development in the first four weeks of growth, switching to increased aboveground growth from four to six weeks, while those plants grown under low PFD show increased root production from 2 weeks. After six weeks there was little difference between the relative growth rates within the three PFD treatments however plants in the high PFD treatment showed high root and shoot biomass, leaf area and root length values (Smith & Shackleton, 1988).

1.2.2.3 Effects of the grass layer on grass seedlings

Studies on the Patagonian steppe have shown that competition between established grass plants and seedlings has different effects depending on water availability. During spring

when water was available in all soil layers the seedlings experienced a reduction in growth compared to seedlings growing without competitive stress, while during summer when available water is only found in the deep soil layers the seedlings experience both a decrease in growth rate and an increase in mortality (Aguiar *et al.*, 1992).

Alternatively some studies have shown that mature plants act as 'nurse plants' creating a favourable environment for seedling germination and establishment (Holmgren & Scheffer, 1997; Niering *et al.,* 1963). Fowler (1986) found that although the soil surface was damp in the areas close to the mature plants the seedling growth and survival rates were higher in the open areas. Despite the fact that both the adult plant and seedling's roots grow straight down and do not intersect the competitive effects of the adult plant were still evident up to 6 cm away (Fowler, 1986). Cook & Ratcliff (1984) found root competition to have a more pronounced influence on the growth of *Panicum maximum* than competition for light. This was done by growing seedlings in varying lengths of root exclusion tubes, increasing the root protection by increasing the length of the tube, and either allowing the surrounding sward to grow or clipping it to simulate heavy grazing. The seedlings in the clipped treatments showed an increase in leaf and tiller numbers, however this was only significant in the treatments with root protection extending below 9 cm deep. It appears that in this case root competition for nutrients was the factor limiting seedling growth as in both clipped and unclipped treatments the seedling leaf width increased with the addition of fertilizer. The greatest increase being observed in the tubes with the least root protection (Cook & Ratcliff, 1984). Snaydon & Howe (1986) found similar results in the competition of *Poa annua*, *Poa trivialis* and *Festuca rubra* seedlings with an established sward of *Lolium perenne*. It is expected that this was as a result of competition for nitrogen as seedling yield increases of up to seven times were observed after the addition of fertilizer (Snaydon & Howe, 1986). This is similar to the results of Haugland & Tawfiq (2001) who found that in the first year of seedling establishment root competition played a significant role, while in the second year aboveground competition had a greater influence.

1.2.3 Co-existence models
1.2.3.1 Walter's 2 layer hypothesis
In a mixed system comprising woody vegetation and a herbaceous layer of forbs, annual grasses and perennial grasses it is possible for the vegetation to reach a state of equilibrium resulting from the trees and herbaceous layer utilizing water resources at different depths in

the soil profile. In the upper soil layers the grasses are more efficient competitors for soil water and utilize water from light rainfall. In the lower soil layers the woody species are more efficient competitors and utilize ground water and anything which filters though the upper soil layers from heavier rainfall (Walker *et al.*, 1981).

Schenk & Jackson (2002) found that in arid regions of less than 500 mm mean annual precipitation and regions with predominantly winter rainfall Walter's two-layer model of soil depth partitioning holds true.

1.2.3.2 Balanced competition

In this situation the species with a stronger competitive ability, in this case the trees, will dominate the system. The individuals of this species are expected to compete more strongly with one another than with other less competitive species, in this case the grass layer. This inter-tree competition results in a limited number of large individuals which allows a population of grass to remain within the system. This grass layer should then outcompete any emerging seedlings preventing increase in woody plant density (Scholes & Archer, 1997). A similar concept applies to emerging seedlings. Ross & Harper (1972) found the factor with the strongest influence on emerging seedling growth was the number of seedlings already emerged. As these seedlings grow their ability to utilize resources and the size of their 'zone of influence' increases thus adversely impacting on the later emerging seedlings (Ross & Harper, 1972). The competition between seedlings emerging at the same time functions slightly differently. The resources within a system can only support a certain biomass of plant material. In the juvenile stages seedlings have a low biomass and thus a larger number of individuals can be present in the system however as the plants grow their individual biomass increases requiring a correlated decrease in the number of individuals present. This mechanism is known as self-thinning (White & Harper, 1970).

1.2.3.3 Tilman's model of differential resource utilization

The basis of Tilman's model is the concept of a zero net growth isocline (ZNGI) (Begon *et al.*, 1990). Begon *et al.* (1990) define this as 'the boundary between the resource combinations which allow the species to survive and reproduce, and the resource combinations which do not'. A graphical representation of this concept is given in Figure 2. In region 1 neither species is able to survive, in region 2 only species a is capable of survival and in region 6 only species b is capable of survival. In region 3 resource Y is a

more limiting factor than resource X placing species a in an advantageous position as it can survive at lower levels of resource Y than species b can. The converse applies in region 5. In region 4 the growth of species a is limited by the availability of resource X, while the growth of species b is limited by the availability of resource Y, allowing the species to co-exist (Begon *et al.*, 1990).
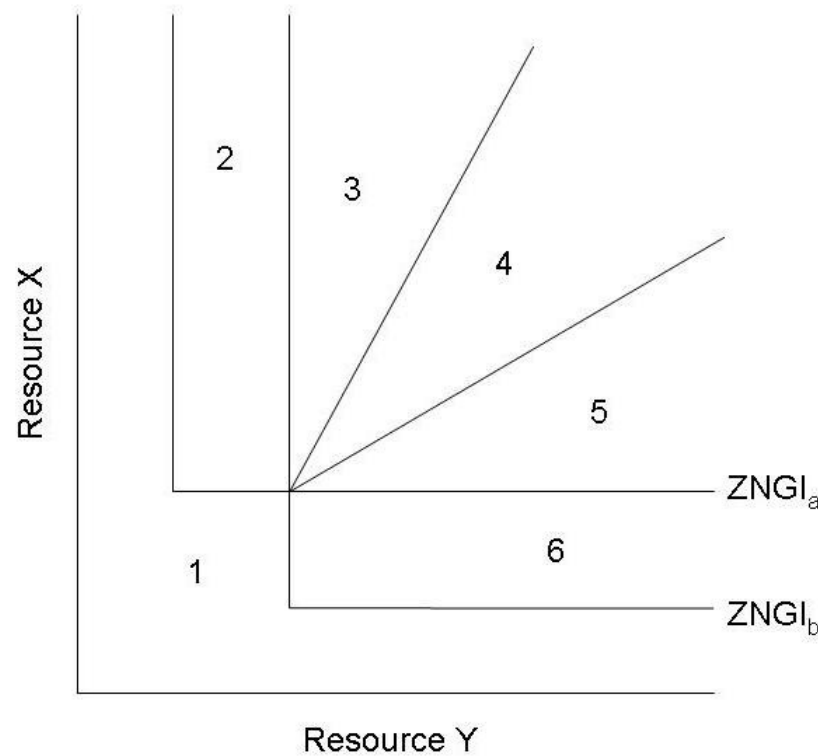
Figure 1.2: Co-existence of two competing species (a and b) at varying levels of two resources (X and Y) (Begon *et al.*, 1990)

Thompson (1987) has several doubts about the ability of this model to account for the structural composition of plant communities. Firstly, in order for a group of species to successfully co-exist the theory requires that they be ranked in order of competitive ability for one limiting resource and ranked in the reverse order for another limiting resource. Field studies have shown that this is not necessarily the case as often the more dominant species will be the superior competitor for both resources. Secondly, the theory states that limitations on above- and belowground resources will affect the plant species differently, while field studies have proven the opposite. Thirdly, early successional plants are regarded as being more efficient extractors of nutrients in nutrient poor soils than the later successional species. Several field studies have observed that the nutrient uptake rate of

plants normally associated with infertile soils is far inferior to the uptake rate of those normally associated with fertile soils, even when both species are grown in a nutrient poor environment. Fourthly, the model states that 'plants that are superior competitors for soil resources may have a higher ratio of absorptive root biomass to shoot biomass, be shorter at maturity, grow rapidly, and reproduce at an earlier age than plants that are superior light competitors'. While these characteristics do describe early successional plants in nutrient rich systems it has already been stated in point three that these plants do not have superior ability to compete for soil nutrients. Finally, Thompson (1987) disagrees with Tilman's statement that the previously mentioned life history differences may be the explanation for similarities observed between the secondary successional phase on nutrient rich soils and the first and second successional stages on nutrient poor soils. He argues that although structurally these stages do appear to be similar the species sequences may be vastly different (Thompson, 1987)

1.2.3.4 Spatial simulation model

This model describes the relationship between woody plants and the herbaceous understory. It takes into account both the stimulatory effects, such as nitrogen fixation, and the competitive effects, such as competition for water, of woody plants on this herbaceous understory. These effects are represented as indices and are multiplied together to obtain a net effect of the trees in the area. The model then allows herbaceous understory production to estimated for communities of varying tree size and density. The model was tested in *Eucalyptus crebra* woodlands in northeastern Australia and *Prosopis glandulosa* woodlands in southwestern U.S.A and produced results correlated with those seen in the literature. When the net effects of woody species where found to be competitive a negative curvilinear relationship was observed with low herbaceous biomass at high tree density, however when the net effects of woody species were stimulatory the maximum herbaceous yield occurred at an intermediate tree density (Scanlan, 1992).

Although all the models described above are theoretically feasible, they do not allow for the wide range of geographic and environmental conditions under which savanna occurs. A complete tree-grass interaction model would require a combination of elements of all the models allowing for variation according to the scale at which the vegetation was being examined and the influences acting upon it at that scale (Scholes & Archer, 1997).

The three major classes of influence on vegetative structure are geological, ecological and meteorological. Geologically the influences may be the soil type, substrate and geology of the area and the topography. All of these factors can exert influence over the vegetation from a micro to a regional scale. Ecologically factors of influence tend to differ over spatial scales. Some of these specific factors are as follows; at the micro scale individual plant interactions and very localised disturbances, at a local scale minor topographic variation, localised fires and herbivory, at the landscape scale severe fires and large herbivores such as elephants and at a regional scale the hydrology of the area, disease outbreaks and herbivore abundance. Meteorologically vegetation is affected by the annual and seasonal rainfall. This applies over a broad range of spatial scales but rarely influences at a level greater than landscape scale (Gillson, 2004).
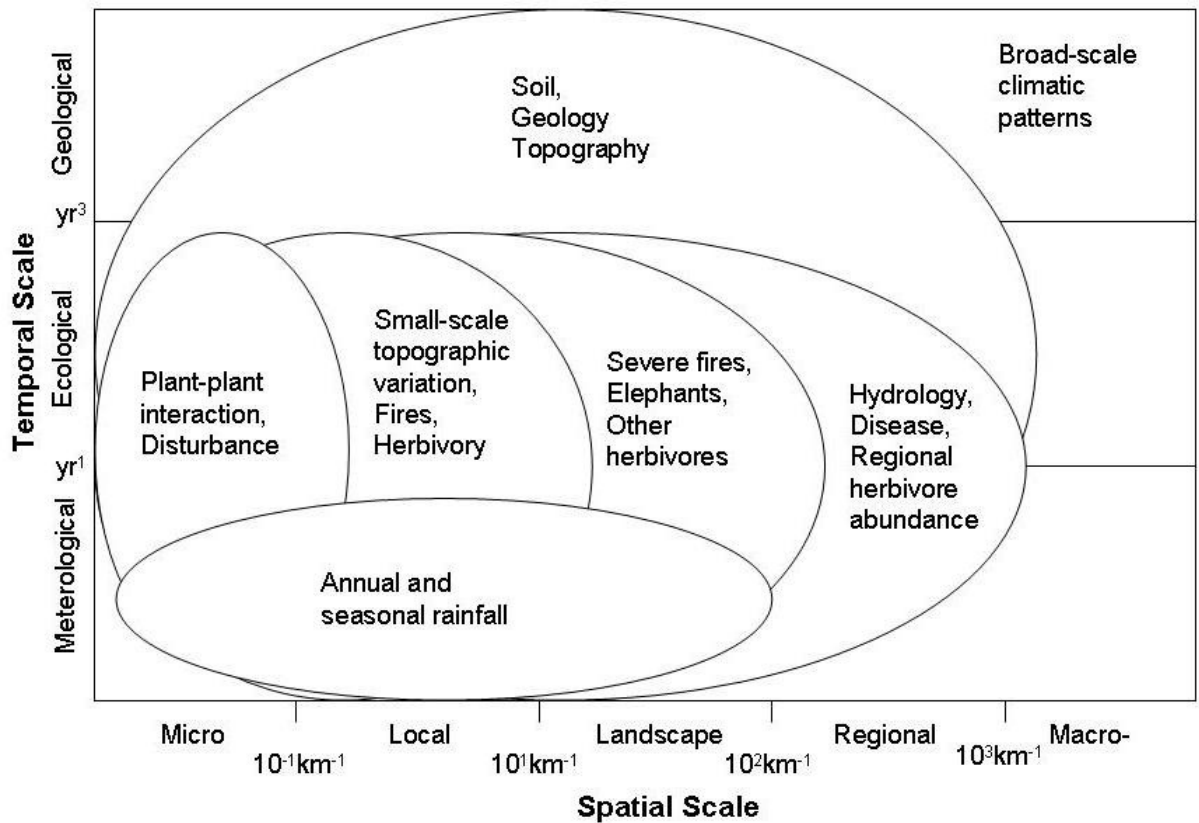
Figure 1.3: Scale of processes influencing tree abundance in savannas (Gillson, 2004)

1.3 COMPETITION

Competition is controlled by levels of resource availability. Cahill (1997) found that under nutrient rich conditions the sum of above- and belowground competition taken as individual measures was much higher than the overall resulting competitive effects experienced by

then plant. By contrast in nutrient poor conditions the sum of above- and belowground competition was much lower than the over competitive effects (Cahill, 1997). For this reason above- and belowground competition cannot be examined individually but must be considered as two parts interacting towards a final competitive effect.

1.3.1 Aboveground competition

Plant aboveground competition occurs mainly for light and as a result space. This form of competition is asymmetric as the larger plant will always have the competitive advantage. When plants colonize an open area the fast growing pioneer species will gain the competitive advantage, while in an established system the mature plants will have a competitive advantage over seedlings (Cahill, 1999).

Trials run using four species of Australian *Acacia* found that 75% shading resulted in increased retention of juvenile leaves, the production of larger, more horizontally orientated leaves, paler and longer stems with an extended period of apical dominance, smaller root areas and lower root and shoot dry masses (Milton, 1982). By contrast grasses may be either positively of negatively affected by shading and in some cases regeneration after defoliation occurs more rapidly when the plants are growing in shaded areas (Belsky, 1994).

1.3.2 Belowground competition

1.3.2.1 Rooting patterns

In the examination of more than 1300 records of root system sizes collected from various studies conducted in deserts, scrublands, grasslands and savannas Schenk & Jackson (2002) observed that maximum rooting depth for all plant growth forms except for trees and shrubs increased with an increase in annual rainfall. While this contradicts the expectation that plants in more arid regions tend to have deeper root systems in order to access ground water it must be noted that the bulk root biomass, between 50 and 95%, was found to be deeper in the more arid regions. As would be expected the lateral root spread was observed to be narrower in the more humid areas and wider in the more arid areas. It is believed that this wide root spread may be the explanation for the low plant densities in arid regions. Rainfall seasonality was found to have some effect on shrub rooting depth with plants in summer rainfall regions having a shallower maximum rooting depth than plants in winter rainfall

regions. Trees were found to be deeply rooted in all environments (Schenk & Jackson, 2002; Lee & Laurenroth, 1994).

Research conducted in the Nylsvley *Burkea* savanna showed that up to 96% of the woody plant root biomass is concentrated in the top 60 cm of soil, although most plants had 'sinker roots' extending as far as 2,2 m to bedrock level. These same species were found to have a lateral root spread of seven times greater than the aboveground canopy spread (Rutherford, 1982). Mordelet *et al.* (1997) found that in humid savanna areas little rooting depth separation is seen as both tree and grass roots were most abundant in the top 20 cm of soil. This is supported by Le Roux *et al.* (1995) and Hipondoka *et al.* (2003). The overall root phytomass was highest under the tree canopy as a result of increased nutrient availability and between 62 and 86 % of this phytomass comprised tree roots (Mordelet *et al.*, 1997). Hipondoka *et al.* (2003) found that in the semi arid regions of Botswana both tree and grass roots were found in high density in the upper soil layers. Although tree roots were found in higher densities beneath the tree canopy than in the open regions grass roots dominated in both situations (Hipondoka *et al.,* 2003). The removal of grass competition results in the white root density of cherry (*Prunus avium*) trees increasing closer to the surface however if the grass is not removed the average depth of the majority of the root biomass increases. Both the effects appear to be aggravated by the addition of nitrogen to the soil (Dawson *et al.*, 2001)

1.3.2.2 Belowground competition

Unlike aboveground competition plants compete for a large range of belowground resources such as water and over twenty essential nutrients of various size and mobility levels. This competition is also more balanced or size-symmetric as larger plants are not able to totally monopolize the nutrient sources as is the case with light competition and the shading of smaller plants. These larger plants are however at an advantage in areas with nutrient rich patches as they are more likely to come across these patches then plants with a smaller root system are (Casper & Jackson, 1997; Cahill & Casper, 2000; Shenk, 2006). Plant responses to belowground competition are very variable. For example the presence of neighbouring plants may result in changes in fine root growth, distribution and structure, while low resource availability may result in changes in resource uptake levels (Cahill, 2003b). While a large proportion of belowground competition is in the form of resource utilization. Interference competition in the form of allelopathy may also play a major role in

belowground interactions. This would result in a more asymmetric form of belowground competitive interaction similar to that of aboveground competition (Cahill & Casper, 2000; Shenk, 2006).

Some species are stronger competitors under certain environmental conditions but there is little evidence to show that these species have a higher nutrient content than those less aggressive competitors. This competitive ability may not only be affected by soil nutrient content but also by season. For example during inflorescence development both nutrient uptake and root growth decreases thus reducing competitive ability (Remison & Snaydon, 1978).

The major processes driving belowground resource utilization are the mass flow of water and nutrients and diffusion. The flow of water and the nutrients dissolved in it is controlled by transpiration rates. As transpiration and stomatal conductance increase water is drawn into the plant through the roots bringing dissolved mineral nutrients with it. When the nutrient concentration within the root epidermal cells is lower than that of the surrounding soil solution a local concentration gradient is created. This results in the diffusion of nutrients across the membrane. These two methods interact to supply Nitrogen, Potassium and Phosphorus, the three major nutrients required for vegetative growth (Casper & Jackson, 1997).

Schultz *et al.* (1955) found major differences in the rooting depth and spread of woody plants grown with and without competition with grasses. Three month old seedlings of the wedgeleaf ceanothus (*Ceanothus cuneatus*) growing in sandy loam soil with no surrounding herbaceous vegetation showed a root depth of 43 inches, lateral root spread of 26 inches and aboveground height of 6 to 8 inches. Similar seedlings growing in the same area but in a plot which had been seeded with ryegrass (*Lolium multiflorum*) were found to have a rooting depth of only 11.5 inches, very little lateral root spread and an aboveground height of 2 inches (Schultz *et al.*, 1955). This is supported by Harmer & Robertson (2003) who found that competition from grass resulted in a decrease in lateral root system development and overall root system length, but an increase in tap root length for six broadleaf tree species. This competition also appeared to increase the proportion of the overall biomass allocated to the root system (Harmer & Robertson, 2003).

While it is known that competition for water and nutrients are important factors in seedling establishment, competition for space also plays an important role (McConnaughay & Bazzaz, 1992). Large aboveground gaps tend to be more suitable for seedling establishment as they are correlated with low root biomass, while smaller gaps which may be suitable in terms of reduced competition for aboveground resources may have a high root biomass as a result of overlapping lateral root spread from the surrounding plants. This is correlated with the findings of Aguiar *et al.* (1992) who found that when root competition was removed by wrapping soil cores in fine nylon mesh both the survival and growth of seedlings was found to increase.

Reduction in the aboveground biomass by clipping did not affect seedling establishment as there was not a correlated decrease in root biomass (Jurena & Archer, 2003; Brown & Archer, 1999). However, Brown & Archer (1989) found that in an area ungrazed for 40 years moderate levels of grass defoliation resulted in eight times the number of *P. glandulosa* seedlings which had an 80% survival rate. While space for lateral root spread is important available depth is a more critical factor for seedling establishment. Jurena & Archer (2003) found that the minimum required area for the establishment of *Prosopis glandulosa* was approximately 80 cm^2 or 10 cm in diameter (Jurena & Archer, 2003). These gaps have an associated root biomass of 62 % while those measuring 20 and 60cm across have root biomasses of 33 and 4 % respectively (Hook *et al.*, 1994). In these gaps a 60% survival rate was observed in the first year of establishment and a 35% survival rate in the second (Jurena & Archer, 2003). This level of successful establishment is as a result of a decrease in belowground competition resulting from a decrease in root biomass. In gaps of approximately 50 cm in diameter root biomass has been found to be 20 % less then under the surrounding vegetation resulting in a 25 % decrease in underground competition (Cahill & Casper, 2002). This is supported by Snaydon & Howe (1986) who found that a decrease in gap size from 80 cm to 10 cm resulted in the average grass seedling weight decreasing by one hundred times. Wilson (1993) found that the presence of root competition had a marked impact on the survival of tree seedlings, but not on the survival of grass seedlings.

1.3.3 Interactions between above- and belowground competition

1.3.3.1 Positive interaction

'One form of competition amplifies the effects of the alternative form' (Cahill, 1999). When one form of competition results in retarded growth in the initial stages the plant loses

its competitive advantage and as a result will always be the weaker competitor within the system. For example initial belowground competition will reduce the plant's aboveground biomass and as a result it's ability to compete for light. Alternatively shading by a mature plant will decrease the level of photosynthates available for root development thus reducing nutrient uptake levels (Cahill, 1999).

1.3.3.2 No interaction

'The effects of one form of competition in no way alter the ability of a plant to compete in the other form of competition' (Cahill, 1999). This form of interaction may occur in one of three situations. Firstly in communities dominated by short plants where competition for light is not a major driving factor; secondly in communities such as forest systems which have an established size hierarchy and understory species are adapted to low light intensity situations and finally when competition is size symmetric, such as in belowground systems (Cahill, 1999).

1.3.3.3 Negative interaction

'One form of competition reduces the severity of the other form' (Cahill, 1999). This occurs in a situation where one of the forms of competition is so limiting that an increase in resource availability which results in a decrease in the other form of competition will have no effect on the growth of the plant. As a result of this the total competitive ability of a plant is not much greater than the competitive ability for that limiting factor (Cahill, 1999).

1.3.4 Root:Shoot Ratios

While actual root density is similar in high and low rainfall regions the root:shoot ratio is higher in low rainfall regions indicating that the plants are allocating a greater volume of resources to belowground growth. This is also the case in low nutrient areas (Belsky *et al*., 1993).

Wilson (1993) found that in the nutrient poor prairies in Canada the presence of root competition had a far more pronounced effect in terms of growth reduction than in the more nutrient rich forest regions. This correlates with the theory that a low standing biomass and a high root:shoot ratio are an indication of high levels of belowground competition (Wilson, 1993). This corresponds with the findings of Aguiar *et al.* (1992) who observed that root competition greatly decreased the number of leaves on grass plants. Cahill (2003a) found

that while root competition between transplanted seedlings and the surrounding old field vegetation resulted in the expected increase in root:shoot ratios this was as a result of the plant size rather then competitive effects as smaller plants tend to have higher root:shoot ratios. During the seedling stage root biomass may be used as an effective indicator of a plant's belowground competitive ability as their major function at this point is nutrient absorption and plant stability. As the plant matures thick storage roots develop forming the bulk of the root biomass and resulting a skewed representation of competitive ability (Cahill, 2003a).

Harmer & Robertson (2003) found that competition with grass increased the root:shoot ratios of broadleaf tree species, while Berendse (1981) found that an increase in plant density resulted in a related decrease in shoot:root ratio. This may be as a result of competition for belowground space or decreased light availability. As light availability decreases the root:shoot ratio decreases as a result of the increased leaf area ratio to compensate for the lower photon flux density (PFD) (Smith & Shackleton, 1988).

1.3.5 Competition on different soil depths and nutrient levels

Lateral root extension tends to be correlated with soil fertility with wider spreads in lower fertility soils with root lengths of up to 27 m being recorded in northern Surinam savanna (Van Donselaar-Ten Bokkel Huinink, 1966). Plants in nutrient rich regions also show a much shallower concentration of root biomass. Mckenzie & Morris (1995) found that the application of nitrogenous fertilizers to perennial ryegrass (*Lolium perenne*) pasture resulted in a shift in root density from 100-200 mm to 0 – 50 mm below ground. Plants grown in competition with other species under nutrient poor conditions have been found to have a Relative Yield Total (RYT), the ratio between species biomass in monoculture and in competition with other plants (Estorninos *et al*., 2002), of greater than 1, indicating that they are avoiding competition by making different demands on the available resources, while plants grown in nutrient rich conditions have a RYT of close to 1, indicating that competition is taking place (Berendse, 1981). As soil nutrient content increases important competitive interactions switch from belowground only to a combination of above- and belowground. Grasses grown under low nutrient conditions without neighbours showed a dry biomass of only 3 to 12% greater than those plants grown with neighbours, while grasses grown under high nutrient conditions without neighbours were up to 58% larger

than those grown with neighbours. This indicates a shift in limiting resources from nutrients only to both light and nutrients as soil nutrient content increases (Wilson & Tilman, 1991).

Competition for space also plays an important role in plant species coexistence. Fargoine & Tilman (2005) state that provided species have different rooting depths and growth periods it is possible for them to coexist. This is supported by Nedrow (1937) who found that plants restricted to a soil depth of approximately 11 cm showed a 55 % decrease in overall plant biomass, while plants restricted to a soil depth of approximately 22 cm showed a decrease of between 42 and 46 %.

1.3.6 Herbivory & competition

While it is generally accepted that resource competition and herbivory result in a multiplication of impacts on plant growth, Haag *et al.* (2004) found that this is may be dependant on the plant species concerned. The removal of insect herbivory alone had little effect on plant biomass, while the interaction between herbivory and competition affected three of the four study species indicating that the impacts of competition are more intense than the impacts of herbivory (Haag *et al.*, 2004). Alternatively grazing may stimulate root growth in some species, while inhibiting it in others (Richards, 1984; McNaughton *et al.*, 1998) resulting in changes in belowground competitive interactions (Cahill, 2003a). When root growth is inhibited there must be a correlated decrease in aboveground growth as a result of decreased nutritional availability (McNaughton *et al.*, 1998). Nedrow (1937) found that the removal of aboveground biomass to a height of approximately 9 cm on plants restricted to a soil depth of 11 cm resulted in an 85 % reduction in overall plant biomass. Similarly, Schuster (1964) found that the overall root biomass comprised 93, 90 and 81% grass root biomass in areas that had been ungrazed, moderately and heavily grazed respectively.

The defoliation of the surrounding grass sward has been found to have little effect on browse biomass production, while total removal of the sward results in a 40 to 166% increase browse production. Unexpectedly, the frequent defoliation of trees has also been found to result in up to a 40% decrease in grass production (Stuart-Hill & Tainton, 1989).

An increase in bush density has long been attributed to high levels of grazing owing to the fact that grazing creates germination gaps making resources available to germinating

seedlings. Alternatively fire has been regarded as having a negative effect on tree seedling establishment, although it too reduces aboveground grass biomass creating gaps with increased available resources in a similar manner to grazing. In addition fire may break dormancy on hard coated seeds resulting in further woody plant germination (Kraaij & Ward, 2006). In semi arid regions grazing is not the sole driving factor behind the increase in bush density. While it creates available niches for seed germination grazing alone is not sufficient to allow for seedling establishment, it is rather the interaction between grazing, fire, rainfall and soil nutrient status. A combination of above average rainfall, high levels of grazing, intermittent fire to break dormancy and low levels of soil nitrogen will result in mass germination and leguminous woody seedling development (Kraaij & Ward, 2006).

1.3.7 Productivity

Catena position plays an important role in woody productivity of a savanna region. Upper-catena areas tend to have lower available water, while lower-catena areas have increased available water as a result of run-on (Smith & Goodman, 1986). The presence of trees within a grassland greatly increases grass productivity however the extent differs depending on water availability. In high rainfall areas the grass understory was 52 % more productive than the open areas, while in the low rainfall regions the understory production was 95 % higher than in the open areas (Belsky *et al*., 1993).

1.4 STUDY SPECIES

1.4.1 Trees

The subfamily Mimosoideae consists of over fifty genera comprising a total of over two thousand species (Carr, 1976). More than half of these species form part the genus *Acacia*, making it the largest genus in the subfamily Mimosoideae and the second largest genus in the family Leguminosae (Ross, 1971). In South Africa forty species, subspecies and varieties of this genus are found, occurring mainly in the savanna biome (Smit, 1999).

1.4.1.1 *Acacia karroo*

Acacia karroo Hayne is one of the most widespread *Acacia* species occurring throughout southern Africa and is classed as both an undesirable plant that should be removed or eradicated if possible and as a valuable fodder plant (Acocks, 1988; Carr, 1976; Davidson & Jeppe, 1981). It grows in a wide variety of habitats from river banks to bushveld, dry thornveld, grassland and coastal dunes (Davidson & Jeppe, 1981). It is able to grow under

variable climatic conditions (Ross, 1971) and is possibly one the most cold-tolerant species (Smit, 1999) being both drought and frost resistant (Thomas & Grant, 2004). It grows on most soil types but is usually associated with high fertility clay and loam soils (Smit, 1999). Tree height is very variable, ranging from five to over twenty metres and plants may be single to many stemmed resulting a dense bushy spreading crown (Davidson & Jeppe, 1981; Carr, 1976; Smit, 1999). The seed pods are sickle-shaped, up to 8 mm wide, 150 mm long and contain between 8 and 10 seeds. These pods are dehiscent, drying, becoming brittle and splitting open to allow dispersal of the seeds. The seeds are a flattened elliptic shape, up to 7 mm long and 5 mm wide and weighing between 0.027 g and 0.051 g (Smit, 1999; Brown, 1965; Story, 1952). Seeds germinate within 3 to 12 days and under favourable conditions can grow up to 1 m per year (Venter & Venter, 2002). *A. karroo* is regarded as a good indicator of soil water, good grazing and is a good fodder and fuel plant (Cotes Palgrave, 2002). All parts are suitable forage for cattle and goats (Thomas & Grant, 2004) and young leaves are sought after browse for black rhino, giraffe, eland, kudu, gemsbok, nyala, sable, impala and springbok (Venter & Venter, 2002).The flowers are eaten by monkeys and many bird species as the pollen has a high protein content (Coates Palgrave, 2002). *A. karroo* is also an important plant in honey production and the bark, which contains up to 19% tannin, is used in tanning leather (Coates Palgrave, 2002; Venter & Venter, 2002). The inner bark can be used to produce rope and the gum is used in both confectionery and adhesive production (Coates Palgrave, 2002). The seeds can be roasted, ground and used as a substitute for coffee (van Wyk & van Wyk, 1997). The wood, which has an air-dry weight of 800kg/m^3, is hard but is prone to borer beetles. It is used in the production of wheel spokes, yokes and tool handles (Thomas & Grant, 2004; van Wyk & van Wyk, 1997; Venter & Venter, 2002). An infusion of the bark can also be used as an antidote to *Moraea* poisoning in cattle (Cotes Palgrave, 2002). The *Acacia karroo* complex has been further divided into six species or varieties, *A. dyeri, A. karroo, A. kosiensis, A. natalitia, A. robbertsei* and *A. theronii. A. natalitia* occurs east of the Drakensberg mountains in KwaZulu-Natal and the Eastern Cape and is most likely to be the variety within the *A. karroo*-complex which is used in these trials (Coates Palgrave, 2002).

1.4.1.2 *Acacia nilotica*

A. nilotica (L.) Willd. Ex Del. is a fairly common species in the dry thornveld, woodland and dry river valleys of southern Africa and is classed as an undesirable plant which should be removed or eradicated if possible (Acocks, 1988; Ross, 1971; Davidson & Jeppe, 1981).

It is generally found on heavy soils with a high clay content, although it may also occur on sodic soils and along the coastline has shown a preference for sandy and alluvial soils (Smit,1999). Trees are both drought and frost resistant (Venter & Venter, 2002). They are usually single stemmed and height can range from five to over ten meters under favourable conditions (Davidson & Jeppe, 1981; Ross, 1971; Smit, 1999). Seeds pods are straight to slightly curved, up to 22 mm wide and 170 mm long and contain up to 16 seeds per pod. They taper to a point at the tip and have distinct constriction between each seed resulting in conspicuous bumps on the surface of the seed pod. These pods are indehiscent and tend break up into single seeded segments after falling from the plant (Smit, 1999). The seeds are round and thickened, up to 9 mm long and 8 mm wide and weighing between 0.076 g and 0.083 g (Smit, 1999; Brown, 1965). Seeds germinate in 7 to 15 days, having between 60 and 90% germination success and plants can grow up to 700 mm per year (Venter & Venter, 2002). *A. nilotica* is considered a good indicator of sweetveld and of soils with a high clay content (Venter & Venter, 2002). Both the leaves and mature pods are utilized as forage by many game and livestock species, such as, black rhino, giraffe, impala, nyala, and cattle (Coates Palgrave, 2002; Thomas & Grant, 2004, Venter & Venter, 2002). This high utilization of the pods plays a major role in the seed dispersal of this species (Thomas & Grant, 2004). Although this is a useful forage species the ripe pods and large amounts of leaf material are toxic to goats and may cause pregnant ewes to abort and adults to die (Venter & Venter, 2002). The wood, which has an air-dry weight of 1100 g/m^3 (Venter & Venter, 2002), is hard, durable and resistant to borer beetles. It has been widely used from the Neolithic period onward. Since approximately 2900 BC *A. nilotica* has been used as a major source of timber for roofing, boat making and furniture (New, 1984; Thomas & Grant, 2004). It has also been used widely in the tanning industry as the bark contains up to 45% tannin (New, 1984; Venter & Venter, 2002). The wood is now mainly used for fuel and fencing posts. The voortrekkers used an extract from the pods to make ink and the gum has been used for confectionery (Coates Palgrave, 2002). *A. nilotica* has many medicinal uses. It can be used as medication for eye diseases and as a tranquilizer, root extract can be used to treat tuberculosis, diarrhoea, toothache and dysentery, while leaf extract can be used for menstrual problems, eye infections, diarrhea, leprosy, stomach ulcers and indigestion (Thomas & Grant, 2004). A decoction made from the bark can also be used to treat coughs (Coates Palgrave, 2002).

1.4.1.3 Seeds and germination

While *A. karroo* is able to germinate under a wide range of temperatures the optimum growing season temperature for seedling establishment is approximately 25°C. It is for this reason that bush encroachment tends to occur following climatic temperature changes (Du Toit, 1967). Germination of *A.* nilotica has also been found to be most successful at approximately 25°C (Brown, 1965). The seedlings of *A. karroo* are sensitive to desiccation and to rapid changes in ambient temperature, as very high soil temperatures can prove fatal to seedlings. It therefore requires long periods of sufficient moisture and appropriate ambient temperature to successfully establish and become invasive (New, 1984). Very little germination of *A. nilotica* has been observed at high moisture levels, possibly due to a lack of available oxygen. This increases as the seeds dry out as the seed coat begins to split at the hilum exposing the radicle and allowing it to grow (Brown, 1965). Root elongation is also more rapid under drier conditions (Brown, 1965). It would appear that *A. nilotica* relies fairly heavily on nutrient supply from the seed cotyledons as seedlings appear to be able to survive browsing provided detachment is above the cotyledons (Brown, 1965)

African *Acacias* produce can produce as much as 45 000 seeds per year resulting in seed banks of up to 9400 seeds per m^2, although up to 85% of these seeds may suffer from predation by bruchid beetles. *A. karroo* has been found to produce as many as 19 000 seeds although this is dependent on the growth from, while *Acacia nilotica* can produce up to 3150 pods. In Hluhluwe-Umfolozi Park the density of adult *A. nilotica* trees was found to be much greater than that of adult *A. karroo* trees, however the density of juvenile *A. karroo* was three times greater than that of *A. nilotica* (Walters & Milton, 2003). This may be due to the fact that *A. karroo* is a shade tolerant species which can germinate under established plants (O' Connor, 1995). Walters & Milton (2003) also found that a proportion of *A. karroo* seeds were able to germinate after attack by bruchid beetles which would further increase seedling numbers. It is therefore possible that *A. karroo* would colonize areas which other *Acacia* species would not be able to (Walters & Milton, 2003). These seeds, particularly those of *A. nilotica*, are able to form persistent seed bank as a result of the hard, thick testa surrounding and protecting the seed. These seeds banks may contain between several hundred and several thousand seeds per square meter and may remain viable for up to five years (Smit, 1999).

Both *A. nilotica* and *A. karroo* have been recognised as problem species in terms of bush encroachment since the 1940's, both being described as 'thicket formers' (West, 1947). *A.*

nilotica, then known as *Acacia arabica*, was noted to provide a crop of pods which were of nutritional value to livestock but should still be carefully monitored and kept under control. *A. karroo* was described as a tree which is difficult to kill and coppices regularly and often as a result of fire (West, 1947; New, 1984).

O'Connor (1995) further examined the widely accepted statement that livestock act as seed dispersal agents for woody plant species, providing a moist, fertile environment within a dung pat for germination. *A. karroo* seeds were used for the experiment and no seeds germinated within a dung pat. It is possible that some seeds may be removed from the dung pat by birds or insects and in this way become part of the seed bank and germinate (O'Connor, 1995), however the likelihood of this occurring on a regular basis is slim and thus it cannot be regarded as a driving force behind bush encroachment. In addition to this the effects of both shading and moisture on seedling establishment were investigated. It was found that shading had no effect on seedling establishment, with equal numbers of seedling germinating in both shaded and unshaded plots. Moisture availability was determined to be the most influential factor in seed germination and seedling establishment, as more than double the number of seedlings germinated in the irrigated plots (O'Connor, 1995). The seedlings are very sensitive to water shortages, often dying as a result of wilt in the first two weeks after germination indicating that an extended period of rainfall, rather than a once-off cloudburst is necessary for successful establishment (Du Toit, 1967). This is supported by Sankaran *et al.* (2005) who found the percentage woody plant cover in arid and semi-arid regions of Africa was controlled by mean annual precipitation.

A low density of *A. karroo* in grassland has been found to have a positive effect on the grass layer, reflecting a higher overall biomass in comparison to areas where no trees are present. This effect was found to be consistent up to a tree density of 300 tree equivalents per hectare (Stuart-Hill *et al.*, 1987). Grass grown in soil collected from below savanna tree canopies was found to have a higher dry biomass than grass grown in soil collected from open areas, indicating that the difference may be as a result of increased soil nutrients. This was confirmed by lab analysis of soil samples (Bosch & van Wyk, 1970). Conversely Du Toit (1968) found no significant correlation between the density of *A. karroo* and species composition and density of the grass sward.

1.4.2 Grasses

1.4.2.1 *Aristida junciformis*

Aristida junciformis Trin. Et Rupr. is a densely tufted perennial grass with thin clums, growing up to 60 cm tall (Chippendall, 1959, Van Oudtshoorn, 2002). The leaves are thin, not more than 3mm wide, wiry and tough (Tainton *et al.*, 1990). They are often rolled or folded towards the base (Chippendall, 1959). In South Africa it occurs in the coastal regions of the Southern and Eastern Cape, in the eastern Free State, KwaZulu Natal and across the southern lowveld (Chippendall, 1959). It is also found further into southern and east Africa (Gibbs Russell *et al.*, 1991, Van Oudtshoorn, 2002). It favours coastal and mistbelt regions where it occurs in the grassland, savanna and fynbos biomes (Tainton *et al.*, 1990, Van Oudtshoorn, 2002). It grows under variable moisture conditions, from high altitude regions with high rainfall and damp vlei areas to dry areas with low rainfall. It is mainly found on poor, gravelly soils but can also grow clay soils such as those found in vlei regions (Van Oudtshoorn, 2002). *A. junciformis* is a pioneer species (Bews, 1918) that increases in density as a result of overgrazing or poor veld management (Tainton *et al.*, 1990). In these situations it may for dominant stands, excluding other species (Van Oudtshoorn, 2002) and is difficult to control as stock will not graze it because of the high level of indigestible cell wall components it contains (Tainton *et al.*, 1990). If it can be kept short it is possible that stock may graze the young shoots (Tainton *et al.*, 1990). Mowing at the time of flowering can also be used as a control method but it will not eradicate this species (Tainton *et al.*, 1990). Although this species has little to no grazing it offers good ground cover which may be useful in preventing erosion (Van Oudtshoorn, 2002).

1.4.2.2 *Eragrostis capensis*

Eragrostis capensis (Thunb.) Trin is a tufted perennial pioneer grass, between 20 and 60 cm tall (Bews, 1918, Chippendall, 1959). Plants can be loosely or densely tufted and growth forms can range from erect to gently ascending from bent nodes (Chippendall, 1959, Tainton *et al.*, 1990). These plants tend to have very few leaves, usually concentrated around the base, and have a tendency to become stemmy (Tainton *et al.*, 1990, Van Oudtshoorn, 2002). The leaf blades are glabrous and rolled, rarely more than 10 cm in length (Tainton *et al.*, 1990). In South Africa it is found along the southern Cape coast, in the Eastern Cape, eastern Free State, KwaZulu Natal and the southern lowveld (Chippendall, 1959). It is also widespread the tropical regions, in southern, central and east Africa as far as Zaire, Kenya and Tanzania as well as Madegascar and Thailand (Gibbs

Russell *et al.*, 1991, Van Oudtshoorn, 2002). It occurs in the grassland, savanna and fynbos biomes where it can grow in sandy, clay or loam soils (Gibbs Russell, 1991, Van Oudtshoorn, 2002). It can survive under variable moisture conditions from dry soils to vlei areas and disturbed areas along roadsides where excess rainwater collects (Tainton *et al.*, 1990, Van Oudtshoorn, 2002). It tends to become dominant on shallow soils where there is little competition from other grasses (Tainton *et al.*, 1990). Although it is relatively palatable it is not an important grazing species but can be useful in mixed veld and sourveld areas (Tainton *et al.*, 1990). It starts to grow early in spring (Tainton *et al.*, 1990) and is one of the first grasses to resprout after a fire (Van Oudtshoorn, 2002). Despite its low leaf production it will be readily utilized by both stock and game until more palatable grasses begin to sprout (Van Oudtshoorn, 2002).

1.4.2.3 *Eragrostis racemosa*

Eragrostis racemosa (Thunb.) Stend. is a short densely tufted perennial grass. The culms are between 10 and 60 cm tall, sturdy, erect and usually glabrous (Chippendall, 1959, Van Oudtshoorn, 2002). The leaf sheath can be hairy or glabrous, while the leaves are covered with long, flexible bulbous-based hairs (Chippendall, 1959, Tainton *et al.*, 1990). The leaves may be expanded or have the margin in-rolled (Chippendall, 1959). It is widespread in South Africa occurring in the Eastern Cape, KwaZulu Natal, Free State, Swaziland and lowveld areas (Chippendall, 1959). It is also found in other areas of southern Africa, East and Central Africa as far north as Sudan and in Madagascar (Gibbs Russell *et al.*, 1991, Van Oudtshoorn, 2002). In these areas it is found in the grassland, savanna and fynbos biomes, tending to avoid the warmer arid regions (Gibbs Russell *et al.*, 1959, Tainton *et al.*, 1990). It favours damp, shallow soils in areas with high rainfall, growing mainly on sandy, gravelly or stony soils but occasionally growing on clay soils (Van Oudtshoorn, 2002). It tends to dominate on shallow soils overlying shale (Tainton *et al.*, 1990) and is often found on disturbed sites (Van Oudtshoorn, 2002). It is palatable but is not a very useful forage species as it has a low leaf yield and most of the leaves are concentrated at the base of the plant (Tainton *et al.*, 1990, Van Oudtshoorn, 2002). It is however useful to prevent erosion on shallow soils and in heavily grazed areas (Gibbs Russell *et al.*, 1991, Tainton *et al.*, 1990, Van Oudtshoorn, 2002).

1.4.2.4 *Hyparrhenia hirta*

Hyparrhenia hirta (L.) Stapf. is a drought-resistant, dense, erect, tufted perennial grass with a dense fibrous root system (Fetene, 2003, Van Oudtshoorn, 2002). It has woody, many nodded stems and tends to branch from the lower nodes (Tainton *et al.,* 1990). Height can vary from 30 to 100 cm (Chippendall, 1959). The leaves are glabrous with a prominent midvein down the centre and blue-green in colour, developing a red tinge when old (Chippendall *et al.*, 1959, Tainton *et al.*, 1990). Lower leaf sheaths are often hairy at the base (Chippendall, 1959). It is one of the most widely distributed South African grass species, occurring in the southern, south-eastern and central Cape, KwaZulu Natal, Free State and lovweld area. It is also found throughout southern and east Africa, the mediterranean regions and Pakistan (Van Oudtshoorn, 2002). It occurs from mid to low altitude areas where it is found in the grassland, savanna, fynbos and Nama-karroo biomes (Gibbs Russell *et al.*, 1991, Tainton, 1990). It grows on well drained soil, particularly gravelly soils in open and disturbed areas but may also be found on heavier soils along rivers and watercourses (Van Oudtshoorn, 2002). In old lands it tends to become dominant and form monotypic swards which may persist for years (Tainton *et al.*, 1990). It is a leafy plant which can be useful fodder if grazed early in the growing season or after burning (Tainton *et* al., 1990, Van Oudtshoorn, 2002). The tall flowering stems appear in mid to late summer and after this plants tend to become stemmy and less useful for grazing (Tainton *et al.*, 1990). This species often grows in association with *Themeda triandra* and together they can form a useful mixed veld fodder base which is palatable for up to 8 months of the year (Tainton *et al.*, 1990). *H. hirta* is also useful for stabilizing hard, gravelly soil and preventing erosion (Van Oudtshoorn, 2002). In many areas the local people also use it as a source of thatching material (Chippendall, 1959, Van Outdtshoorn, 2002). It has been observed to be a highly competitive species in a low nutrient situation with decreasing competitive ability as the soil N content increases (Fynn *et al.*, 2005). This may be as a result of the structure of the root system (Fetene, 2003).

1.4.2.5 *Panicum maximum*

Panicum maximum Jacq. is a leafy, erect, loosely tufted perennial grass (Chippendall, 1959, Gibbs Russell *et al.*, 1991, Van Oudtshoorn, 2002). It roots from the lower nodes and often has short creeping rhizomes (Chippendall, 1959). Height is very variable from a little as 60 cm to as much as 300 cm in tropical regions where it begins to take on a reed-like appearance (Chippendall, 1959, Van Oudtshoorn, 2002). The broad, expanded leaves are sometimes glabrous but more often hairy covered with hard, tubercle-based hairs

(Chippendall, 1959). It is widely distributed in the eastern half of South Africa and occurs in the grassland, savanna and Nama-karroo biomes (Gibbs Russell *et al.*, 1991). Although it originated in Africa it has since spread to many tropical areas (Van Oudtshoorn, 2002). It favours shady, cool, damp places with fertile soils, such as low-lying coastal areas and interior basins, and is often associated with trees in open woodland areas (Chippendall, 1959, Tainton *et al.*, 1990, Van Oudtshoorn, 2002). In areas with a high tree density this grass often dominates (Tainton *et al.*, 1990). It is a useful fodder plant in tropical and subtropical Africa as it remains green until late winter and is often used to make hay or as a pasture grass (Chippendall, 1959, Van Oudtshoorn, 2002) although it does not persist under high grazing pressure (Tainton *et al.*, 1990). When moisture is not a limiting factor it grows rapidly (Chippendall, 1959), producing up to 12 tonnes per hectare with a crude protein level of between 10 and 20 percent (Tainton *et al.*, 1990). *P. maximum* has been observed to be a highly competitive species in a high nutrient situation, being strongly influenced by the interaction between Nitrogen (N) and Potassium (P) levels, while in a low nutrient situation when both competing species were subjected to defoliation it was outcompeted by *Themeda triandra* (Fynn *et al.*, 2005).

1.4.2.6 *Sporobolus africanus*

Sporobolus africanus (Poir.) Robyns & Tournay, previously classified as *Sporobolus capensis* (Willd.) Kunth, is a relatively small, tufted, perennial, pioneer grass (Bews, 1918, Chippendall, 1959, Tainton *et al.*, 1990). The culms and lower leaf sheaths are compressed and keeled towards the base, growing away from the rooting point at an angle, particularly if heavily grazed or trampled (Chippendall, 1959, Tainton *et al.*, 1990). It has a strong root system which makes it difficult to uproot and the leaves are tough and difficult to break (Van Oudtshoorn, 2002). It is widely distributed in the southern Cape and the eastern region of South Africa, but does not occur in the dry Karroo regions (Chippendall, 1959). It is also found in other regions of southern and east Africa and as far north as Ethiopia (Van Oudtshoorn, 2002). It is found in the grassland, savanna and fynbos biomes (Gibbs Russell *et al.*, 1991) and favours poor soils and disturbed areas, such as overgrazed veld (Chippendall, 1959, Tainton *et al.*, 1990). It is often found on compacted soil, particularly in damp places, such as around water points (Van Oudtsoorn, 2002) and is an indication of disturbed areas or mismanagement of the veld (Tainton *et al.*, 1990). Although the species is fairly palatable it has little leaf material and is generally only grazed when the plant is young or there is a high concentration of animals on the veld (Tainton *et al.*, 1990, Van

Oudtshoorn, 2002). It can however be useful late into winter as the stems remain succulent (Tainton *et al*., 1990).

1.4.2.7 *Themeda triandra*

Themeda triandra Forsk. is a tufted perennial climax grass, between 30 and 180 cm tall (Chippendall, 1959, Tainton *et al.*, 1990). It has very variable morphology with leaf blades ranging from glabrous to hairy and folded to expanded (Chippendall, 1959). There are four different varieties of this species recognized with various combinations of leaf characteristics, glabrous and green, glabrous and blueish, hairy and green and hairy and blueish. Leaf blades often have a reddish tinge (Chippendall, 1959). It occurs widely throughout southern and east Africa, being found in the grassland, savanna, fynbos and Nama-karroo biomes (Gibbs Russell *et al*., 1991, Van Oudtshoorn, 2002). It can grow in most soil types but tends to favour clay (Van Oudtshoorn, 2002). It can withstand various moisture levels, from average to high rainfall, and altitude ranging from 1300 m to 3000 m, with the shorter varieties occurring at high altitudes and the taller varieties at low altitudes (Tainton *et al.,* 1990, Van Oudtshoorn, 2002). It is a valuable fodder crop and is an indicator of veld in good condition (Chippendall, 1989, Tainton *et al.*, 1990). It is palatable but it's major value is that it tends to form dense, fairly monotypic stands and will increase in abundance with regular burning, provided it is not overgrazed (Van Oudtshoorn, 2002). A *T. triandra* dominated grass sward is also fairly stable and requires very little input other than correct management to maintain maximum productivity (Tainton *et al.*, 1990).

This thesis aims to answer the following questions:

Chapter 2

What is the effect of nutrient level (low or high) and competing grass species on:

(1) Temporal growth?

(2) Final above ground biomass?

(3) Total root biomass?

(4) Biomass distribution?

(5) Relative Interaction Index (RII)?

Chapter 3

(1) What are the relative effects of above and belowground competition from grass on the biomass and height of two species of *Acacia*?

and (2) were these effects dependant upon environment, specifically varying soil depth down a landscape catena?

Chapter 4

What are the relative effects of above- and belowground competition and their interactions on: (1) aboveground growth percentage, in terms of biomass, and tuft size, in terms of tiller number, of three locally common grass species and the effects of soil depth on these interactions?

and (2) growth pattern of the three grass species over a 24 week period across three levels of soil depth?

and (3) does soil depth mediate competitive interactions between grass seedlings and the surrounding sward?

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CHAPTER TWO

THE EFFECT OF DIFFERENT GRASS SPECIES ON THE GROWTH OF *ACACIA* SEEDLINGS UNDER DIFFERENT SOIL NUTRIENT REGIMES

2.1 ABSTRACT

The structure and composition of savanna vegetation is influenced by resource availability and disturbance. Grasses, a major component of savannas, influence this resource availability by competing directly with trees for light, water and soil nutrient resources. The direct causes of bush encroachment are not always apparent, but are commonly ascribed to overgrazing and consequent decreased grass competition. The impact of competition exerted by different grass species on tree growth was identified as a critical focus area to improve understanding of bush encroachment. In order to investigate this seedlings were planted in pots with a tree seedling, either *Acacia karroo* or *Acacia nilotica*, as the central phytometer with four grass seedlings of the same species, planted around it. The major competitive effects experienced by the tree seedlings were dependant on grass species and nutrient level ($p < 0.001$). *A. nilotica* was affected by aboveground competition while *A. karroo* was affected by belowground competition. *E. capensis* caused the greatest decrease in *A. karroo* plant biomass ($p = 0.020$). Both *E. capensis* and *H. hirta* had large competitive effects on the aboveground biomass of *A. nilotica* ($p = 0.020$), while *S. africanus* had the greatest effect on belowground biomass. Increasing nutrient availability resulted in an increase in the competitive effect exerted on *A. karroo*, while the little to no change was seen in the competitive effect exerted on *A. nilotica*. Changes in savanna composition and structure are thus likely to be influenced by initial species composition and soil nutrient composition.

This experiment aimed to answer the following questions:

What is the effect of nutrient level (low or high) and competing grass species on:

(1) Temporal growth?

(2) Final above ground biomass?

(3) Total root biomass?

(4) Biomass distribution?

(5) Relative Interaction Index (RII)?

2.2 INTRODUCTION

Scholes & Archer (1997) define savannas as "communities or landscapes with a continuous grass layer and scattered trees". The species composition within these communities is controlled by various factors such as fire, herbivory, climate and resource availability. The level of influence that these factors have on individual plants is largely dependent on tree size (Sankaran *et al*., 2004). It has been observed that grasses compete with trees both directly and indirectly. They compete directly for light, water and nutrient resources, while they compete indirectly by providing a fire fuel load, which affects the frequency and intensity of burns (Scholes & Archer, 1997). Increased frequency of trees in savanna areas, known as bush encroachment, has significantly impacted commercial farming. This problem is suggested to occur as a result of heavy and sustained grazing pressure and causes grass production to decrease rapidly thus forming a positive feedback system (Teague & Smit, 1992). Landowners are reluctant to lower their stocking rates to allow the grass sward to recover and often have to spend large amounts of money mechanically clearing the land before it becomes productive again (Teague & Smit, 1992; Smit, 2004).

In addition the increasing atmospheric CO_2 levels are believed to be aggravating the bush encroachment problem (Meadows, 2006). As CO_2 is a major component in the process of photosynthesis an increase in the availability of this compound may result in an increase in savanna productivity. This is known as the 'CO_2 fertilization effect' and has a greater impact on the productivity of C_3 plants, such as trees, than on the productivity of C_4 plants, such as grasses (Scholes & Bailey, 1996). This increased productivity should allow the trees to grow bigger, more quickly, which would allow tree seedlings to escape the zone of most intense competition with the grass sward rapidly and would further increase the competitive ability of woody plants in areas where the grass layer has already been impacted (Scholes & Bailey, 1996). However, further study has revealed that the growth of C_4 plants is also to some extent affected by CO_2 fertilization although this may be dependent on the growth stage of the plant concerned (Ghannoum, *et al.*, 2000; Wand, Midgley & Stock, 2002; Wand & Midgley, 2004). Consequently research into grass-tree competition and interactions has become an important scientific focus (Scholes & Archer, 1997). Several studies have examined combinations of root and shoot competition and attempted to determine relations between the two, but producing contrasting results (Cahill, 2002). Most have implied that reduced shoot and root competition by grasses facilitates tree growth but no quantitative measure of relative strength has been formulated.

2.3 METHODS

In order to investigate the competitive effect of specific grass species on tree seedlings various combinations of grass and tree species were grown under both nutrient rich and nutrient poor conditions. These combinations were planted in pots with a volume of 1178 cm^3, filled with sand with a tree species as the central phytometer with four grass seedlings planted around it. Tree seedlings were also planted alone. Plants were grown in an open area at the University of KwaZulu-Natal Arboretum in Pietermaritzburg and irrigated to ensure sufficient water availability. Seed used for this experiment was collected in the Pietermaritzburg area during 2004 and 2005, was inspected to ensure no bruchid beetle damage and scarified by soaking in sulphuric acid before sprouting. The experiment was a full factorial and pots were laid out in a completely randomised manner with six replications of each treatment. The tree seedlings used were *Acacia nilotica* and *Acacia karroo,* while the grass species used were *Themeda triandra, Eragrostis capensis, Hyparrhenia hirta, Aristida junciformis, Sporobolus africanus* and *Panicum maximum.* Both *A. nilotica* and *A. karroo* have been recognised as species with high potential to rapidly increase in density since the 1940's, both being described as 'thicket formers' (West, 1947). The six grass species were selected because they vary in structure, with differing leaf heights and tillering ability varying from short plants with small leaves forming dense tufts to tall plants with relatively few tillers but large leaves (unpublished data, RWS Fynn).

The nutrient rich treatments were watered with 300 ml of 80% Hoagland's nutrient solution (Hoagland & Arnon, 1950) every four days while the nutrient poor treatments were given the same amount of water but no additional nutrients. Every two weeks plant height and number of leaves per tree seedling were measured. The trial was run from 12 October 2005 to 11 April 2006. After 26 weeks final measurements were taken and plants were then removed from the pots and the roots washed with water to remove excess sand. Tree and grass roots were separated and the maximum length of both tree and grass roots was measured. Above- and belowground material was separated and belowground material split into five belowground levels, 0-50 mm, 50-100 mm, 100-150 mm, 150 – 250 mm and 250-500 mm. This material was then dried for 24 hours at 60°C and weighed.

2.4 ANALYSIS

Change in mean tree height for high and low fertility conditions were graphed against time for each competing grass species and for both tree species growing alone. Relative root dry biomass (RRDB) was calculated by dividing the dry biomass for each soil level by the depth of that level in mm to get a value in grams of dry mass per millimetre soil depth. These values were then plotted as stacked column plots according to treatment. Root/shoot biomass ratios were calculated according to Monk (1966) by dividing the mean belowground biomass, calculated by adding together the dry biomass values for each soil level, by the mean aboveground biomass for that particular treatment combination.

Relative interaction indices (RII) were calculated for both above- and belowground biomass of each species within each combination and treatment. RII was calculated according to Armas, Oridiales & Pugnaire (2004). The index is a ratio representing the net loss or gain of a measurable trait, generally biomass, as a result of inter-specific interaction relative to value of that trait when this inter-specific interaction is absent. The values of this ratio range from -1 to 1, with negative values indicating competition, zero indicating symmetry and positive values indicating facilitation. The ratio is calculated as follows:

$$RII = (B_W - B_O)/(B_W + B_O)$$

where B_W is the biomass of plants growing with inter-specific interaction and B_O is the biomass of plants growing without inter-specific interaction (Armas, Oridiales & Pugnaire, 2004). RII was calculated for each treatment combination, for of the six competing species regardless of nutrient conditions and also for high and low nutrient levels averaged across competing species. In addition belowground root biomass was plotted to show root distribution (g/mm) down the soil profile.

A three-way ANOVA was used to assess the effects of tree species, grass species, nutrient level and their interaction, on RII based on: (1) aboveground or leaf and stem biomass, (2) belowground or root biomass and (3) whole plant biomass. When the ANOVA (f-test) revealed significant differences, the least significant Fisher's test (LSD) for $p \leq 0.05$ was used to separate means.

2.5 RESULTS

The main effects of tree species, grass species and nutrient level were significant at a 5% level for both above- and belowground biomass, while only grass species and nutrient level had a significant effect on whole plant biomass. The interaction of tree species and nutrient level was significant for above-, belowground and whole plant biomass, while the interaction of grass species and nutrient level was only significant for aboveground biomass (Table 2.1).

Table 2.1: Results of analysis of variance of main effects and interactions for mean RII of (a) aboveground biomass, (b) belowground biomass and (c) whole plant biomass showing degrees of freedom (d.f.), sum of squares (s.s.), mean squares (m.s.), F-ratio and p-value with significant effects ($p < 0.05$) in bold

(a)

Source of variation	d.f.	s.s.	m.s.	F-ratio	p-value
Tree Species	1	0.417	0.417	7.870	**0.006**
Grass Species	5	1.330	0.266	5.020	**<0.001**
Nutrient Level	1	4.985	4.985	93.990	**<0.001**
Tree Species.Grass Species	5	0.274	0.055	1.030	0.402
Tree Species.Nutrient Level	1	2.757	2.757	51.990	**<0.001**
Grass Species.Nutrient Level	5	0.743	0.149	2.800	**0.020**
Tree Species.Grass Species.Nutrient Level	5	0.125	0.025	0.470	0.798
Residual	108	5.728	0.053		
Total	131	15.748			

(b)

Source of variation	d.f.	s.s.	m.s.	F-ratio	p-value
Tree Species	1	0.378	0.378	6.930	**0.010**
Grass Species	5	1.119	0.224	4.100	**0.002**
Nutrient Level	1	1.429	1.429	26.170	**<0.001**
Tree Species.Grass Species	5	0.220	0.044	0.810	0.548
Tree Species.Nutrient Level	1	2.304	2.304	42.180	**<0.001**
Grass Species.Nutrient Level	5	0.440	0.088	1.610	0.163
Tree Species.Grass Species.Nutrient Level	5	0.387	0.077	1.420	0.224
Residual	109	5.953	0.055		
Total	132	11.733			

(c)

Source of variation	d.f.	s.s.	m.s.	F-ratio	p-value
Tree Species	1	0.031	0.031	0.680	0.413
Grass Species	5	1.123	0.225	4.960	**<0.001**
Nutrient Level	1	2.554	2.554	56.450	**<0.001**
Tree Species.Grass Species	5	0.138	0.028	0.610	0.694
Tree Species.Nutrient Level	1	2.261	2.261	49.970	**<0.001**
Grass Species.Nutrient Level	5	0.487	0.097	2.150	0.064
Tree Species.Grass Species.Nutrient Level	5	0.217	0.043	0.960	0.447
Residual	109	4.931	0.045		
Total	132	11.278			

The competing grass species had a greater competitive effect on aboveground than belowground biomass of *A. nilotica* and, while the opposite effect was apparent for *A. karroo*, none of these effects were significant at a 5% level. *E. capensis* had the greatest competitive effect on *A. karroo* for above-, belowground and whole plant biomass. *E. capensis* and *H. hirta* had the greatest competitive effect on the aboveground biomass of *A. nilotica*, while *S. africanus* had the greatest competitive effect on belowground biomass. Whole plant biomass of both tree species was most affected by competition with *E. capensis* and *S. africanus* (Figure 2.1).

Under high nutrient levels, *A. karroo* experiences greater competitive effects from grass than *A. nilotica*, while under low nutrient conditions *A. nilotica* experiences greater competitive effects than *A. karroo* for aboveground, belowground and whole plant biomass. Under both high and low nutrient conditions *A. nilotica* experienced greater competitive effects aboveground than belowground. The same was observed for *A. karroo* under high nutrient conditions, while under low nutrient conditions the competitive effect experienced aboveground was greater than that experienced belowground (Figure 2.2).

Under both high and low nutrient conditions *E. capensis* exhibited the greatest aboveground competitive effect on tree seedlings although it was not significantly different from *H. hirta*, *S. africanus* and *T. triandra* under high nutrient conditions and from *A. junciformis* and *H. hirta* under low nutrient conditions. For belowground and whole plant biomass *E. capensis* was the most competitive species under low nutrient conditions, while *S. africanus* was the most competitive under high nutrient conditions. These results were not, however, significant at a 5% level (Figure 2.3).
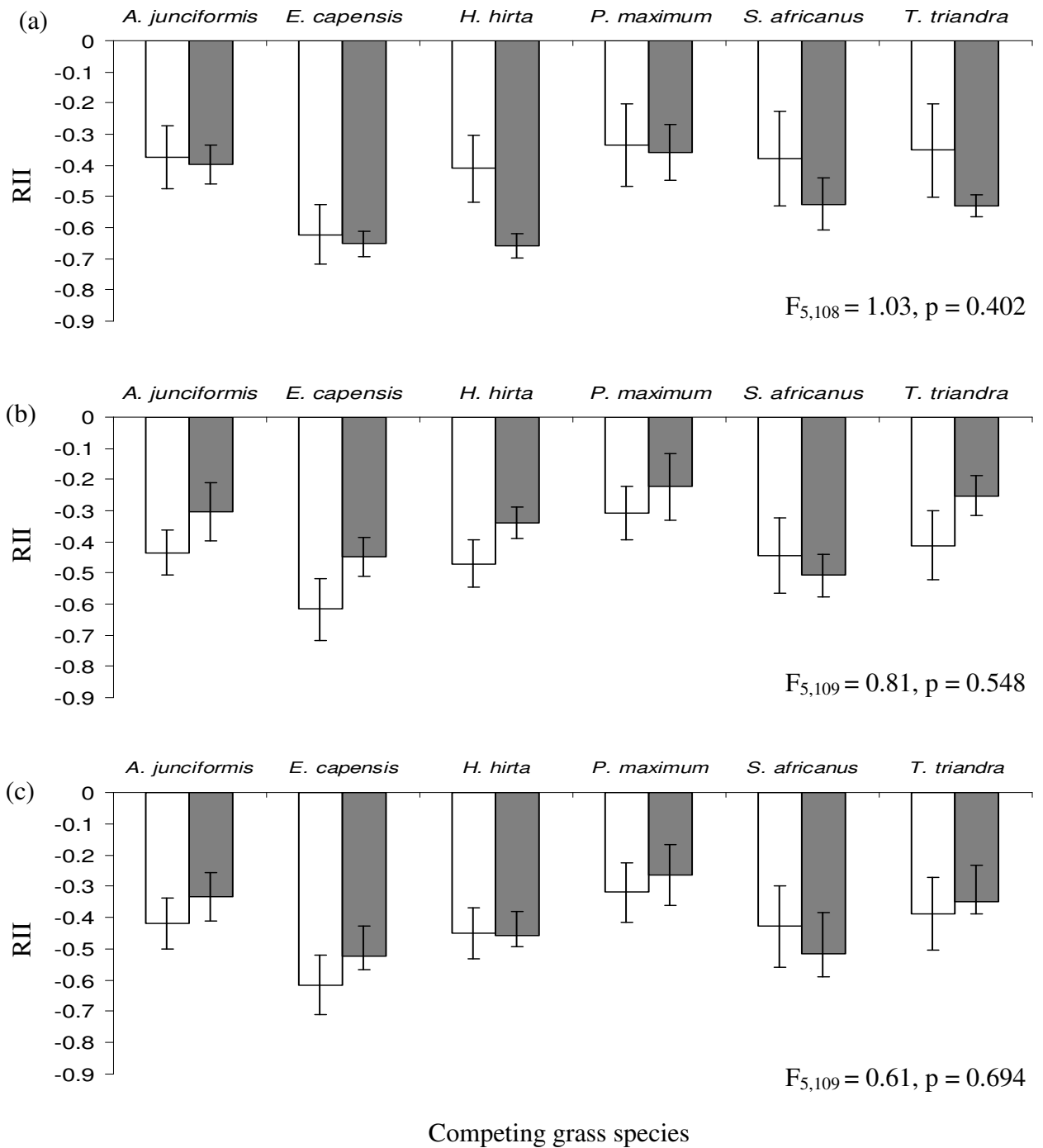
Figure 2.1: Mean RII (±SE) from final dry biomass for *A. karroo* (open) and *A. nilotica* (black) for (a) aboveground dry biomass, (b) belowground dry biomass and (c) whole plant dry biomass, comprised of both high and low nutrient treatments.
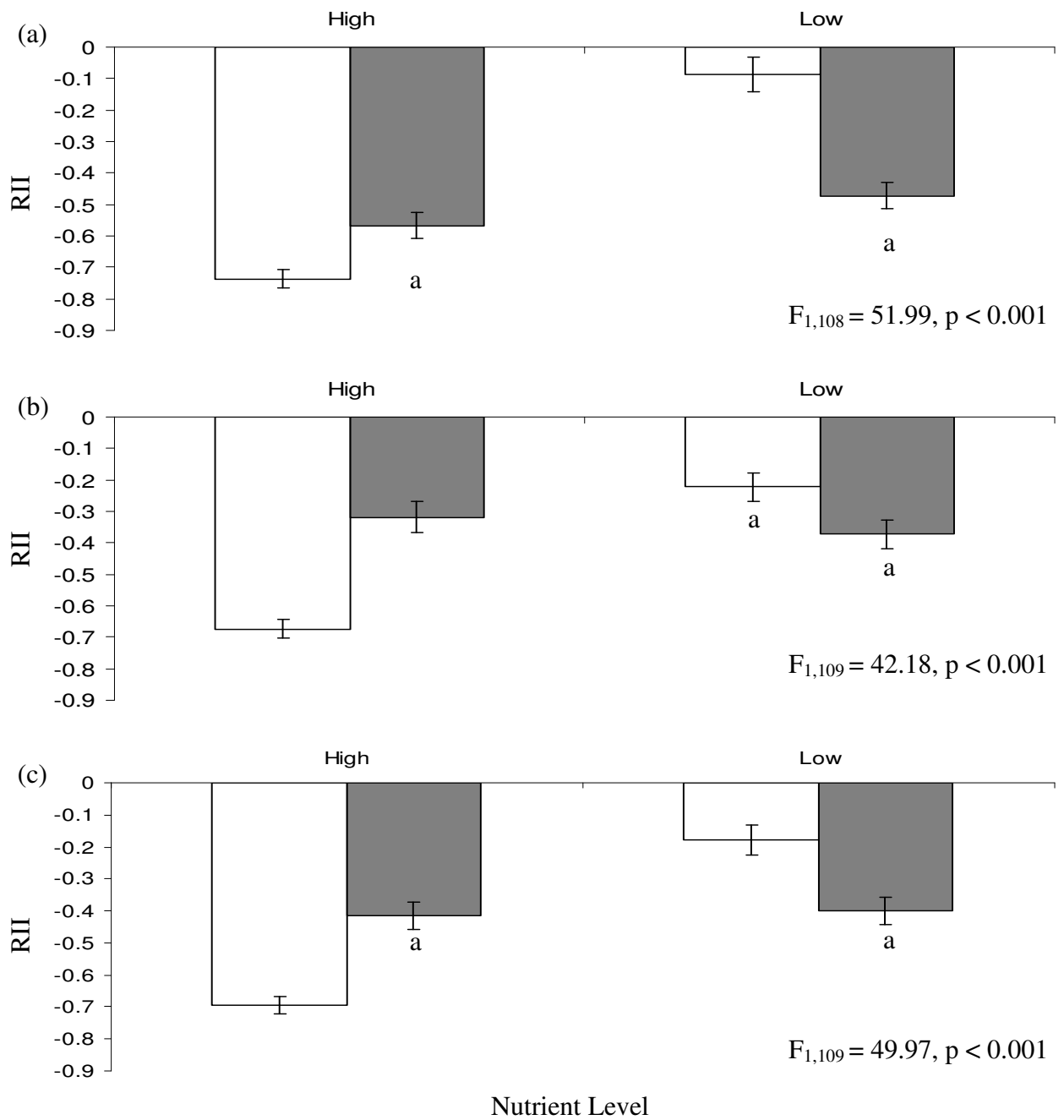
Figure 2.2: Mean RII (±SE) from final dry biomass for *A. karroo* (open) and *A. nilotica* (grey) for (a) aboveground dry biomass, (b) belowground dry biomass and (c) whole plant dry biomass, for high and low nutrient levels, comprised of all competing grass species and showing results of means comparisons (LSD). Treatments with letters in common are not different. (p>0.05).
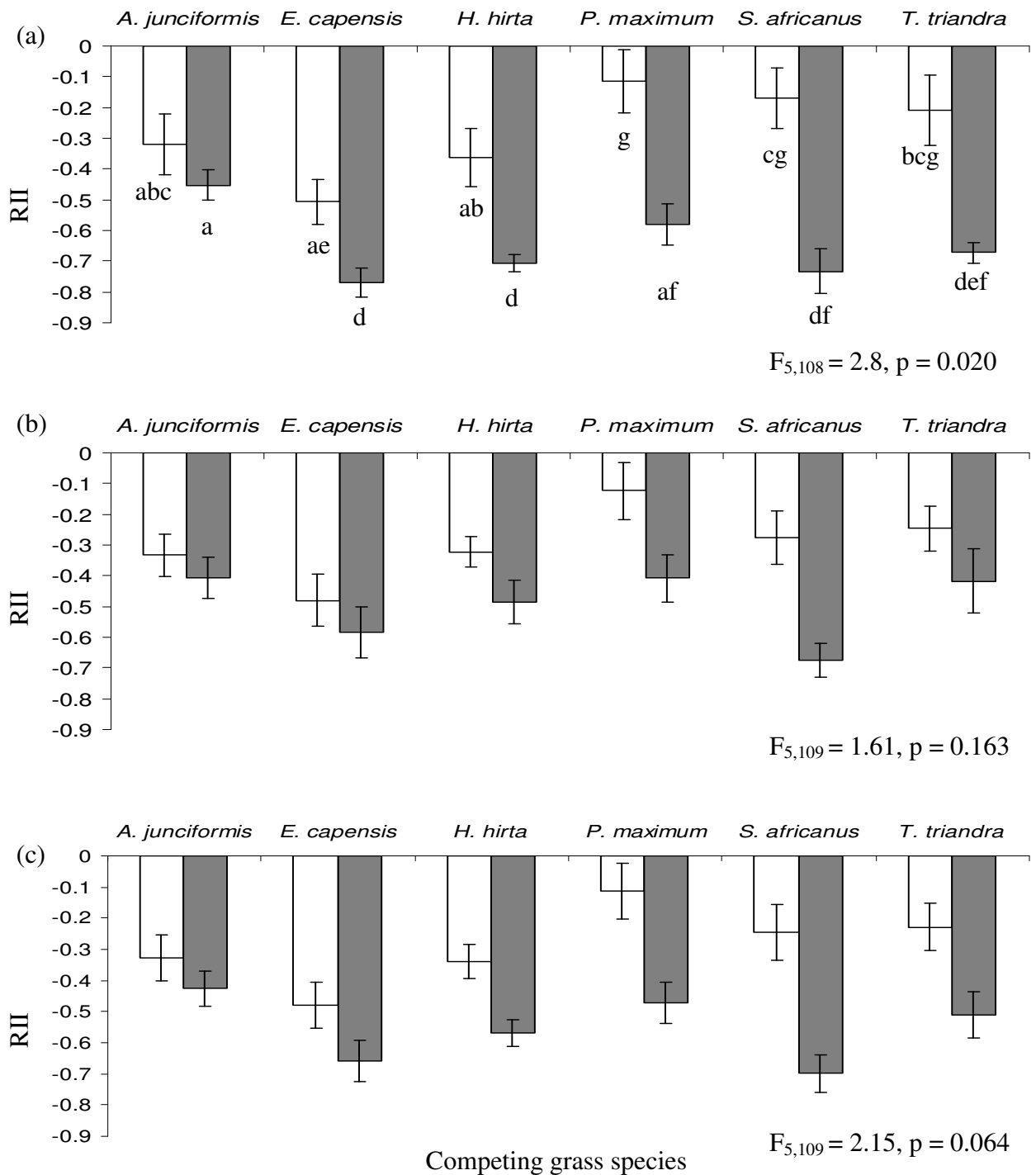
Figure 2.3: Mean RII (±SE) from final dry biomass for low (open) and high (grey) nutrient level for (a) aboveground dry biomass, (b) belowground dry biomass and (c) whole plant dry biomass, comprised of all competing grass species and showing results of means comparisons (LSD). Treatments with letters in common are not different (p>0.05).

The growth curves for high and low nutrient conditions began to diverge after 36 days from the outset of the trial. At this point the additional nutrients appear to have begun to affect plant growth. This effect was consistent over all treatments except for *A. nilotica* growing with *E. capensis* and both *Acacia* species growing with *T. triandra* which began to diverge after 50 days and *A. nilotica* growing with *S. africanus* which began to diverge after 64 days (Figure 2.4).

A. nilotica decreased in relative root dry biomass (RRDB) under both high and low nutrient conditions with all competing species, except *T. triandra* under high nutrient conditions where the RRDB remained the same. When growing with *S. africanus*, *A. nilotica* the RRDB decreased substantially under both the high and low nutrient conditions. The RRDB of *A. karroo* also decreased under both high and low nutrient conditions with all competing grass species, except when growing under low nutrient conditions with *S. africanus* and *T. triandra* where it remained the same and with *P. maximum* where a small increase was observed. When growing alone under low fertility conditions, the RRDB of *A. nilotica* doubled compared to when growing under high fertility conditions (Figure 2.5 to 2.11).

There does not appear to be a consistent response in the RRDB of the grasses growing with the two tree species. The RRDB of *A. junciformis* decreased at all soil levels when growing with both tree species. When growing alone under low nutrient conditions *E. capensis* had a greater RRDB than when growing alone under high nutrient conditions, while the plants growing under high nutrient conditions with both *A. karroo* and *A. nilotica* showed a greater RRDB than those growing with trees under low nutrient conditions. The RRDB of *H. hirta* decreased slightly when growing under high nutrient conditions with *A. karroo* and decreased still further when growing under the same conditions with *A. nilotica*, while under low nutrient conditions the RRDB increased when growing with both trees. When growing with *A. karroo*, the RRDB of *P. maximum* decreased regardless of the nutrient level while it increased when growing with *A. nilotica* under high nutrient conditions but stayed the same when growing under low nutrient conditions. The RRDB of *S. africanus* decreased regardless of soil nutrient conditions when growing with *A. karroo* and when growing under low nutrient conditions with *A. nilotica*, while it increased when growing under high nutrient conditions when growing with *A. nilotica*. The RRDB of *T. triandra* increased in the 0-50 mm stratum and below 150 mm while staying the same in the 50-100 mm and 100-150 mm strata when growing under high nutrient conditions with *A. karroo*.

Similarly the RRDB of *T. triandra* increases when growing under low nutrient conditions with *A. karroo*. A large increase in the RRDB of *T. triandra* was seen when growing under high nutrient conditions with *A. nilotica*, while a small increase was seen in the 0-50 mm stratum, with all the other levels remaining the same when growing under low nutrient conditions with *A. nilotica* (Figure 2.5 to 2.11).

When growing with *H. hirta*, *T. triandra* and growing alone *A. karroo* had a higher root:shoot ratio under low fertility conditions, while *A. nilotica* had a higher ratio growing under high fertility conditions. When growing with *P. maximum* under high fertility conditions *A. karroo* appeared to have a greater root:shoot ratio, while root growth was favoured in *A. nilotica* growing low fertility conditions (Figure 2.12).

The greatest root:shoot ratio for *A. karroo* occurred when the tree was growing alone under low fertility conditions while the highest ratio for *A. nilotica* was observed when growing with H. hirta under high fertility conditions. The lowest ratio for both tree species was recorded when the plant was growing alone, under high fertility conditions for *A. karroo* and under low fertility conditions for *A. nilotica* (Figure 2.12).

The greatest effect of fertility on root:shoot ratios was found when *A. karroo* was growing alone and when *A. nilotica* was growing with *A. junciformis*, while the smallest difference was observed when *A. karroo* was growing with *P. maximum* and when *A. nilotica* was growing with *E. capensis* (Figure 2.12).
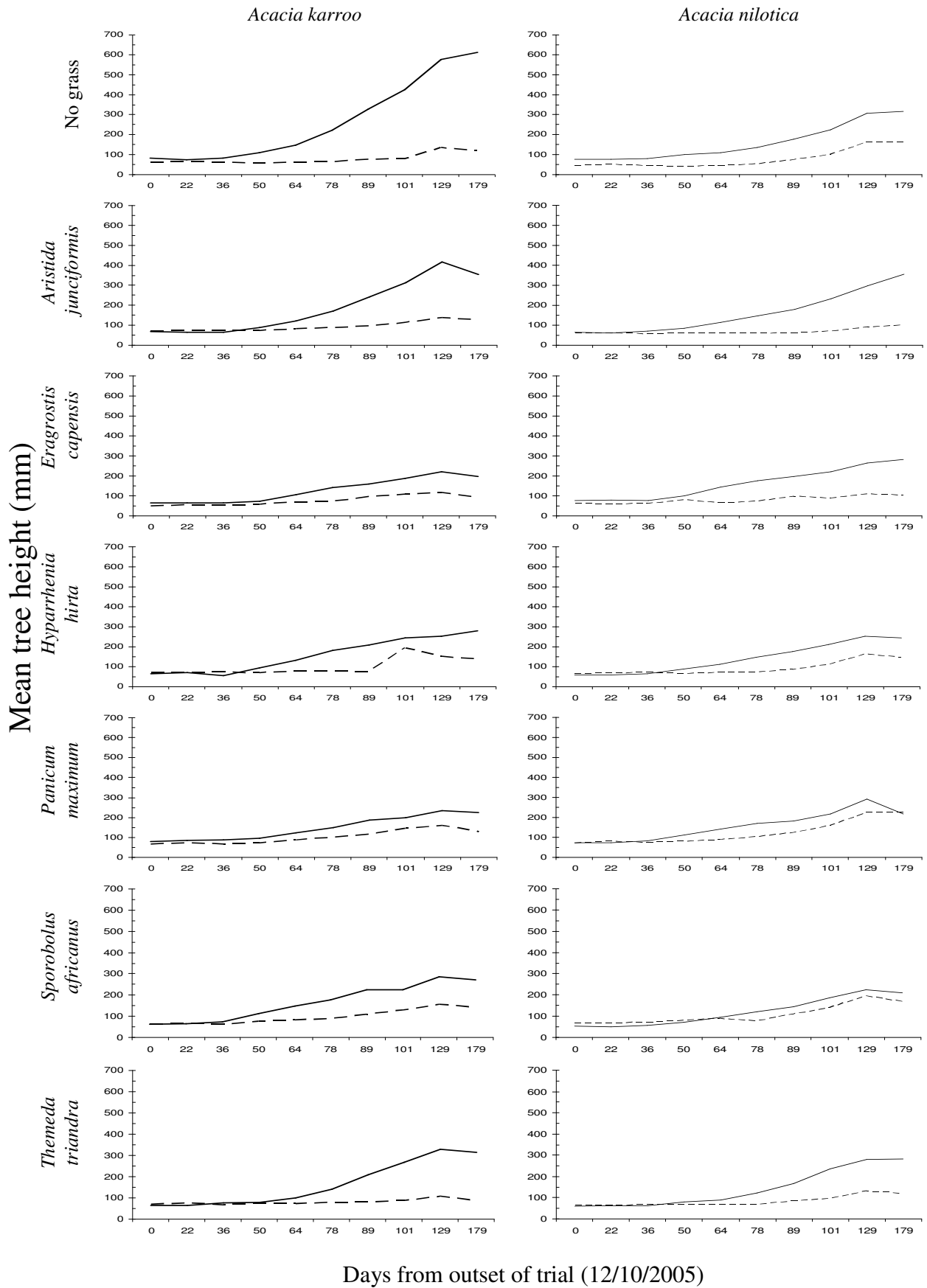
Figure 2.4: Change in mean tree height for *A. karroo* and *A. nilotica* under high (solid line) and low (dashed line) nutrient conditions growing with various competing grass species.
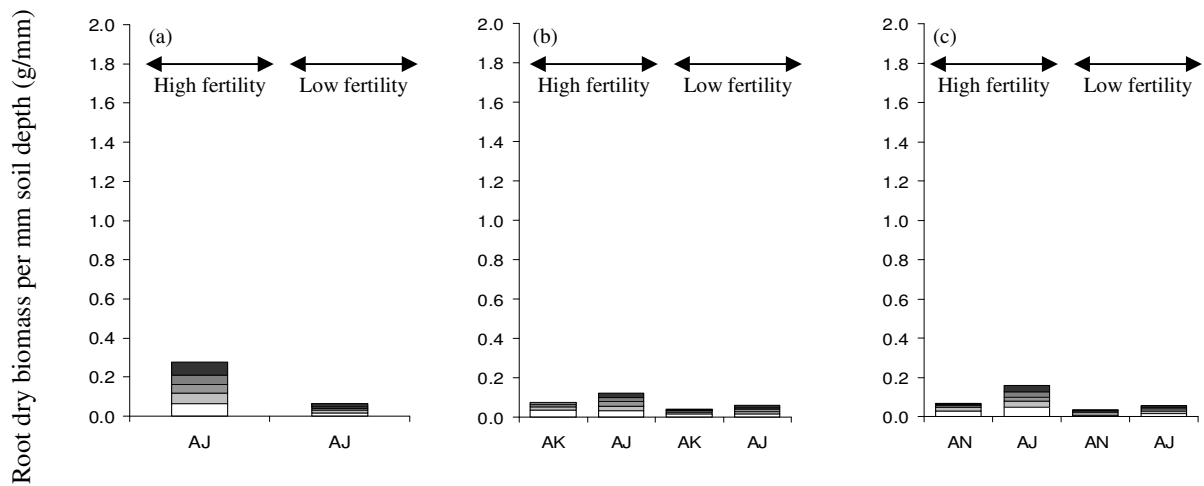
Figure 2.5: Distribution of relative root dry biomass for *A. junciformis* (AJ) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▣), 100-150 mm (▩), 150-250 mm (▦) and 250-500 mm (■) below ground level.
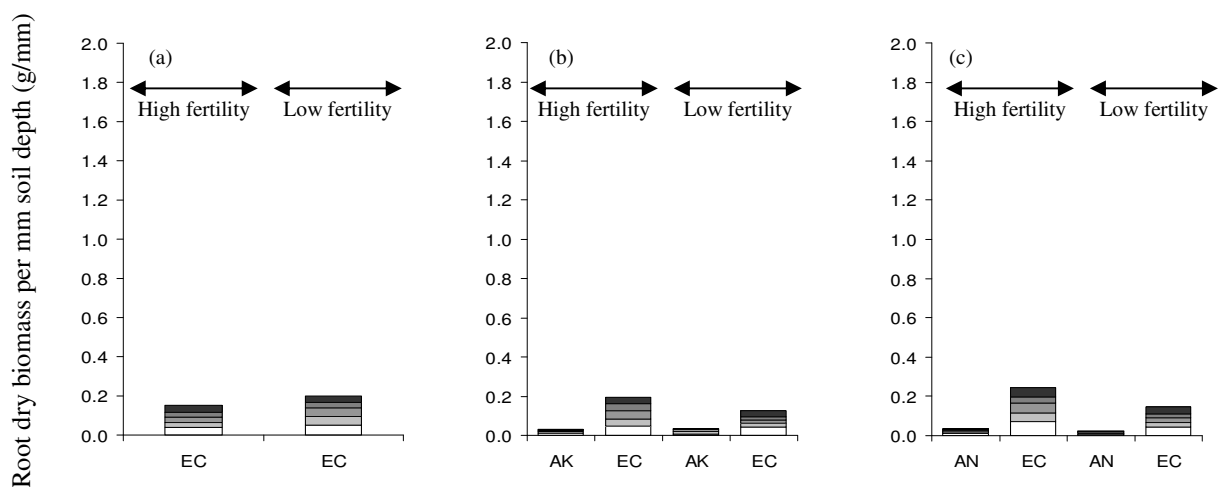
Figure 2.6: Distribution of relative root dry biomass for *E. capensis* (EC) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▣), 100-150 mm (▩), 150-250 mm (▦) and 250-500 mm (■) below ground level.
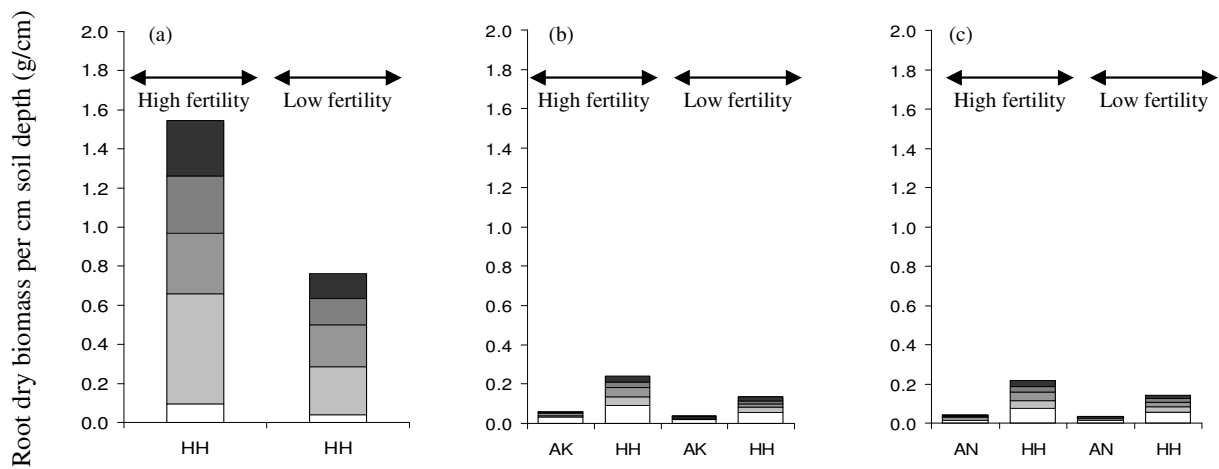
Figure 2.7: Distribution of relative root dry biomass for *H. hirta* (HH) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▨), 100-150 mm (▩), 150-250 mm (▦) and 250-500 mm (■) below ground level.
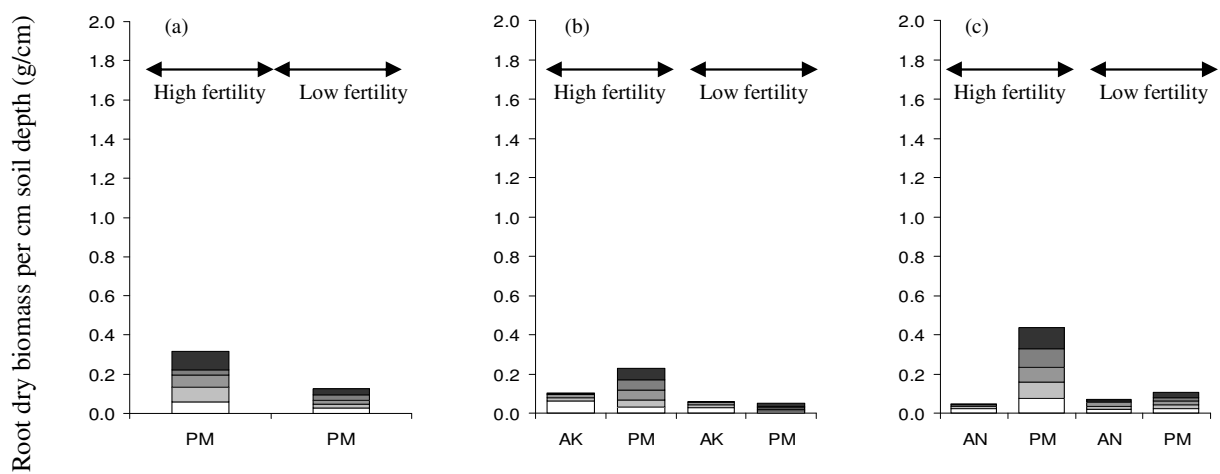
Figure 2.8: Distribution of relative root dry biomass for *P. maximum* (PM) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▨), 100-150 mm (▩), 150-250 mm (▦) and 250-500 mm (■) below ground level.
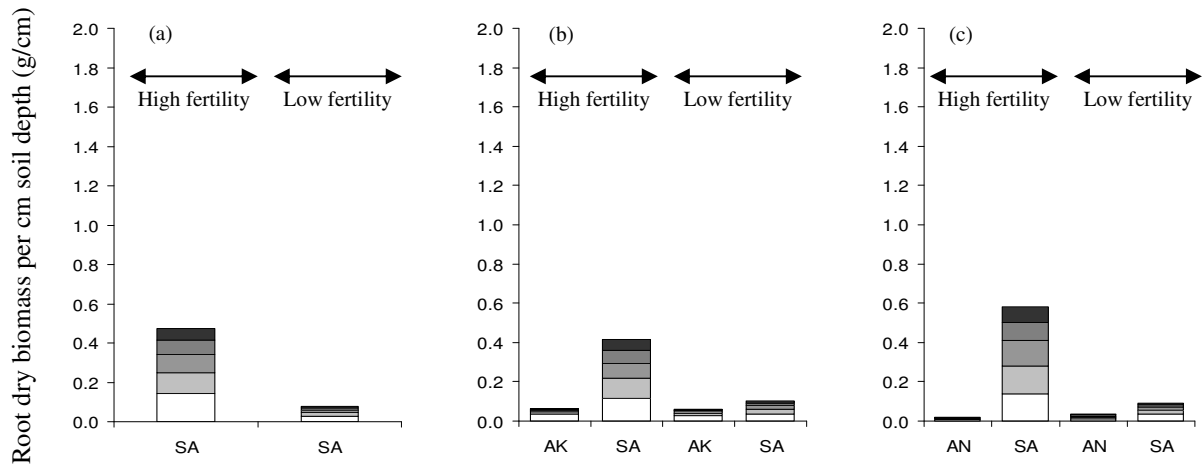
Figure 2.9: Distribution of relative root dry biomass for *S. africanus* (SA) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▣), 100-150 mm (▣), 150-250 mm (▣) and 250-500 mm (■) below ground level.
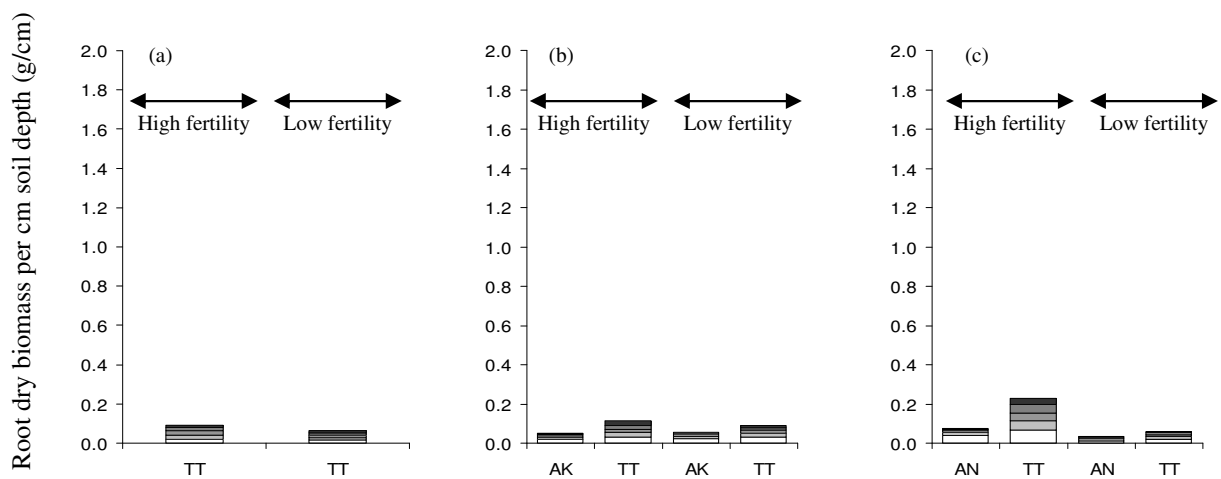
Figure 2.10: Distribution of relative root dry biomass for *T. triandra* (TT) (a) growing alone, (b) growing with *A. karroo* (AK) and (c) growing with *A. nilotica* (AN) at 0-50 mm (□), 50-100 mm (▣), 100-150 mm (▣), 150-250 mm (▣) and 250-500 mm (■) below ground level.
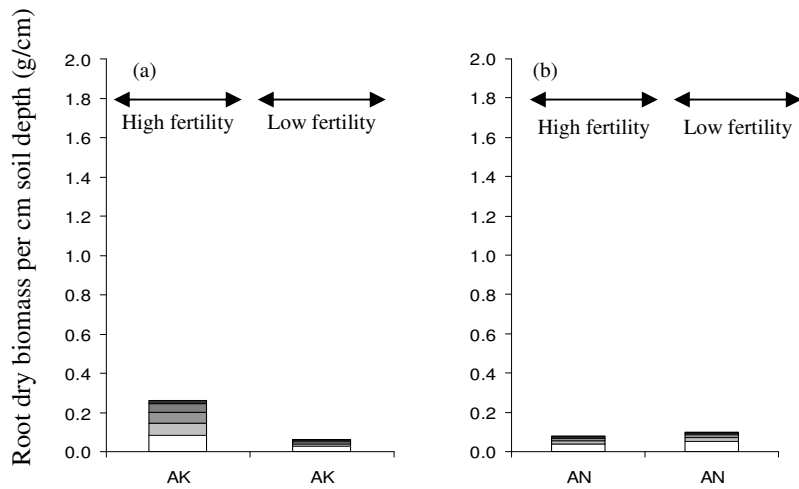
Figure 2.11: Distribution of relative root dry biomass for (a) *A. karroo* (AK) and (b) *A. nilotica* (AN) growing alone at 0-50 mm (□), 50-100 mm (▨), 100-150 mm (▦), 150-250 mm (▩) and 250-500 mm (■) below ground level.

(a)

(b)

Competing grass species
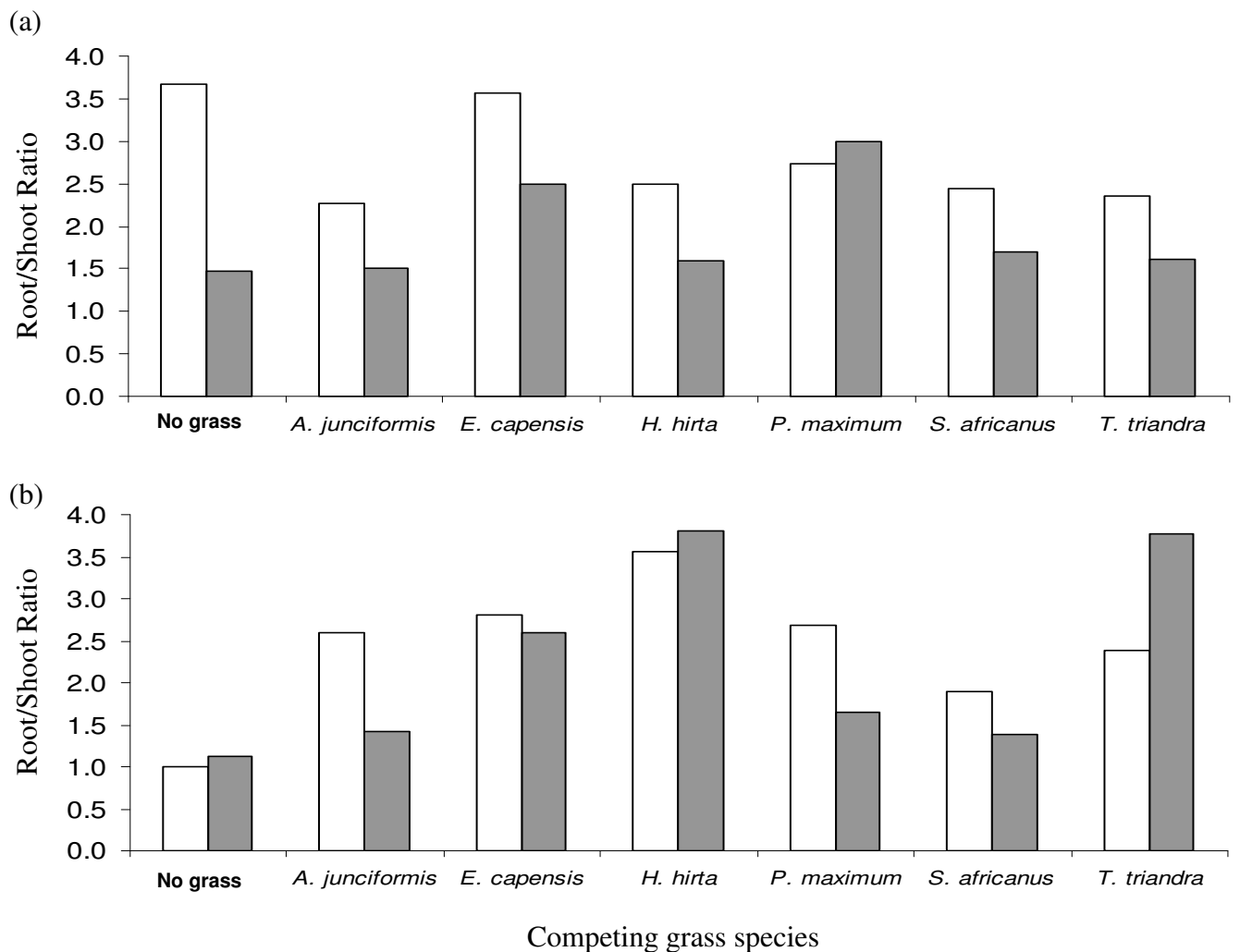
Figure 2.12: Root:shoot biomass ratios of (a) *A. karroo* and (b) *A. nilotica* under low (open) and high (grey) nutrient conditions.

2.6 DISCUSSION

In most cases the effect of soil nutrient conditions became apparent only after 36 days. It is only after this that competition or facilitation can begin to play a major role in plant interactions. *A. nilotica* when growing with *E. capensis* and both *Acacia* species growing with *T. triandra* only showed the effects of external nutrient availability after 50 days, while *A. nilotica* growing with *S. africanus* showed the effects after 64 days.

Both tree species, except for *A. karroo* growing with *P. maximum* and *A. nilotica* growing with *H. hirta* and *T. triandra*, showed a higher root:shoot biomass ratio when growing under low fertility conditions, indicating that the trees favoured root growth over shoot growth. The same effect is seen in plants in dry regions where more resources are allocated to producing a greater root volume in order to obtain necessary water resources (Monk, 1966). The trees growing under low nutrient conditions appear to be reacting in the same way by developing a larger root system to exploit a larger volume of soil nutrients.

The surrounding grass exerted similar competitive effects on the two tree species, with *E. capensis* reducing the aboveground biomass, compared to the control plant growing without the surrounding grass, to the largest extent and *P. maximum* the least ($p < 0.001$). The addition of nutrients increased the competitive effect of all grass species on *A. karroo* considerably ($p < 0.001$), while appearing to have little to no effect on *A. nilotica*. Similar competitive effects were observed on the root biomass of *A. karroo*, with *E. capensis* being the most, and *P. maximum* the least, competitive grass species.

It is possible that the competitive effect of specific grass species and the impact which that species has on the seedling may be as a result of grass root morphology. During the harvesting process, *E. capensis* was observed to have fine, hair-like roots, while *P. maximum* was observed to have much thicker, robust roots (Hartnett *et al.*, 2004) which may affect the intensity of belowground competition for nutrients. *E. capensis* and *H. hirta* are fairly tall species, ranging from 20 to 60 cm and 60 to 100 cm, respectively (Van Oudtshoorn, 2002). The tillers of both these species grow directly upright and form fairly dense shady tufts which may result in high aboveground competition as observed when growing with *A. nilotica*.

Acacia karroo appears to be more susceptible to aboveground competition while *A. nilotica* appears to be more susceptible to belowground competition, although these competitive effects may have been aggravated in this trial due to the plant roots being confined in pots rather than growing in an open soil profile. This may be due to the fact that *A. karroo* is a fast growing species, growing up to or more than one metre per year (Venter & Venter, 2002), and it relies on this fast growth rate to get out of the zone of most intense light competition as fast as possible, while *A. nilotica* is slower growing, only growing up to 700 mm per year (Venter & Venter, 2002) and therefore is possibly better adapted to dealing with belowground competition. Cramer *et al.* (2007) found similar results when growing a variety of *Acacia* seedlings in both cleared and grassed plots in a natural grass sward. *A. karroo* was found to have a higher stem elongation rate, in mm/day, than *A. nilotica* when competing with grass, while in the cleared plots the elongation rate was the same (Cramer *et al.*, 2007). The ability to develop root nodules and thus utilize atmospheric N_2 which is unavailable to other plant species is thought to give leguminous plant species a growth advantage over non-leguminous species when competing with the grass sward. This is however an energy expensive process, and if combined N is readily available it is unlikely that trees will form these nodules (Cramer *et al.*, 2007). Cramer *et al.* (2007) also found that the proportion of nitrogen (N) derived from N_2 fixation was over 80 % after a growth period of 112 days for all five *Acacia* species studied when growing in competition with the grass sward. This decreased to just over 40% after 261 days (Cramer *et al.*, 2007) indicating that the tree roots may be growing deep enough to be out of the zone of intense root competition. The trees growing with no grass competition were found to have less than 20% of the N accounted for by N_2 fixation (Cramer *et al.*, 2007). Forty eight percent of the woody plants on the Conservation of Agricultural Resources Act, No. 43 of 1983, Declared indicators of bush encroachment list are leguminous species and 46 % of the species on this list are *Acacia* species. These listed *Acacia* species account for half of the total number of *Acacia* species recognised in South Africa (Smit, 1999). It is possible that this ability to fix nitrogen may be one of the traits allowing these *Acacia* species to outcompete the grass sward by allowing the roots of these encroaching species to grow beyond the zone of most intense nutrient competition.

Although, it has been demonstrated that grazing leads to short-term changes in root biomass (Rodríguez, Alvarez & Gómez-Sal, 1996; Milchunas & Lauenroth, 1989) and a long-term change in sward species composition (O'Connor, 1985), it appears that factors other than

disturbance may be contributing to bush encroachment may be more than just disturbance and that both tree and grass species and soil nutrient content and the interactions between the three play an important role in determining if a savanna region will become encroached by woody plants.

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CHAPTER THREE

ABOVE- AND BELOW-GROUND INTERACTIONS BETWEEN TWO TREE SPECIES
AND THE SURROUNDING NATIVE GRASS SWARD ON THREE SITES OF
DIFFERING SOIL DEPTH

3.1 ABSTRACT

The interaction, both above and belowground, between tree seedlings and the surrounding grass sward is dependant on many factors, such as soil depth, tree species and sward composition. These factors, as well as the presence or absence of defoliation, in the form of grazing or fire dictate whether the system will remain in a transition state as savanna or move towards a stable woodland state. The individual effects of above and belowground competition two species of *Acacia* and the effects of soil depth on these interactions were examined by planting *Acacia karroo* and *Acacia nilotica* seedlings into a natural grass sward on three different soil depths. Three aboveground treatments; full light competition, no light competition and simulated grazing, and two belowground treatments; full belowground and no belowground competition, were used. Soil depth constrained plant size in both tree species, with tallest and heaviest plants growing on the deepest soils. The intensity of belowground interactions on tree biomass was unaffected by soil depth, while aboveground competition had a significant effect on shallow soils ($p = 0.027$), with clipping the surrounding sward increasing biomass by 47 %. Belowground competition was also of greater importance than aboveground competition in dictating tree seedling height ($p < 0.001$). Encroachment on shallow soils may be as a result of decreased root vigor of the surrounding grasses allowing the tree seedlings access to water and nutrient resources, while on deep soils this decrease in surrounding sward root vigor, coupled with the increase in available light resources may allow the tree seedlings to increase root elongation and access soil water and nutrients in deeper soil layers inaccessible to the grass sward. Encroachment is thus more likely to occur on intensively grazed shallow and deep soils than on medium depth soils.

3.2 INTRODUCTION

South African savanna ecosystems are commonly maintained in a pre-climax state by the presence of fire. In many savanna regions unburnt patches exist and support a high density of trees and woody plants. These patches may serve as an indication that in the absence of fire these areas may be capable of supporting thicket or forest vegetation (Bond *et al.*,

2003). Fire serves a similar function to herbivory but behaves as a general defoliator, removing living and dead material from both woody and herbaceous plants (Bond & Keeley, 2005). Fire therefore reduces the density of tree seedlings by destroying them before they are able to grow above the grass layer but causes little mortality of established trees above the grass layer (Trollope, 1980).

The fire intensity and its ability to destroy seedlings is dependant on four factors, namely air temperature, relative humidity, fuel load and fuel moisture (Trollope, 1980). At high grazing intensities there is usually insufficient grass fuel to sustain a hot fire and fires are less frequent. As a result, woody seedlings are able to grow beyond the grass layer and escape the zone of the most intense heat thus increasing the chances of the plant surviving the next fire (Trollope, 1980). If intense grazing is maintained more seedlings will grow beyond the grass layer and the density of woody plants will increase (Stuart-Hill, 1985; Skarpe, 1992; Tobler *et al*, 2003) until ultimately an impenetrable woody thicket is formed. In addition to the reduction of grass fuel load high intensity grazing decreases the competitive ability of the grass layer allowing water and soil nutrients to infiltrate deeper into the soil profile into regions inaccessible to grasses but accessible to trees (Stuart-Hill, 1985; Tobler *et al*, 2003; Skarpe, 1992). While extended periods of intense grazing pressure and a lack of fire may be regarded as major driving factors behind bush encroachment it may also result from low grazing pressure and from incorrect burning practices (Skarpe, 1992; Ward, 2003). Large herbivores accelerate the nutrient cycle in savanna regions and the exclusion of these animals allows nutrients to infiltrate to deeper soil layers where grasses are unable to utilize them, thus promoting woody plant growth (Skarpe, 1992).

Savanna is regarded as a transition state between grassland and woodland which is kept from moving towards a stable woodland state by disturbances, such as fire, bush clearing and livestock utilization (Scholes and Archer, 1997; Ward, 2003). In such a system it is possible for the vegetation to reach some level of equilibrium by resource partitioning as described by Walter's 2-layer hypothesis. The trees and herbaceous layer utilize water resources at different depths in the soil profile. In the upper soil layers the grasses are more efficient competitors for soil water and utilize water from light rainfall. In the lower soil layers the woody species are more efficient competitors and utilize ground water and anything which filters though the upper soil layers from heavier rainfall (Walker *et al.*, 1981).

As well as utilizing the same aboveground niche, tree seedlings also utilize the same belowground niche and cannot escape competition by resource partitioning until later growth stages (Ward, 2003). This resource partitioning is thought to be the major driving force in terms of tree grass interactions in savanna regions (Mopipi, 2005), although there is some debate surrounding this theory as bush encroachment has been observed in regions where both tree and grass roots are confined within a soil layer of between 50 and 150 mm deep, a depth not sufficient to allow for this differentiation (Ward, 2003, Wiegand *et al.*, 2005). Nevertheless it has been stated that, in grassland and savanna regions, belowground interactions have greater impacts on plant growth than aboveground interactions. These belowground interactions are also more important in grassland and savanna than in thicket and forests as the aboveground biomass in the grass dominated regions is regularly removed by fire and grazing (Donald, 1958 cited in Carlen *et al.*, 2002: Johnson & Matchett, 2001; Wilson, 1988) thus potentially altering the competitive effect of grasses on trees. Belowground biomass is often three to four times greater than the aboveground biomass (Jackson *et al.,* 1996) and is the major contributor of organic matter and carbon into grassland soils (Johnson & Matchett, 2001).

This experiment aimed to answer the following questions:

(1) what are the relative effects of above and belowground competition from grass on the biomass and height of two species of *Acacia*?

and (2) were these effects dependant upon environment, specifically varying soil depth down a landscape catena?

3.3 METHODS

3.3.1 *Study Area*

The experiment was carried out at Ukulinga Research Farm, Pietermaritzburg, South Africa (29°24'E, 30°24'S). The mean annual rainfall calculated over the last 24 years is 694 mm and falls predominantly during the summer months (September to April). The summer months are hot, with a mean monthly maximum of 26.4°C occurring in February, while winters are mild with some frost, with a mean monthly minimum of 8.8°C occurring in July. The combination of these climatic variables results in a growing season from October to April (Fynn & O'Connor, 2005). The vegetation falls into the grassland biome

(Rutherford & Westfall, 2003) and is classified by Acocks (1988) as Natal Mist Belt 'Ngongoni Veld, dominated by *Aristida junciformis, Themeda triandra*, and *Tristachya leucothrix*, while it falls into the transition zone between Ngononi Veld and KwaZulu-Natal Hinterland thornveld as classified by Mucina & Rutherford (2006).

Figure 3.1: Ukulinga Research Farm monthly rainfall for August 2005 to May 2006.

The three experimental plots were located within 1 km of one another along a catenal gradient, with the shallow soil plot at the top, the medium soil plot part of the way down, and the deep soil plot at the bottom of the catena. The soils at these three points are classified as Westleigh, Mayo and Bonheim forms respectively (Anon, 1991). The plots were approximately 10 m by 15 m. The soil underlying the shallow plot ranged from 150 to 250 mm deep, while the soils underlying both the medium dystrophic and the deep eutrophic plots were both deeper than 1500 mm. The dominant grass species in the shallow soil plot were *Melinis nerviglumis*, *Eragrostis racemosa*, *T. leucothrix*, *Eragrostis capensis* and *Eragrostis curvula*. The dominant non-grass herbaceous species were *Hypoxis* sp. and *Senecio* sp. and there were no trees in the immediate vicinity. The dominant grass species in the medium soil plot were *T. triandra* and *E. curvula*, while the dominant non-grass herbaceous species were *Hypoxis* sp. There was one small *Acacia* (less than 0.5 m tall) in the plot but no other trees in the immediate vicinity. The dominant grass species in the deep soil plot were *E. curvula* and *Setaria sphacelata*. There was one *Acacia* (less than 2 m tall) in the plot and a large number of *Acacias* (greater than 2 m tall) around the plot.

3.3.2 *Experimental Design*

Seedlings of two tree species, *Acacia karroo* and *Acacia nilotica*, were used as experimental units. Both *A. nilotica* and *A. karroo* have been recognised as problem species in terms of bush encroachment since the 1940's, both being described as 'thicket formers' (West, 1947). These plants were subjected to various combinations of above- and belowground competition from the surrounding sward, created by various treatments. Each

treatment was applied to the sward in a 0.5 x 0.5 m area with the tree phytometer (study plant) in the centre.

The three aboveground treatments (AG) were: full light competition, partial light competition and no light competition. In the full light competition treatment the sward was allowed to grow undisturbed to provide full competition for light. Partial light competition was created by clipping the sward at 6, 4 and 2 week intervals for the shallow, medium and deep swards respectively to a height of approximately 4 cm to simulate intensive grazing. The no light competition treatment was created by holding the surrounding aboveground grass material down using a 0.5 m by 0.5 m square of netting with holes 2 cm by 2 cm. A hole was cut in the centre of the netting to allow the tree phytometer to emerge. The four corners of the net and four points around the central hole were pegged to the ground (adapted from Cahill, 1999). Treatments were checked, the net maintained and clipping done at 2, 4 and 6 weekly intervals for the deep, medium and shallow plots respectively. The percentage shading given by these treatments at each of the three plots was determined by taking ten light intensity readings on each treatment at midday on a cloudless day at the outset of the trial using a Decagon PAR/LAI Ceptometer Accupar LP-80 light meter.

Following the methods of Cahill (1999), two belowground treatments (BG) were applied: full root competition; and no root competition, or root exclusion. For both of these treatments, PVC tubes, 150 mm in diameter were used. For the shallow plot, tubes were cut to a length of 200 mm and three rectangular holes 80 mm wide and 140 mm long were cut in the sides. For the medium and deep plots the tubes were cut to a length of 500 mm and six holes 80 mm wide by 180 mm long were cut in the sides. In the root exclusion treatment these holes were then covered with 43 μm NITEX mesh (produced and supplied by Meshcape Industries, Durban, South Africa) to prevent root interaction but allow the lateral movement of soil water and nutrients. In the full root competition treatment holes were left uncovered.

The treatments were combined in a full factorial design with all combinations of: full, partial and no light competition to create varying levels of aboveground competition and full and no root competition to create varying levels of belowground competition. The treatments were then laid out in a completely randomized design with four replications per treatment.

In each plot, 72 holes were dug with a petrol powered auger, to a depth of 200 mm in the shallow plot and 500 mm in the medium and deep plots. The soil was removed from the holes and mixed to reduce the effects of soil heterogeneity. PVC tubes were randomly allocated to the holes and then filled with the mixed soil. The tree phytometers, approximately 50 mm tall tree seedlings, were then planted into the tubes. Plants were watered for the first two weeks after planting to ensure survival. Thereafter, growth depended on natural rainfall.

3.3.3 *Sampling*

The trial was run from 5 Dec 2005 to 22 May 2006. Tree height was measured every four weeks. After 24 weeks the final height measurements were taken and the tree aboveground biomass was harvested, dried at 60°C and weighed to provide a measure of tree performance under different treatments. In addition, rainfall was monitored for the duration of the study and the mean standing dry biomass of the surrounding sward was measured for each plot by taking clippings from ten $1m^2$ quadrats randomly located around each plot but at a suitable distance to remain unaffected by the treatments.

3.4 ANALYSIS

Changes in mean tree height for shallow, medium and deep soil levels were graphed against time for both tree species separately. Three way ANOVA (species x AG x BG) was performed on both the mean final height and the mean dry biomass for each tree species. Residuals were examined to confirm that the assumptions of ANOVA were met. When the ANOVA (F-test) revealed significant differences, the least significant differences test (LSD) for $p \leq 0.05$ was used to separate means. In addition, the percentage change in yield (Ry) resulting from the treatment effect was calculated by comparing each treatment to the control of both full above and full belowground competition using the following formula:

$$Ry = [(Y_t - Y_c)/Y_c]*100$$

Where Y_t is the mean final value for treatment and Y_c is the mean final value for the control.

3.5 RESULTS

Percentage shade given by the aboveground treatments increased from the partial light competition treatment (clipped), to the no light competition treatment (none), to the full

light competition treatment (full). The shallow soil site was characterized by short grass species and as a result did not reduce incident light by more than half the available light when exerting full aboveground competition. The sward on the medium soil depth gave the highest level of shading at full competition, while the sward on the deep soil shaded the plants slightly less (Figure 3.2).
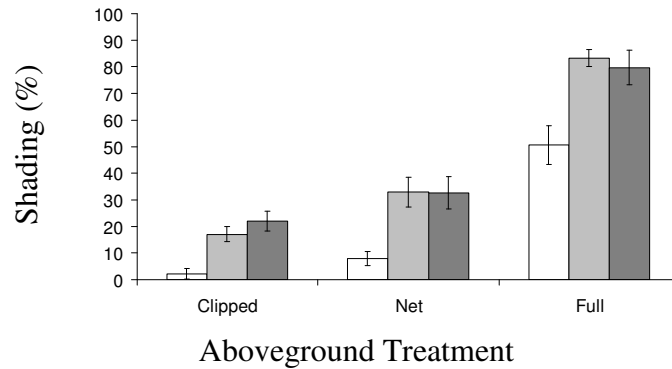
Figure 3.2: Mean percentage shading (±SE) given by three aboveground treatments for shallow (open), medium (grey) and deep soils (black), based on ten readings taken in each treatment area at the outset of the trial.

Biomass of the surrounding sward at the end of the growing season when the trial was harvested increased with increasing soil depth (Figure 3.3).
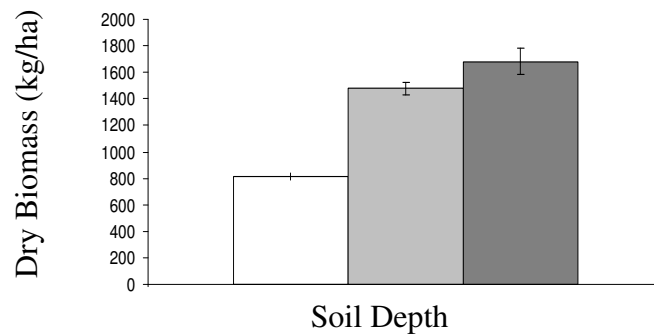
Figure 3.3: Standing dry biomass (±SE) of surrounding sward for shallow (open), medium (grey) and deep soils (black) based on ten quadrats harvested in each experimental area.

Table 3.1: Results of analysis of variance of the main effects and interactions for mean aboveground dry biomass (g) and mean final height (mm) of *A. karroo* & *A. nilotica* on (a) shallow (b) medium and (c) deep soil sites showing degrees of freedom (d.f.), sum of squares (s.s.), mean squares (m.s.), F-ratio and p-value, with significant effects ($p < 0.05$) in bold

a)

Source of variation		Biomass				Height			
	d.f.	s.s.	m.s.	F-ratio	p-value	s.s.	m.s.	F-ratio	p-value
Species	1	21.246	21.246	11.300	**0.003**	3746	3746	1.020	0.323
Aboveground (AG)	2	15.786	7.893	4.200	**0.027**	1228	614	0.170	0.847
Belowground (BG)	1	23.404	23.404	12.450	**0.002**	34203	34203	9.290	**0.006**
Species.AG	2	6.167	3.083	1.640	0.215	4040	2020	0.550	0.585
Species.BG	1	2.224	2.224	1.180	0.288	6409	6409	1.740	0.199
AG.BG	2	6.774	3.387	1.800	0.187	905	453	0.120	0.885
Species.AG.BG	2	2.544	1.272	0.680	0.518	7170	3585	0.970	0.392
Residual	24	45.117	1.880			88314	3680		
Total	35	104.750				133922			

b)

Source of variation		Biomass				Height			
	d.f.	s.s.	m.s.	F-ratio	p-value	s.s.	m.s.	F-ratio	p-value
Species	1	53.730	53.730	18.370	**<0.001**	102269	102269	9.770	**0.004**
Aboveground (AG)	2	0.201	0.100	0.030	0.966	70970	35485	3.390	**0.050**
Belowground (BG)	1	59.521	59.521	20.350	**<0.001**	160192	160192	15.300	**<0.001**
Species.AG	2	5.933	2.966	1.010	0.377	5060	2530	0.240	0.787
Species.BG	1	4.472	4.472	1.530	0.228	54334	54334	5.190	**0.032**
AG.BG	2	20.535	10.267	3.510	**0.045**	831	415	0.040	0.961
Species.AG.BG	2	1.230	0.615	0.210	0.812	31878	15939	1.520	0.238
Residual	25	73.131	2.925			261668	10467		
Total	36	170.441				516923			

c)

Source of variation		Biomass				Height			
	d.f.	s.s.	m.s.	F-ratio	p-value	s.s.	m.s.	F-ratio	p-value
Species	1	5.315	5.315	0.730	0.400	3432	3432	0.390	0.536
Aboveground (AG)	2	48.068	24.034	3.320	0.053	8317	4158	0.480	0.626
Belowground (BG)	1	57.439	57.439	7.940	**0.010**	142168	142168	16.310	**<0.001**
Species.AG	2	10.436	5.218	0.720	0.497	17506	8753	1.000	0.381
Species.BG	1	0.587	0.587	0.080	0.778	15371	15371	1.760	0.197
AG.BG	2	6.877	3.439	0.480	0.628	8448	4224	0.480	0.622
Species.AG.BG	2	10.885	5.442	0.750	0.482	47971	23986	2.750	0.084
Residual	24	173.720	7.238			209194	8716		
Total	35	284.782				366174			

At the shallow soil site significant effects ($p < 0.05$) were found in the main effects of tree species as well as above- and belowground treatments on mean dry biomass. Mean height of plants was affected by belowground treatment (Table 3.1a). At the medium depth soil site, the main effects of species and belowground treatment and the interaction of above- and belowground treatments on the mean dry biomass, the main effects of tree species, above- and belowground treatment, and the interaction of species and belowground treatment on mean height were significant ($p < 0.05$) (Table 3.1b). On the deep soil site, the main effect of belowground treatment on both mean dry biomass and mean height was significant ($p < 0.05$) (Table 3.1c). These significant effects are illustrated in figures 3.4 to 3.11. All responses are presented in Appendix 1.

Acacia nilotica increased in both height and dry biomass from the shallow soil site to the medium and deep soil sites. The seedlings on the medium soil site had a greater dry biomass than those on the deep soil site although they were similar in height. *A. nilotica* had a higher dry biomass than *A. karroo* across all three soil depths (Figure 4a). The two species were similar in height on the shallow and deep soils, while *A. nilotica* was approximately 37% taller than *A. karroo* on the medium soil depth (Figure 4b). Both the dry biomass and height of the *A. karroo* seedlings increased consistently with increasing soil depth (Figure 3.4).
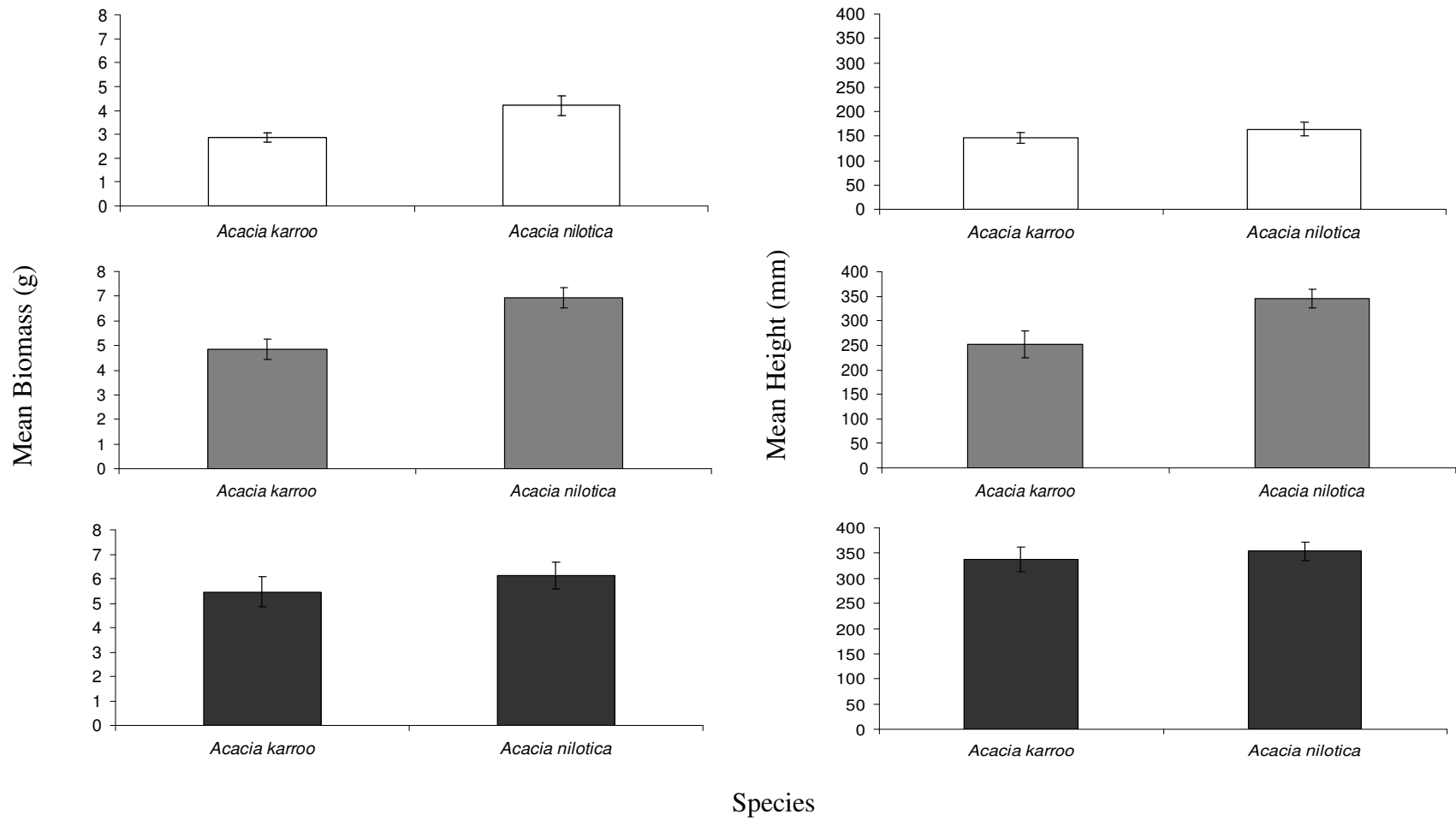
Figure 3.4: Mean (±SE) aboveground dry biomass and final height for species across all treatments on shallow (open), medium (grey) and deep soils (black).

Tree seedling biomass on shallow soil increased across the three aboveground treatments. It was least on the full competition treatment increasing under no competition and then clipping surrounding sward, with a significant difference in biomass between full competition and clipping the surrounding sward ($P < 0.05$) (Figure 3.5). Tree height was constant across all the aboveground treatments on shallow soil ($P > 0.05$) (Figure 3.5).

Tree seedling biomass remained constant across all three aboveground treatments on the medium soil depth (Figure 3.5), while tree seedling height decreased from full competition to no competition to clipping the surrounding sward (Figure 3.5).

There was a steady increase in tree seedling biomass with decreasing aboveground competition observed on the deep soil (Figure 3.5) although seedling height was similar in the full and no aboveground competition treatments and slightly greater than these in the clipped aboveground treatment (Figure 3.5). None of these differences were however significant ($P > 0.05$).

Height and dry biomass were greatest in the full aboveground competition treatment on the medium soil depth, followed by those growing on deep soil and then those on shallow soil having the lesser values. The seedlings with no aboveground competition had similar dry biomass on the medium and deep soils while those on the shallow soil had lower dry biomass. There was a consistent increase in height with increasing soil depth ($P < 0.05$). Clipping the surrounding sward resulted in a consistent increase in both dry biomass and height with increasing soil depth (Figure 3.5).

There was a consistent increase in both dry biomass and height with increasing soil depth for both belowground treatments. There was also an increase in both height and dry biomass when belowground competition was removed (Figure 3.6).
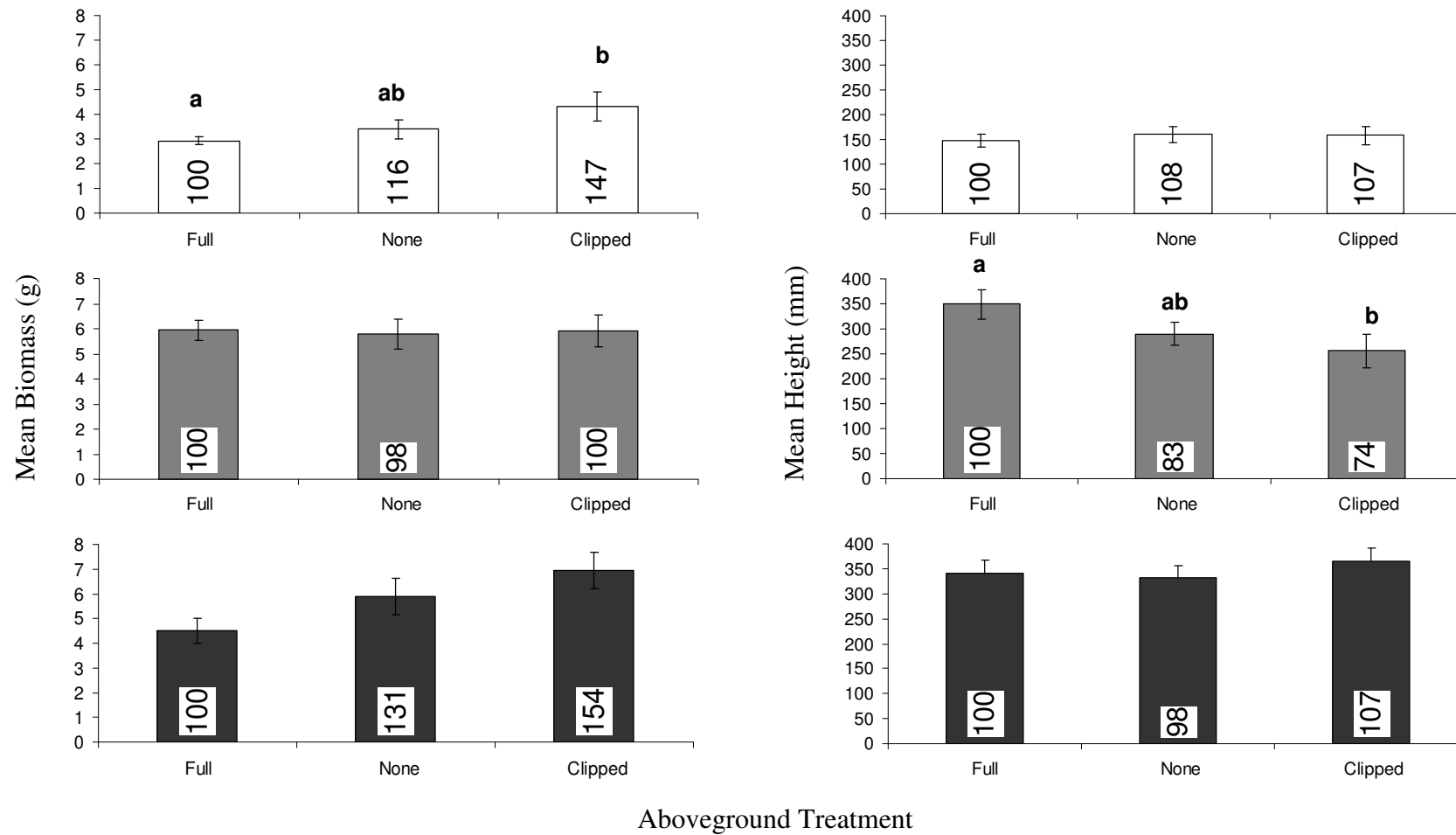
Figure 3.5: Means (±SE) for aboveground dry biomass and final height as a mean for both species under three aboveground treatments on shallow (open), medium (grey) and deep soils (black) and showing percentage yield relative to the control inside bars. Treatments with superscript letters in common are not different (P < 0.05, shallow depth $LSD_{biomass}$ = 1.0 and medium depth LSD_{height} = 74.5).
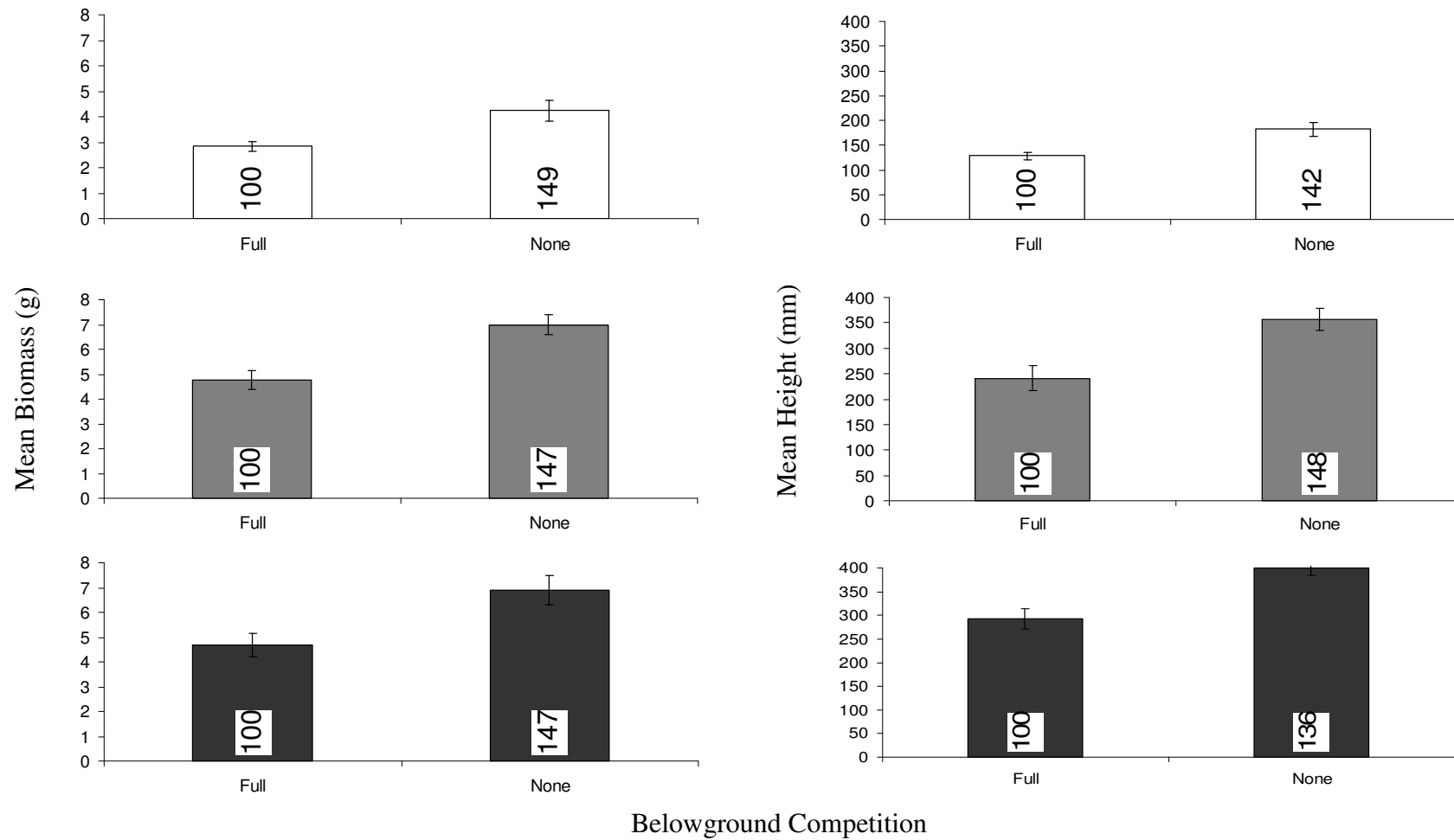
Figure 3.6: Means (±SE) for belowground dry biomass and final height as a mean for both tree species under two belowground competition treatments (full & none) on shallow (open), medium (grey) and deep soils (black) and showing percentage yield relative to the control.

There was an increase in height for both species with the removal of belowground competition. This increase was more pronounced in *A. karroo* than in *A. nilotica*. *Acacia nilotica* was significantly taller than *A. karroo* (P < 0.05) in the full belowground competition treatment (Figure 3.7).
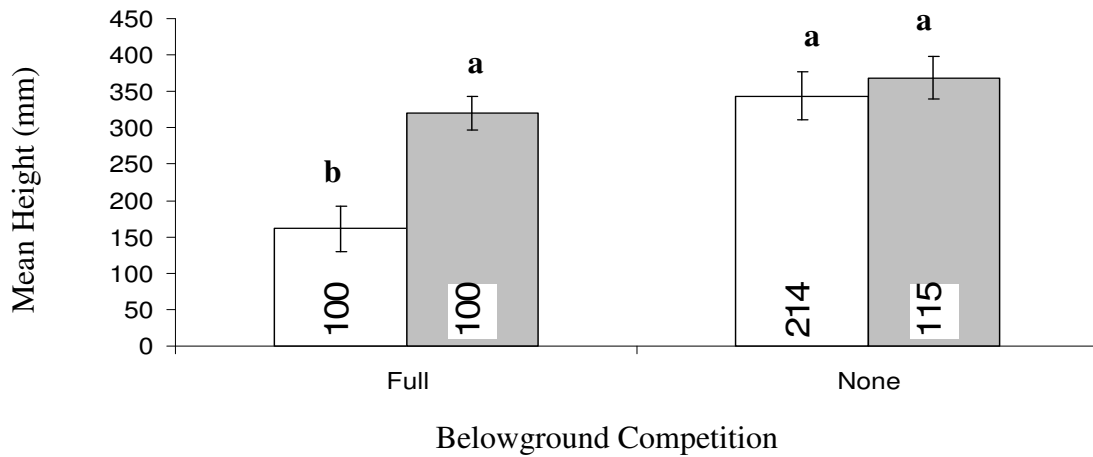
Figure 3.7: Mean final height for *A. karroo* (white) and *A. nilotica* (grey) seedlings growing under two levels of belowground competition growing on medium depth soil showing the percentage yield relative to the control. Treatments with superscript letters in common are not different (P < 0.05, LSD = 86.0).

The removal of belowground competition increased dry biomass across all three aboveground treatments, most substantially when there was no aboveground competition, where it doubled the dry biomass. The seedlings with no above or belowground competition had the greatest dry biomass followed by those where the surrounding sward had been clipped coupled with no belowground competition and then by those with full aboveground competition and no belowground competition. The removal of above aboveground competition, both by tying plants back and by clipping the surrounding sward, when seedlings were subjected to full belowground competition caused a decrease in dry biomass of 31% and 10% respectively (Figure 3.8).

Seedlings showed an asymptotic growth pattern, flattening out from 84 days after the start of the trial. On the shallow soil level seedlings responded in a similar way regardless of species and treatment combination. Maximum seedling height was just over 200 mm and was observed in the *A*. nilotica full root competition treatment where the surrounding sward was clipped (Figures 3.9 – 3.11).

Seedlings on both the medium and deep soils were taller than those on the shallow soil depth and showed more distinct treatment effects. On the medium soil depth plots the seedlings with full aboveground competition for both *A. karroo* without root competition and *A. nilotica* with root competition were the tallest, followed by the seedlings with no aboveground competition and finally the seedlings which had had the surrounding sward clipped. The shortest seedlings on the medium soil depth were those of *A. karroo* with full root competition (Figures 3.9 – 3.11).

The seedlings in both belowground treatments of *A. karroo* on the deep soil were similar in height regardless of aboveground treatment. *A. nilotica* with full root competition showed the most distinct separation of aboveground treatment effects with the seedlings under full above ground competition being the tallest followed by the seedlings which had the surrounding sward clipped and finally the seedlings with no aboveground competition. Across all three soil depths the seedlings of *A. karroo* with full root competition were the shortest regardless of aboveground treatment (Figures 3.9 – 3.11).
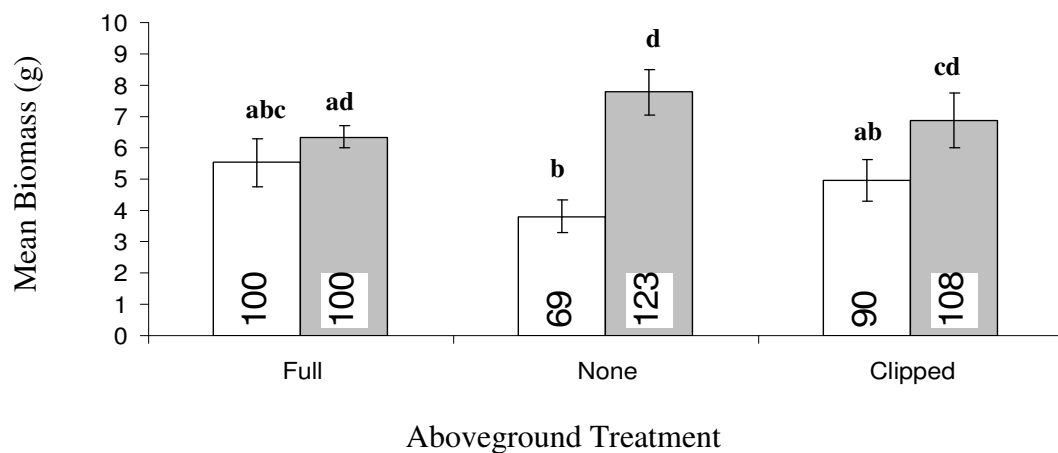
Figure 3.8: Mean (±SE) aboveground dry biomass for seedlings of both species growing under full (white) and no (grey) belowground competition under three aboveground treatments on medium depth soil and showing percentage yield relative to the control. Treatments with superscript letters in common are not different (P < 0.05, LSD = 1.761).
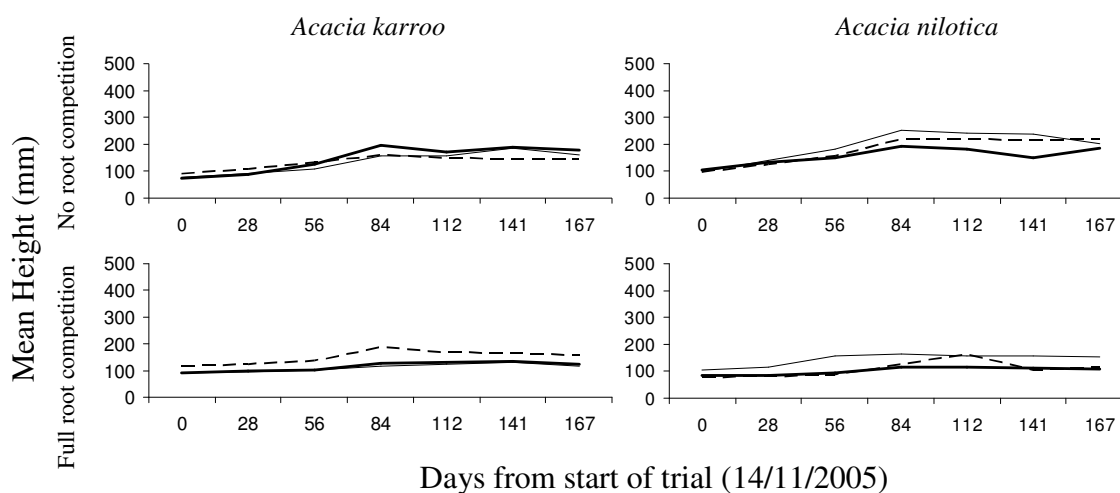
Figure 3.9: Change in mean height over time for three aboveground treatments: clipped (thin solid line), full (thick solid line) and none (dashed line), at two levels of belowground competition on the shallow soil site.
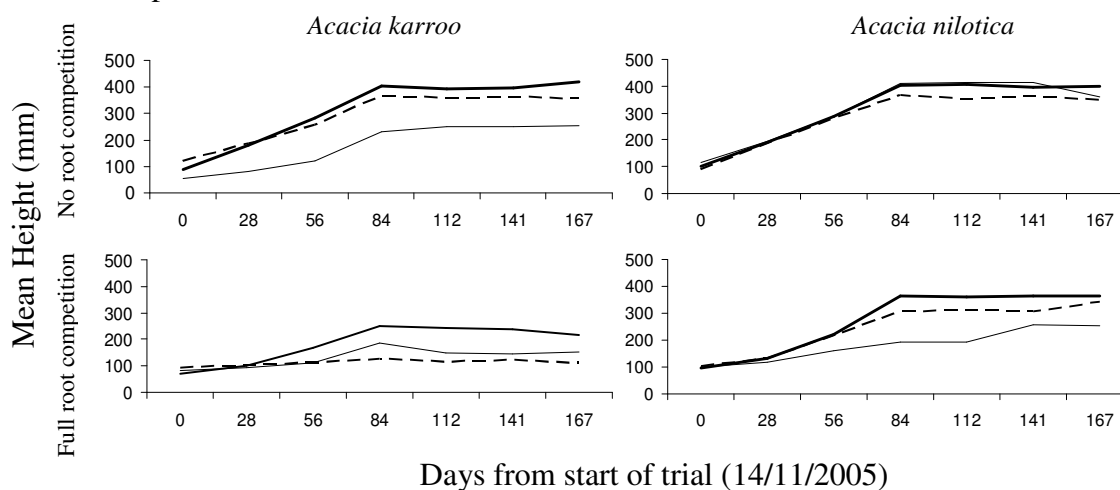
Figure 3.10: Change in mean height over time for three aboveground treatments: clipped (thin solid line), full (thick solid line) and none (dashed line), at two levels of belowground competition on the medium soil depth site.
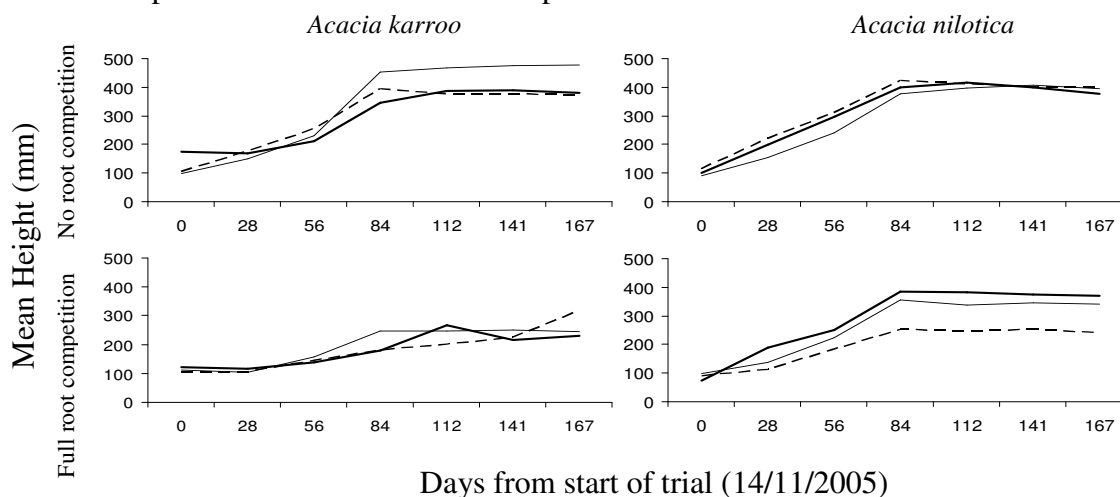
Figure 3.11: Change in mean height over time for three aboveground treatments: clipped (thin solid line), full (thick solid line) and none (dashed line), at two levels of belowground competition on the deep soil site.

In summary, soil depth was found to constrain plant size in both tree species. Plants grew taller and had a greater biomass with increasing soil depth. One exception to this is that *A. nilotica* seedlings on the medium soil depth had a slightly greater biomass than those grown on deep soil (Figure 3.4).

No effect of soil depth on the intensity of belowground competition was detected (Figure 3.6) although the importance of belowground competition in dictating tree seedling biomass was significant with increasing soil depth ($P < 0.05$) (Table 3.1). The opposite is true for aboveground competition as this only had a significant effect on biomass on shallow soils ($p < 0.05$), increasing biomass by 16% when competition was removed by tying back the surrounding grass and by 47% when the grass was clipped (Figure 3.5). On medium depth soils it was only significant when coupled with belowground competition ($p < 0.05$) (Table 3.1).

Belowground competition was also of greater importance than aboveground competition in dictating tree seedling height. Aboveground competition, irrespective of belowground competition, only had a significant effect on tree seedling height on medium depth soils ($p < 0.05$), with the fully shaded seedlings growing taller than those fully shaded on the shallow and deep soils (Table 3.1; Figure 3.5).

Simulated grazing, by clipping increased both biomass and height on shallow and deep soils, relative to those plants under full aboveground competition while it resulted in a decrease in height with no change in biomass on the medium soil depth. The effect of clipping on biomass was greater than the effect of removal of aboveground competition as on all three soil levels. This effect was also occurred in the height of seedlings on the medium and deep soil, while there was no difference in seedling height growing on shallow soil regardless of whether the surrounding grass was clipped or tied back (Figure 3.5).

The effects of clipping the surrounding sward were manifested on all soil depths after 28 days while the effects of full and no aboveground were observed after 28 days on the deep soils and only after 56 days on the shallow and medium soil depths (Figures 3.9 – 3.11).

3.6 DISCUSSION

The decline in the importance of aboveground competition with increasing soil depth is surprising as the dominant grasses on the shallow soil did not reduce incident sunlight by more than 50 % of the available sunlight, while the sward on medium depth soil comprised of taller grasses with a large number of longer leaves growing mainly from the base of the plant (pers. observation) shading up to 85 % of the available sunlight. The grass species dominating the deeper soils, while being tall species with long stems and few leaves located up the stem not shading more than 80 % of the available sunlight (Figure 2). The trend of increasing biomass with decreasing aboveground competition is supported by Kantz (2001) who found that *Acacia* seedlings survived better under reduced aboveground competition owing to grass cover reducing incident light availability. Shaded plants had lower leaf to height ratios indicating that plants are increasing in height rather than increasing leaf biomass in an attempt to escape light competition (Kantz, 2001).

The increase in tree biomass and height as a result of clipping may be due to a decrease in root productivity resulting from plant stress (Richards, 1984; McNaughton *et al.*, 1998). Defoliation by herbivory, has been observed to decrease root growth by up to 30 %, resulting from carbon limitation caused by shoot regrowth. As a result soil respiration decreases by up to 50 %, while nitrogen mineralization increases from approximately 90 % to 617 % and nitrogen cycling and availability increases as the removed nitrogen is returned in the form of urine and dung (Johnson & Matchett, 2001, Cahill & Casper, 2002). It is surprising then that defoliation had little impact on plant size on the medium soil depth. There are, however, contrasting opinions regarding the effects of grazing. Some studies have found grazing to have a stimulatory effect on root growth, while others have found that it has no effect at all (McNaughton *et al.*, 1998; Milchunas & Laurenroth, 1989). In decreasing root growth grazing essentially creates root gaps which tree seedling roots can colonise. However, greenhouse experiments have shown that this heavy grazing alone is not sufficient to cause bush encroachment. In addition, sufficient rainfall and soil nutrient levels low enough to prevent excessive grass growth but sufficient to allow for woody plant growth are required for bush encroachment to take place (Kraaij & Ward, 2006).

Contrary to the findings of Grime (1973) the removal of belowground competition appears to increase the seedling aboveground biomass by approximately 50% across all three soil levels. This may follow the predictions of Tilman (1985), who stated that each species has a limiting nutrient concentration (R*) below which the species cannot survive. If species are

limited by the same nutrient then the species with the lowest R* should displace its competitors in a nutrient limited environment (Tilman, 1985). Fynn *et al.* (2005) also presented evidence for these competitive hierarchies indicating the importance of trade-offs such as leaf width, specific leaf area and height in determining the competitive ability of a species along a fertility gradient (Fynn *et al.*, 2005). This consistent increase in both biomass and height with the removal of belowground competition, regardless of the degree of aboveground competition and soil depth further illustrates the importance of belowground competition in grassland and savanna systems as stated by various researchers over the last fifty years (Donald, 1958 cited in Carlen *et al.*, 2002: Johnson & Matchett, 2001; Wilson, 1988).

The height and biomass of *A. karroo* were very strongly correlated with soil depth resulting in taller, heavier plants on the deepest soils. It has been noted that available soil depth is more important than available horizontal space with plants successfully establishing in gaps only 10 cm in diameter (Jurena & Archer, 2003). *Acacia nilotica* also tended to increase in biomass and height with increasing soil depth but this trend was not as marked as for *A. karroo* and the plants on medium and deep soils were much the same size. Overall, *A. nilotica* is a larger plant in terms of both biomass and height and did not appear to be as strongly affected by belowground competition as *A. karroo*. Although *A. nilotica* has been observed to have an advantage over *A. karroo* in terms of surviving grass competition it has been observed that *A. karroo* has higher seed emergence rates (Kantz, 2001) and thus may make up for this sensitivity to competition by sheer number of seedlings produced.

To conclude, belowground competition appears to be more important than aboveground competition in determining the outcome of the interactions between tree seedlings and the surrounding grass sward and the intensity of the effect of belowground competition does not appear to be influenced by increasing soil depth. Shallow and deep soils appear to be more likely to become encroached as a result of intense grazing than medium depth soils. On shallow soils this may be as a result of decreased root vigor of the surrounding grasses allowing the tree seedlings access to water and nutrient resources (Johnson & Matchett, 2001; Cahill & Casper, 2002; Wiegand *et al.*, 2005). On deep soils this decrease in surrounding sward root vigor, coupled with the increase in available light resources may allow the tree seedlings to increase root elongation and access soil water and nutrients in deeper soil layers inaccessible to the grass sward (Walker *et al.*, 1981).

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CHAPTER FOUR

ABOVE- AND BELOWGROUND INTERACTIONS BETWEEN SEEDLINGS OF
THREE GRASS SPECIES AND THE SURROUNDING NATIVE GRASS SWARD ON
THREE SITES OF DIFFERING SOIL DEPTH

4.1 ABSTRACT

Interactions between mature grass plants and grass seedlings have been found to be both
facilitative and competitive (Aguiar, *et al*., 1992). The degree of competition exerted by
interactions depends largely on the species of the mature plant and the seedling, the soil
conditions and the available resources. To examine the effects of combinations of above
and belowground competition on growth percentage, in terms of biomass, and tuft size, in
terms of tiller number and the effects of soil depth on these interactions, seedlings of three
locally common grass species, *Eragrostis racemosa, Themeda triandra* and *Panicum
maximum*, were planted into a natural grass sward on three different parts of the landscape
that varied in soil depth. Three aboveground treatments, full light competition, no light
competition and clipping to simulate grazing, and two belowground treatments, full
belowground competition and no belowground competition, were used. Seedlings growing
on all three soil depths the three grass species differed in mean mass, with *E. racemosa*
having the least mass and *T. triandra* having the greatest. Results for number of tillers
were more complex as some species, such as *P. maximum*, were tall but had a low number
of tillers. Simulated grazing by clipping the surrounding sward created niches for seedling
establishment while heavy grazing has been observed to increase seedling mortality. This
highlights the importance of maintaining stocking rates at a level which promotes seedling
establishment.

4.2 INTRODUCTION

Adult grasses and grass seedlings respond differently to competition from the surrounding
sward. Interactions between adult grass plants and grass seedlings have been found to be
both competitive and facilitative (Niering *et al.,* 1963; Fowler, 1986; Aguiar *et al*., 1992;
Holmgren & Scheffer, 1997). In the case of a competitive interaction adult grass plants
may prevent the establishment of grass seedlings resulting in increasingly large areas of
bare ground (Aguiar *et al*., 1992). Water plays a large role in this interaction. In a survey
during the rainy season when water is available in all soil layers the seedlings growing near
adult plants suffered some reduction in growth but survived the season, while during the

dry season those seedlings growing in close proximity to adult plants showed both a decrease in growth rate and an increase in mortality (Aguiar *et al*., 1992). Other studies (Niering *et al.,* 1963; Fowler, 1986; Holmgren & Scheffer, 1997) have found that adult plants may behave as 'nurse plants', creating a favourable microclimate which favours seedling establishment by keeping the soil surface damp as a result of shading.

In grassland regions in particular, belowground competition is believed to impact seedling establishment more than aboveground competition (Donald, 1958 cited in Carlen *et al*., 2002; Wilson, 1988), while after the first year of growth aboveground competition appears to become more influential (Haugland & Tafiq, 2001). These effects may, however, be influenced by soil type as regions with fertile soil have been observed to be dominated by plants with fast growth rates and rapid nutrient uptake and a large aboveground biomass, indicating that aboveground competition is more influential than belowground (Grime, 1979). Several studies have shown that in cases where plants have been subjected to belowground competitive stress the addition of nutrients has relieved this stress, resulting in increased growth rates and final yield irrespective of the level of aboveground competition (Fowler; 1986; Snaydon & Howe, 1986; Cook & Ratcliff, 1984). This response may result from the ability of adult grass plants to exert competitive effects up to 60 mm away from the actual root (Fowler, 1986) thus creating a large zone of influence around the plant. This competition would be compounded in a dense grass sward by the overlap of this zone with those of surrounding plants. These effects may differ according to plant shoot and root structure, competitive effect and response, defoliation regrowth response of competing species and season or time of dormancy (Carlen *et al*., 2002).

This experiment aimed to answer the following questions: what are the relative effects of above- and belowground competition and their interactions on
(1) aboveground growth percentage, in terms of biomass, and tuft size, in terms of tiller number, of three locally common grass species and the effects of soil depth on these interactions?
and (2) growth pattern of the three grass species over a 24 week period across three levels of soil depth?
and (3) does soil depth mediate competitive interactions between grass seedlings and the surrounding sward?

4.3 METHODS

4.3.1 *Study Area*

The experiment was carried out at Ukulinga Research Farm, Pietermaritzburg, South Africa (29°24'E, 30°24'S). The mean annual rainfall calculated over the last 24 years is 694 mm and falls predominantly during the summer months (September to April). The summer months are hot, with a mean monthly maximum of 26.4°C occurring in February, while winters are mild with some frost, with a mean monthly minimum of 8.8°C occurring in July. The combination of these climatic variables results in a growing season from October to April (Fynn & O'Connor, 2005). The vegetation falls into the grassland biome (Rutherford & Westfall, 2003) and is classified by Acocks (1988) as Natal Mist Belt 'Ngongoni Veld, dominated by *Aristida junciformis, Themeda triandra*, and *Tristachya leucothrix*, while it falls into the transition zone between Ngononi Veld and KwaZulu-Natal Hinterland thornveld as classified by Mucina & Rutherford (2006).

Figure 4.1: Ukulinga Research Farm monthly rainfall for August 2005 to May 2006.

The three experimental plots were located within 1 km of one another along a catenal gradient, with the shallow soil plot at the top, the medium soil plot part of the way down, and the deep soil plot at the bottom of the catena. The soils at these three points are classified as Westleigh, Mayo and Bonheim forms respectively (Anon, 1991). The plots were approximately 10 m by 15 m. The soil underlying the shallow plot ranged from 150 to 250 mm deep, while the soils underlying both the medium dystrophic and the deep eutrophic plots were both deeper than 1500 mm. The dominant grass species in the shallow soil plot were *Melinis nerviglumis, Eragrostis racemosa, T. leucothrix, Eragrostis capensis* and *Eragrostis curvula*. The dominant non-grass herbaceous species were *Hypoxis* sp. and *Senecio* sp. and there were no trees in the immediate vicinity. The dominant grass species in the medium soil plot were *T. triandra* and *E. curvula*, while the dominant non-grass herbaceous species were *Hypoxis* sp. There was one small *Acacia* (less than 0.5 m tall) in

the plot but no other trees in the immediate vicinity. The dominant grass species in the deep soil plot were *E. curvula* and *Setaria sphacelata*. There was one *Acacia* (less than 2 m tall) in the plot and a large number of *Acacias* (greater than 2 m tall) around the plot.

4.3.2 *Experimental Design*

Seedlings of three local grass species, *E. racemosa*, *T. triandra* and *Panicum maximum*, were used. These three species vary in structure, with differing leaf heights and tillering ability. *E. racemosa* is short (< 300 mm) with a large number of tillers, *T. triandra* is medium height (< 600 mm) with less tillers than *E. racemosa* and *P. maximum* is tall (< 1400 mm) with less tillers than *T. triandra* (unpublished data, RWS Fynn). These plants were subjected to various combinations of above- and belowground competition, created by various treatments. Each treatment was applied in a 0.5 x 0.5 m area with the grass phytometer (study plant) in the centre.

The three aboveground treatments (AG) were: full light competition, partial light competition and no light competition. In full light competition the sward was allowed to grow undisturbed to provide full competition for light. Partial light competition was created by clipping the sward at 6, 4 and 2 week intervals for the shallow, medium and deep swards respectively to a height of approximately 4 cm to simulate intensive grazing. The no light competition was created by holding the surrounding aboveground grass material down using a 0.5 m by 0.5 m square of netting with holes 2 cm by 2 cm. A hole was cut in the centre of the netting to allow the grass phytometer to emerge. The four corners of the net were pegged to the ground and four points around the central hole were also pegged to the ground (adapted from Cahill, 1999). Treatments were checked, the net maintained and clipping done at 2, 4 and 6 weekly intervals for the deep, medium and shallow plots respectively. The percentage shading given by these treatments at each of the three plots was determined by taking ten light intensity readings on each treatment at midday on a cloudless day at the outset of the trial using a Decagon PAR/LAI Ceptometer Accupar LP-80 light meter.

Following the methods of Cahill (1999) two belowground treatments (BG) were applied: full root competition and no root competition, or root exclusion. For both of these treatments PVC tubes 150 mm in diameter were used. For the shallow plot tubes were cut to a length of 200 mm and three rectangular holes 80 mm wide and 140 mm long were cut

in the sides. For the medium and deep plots the tubes were cut to a length of 500 mm and six holes 80 mm wide by 180 mm long were cut in the sides. In the root exclusion treatment these holes were then covered with 43 μm NITEX mesh (produced and supplied by Meshcape Industries, Durban, South Africa) to prevent root interaction but allow the lateral movement of soil water and nutrients. In the full root competition treatment these holes were left uncovered.

The treatments were combined using a full factorial design with all combinations of: full, partial and no light competition to create varying levels of aboveground competition and full and no root competition to create varying levels of belowground competition. The treatments were then laid out in a completely randomized design with four replications per treatment.

In each plot, 72 holes were dug with a petrol powered auger, to a depth of 200 mm in the shallow plot and 500 mm deep in the medium and deep plots. The soil was removed from the holes and mixed to reduce the effects of soil heterogeneity. PVC tubes were randomly allocated to the holes and then filled with the mixed soil. The grass phytometers were then planted into the tubes. These plants were watered for the first two weeks after planting to ensure survival. Thereafter, growth depended on natural rainfall.

4.2.3 *Sampling*

The trial was run from 5 Dec 2005 to 22 May 2006. Grass height was measured every four weeks. After 24 weeks the final height measurements were taken and the grass aboveground biomass was harvested, dried at 60°C and weighed to provide a measure of grass performance under different treatments. In addition rainfall was monitored for the duration of the study and the mean standing dry biomass of the surrounding sward was measured for each plot by taking clippings from ten 1 x 1 m quadrats randomly located around each plot but at a suitable distance to be unaffected by the treatments.

4.4 ANALYSIS

Changes in mean height for shallow, medium and deep soil levels were graphed against time for each grass species separately. Three way ANOVA (species x AG x BG) was performed on both the mean final height and the mean dry biomass for each grass species. Residuals were examined to confirm that the assumptions of ANOVA were met. Data were

transformed where necessary to fit these assumptions. When the ANOVA (f-test) revealed significant differences, the least significant Fisher's test (LSD) for p ≤ 0.05 was used to separate means. In addition the percentage change in yield (Ry) resulting from the treatment effect was calculated by comparing each treatment to the control of both full above and full belowground competition using the following formula:

$$Ry = [(Y_t - Y_c)/Y_c]*100$$

Where Y_t is the final mean value for treatment and Y_c is the final mean value for the control.

4.5 RESULTS

Percentage shade given by the aboveground treatments increased from clipped, where the surrounding sward was clipped to simulate intensive grazing, to net, where the surrounding grass was held back by netting to remove aboveground competition, to full, where the surrounding sward was allowed to grow naturally and exhibit maximum aboveground competition. The shallow soil site was characterized by short grass species and as a result did not shade more than half the available light when exerting full aboveground competition. The sward on the medium soil depth gave the highest level of shading at full competition, with the sward on the deep soil shaded the plants slightly less (Figure 2).
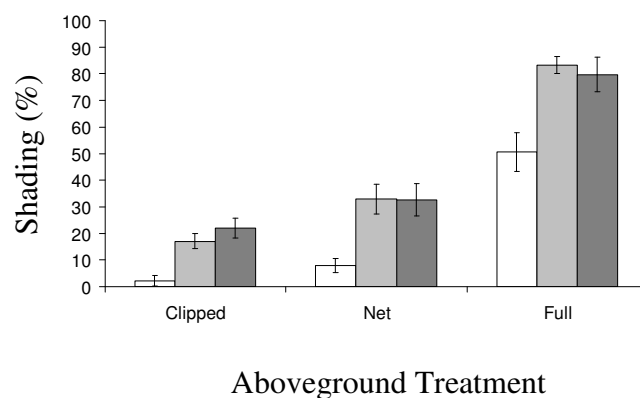
Figure 4.2: Percentage shading given by three aboveground treatments for shallow (open), medium (grey) and deep soils (black). A mean value calculated from ten readings taken on each treatment at the outset of the trial.

Biomass of the surrounding sward was sampled at the end of the growing season when the trial was harvested and showed the expected increase with increasing soil depth (Figure 3).
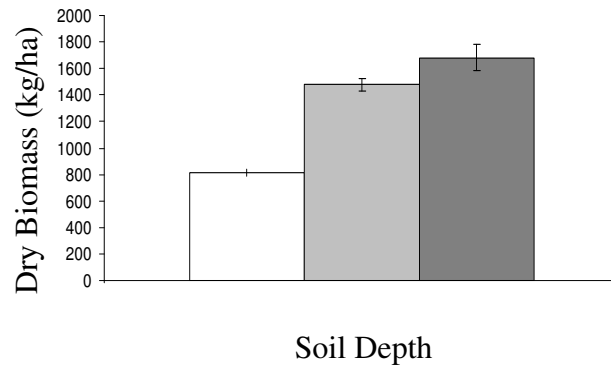
Figure 4.3: Standing dry biomass of surrounding sward for shallow (open), medium (grey) and deep soils (black).

Table 4.1: Results of analysis of variance of main effects and interactions for grass mean aboveground dry biomass (g) and mean final number of tillers on (a) shallow, (b) medium and (c) deep soil sites showing degrees of freedom (d.f.), sum of squares (s.s.), mean squares (m.s.) F-ratio and p-value with significant effects (p < 0.05) in bold. Analyses for medium and deep soils performed on log transformed data

a)

Source of variation	Biomass					Tillers				
	d.f.	s.s.	m.s.	F-ratio	p-value	d.f.	s.s.	m.s.	F-ratio	p-value
Species	2	262.06	131.03	10.510	**<0.001**	2	74569.10	37284.50	76.560	**<0.001**
Aboveground (AG)	2	127.13	63.57	5.100	**0.010**	2	4582.60	2291.30	4.710	**0.013**
Belowground (BG)	1	115.52	115.52	9.270	**0.004**	1	249.40	249.40	0.510	0.477
Species.AG	4	35.71	8.93	0.720	0.585	4	6551.30	1637.80	3.360	**0.016**
Species.BG	2	3.17	1.58	0.130	0.881	2	1338.80	669.40	1.370	0.262
AG.BG	2	9.32	4.66	0.370	0.690	2	543.90	271.90	0.560	0.576
Species.AG.BG	4	41.33	10.33	0.830	0.513	4	117.20	29.30	0.060	0.993
Residual	50	623.10	12.46			51	24836.30	487.00		
Total	67	1162.92				68	106951.90			

b)

Source of variation	Biomass (log transformed)					Tillers (log transformed)				
	d.f.	s.s.	m.s.	F-ratio	p-value	d.f.	s.s.	m.s.	F-ratio	p-value
Species	2	1.403	0.702	28.270	**<0.001**	2	13.07	6.54	145.33	**<0.001**
Aboveground (AG)	2	0.144	0.072	2.910	0.064	2	0.19	0.09	2.09	0.134
Belowground (BG)	1	0.818	0.818	32.960	**<0.001**	1	0.00	0.00	0.02	0.883
Species.AG	4	0.063	0.016	0.640	0.638	4	0.37	0.09	2.06	0.099
Species.BG	2	0.077	0.039	1.560	0.221	2	0.20	0.10	2.24	0.116
AG.BG	2	0.014	0.007	0.290	0.750	2	0.76	0.38	8.49	**<0.001**
Species.AG.BG	4	0.148	0.037	1.490	0.219	4	0.19	0.05	1.03	0.399
Residual	50	1.241	0.025			52	2.34	0.05		
Total	67	3.683				69	16.67			

c)

Source of variation	Biomass (log transformed)					Tillers (log transformed)				
	d.f.	s.s.	m.s.	F-ratio	p-value	d.f.	s.s.	m.s.	F-ratio	p-value
Species	2	3.051	1.526	29.290	**<0.001**	2	56.74	28.37	143.88	**<0.001**
Aboveground (AG)	2	0.874	0.437	8.390	**<0.001**	2	6.05	3.03	15.340	**<0.001**
Belowground (BG)	1	1.548	1.548	29.710	**<0.001**	1	1.25	1.25	6.32	**0.016**
Species.AG	4	0.074	0.018	0.350	0.840	4	1.35	0.34	1.71	0.164
Species.BG	2	0.199	0.100	1.910	0.160	2	0.33	0.16	0.83	0.442
AG.BG	2	0.021	0.011	0.210	0.815	2	0.80	0.40	2.01	0.146
Species.AG.BG	4	0.063	0.016	0.300	0.876	4	0.37	0.09	0.46	0.761
Residual	44	2.292	0.052			44	8.68	0.20		
Total	61	7.430				61	62.92			

All three main effects had a significant influence ($p < 0.05$) on grass seedling biomass on both shallow and deep soil levels (Table 4.1a & c), while only the effects of species and belowground treatment were found to be significant ($p < 0.001$) on the medium soil level (Table 4.1c). On the shallow soil the main effects of species and aboveground competition and the interaction of species and aboveground treatment had a significant effect ($p < 0.05$) on the final number of tillers (Table 4.1a). Species differed in biomass on the medium soil level, while above- and belowground only exerted significant ($p < 0.001$) competitive effects when interacting with one another (Table 4.1b) On the deep soil level only the three main effects are significant (Table 4.1c). These significant effects are illustrated in figures 4.4 to 4.11. All responses are presented in Appendix 2.

The biomass of both *P. maximum* and *T. triandra* increased with increasing soil depth, while biomass of *E. racemosa* remained fairly consistent. *Themeda triandra* had the largest biomass on the shallow and medium soil depths, while *P. maximum* had the largest biomass on the deep soil. On shallow soil the biomass of *T. triandra* was significantly different to the other two species ($p < 0.05$), while on deep soil the biomass of *E. racemosa* was significantly different to the other two species ($p < 0.05$). On the medium soil depth the dry biomass of all three species were different ($p < 0.05$) to one another (Figure 4.4).

Themeda triandra had the greatest number of tillers on all three soils, followed by *E. racemosa* and then *P. maximum* with the least number of tillers. Despite increasing in biomass, *P. maximum* tiller number decreased with increasing soil depth, while *T. triandra* tiller number increased consistently with increasing soil depth. Mean tiller number differed between species ($p < 0.001$) all three species for all three soil levels (Figure 4.4).
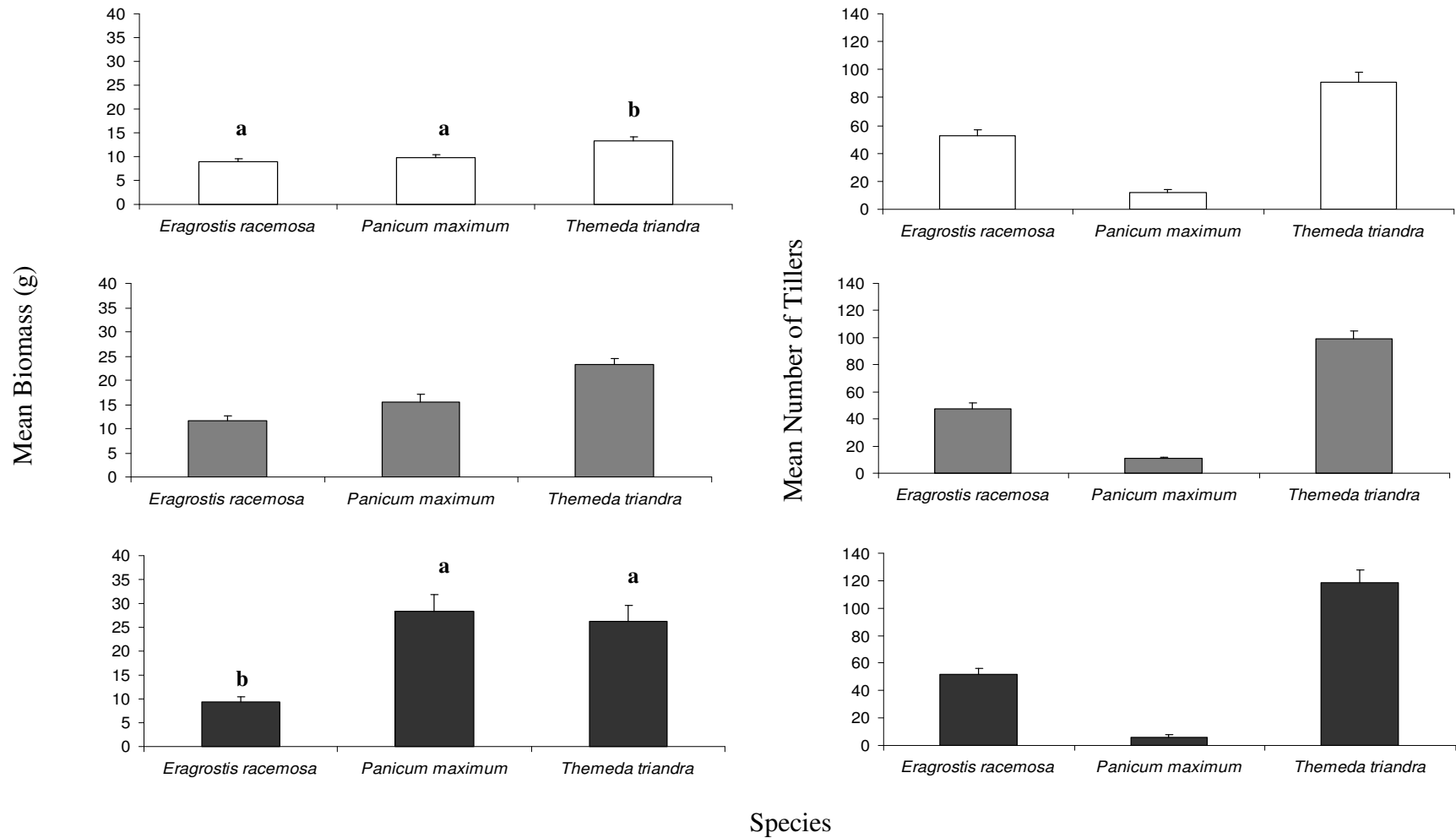
Figure 4.4: Means (±SE) for species aboveground dry biomass and final number of tillers comprising all treatments on shallow (open), medium (grey) and deep soils (black), showing results of means comparisons (LSD) using untransformed data for shallow soil and log transformed data for medium and deep soils. Treatments with letters in common are not different (P < 0.05, shallow soil $LSD_{biomass}$ = 2.047).

Biomass increased consistently with increasing soil depth in all three of the aboveground treatments. Soil depth had the greatest effect on the biomass of those plants around which the sward had been clipped, with the relative yield increasing from 34% more the control on the shallow soil to 91% on the deep soil (Figure 4.5). On the shallow and deep soils the dry biomass of the plants where the surrounding sward had been clipped were larger than those plants on the other two aboveground treatments ($p < 0.001$) (Figure 4.5).

Tiller number increased as aboveground competition was reduced on shallow and deep soils: plants where the surrounding sward had been clipped had the most, no competition fewer and full competition the least. Under clipping, soil depth did not have as large an effect on the number of tillers as it did on dry biomass, with an increase of 46% (19.5 g) on the shallow soils and 59% (29.5 g) on the deep soils relative to the size of the control plants. The removal of aboveground competition decreased tiller number from a 24% (10 tillers) increase relative to the control plants to an 11% (5.4 tillers) increase, on shallow and deep soils respectively (Figure 4.5).

There was a consistent increase in dry biomass with increasing soil depth for both levels of belowground competition, with a greater increase observed in the absence of belowground competition. The effect of the removal of belowground competition increased from a 27% (2.53 g) increase relative to the biomass of the control plants on shallow soil to a 68% (10.8 g) increase on deep soil (Figure 4.6).

There was also a consistent increase in number of tillers with increasing soil depth under both full and no belowground competition, although the effect was of a lesser magnitude than was observed in the aboveground dry biomass. The effect of the removal of belowground competition increased from 8% (4.2 tillers) on shallow soil to 13% (5.3 tillers) to deep soil (Figure 4.6).
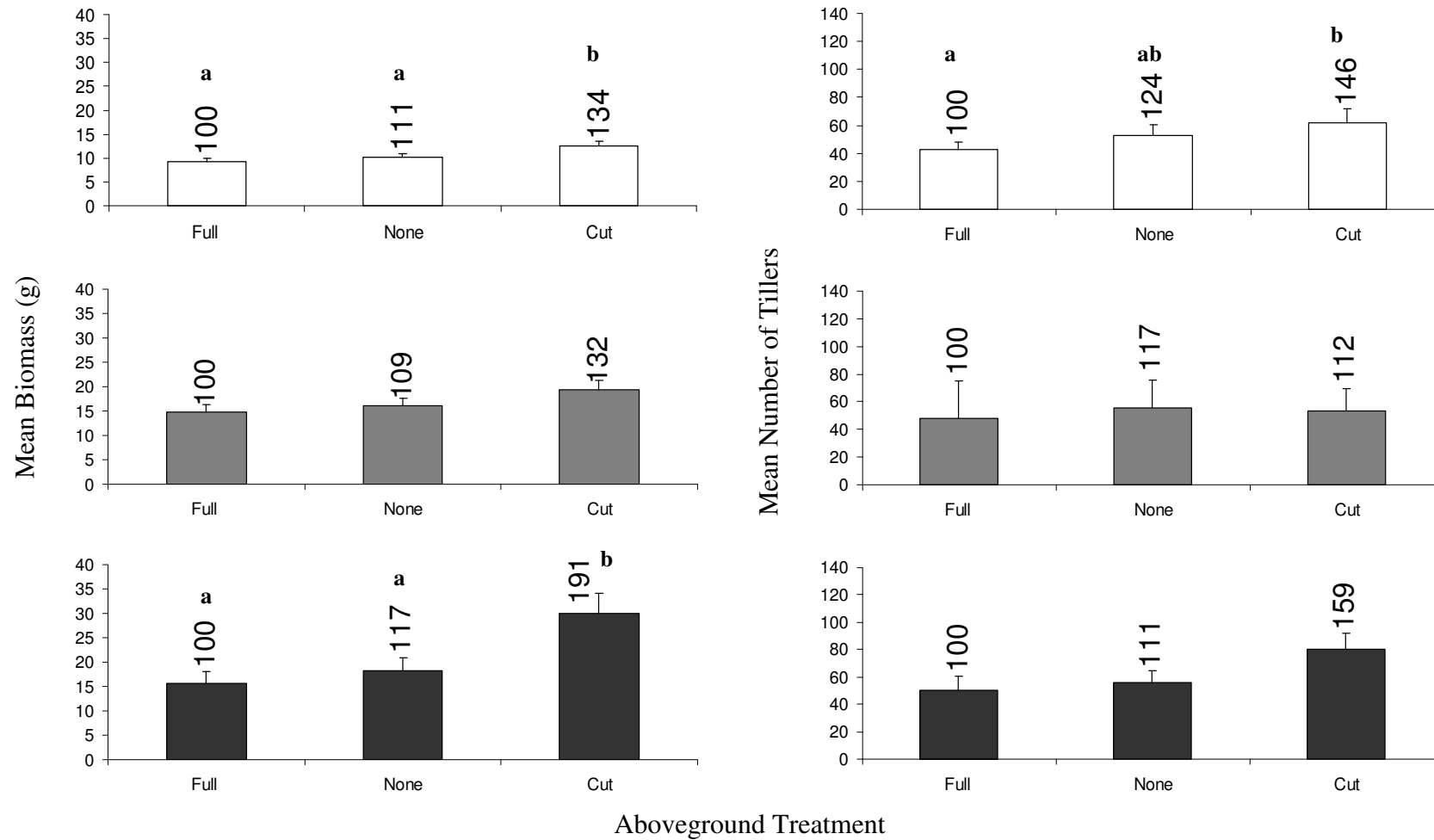
Figure 4.5: Means (±SE) for aboveground dry biomass and final number of tillers comprising all three grass species and both belowground treatments under three aboveground treatments on shallow (open), medium (grey) and deep soils (black), showing results of means comparisons (LSD) using untransformed data for shallow soil and transformed data for medium and deep soils and percentage yield relative to the control above bars. Treatments with letters in common are not different (P < 0.05, shallow soil $LSD_{biomass}$ = 2.047 and $LSD_{tillers}$ = 12.79).
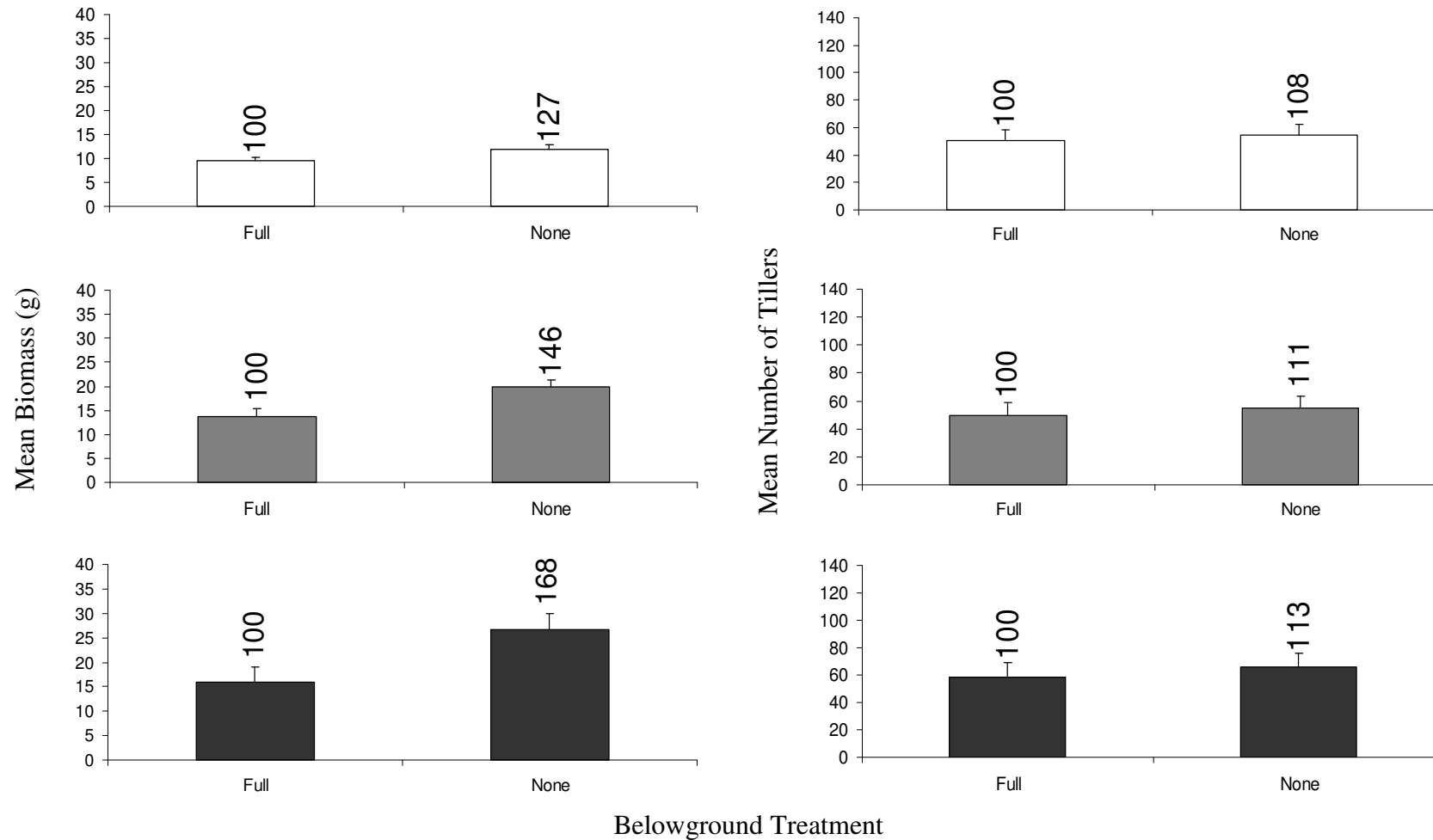
Figure 4.6: Untransformed data means (±SE) for aboveground dry biomass and final number of tillers comprising all three species and three aboveground treatments under two belowground treatments (Full and None) on shallow (open), medium (grey) and deep soils (black) and showing percentage yield relative to the control above bars.

For *P. maximum,* the number of tillers increased by 61% (6.5 tillers) when the sward was clipped compared to full competition, while there was a 13% (1.4 tillers) decrease when aboveground competition was removed. Conversely *E. racemosa* tiller number increased by 15% (7.3 tillers) when aboveground competition was removed, while it only increased by 2% (0.8 tillers) when the surrounding sward was clipped. There was a consistent increase in the tiller number of *T. triandra*: full aboveground competition had the least, no aboveground competition had more with an increase of 35% (23.2 tillers) compared to full competition and plants where the surrounding sward was clipped had the most with a 78% (51.4 tillers) increase (Figure 4.7).

Under full aboveground competition *P. maximum* had significantly less tillers than both *E. racemosa* and *T. triandra* ($p < 0.05$), while under no aboveground competition and when the surrounding sward was clipped all three species had different tiller numbers ($p = 0.016$) (Figure 4.7).
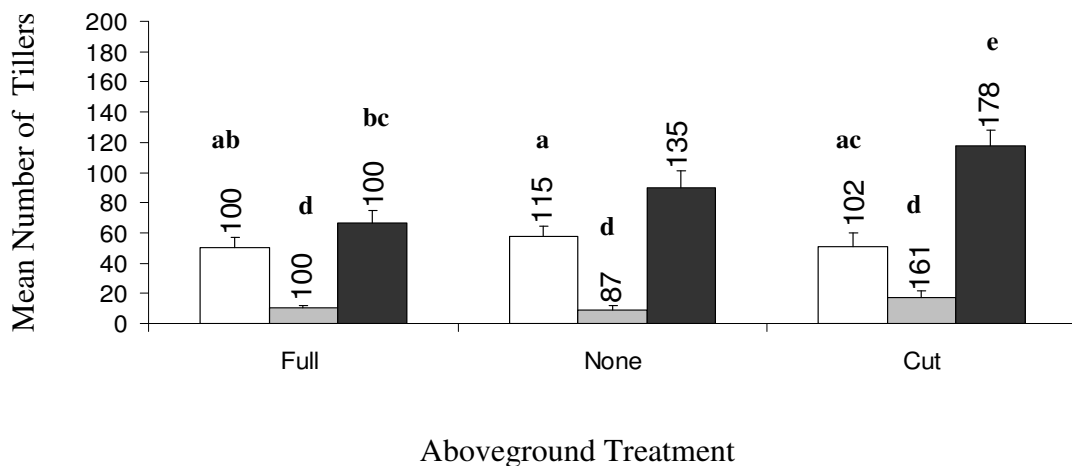
Figure 4.7: Mean final number (±SE) of tillers for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) on shallow soil comprised of both belowground treatments under three aboveground treatments, showing results of means comparisons (LSD) using untransformed data for shallow soil and transformed data for medium and deep soils and percentage yield relative to the control above bars. Treatments with superscript letters in common are not different ($P < 0.05$, LSD = 22.15).

Tiller number increased by 55% (21.7 tillers) as a result of clipping the surrounding sward despite the fact that belowground competition remained unchanged. The removal of both above- and belowground competition resulted in a 61% (24.2 tillers) increase in tiller number ($p < 0.001$) (Figure 4.8).
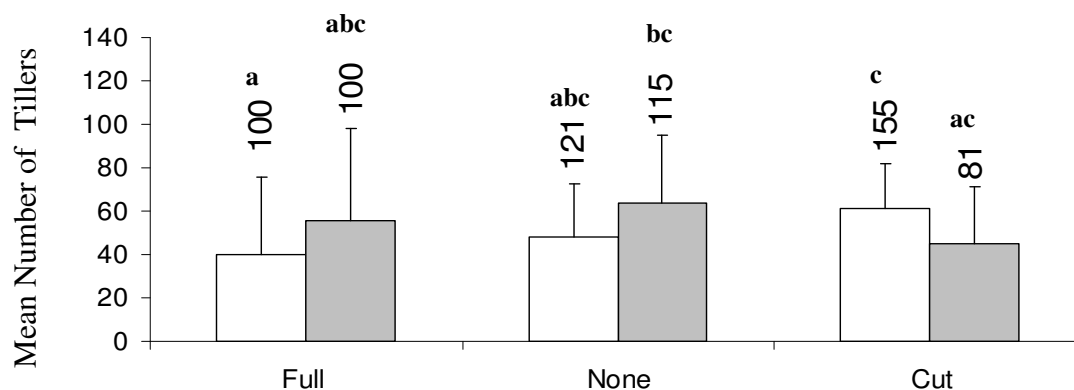
Figure 4.8: Mean final number (±SE) of tillers from untransformed data on medium soil for full belowground competition (open) and no belowground competition (grey) under three aboveground treatments and showing percentage yield relative to the control above bars.

Seedlings showed an asymptotic growth pattern, flattening out between 56 and 112 days from the outset of the trial. Clipping the surrounding sward resulted in the most rapid increase in tiller number for all species regardless of belowground treatment on deep soil (Figures 4.9 – 4.11).

Themeda triandra responded the most to changes in the degree of aboveground competition in both the presence and absence of belowground competition. Treatment effects became apparent after 56 days from the outset of the trial on shallow and deep soils and 112 days on the medium depth soil. Under full belowground competition *E. racemosa* only exhibits the effects of the aboveground treatments on deep soil, while when belowground competition is absent some aboveground treatment separation can be seen on all three soil depths. There was little difference in the change in *P. maximum* tiller number over time regardless of treatment and soil depth (Figures 4.9 – 4.11).
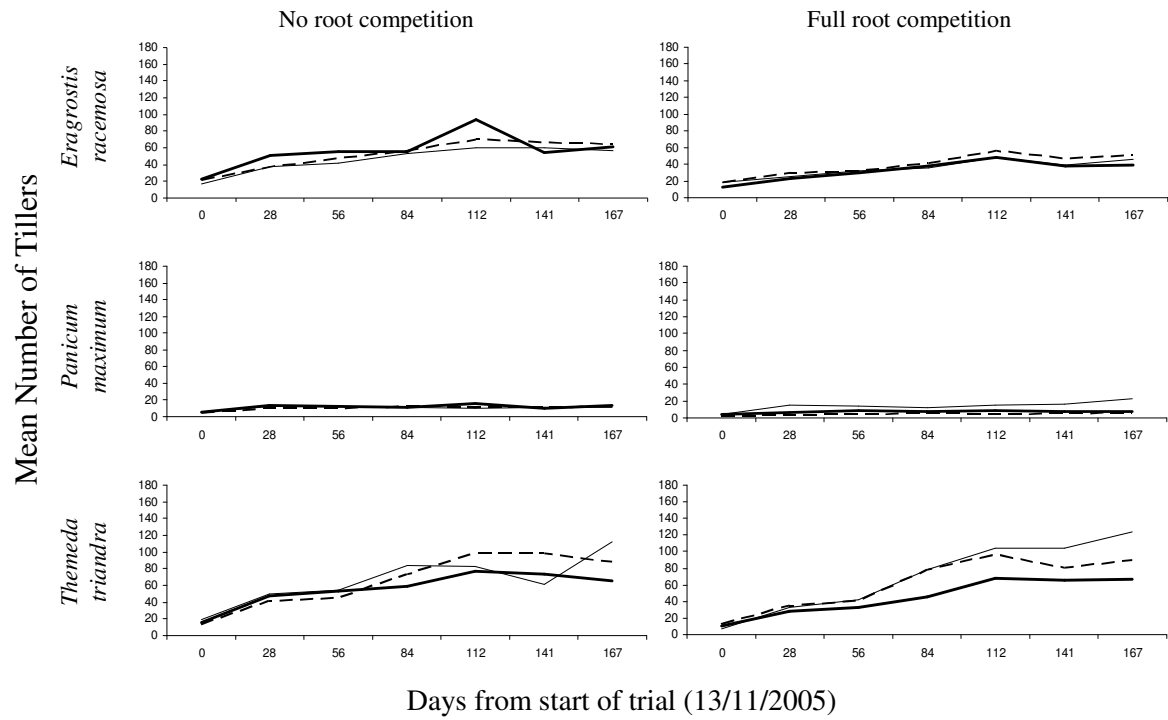
Figure 4.9: Change in mean tiller number over time for three aboveground treatments, cut (thin solid line), full (thick solid line) and none (dashed line), under two belowground treatments, on the shallow soil level.
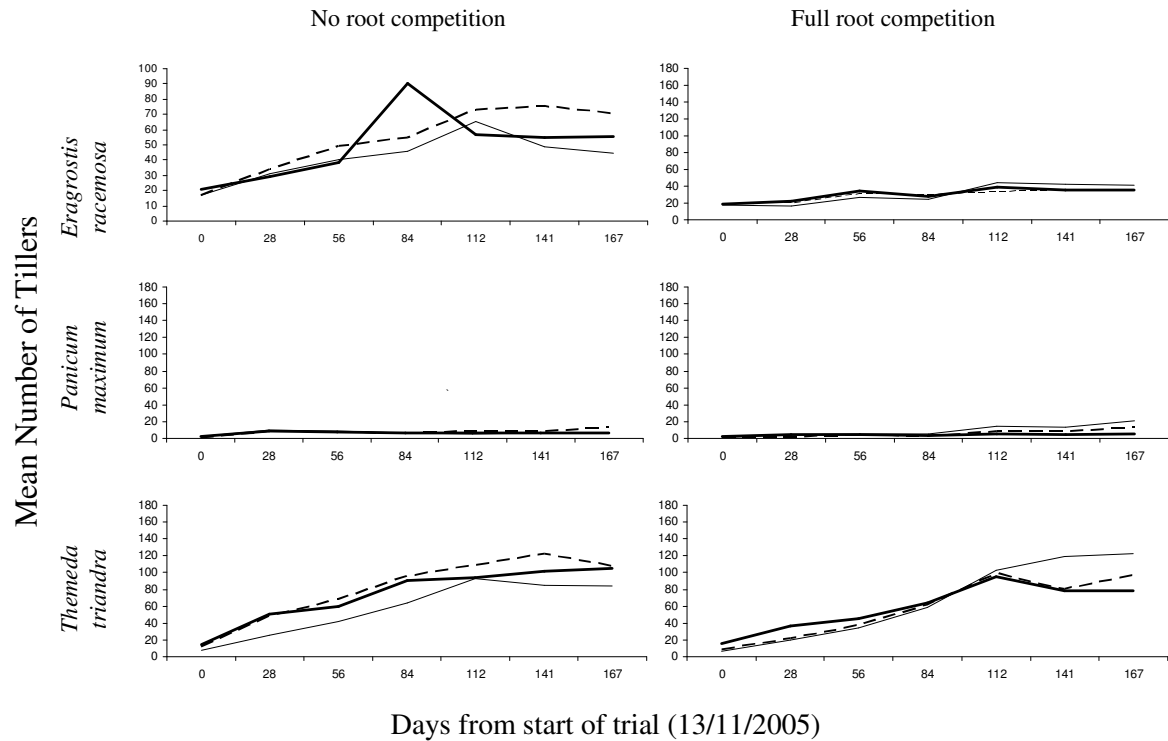
Figure 4.10: Change in mean tiller number over time for three aboveground treatments, cut (thin solid line), full (thick solid line) and none (dashed line), under two belowground treatments on medium soil level.
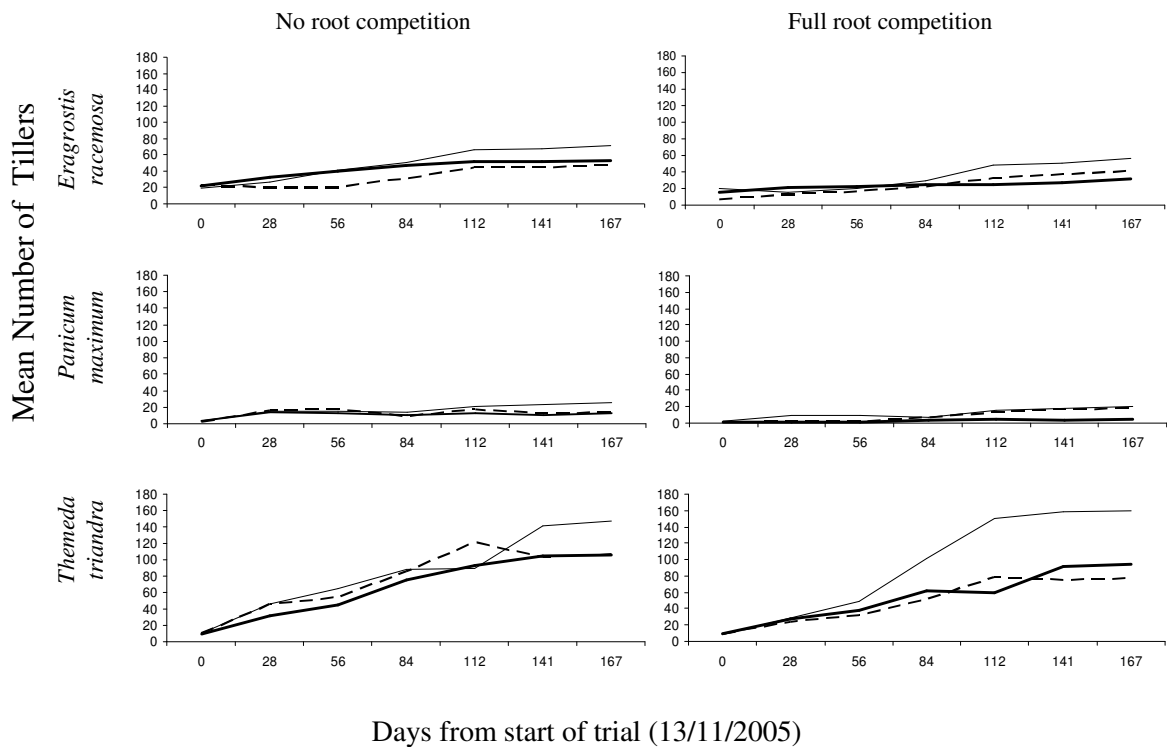
Figure 4.11: Change in mean tiller number over time for three aboveground treatments, cut (thin solid line), full (thick solid line) and none (dashed line), under two belowground treatments on the deep soil level.

In summary, on all three soil depths the three grass species differed in mean mass with *E. racemosa* having the least mass and *T. triandra* having the greatest. Above- and belowground competition had consistent effects, decreasing in intensity with increasing soil depth. There were no effects of interaction between above- and belowground competition. Results for number of tillers were more complex as some species, such as *P. maximum*, were tall but had relatively few tillers.

4.6 DISCUSSION

Biomass of all species increased with increasing soil depth across all levels of above- and belowground competition. Biomass gain was affected by both above- and belowground competition on shallow and deep soils, while only belowground competition affected plant biomass on medium soil depths. The removal of aboveground competition increased tiller number on both shallow and deep soils, while clipping the surrounding sward amplified this response still further. The removal of belowground competition only increased tiller

number on deep soils. On shallow and medium soils, above and belowground competition respectively, had some effect of tiller number but this effect varied between species. Thus grass aboveground competition may play a more important role in determining seedling success on shallow soils, with belowground competition increasing in importance with increasing soil depth.

Cook & Ratcliff (1984) found that root competition had a more pronounced influence on the growth of *P. maximum* than competition for light. This is believed to be as a result of nutrient limitation as the plants suffering from root competition showed an increase in leaf diameter correlated with increasing intensity of root competition resulting from fertilization (Cook & Ratcliff, 1984). Snaydon & Howe (1986) found similar results in the competition of *Poa annua*, *Poa trivialis* and *Festuca rubra* seedlings with an established sward of *Lolium perenne* and attributed this to competition for nitrogen, as seedling yield increases of up to seven times were observed after the addition of fertilizer (Snaydon & Howe, 1986). It has been suggested that in the first year of seedling establishment root competition plays a significant role, while in the second year above ground competition had a greater influence (Haugland & Tawfiq, 2001).This is supported by Remison & Snaydon (1978) who found that root competitive ability was dependant on fertilizer level and changed over time, possibly being influenced by seasonal growth patterns. Species observed to be aggressive competitors on nutrient poor soils were found to become less competitive on nutrient rich soils (Remison & Snaydon, 1978).

Although not significant at the 5% level, a consistent increase in plant biomass was observed with the removal of belowground competition regardless of aboveground treatment. The three species responded differently to increasing soil depth. *Eragrostis racemosa* increased tiller number, while *P. maximum* and *T. triandra* increased in biomass. This may be due to variation in plant physical traits as *E. racemosa* tends to be a short grass, usually found on shallow, rocky soils (Van Oudtshoorn, 2002), while *P. maximum* and *T. triandra* are taller plants and are possibly more efficient at increasing aboveground biomass by increasing plant height.

Cutting the surrounding sward resulted in a greater increase in biomass than removing aboveground competition by holding back the surrounding sward across all three soil depths. The magnitude of this effect increased with increasing soil depth, with a difference

of 13%, 23% and 74% between clipped and holding back the sward on shallow, medium and deep soils respectively. Effects on number of tillers were inconsistent, with an increase on deep soil, a decrease on medium soil depth and little to no change on shallow soil. *P. maximum* has previously been observed to increase in both leaf and tiller number as a result of cutting the surrounding sward (Cook & Ratcliff, 1984), while *Festuca pratensis* showed no change in the relative importance of root and shoot competition in the first growing season in response to cutting the competing plants (Carlen *et al.*, 2002). These variable responses may be as a result of physiological characteristics of the focus plant or the response of the surrounding sward to being cut. Defoliation has been found to decrease root elongation by up to 50 % in defoliation sensitive grasses while it had no effect in grazing tolerant species (Richards, 1984). This decrease in root elongation was correlated to an increase in aboveground photosynthetic material. Such a response may allow grazing intolerant species to both survive grazing and maintain aboveground competitive ability (Richards, 1984).

Grass species differ in their responses to resource availability both in terms of biomass accumulation and tillering patterns. While a species may be able to grow on various soil types if growing alone, the presence of other species which may be stronger competitors on certain soil types may dictate where species occur. This may be influenced by physical traits; such as height, leaf width, leaf length, the presence of root hairs, root production and root structure, behavioural characteristics; such as tendency to produce tillers and root nutrient uptake ability; the interaction of above and belowground competitive ability and other impacts on the ecosystem such as grazing and other disturbances (Cahill, 2003). This contradicts the neutral theory of biodiversity (Hubbell, 2001) which assumes that species within the same trophic level are ecologically similar and respond in the same way to resource limitation (Hubbell, 2001).

For example, while it may be possible for *E. racemosa* to grow on deep soils it does not thrive there as other species are able to utilize a larger proportion of the available resources. *P. maximum* grows approximately four times taller than *E. racemosa* (Unpublished data, RWS Fynn) and has a much greater biomass on deep soil, while on shallow soil the biomass of the two species is similar. *P. maximum* appears to utilize resources more effectively on deep soils and is able to grow tall and outcompete *E. racemosa* for light resources.

As clipping the surrounding sward resulted in an increase in grass seedling biomass on all three soil depths, it follows that grazing creates available niches for grass seedlings to establish. Savory & Butterfield (1999) describe both grazing and animal impact as important tools for ecosystem management. Low grazing impact maintains the health of individual plants, while the low animal impact associated with low intensity grazing decreases the likelihood of new plants establishing (Savory & Butterfield, 1999) and thus colonization of gaps is usually as a result of vegetative propagation (Belsky, 1986). Conversely, high intensity grazing decreases vigour of individual plants leading to die back of established grass tufts, but is associated with high intensity animal impact which chips the soil surface to prevent crusting and improve infiltration, improves soil aeration (Savory & Butterfield, 1999) and improves seed-to-soil contact resulting in greater seedling establishment (Griffith *et al.*, 1984; Savory & Butterfield, 1999; van der Merwe & Kellner, 1999).

Although animal impact creates hollows and furrows (van der Merwe & Kellner, 1999) which provide microsites for seed germination, this impact alone is not sufficient to ensure seedling establishment. The timing of the impact with respect to the season's first rainfall is crucial as disturbance more than one month after a rainfall event will result in little to no seedling establishment (Von Maltitz, 1990). Factors likely to further limit seedling establishment are moisture limitation (Donaldson, 1967; Ndawlula-Senyimba, 1972), uprooting by heavy rainfall (Veenendaal,1991), heavy grazing (Dankwerts & Stuart-Hill, 1988) and fire (O'Connor & Everson, 1998). It is therefore critical that land managers maintain stocking rates at a level which allows sufficient animal impact to promote seed germination but not create excessively large gaps as these areas tend to develop a soil crust and lack soil moisture thus inhibiting seedling establishment and creating opportunities for soil erosion.

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CHAPTER FIVE

SYNTHESIS AND MANAGEMENT RECCOMENDATIONS

5.1 Synthesis

The mechanisms of co-existence of tree and grass species in the savannas of the world have been the subject of research from the 1940's. Early interest was mainly as a result of the developing problem of bush encroachment (West, 1947) or the increasing density of woody shrubs and the correlated decrease in available grazing land. Later research was focused on understanding the mechanisms by which this co-existence was possible and led to theories suggesting some form of niche differentiation (Walter, 1971; Walker & Noy-Meir, 1982). These theories were limited in their application as in many systems the level to which this niche separation occurs remains unclear (Teague & Smit, 1992; Scholes & Walker, 1993) indicating that additional factors must be driving the maintenance of this co-existence. Several models attempting to describe the factors contributing to this co-existence have been produced (White & Harper, 1970: Ross & Harper, 1972; Tilman, 1985; Townsend, 1987; Scanlan, 1992; Scholes & Archer, 1997; Gillson, 2004; Smit, 2004). Although all these models are theoretically feasible, they do not allow for the wide range of geographic and environmental conditions under which savanna occurs. A complete tree-grass interaction model would require a combination of elements of all the models allowing for variation according to the scale at which the vegetation was being examined and the influences acting upon it at that scale (Scholes & Archer, 1997).

Jeltsch, Weber and Grimm (2000) proposed an alternative method of explaining savanna system functioning in terms of ecological buffering. This concept suggests that the combination of tree and grass species do not form a stable co-existing state but that the system is unstable and prevented from moving towards a stable grassland or woodland state by buffers. These buffers can be grouped into two classes, those which hinder the transition towards grassland and those which hinder the transition towards woodland. Those mechanisms described as hindering the transition towards a grassland state are: (1) the presence of micro sites with suitable germination conditions allowing tree seedlings to become established, (2) heavy grazing which reduces the species diversity, density, growth and reproduction of grass plants, (3) dormancy mechanisms in the seeds of woody plants allowing them to remain in the seed bank until suitable environmental conditions allow for germination and (4) the response of trees to environmental stress, such as limited water resources, to increase seed production further contributing to the seed bank. The factors

described as hindering the progression towards a woodland state are: (1) fire, as it decreases woody plant density by killing small trees, (2) large browsers, such as elephant, which push over and uproot trees, (3) other browsers, that place the trees under pressure by removal of biomass thus reducing vigor, tree density and reproduction, (4) anthropogenic utilization of the woody component by wood cutting, which further reducing plant density and growth, (5) seed predators decreasing germination levels and (6) insect disease vectors, such as tsetse fly, which reduce the density of grazers and thus decrease utilization pressure on the grass sward (Jeltsch *et al.*, 2000). In addition to this, trampling by grazers and competition from the surrounding grass sward has been found to affect tree density by reducing tree seedling establishment (Scholes & Archer, 1997; Kraaij & Ward, 2006). As these factors listed above are regarded as the most important forces maintaining savanna regions in a mixed tree-grass system it follows that manipulation of these factors will result in movement towards either grassland or woodland.

In this study tree seedlings had a greater competitive advantage than grass seedlings when growing on heavily grazed shallow soils, as indicated by the 47 % increase relative to the biomass of the control in tree seedling biomass compared to the 34 % increase in grass seedling biomass in the clipped treatment. Intensive grazing, in terms of both complete sward over-utilization and selective grazing and particularly when interrupted by a seasonal rest (Tainton, 1972; Morris *et al.*, 1992), creates favourable micro sites which allow tree seedlings to germinate and establish within a grass sward, which would otherwise outcompete the seedlings (Jeltsch *et al*., 2000). In addition grass species in heavily grazed short grasslands tend to propagate by vegetative mechanisms rather than producing seed (O' Connor & Everson, 1998). As expected from the findings of Chirara (2001), tree seedlings also showed a greater increase in biomass than grass seedlings when aboveground competition was removed. This occurred on both shallow and deep soils, while grass seedlings showed the greater increase on medium depth soils.

On heavily grazed medium and deep soils, grass seedlings appeared to have a greater competitive advantage than tree seedlings with a biomass increase of 32 % and 91 % relative to that of the control respectively, as opposed to tree seedlings which showed no increase on medium depth soil and 54 % increase in biomass on deep soil (Table 5.1a, Figure 3.5, Figure 4.5). These differences in the competitive response of grass seedlings across the three sites may be as a result of increasing soil nutrient content with increasing

soil depth (Anon, 1991). Owing to the fact that *Acacia* species have the ability to fix air-borne nitrogen, these tree seedlings are able to produce nutrients which sustain growth during the seedling stage (Mopipi, 2005). This is supported by Cramer *et al*. who observed that seedlings of *A. karroo*, *A. nilotica, A. tortilis* and *A. nigrescens* all nodulated when growing in competition with grass (Cramer *et al.*, 2007). As grass seedlings are unable to do this they are reliant on soil nutrients for seedling growth and it is therefore expected that tree seedlings should have a greater increase in plant biomass than grass seedling on shallow, infertile soils.

The removal of belowground competition, by root exclusion tubes resulted in a tree seedling biomass increase of between 47 and 49 % on all three soil depths. Grass seedlings, on the other hand, showed an increase in biomass with increasing soil depth following the removal of belowground competition, with plants on the deep soil gaining more than double that of those on the shallow soil. These results may indicate that grass seedlings are more strongly affected by soil depth than tree seedlings. Growing on shallow soil, tree seedlings had a competitive advantage over grass seedlings when belowground competition was removed, while grass seedlings had an advantage when growing on deep soils, gaining 68 % biomass as opposed to 47 % biomass gained by the tree seedlings (Table 5.1b, Figure 3.6, Figure 4.6). Few significant interactions were observed between above- and belowground competition (Table 3.1, Table 3.2).

Acacia karroo is expected to encroach into infertile areas as the surrounding grass exerts a lower competitive effect on the seedlings. Although *Acacia* species tend to dominate nutrient-rich savanna regions (Wilson & Witkowski, 1998) *A. karroo* seedlings are able to adapt to resource limitation (Chirara, 200). *A. nilotica* shows a similar competitive response on both fertile and infertile soils (Figure 2.2). In addition there has been evidence that encroaching tree species are able to utilize soil water at a lower matric potential than grasses and thus are able to take advantage of water resources from light rainfall events which are unavailable to the grass layer (Smit & Rethman, 2000).

Table 5.1: Biomass of treatment plants (%) relative to that of the control growing in a natural grass sward for changes in the levels of (a) aboveground competition and (b) belowground competition for tree and grass seedlings growing on shallow, medium and deep soils

a)

Soil	Tree seedlings			Grass seedlings		
	Full	None	Clipped	Full	None	Clipped
Shallow	100	116	147	100	111	134
Medium	100	98^{NS}	100^{NS}	100	109^{NS}	132^{NS}
Deep	100	131^{NS}	154^{NS}	100	117	191

b)

Soil	Tree seedlings		Grass seedlings	
	Full	None	Full	None
Shallow	100	149	100	127
Medium	100	147	100	146
Deep	100	147	100	168

NS – Non-significant

In the undisturbed sward the individual grass species attain the greatest biomass when growing on the soil depth which they are adapted to, despite the fact that the deeper soils had a higher soil nutrient content. For example, the greatest biomass attained by *E. racemosa* was on the shallow and medium soils, while for *P. maximum* it was on the deep soils. When the sward was subjected to simulated grazing an entirely different trend appeared. Grass biomass increased with increasing soil depth indicating that the competitive ability of the surrounding sward which prevented these plants from thriving in the undisturbed sward had decreased (Table 5.2a). Both tree species had the greatest biomass in the undisturbed sward, while under simulated grazing *A. karroo* seedlings were the largest on deep soil. In contrast, *A. nilotica* seedlings were of similar size on both medium and deep soils (Table 5.2b). It would thus be expected that heavily grazed swards on shallow and deep soils would be the most likely to be encroached.

Table 5.2: Dry biomass (±SE) (g) of (a) three grass and (b) two tree species growing in an undisturbed sward and a sward where grazing has been simulated by clipping on shallow, medium and deep soils

a)

Grass	Undisturbed Sward			Grazed Sward		
Species	Shallow	Medium	Deep	Shallow	Medium	Deep
E. racemosa	7.00 ± 1.18	7.60 ± 0.42	5.20 ± 0.59	7.95 ± 1.85	7.53 ± 1.06	9.3 ± 3.46
T. triandra	8.85 ± 1.77	17.05 ± 1.34	15.80 ± 6.02	15.55 ± 2.90	24.55 ± 2.65	43.0 ± 17.08
P. maximum	6.65 ± 1.73	8.75 ± 2.65	8.90 ± 5.12	10.90 ± 1.65	20.45 ± 8.75	25.1 ± 6.41

b)

Tree	Undisturbed Sward			Grazed Sward		
species	Shallow	Medium	Deep	Shallow	Medium	Deep
A. karroo	2.33 ± 0.06	4.27 ± 0.86	3.01 ± 0.71	2.13 ± 0.25	3.33 ± 0.25	5.70 ± 1.48
A. nilotica	3.07 ± 0.12	6.80 ± 1.06	4.53 ± 1.00	4.20 ± 0.61	6.60 ± 0.42	6.40 ± 1.70

Encroachment on shallow soils is due to decreased competitive ability of the grass sward and the ability of *Acacia* plants to fix air-borne nitrogen allowing the tree seedlings accesses to an additional nutrient source not available to the grass layer (Mopipi, 2005, Cramer *et al*., 2007). Encroachment has been observed in regions with shallow soil with trees averaging less than 0.5 m forming high density thickets ($\geq$ 5000 trees ha^{-2}) and trees at lower densities ($<$ 2000 trees ha^{-2}) growing to over 1.2 m tall despite insufficient soil depth for tree and grass roots to exploit separate soil layers (Wiegand *et al*., 2005). The deep soils are unlikely to be nutrient limited and thus tree-grass interactions are controlled by soil water availability as proposed by Walter (1971). These soils are deep enough to allow for root niche separation, where trees have access to water resources in deep soil layers and grasses utilize water in layers closer to the soil surface (Walter, 1971). The decrease in grass aboveground biomass and associated decrease in grass root biomass resulting from defoliating the grass sward on deep soils decreases the belowground competitive effect grasses exert on tree seedling roots (McNaughton *et al*., 1998). This could allow the tree seedling roots to grow past the depth attainable by grass roots and to utilize resources from the deeper soil layers.

It is also possible for an undisturbed sward to become encroached, as reported by Titshall *et al*. (2000) when assessing the species composition of several long-term trials of between 34 to 49 years duration. Exclosure plots protected from both fire and grazing for the duration of the trial and were all found to have substantial tree encroachment. One of the trials, located within 1 km of the study site for this project on soil between 0.5 and 0.8 m deep,

had after 49 years of no disturbance a tree density of greater than 10 000 trees/ha, with some stem diameters measuring over 0.5 m (Titshall *et al.*, 2000). Westfall *et al.* (1982) also documented the progression of grassland to scrub forest in areas protected from fire for up to forty years. In this trial tree seedlings growing on the medium soil depth had the greatest biomass and thus have the greatest likelihood of encroaching.

5.2 Management recommendations

The ecological buffers described by Jeltsh *et al.* (2000) provide a sound platform from which to determine the best management tactics to combat increasing bush density. In order to maximize grass forage production the intensity of those factors described as hindering system transition towards grassland need to be minimized, while the intensity of those factors described as hindering system transition towards woodland should be increased. The first two buffers described as preventing transition towards a grassland state, namely (1) the presence of micro sites with suitable germination conditions allowing tree seedlings to become established, (2) heavy grazing which reduces the density, growth and reproduction of the grass sward (Jeltsh *et al.*, 2000), can be examined together as both of these factors as linked to the level of grazing applied by managers.

This study has highlighted the importance of competition from the surrounding sward, particularly belowground, in decreasing the biomass accumulation of tree seedlings, particularly in nutrient rich soils. As intensive grazing decreases both above and belowground sward biomass (McNaughton *et al.*, 1998) micro sites of increased resource availability develop allowing tree seedlings the opportunity to establish (O'Connor, 1997). In order to prevent this, management should be aimed at maintaining as vigorous a grass sward as possible, while maintaining animal condition. This may be done by grazing regularly, while allowing the sward sufficient rest periods to increase vigor and improve species composition. Possibly more critical than the grazing system used is the type of animal stocked, the rate at which they were stocked and the management ability of the land manager (O' Reagain & Turner, 1992; Kantz, 2001, Briske *et al.*, 2008). Stocking with mixed species may also assist in the long term reduction of bush density (Trollope, 1983; Hardy, 1994; Kantz, 2001) as grazing by cattle alone has been found to be beneficial to the development of tree seedlings (Kantz, 2001). Grazing by sheep alone may decrease the vigour of the veld even further than grazing by cattle alone (Kirkman, 1999) despite the fact that sheep have a greater selective ability than cattle and utilize a greater proportion of tree

seedlings than cattle (Kantz, 2001). A combination of cattle and sheep has been suggested at a ratio of 1 AU cattle to 1 AU sheep or a ratio which favours cattle (Hardy, 1994). Kirkman and Moore (1995) suggest a four block, four year rotational grazing system with a low sheep:cattle ratio where two blocks are grazed by cattle, one by sheep and one rested each growing season (Kirkman & Moore, 1995). This system may be modified to include burning of the rested veld when necessary or to allow sheep and cattle to graze together on the same block, although one specific block should not be grazed by sheep for more than one season consecutively (Kirkman & Moore, 1995).

Resting allows the veld to increase in vigor, to accumulate biomass for both grazing and burning to reduce woody plant density, to improve species composition, to increase grass seedling establishment and for individual grass plants to grow rapidly, produce seed, produce vegetative parts, increasing tuft size and reduce differences in vigor between lightly and heavily utilized plants (Tainton, 1971; Peddie, 1994; Kirkman, 1999). Veld that has been grazed for two seasons should be rested for a minimum of one season. As sheep have a greater impact on grass vigour than cattle it is recommended that when stocking with high numbers of sheep relative to cattle veld should be rested more regularly (Kirkman & Moore, 1995).

The remaining two factors preventing the transition of savanna systems to grassland, that is: (3) seed dormancy mechanisms and (4) the positive effect of stress on seed production (Jeltsch *et al.*, 2000), are not relevant as potential management tactics as these factors cannot be manipulated.

The first and possibly most important ecological buffer preventing the progression of savanna towards woodland is fire as it decreases woody plant density by killing small individuals (Trollope, 1983; Jeltsch *et al.*, 2000). The potential for the inclusion of fire within a rotational grazing system has already been mentioned. Fire is a useful management tactic as it is a natural factor in African ecosystems and is fairly inexpensive to utilize (Trollope, 1983). In an unencroached multi paddock system burning every four years is thought to be sufficient to maintain the system in an unencroached state (Hardy, 1994). Triennial burning has been observed to exclude woody species on long term trials at Ukulinga Research Farm, Pietermaritzburg (Titshall *et al.*, 2000) but may also result in a change in sward composition, from short to tall grass species as a result of increased soil

nitrogen (Fynn *et al*., 2005). Careful attention must be paid to the type of fire used and season of burning when burning to reduce bush density as burning during the dry season may result in an increase in woody plant density due to the fact that the grasses cannot maintain their initial post-fire growth spurt and subsequently die (Everson, 1985; Skarpe, 1992). For effective control of bush encroachment a high intensity surface head fire is recommended. Although a head fire is cooler than a back fire it has been found that back fires have negative impacts on grass regrowth (Trollope, 1974). The conditions required for an intense head burn to take place are as follows; air temperature >25°C, relative humidity <30%, fuel load >3000kg/ha and fuel moisture <40% (Trollope, 1980).

Two ecological buffers preventing the transition of savanna to grassland involve browsers, including large browsers, such as elephant, which push over and uproot trees and smaller ungulates, which place the trees under pressure by removal of biomass (Jeltsch *et al.*, 2000). Within a wildlife system large browsers play a significant role in decreasing bush density, while in a domestic system other browsers such as sheep and goats can be used to fulfill this role. The use of a mixed species system incorporating sheep into a cattle system owing to their ability to select forage on a finer scale than cattle and their negative impact on tree seedlings has been discussed in conjunction with grazing systems with regard to the prevention of the transition from savanna to grassland. In some regions goats have been used rather than sheep to decrease woody species density as sheep spend only ten percent of their foraging time utilizing browse, while goats browse for as much as fifty percent of their foraging time (Du Toit, 1972; Trollope, 1983). Burning can be used in conjunction with browsing by goats to reduce bush density, as a surface head fire tends to cause extensive top kill of plants over 2 m tall thus bringing the woody layer down to a level where goats are able to browse. Continuous stocking with goats has been found to substantially decrease the percentage of coppicing bushes, but stocking rates must be decreased as bush density decreases to prevent over-utilization of the recovering grass sward (Trollope, 1983).

Finally, the anthropogenic utilization of the woody component by wood cutting reduces plant density and growth (Jeltsch *et al*., 2000). Originally the most effective method of bush clearing was thought to be the mechanical removal or poisoning of trees. In the clearing of seedlings cutting must be done as low to the ground as possible as plants cut above the point of cotyledon attachment tend to coppice and produce multiple stems (Brown & Booysen, 1967). West (1947) recommended using machinery such as bulldozers, power

winches and chainsaws, followed by poisoning individual plants with paraffin or arsenic based solutions. Although these methods are effective, they can become very expensive as regular applications are required before the problem is under control (West, 1947, Smit *et al.*, 1999).

The remaining two factors preventing the transition of savanna systems to woodland (5) seed predators decreasing germination levels and (6) insect disease vectors, such as tsetse fly, which reduce the density of grazers and thus decrease utilization pressure on the grass sward (Jeltsch *et. al*, 2000) are not relevant as potential management tactics as these factors cannot be manipulated.

With careful manipulation of the aforementioned ecological buffers and ensuring the grass sward remains vigorous by resting and monitoring stocking rates to ensure veld is not over-utilized it is possible to reduce bush density and maintain some form of tree-grass coexistence at a level where available grazing is not compromised.

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APPENDIX ONE

FULL RESULTS OF DATA ANALYSES FOR ABOVE AND BELOW GROUND INTERACTIONS BETWEEN TWO TREE SPECIES AND THE SURROUNDING SWARD ON THREE DIFFERENT SOIL LEVELS

Table 1: Shallow soil – means (± standard error) for aboveground dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground								
		Full			None			Partial		
Acacia karroo	Full	2.33	±	0.06	2.70	±	0.21	2.13	±	0.25
	None	2.80	±	0.17	3.13	±	0.25	4.13	±	0.75
Acacia nilotica	Full	3.07	±	0.12	2.60	±	0.14	4.20	±	0.61
	None	3.47	±	0.40	5.15	±	0.83	6.73	±	1.77
	Grand mean	3.54	±	0.25						

b)

Belowground	Aboveground										Mean		
	Full			None			Partial						
Full	2.70	±	0.15	2.65	±	0.11	3.17	±	0.50	2.84	±	0.20
None	3.13	±	0.24	4.14	±	0.57	5.43	±	1.00	42.4	±	0.41
Mean	2.92 [a]	±	0.15	3.40 [ab]	±	0.38	4.30 [b]	±	0.59			

c)

	Aboveground									Belowground									Mean		
	Full			None			Partial			Full			None								
Acacia karroo	150.20	±	2.68	152.30	±	15.77	132.20	±	20.27	131.40	±	11.94	161.70	±	16.29	146.5	±	10.48
Acacia nilotica	146.50	±	18.26	167.80	±	27.01	178.30	±	28.70	125.90	±	10.40	202.40	±	21.62	164.2	±	14.18

Table 2: Shallow soil – means (± standard error) for final height (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground					
		Full		None		Partial	
Acacia karroo	Full	122.00 ± 13.23		157.50 ± 10.25		114.70 ± 31.16	
	None	178.30 ± 37.00		147.00 ± 30.43		159.70 ± 26.51	
Acacia nilotica	Full	109.00 ± 13.23		115.60 ± 24.00		153.30 ± 18.46	
	None	184.00 ± 24.71		220.00 ± 31.93		203.30 ± 62.39	
	Grand mean	155.40 ± 8.93					

b)

	Aboveground			Belowground			
	Full	None	Partial	Full	None	Mean	
Acacia karroo	150.20 ± 20.68	152.30 ± 15.77	132.20 ± 20.27	131.40 ± 11.94	161.70 ± 16.29	146.50 ± 10.48	
Acacia nilotica	146.50 ± 18.26	167.80 ± 27.01	178.30 ± 28.70	125.90 ± 10.40	202.40 ± 21.62	164.20 ± 14.18	

c)

Belowground	Aboveground			
	Full	None	Partial	Mean
Full	115.50 ± 6.46	136.50 ± 13.79	134.00 ± 17.33	128.70 ± 7.63
None	181.20 ± 19.93	183.50 ± 24.48	181.50 ± 13.47	182.10 ± 13.99
Mean	148.30 ± 13.16	160.00 ± 15.87	157.70 ± 17.75	

Table 3: Medium soil - means (± standard error) for aboveground dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground								
		Full			**None**			**Partial**		
Acacia karroo	**Full**	4.27	±	0.86	2.62	±	*	3.33	±	0.25
	None	5.93	±	0.40	7.40	±	0.75	5.40	±	1.31
Acacia nilotica	**Full**	6.80	±	1.06	5.00	±	0.59	6.60	±	0.42
	None	6.75	±	0.54	8.15	±	1.29	8.35	±	0.90
	Grand mean	5.88	±	0.31						

b)

	Aboveground									Belowground							Mean		
	Full			**None**			**Partial**			**Full**			**None**				**Mean**		
Acacia karroo	317.00	±	55.35	235.00	±	47.61	205.00	±	39.64	161.00	±	30.28	344.00	±	32.62	252.00	±	27.95
Acacia nilotica	381.00	±	26.60	46.00	±	24.93	307.00	±	48.22	320.00	±	22.96	369.00	±	29.56	344.00	±	19.01

c)

	Aboveground											
Belowground	**Full**			**None**			**Partial**			**Mean**		
Full	5.53	±	0.78	3.81	±	0.52	4.97	±	0.66	4.77	±	0.38
None	6.34	±	0.35	7.77	±	0.73	6.87	±	0.89	7.00	±	0.40
Mean	5.94	±	0.41	5.79	±	0.61	5.92	±	0.63			

* - insufficient number of reps to calculate a standard error

Table 4: Medium soil – means (± standard error) for final height (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground					
		Full		None		Partial	
Acacia karroo	Full	215.00 ± 75.04		113.00 ± *		154.00 ± 36.87	
	None	419.00 ± 43.41		356.00 ± 34.67		255.00 ± 67.61	
Acacia nilotica	Full	363.00 ± 25.82		345.00 ± 49.55		54.00 ± 49.55	
	None	398.00 ± 46.96		347.00 ± 21.10		360.00 ± 21.10	
	Grand mean	298.00 ± 17.30					

b)

	Aboveground			Belowground		Mean
	Full	None	Partial	Full	None	
Acacia karroo	317.00 ± 55.35	235.00 ± 47.61	205.00 ± 39.64	161.00 ± 30.28	344.00 ± 32.62	252.00 ± 27.95
Acacia nilotica	381.00 ± 26.60	46.00 ± 24.93	307.00 ± 48.22	320.00 ± 22.96	369.00 ± 29.56	344.00 ± 19.01

c)

Belowground	Aboveground			Mean
	Full	None	Partial	
Full	289.00 ± 45.62	229.00 ± 24.48	204.00 ± 6.46	241.00 ± 24.31
None	409.00 ± 29.67	352.00 ± 17.74	308.00 ± 19.92	356.00 ± 21.45
Mean	349.00 [a] ± 29.82	290.00 [ab] ± 23.36	256.00 [b] ± 33.62	

* - insufficient number of reps to calculate a standard error

Table 5: Deep soil - means (± standard error) for aboveground dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground								
		Full			None			Partial		
Acacia karroo	Full	3.01	±	0.71	4.07	±	1.19	5.70	±	1.48
	None	5.40	±	1.84	8.20	±	2.23	6.40	±	0.14
Acacia nilotica	Full	4.53	±	1.00	4.50	±	0.60	6.40	±	1.70
	None	5.13	±	0.93	6.85	±	1.18	9.35	±	1.51
	Grand mean	5.80	±	0.41						

b)

	Aboveground									Belowground							Mean		
	Full			None			Partial			Full			None				Mean		
Acacia karroo	306.00	±	51.92	345.00	±	35.51	361.00	±	54.93	265.00	±	32.51	410.00	±	28.22	338.00	±	24.94
Acacia nilotica	374.00	±	28.74	322.00	±	34.84	367.00	±	31.96	318.00	±	29.05	391.00	±	17.04	354.00	±	18.39

c)

Belowground	Aboveground									Mean		
	Full			None			Partial			Mean		
Full	3.77	±	0.63	4.28	±	0.58	6.05	±	1.05	4.70	±	0.47
None	5.27	±	0.80	7.53	±	1.12	7.87	±	0.99	6.89	±	0.60
Mean	4.52	±	0.51	5.90	±	0.73	6.96	±	0.74			

Table 6: Deep soil - means (± standard error) for final height (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions

a)

Species	Belowground	Aboveground								
		Full			None			Partial		
Acacia karroo	Full	232.00	±	52.68	319.00	±	70.59	245.00	±	58.69
	None	381.00	±	88.39	372.00	±	28.36	477.00	±	34.65
Acacia nilotica	Full	371.00	±	47.92	242.00	±	33.07	340.00	±	55.23
	None	378.00	±	42.73	401.00	±	19.22	394.00	±	35.16
	Grand mean	346.00	±	14.76						

b)

	Aboveground									Belowground								
	Full			None			Partial			Full			None			Mean		
Acacia karroo	306.00	±	51.92	345.00	±	35.51	361.00	±	54.93	265.00	±	32.51	410.00	±	28.22	338.00	±	24.94
Acacia nilotica	374.00	±	28.74	322.00	±	34.84	367.00	±	31.96	318.00	±	29.05	391.00	±	17.04	354.00	±	18.39

c)

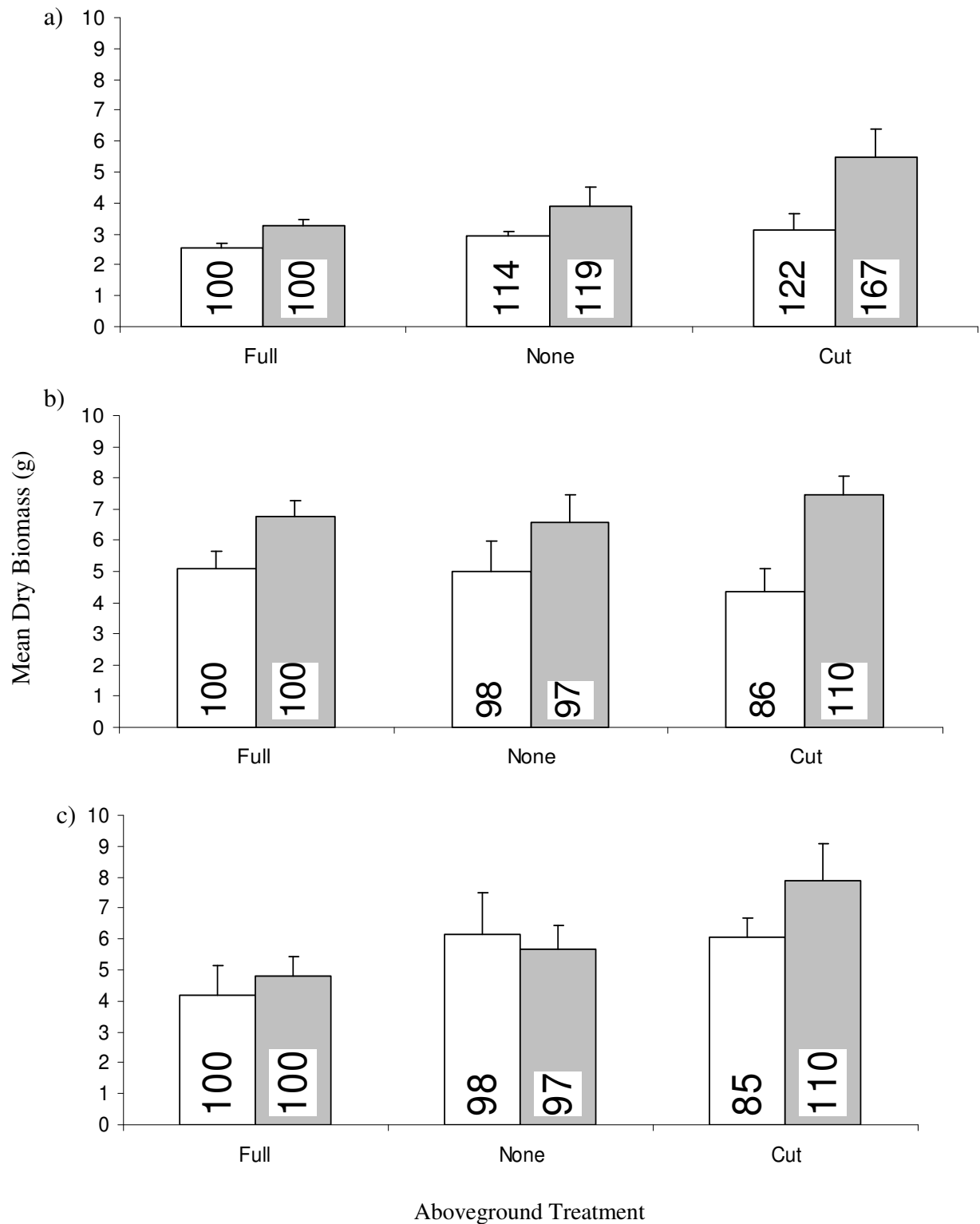| Belowground	Aboveground											
	Full			None			Partial			Mean		
Full	301.00	±	40.63	281.00	±	36.25	293.00	±	13.79	292.00	±	21.25
None	379.00	±	37.86	386.00	±	16.03	436.00	±	24.48	400.00	±	15.08
Mean	340.00	±	27.5	333.00	±	24.05	364.00	±	27.15			

Figure 1: Mean aboveground dry biomass for *A. karroo* (white) and *A. nilotica* (grey) seedlings under three aboveground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.
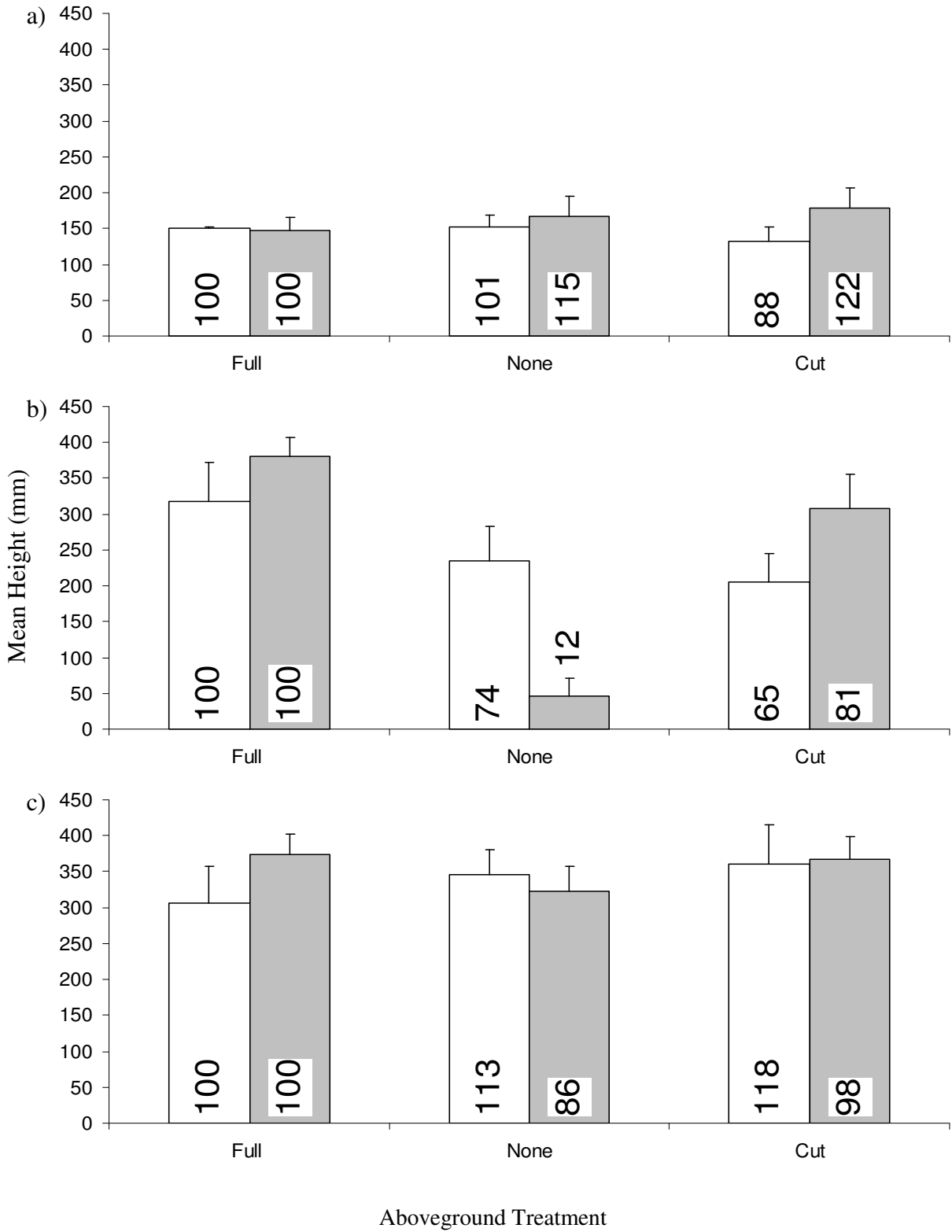
Figure 2: Mean final height for *A. karroo* (white) and *A. nilotica* (grey) seedlings under three aboveground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.
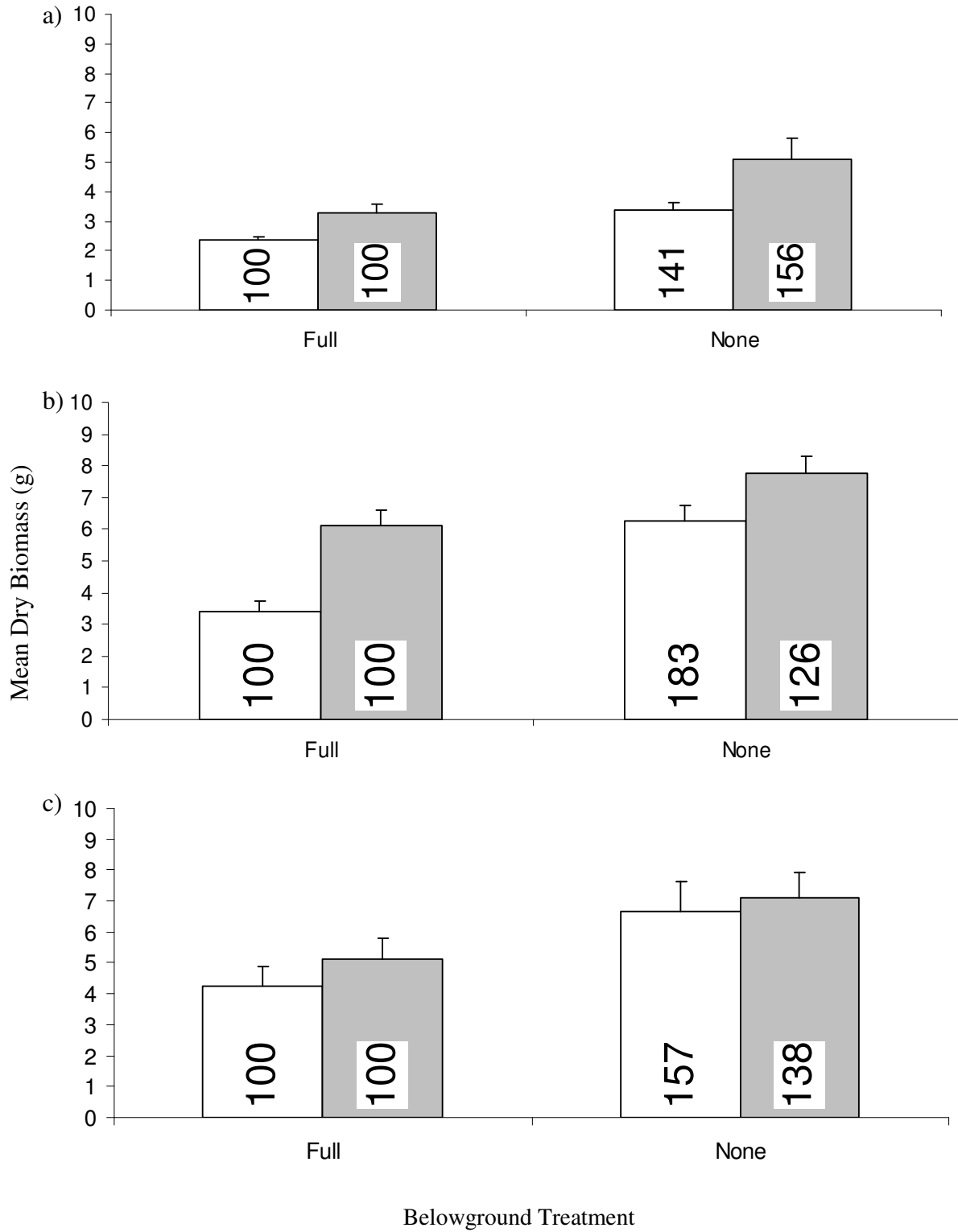
Figure 3: Mean aboveground dry biomass for *A. karroo* (white) and *A. nilotica* (grey) seedlings under two belowground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.

Figure 4: Mean final height for *A. karroo* (white) and *A. nilotica* (grey) seedlings under two belowground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.
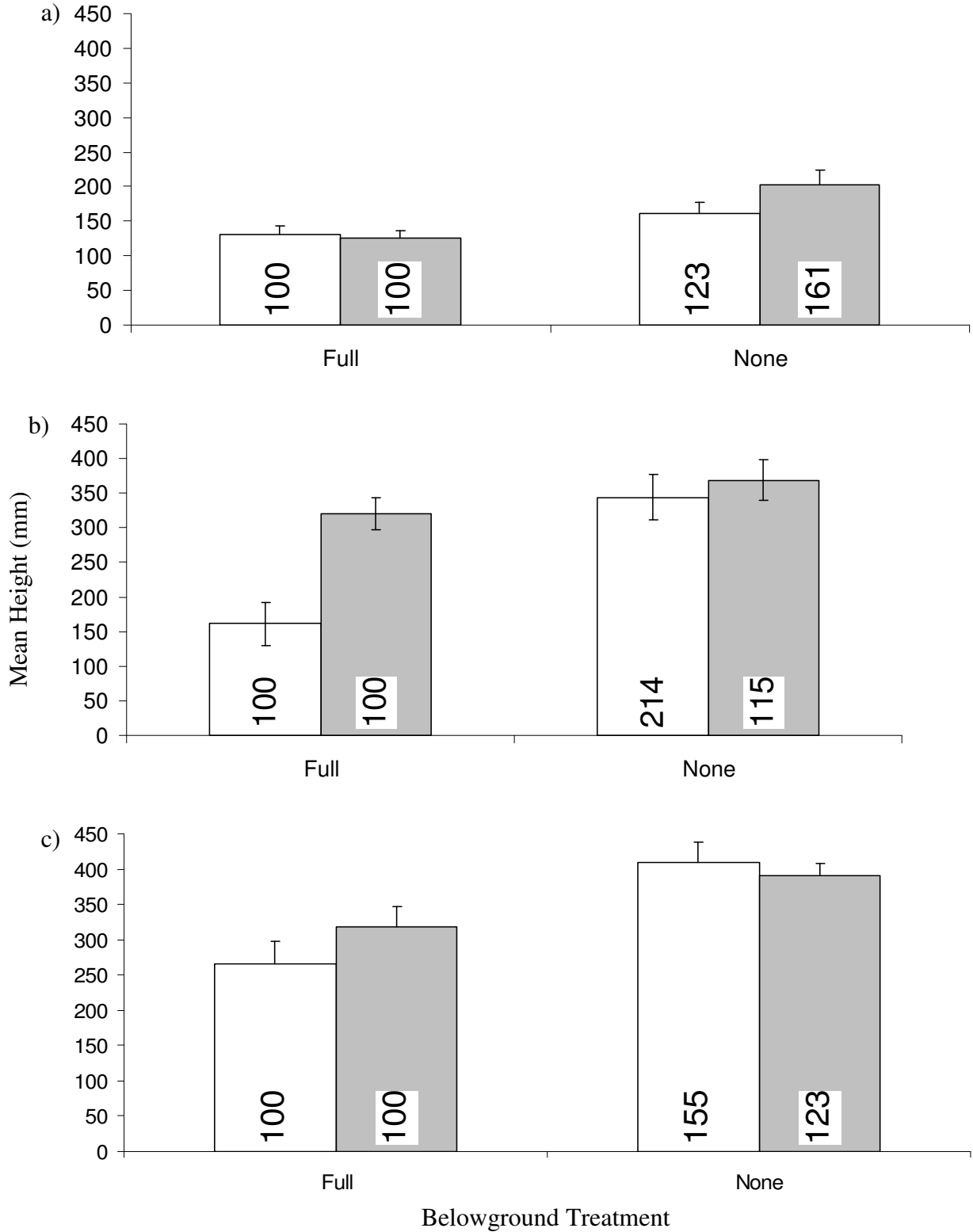
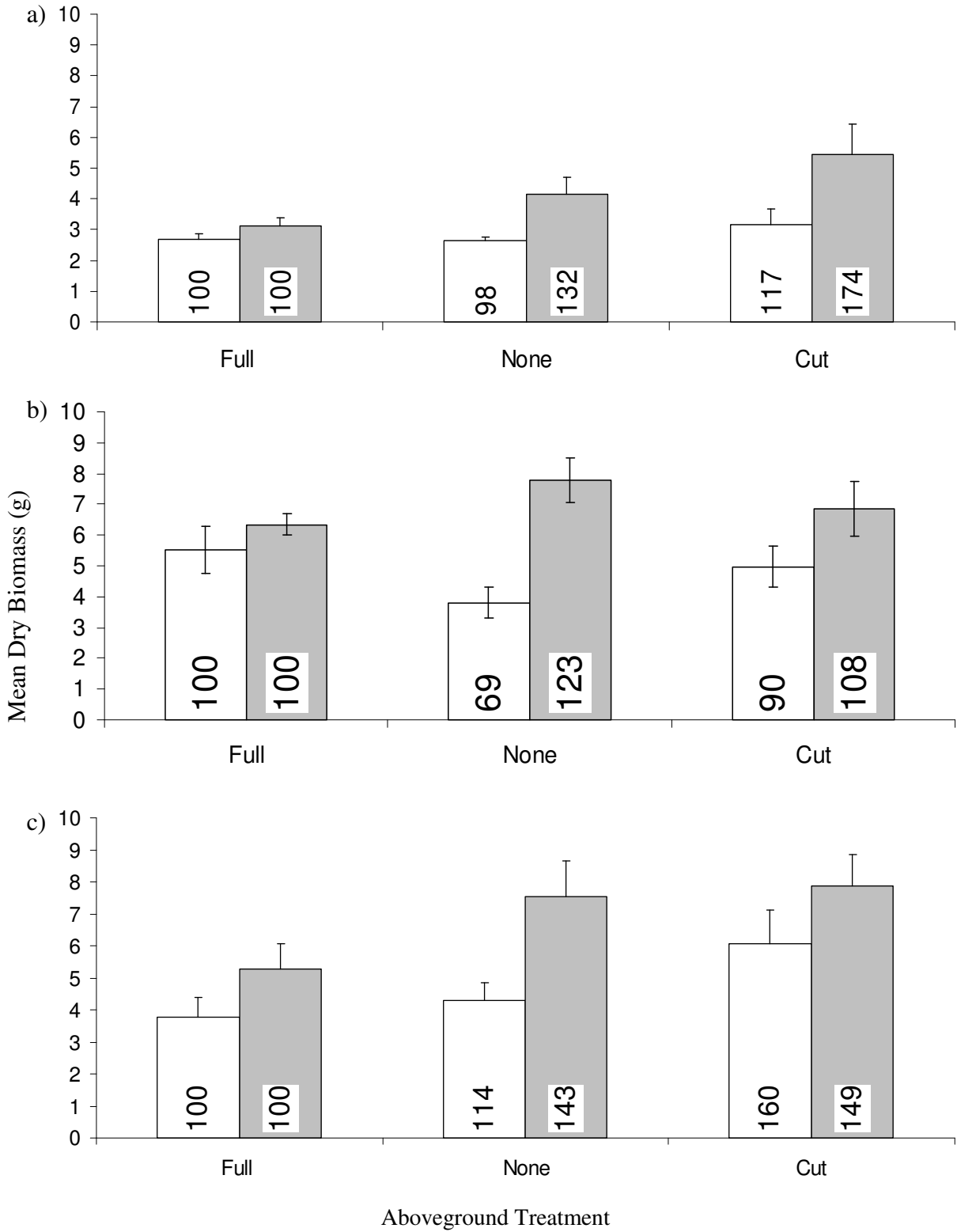Figure 5: Mean aboveground dry biomass for two belowground treatments under three aboveground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.
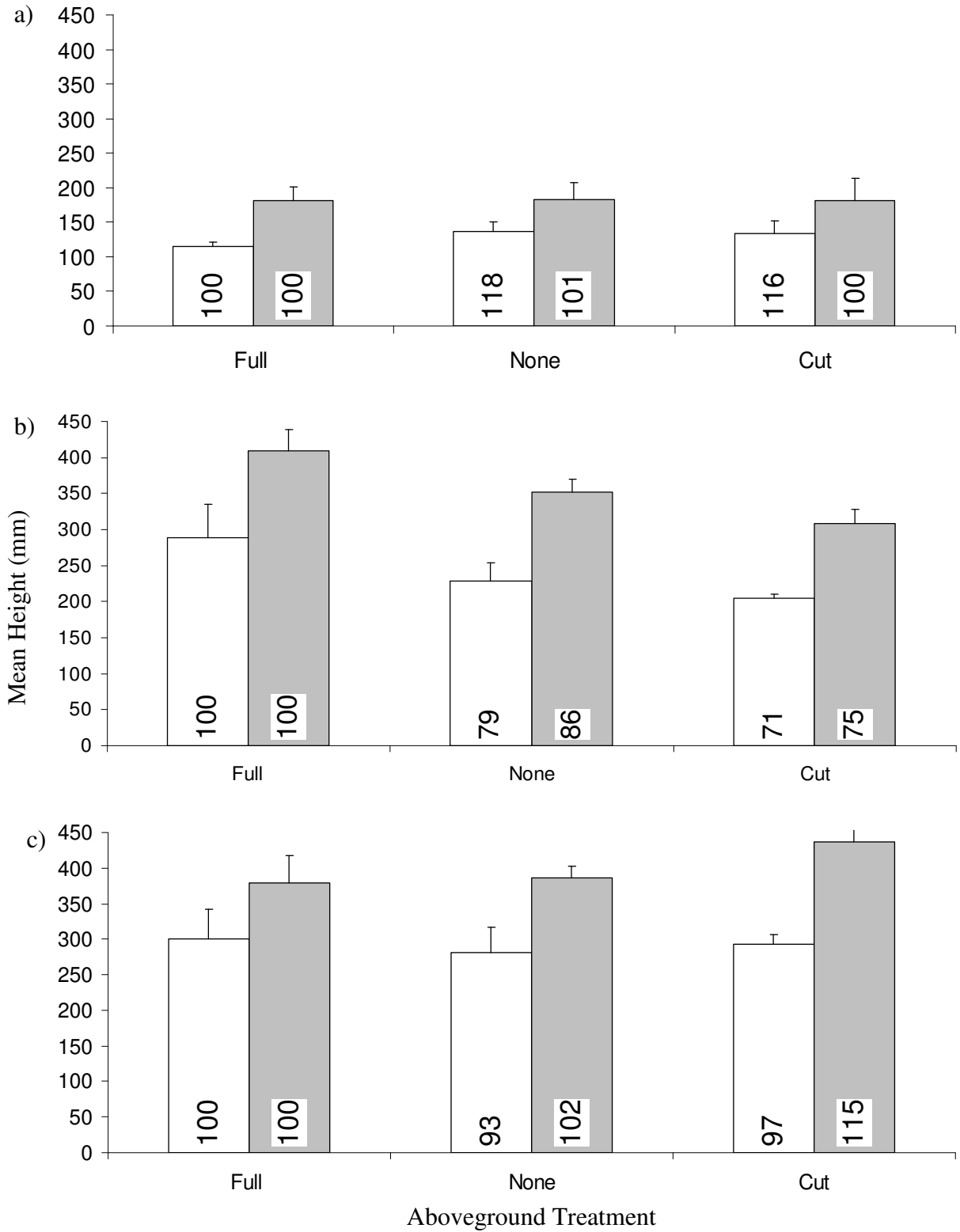
Figure 6: Mean final height for two belowground treatments under three aboveground treatments showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.

Figure 7: Mean aboveground dry biomass for *A. karroo* (white) and *A. nilotica* (grey) seedlings for six aboveground and belowground treatment combinations showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.

Figure 8: Mean final height for *A. karroo* (white) and *A. nilotica* (grey) seedlings for six aboveground and belowground treatment combinations showing percentage yield relative to the control across shallow (a), medium (b) and deep (c) soils.

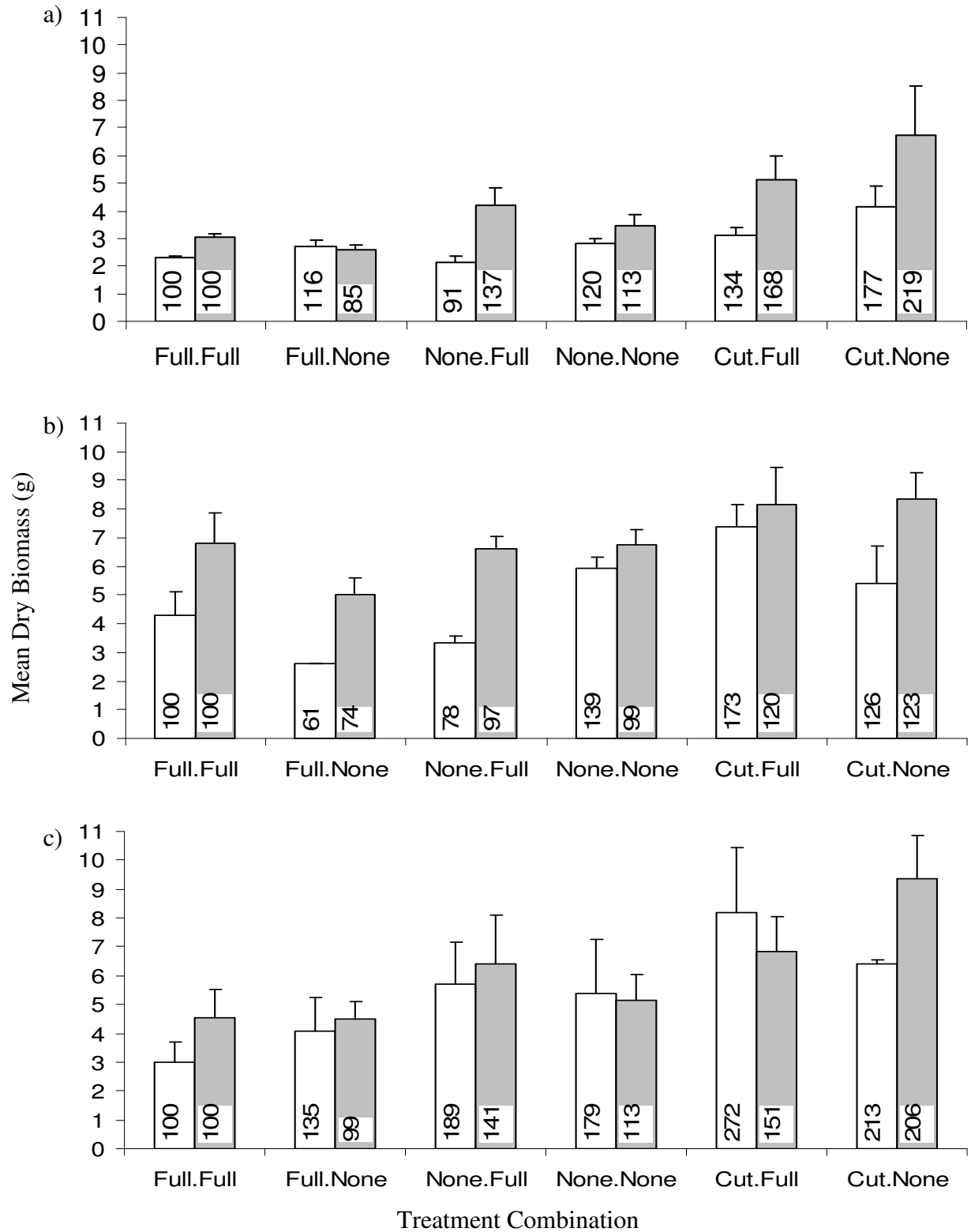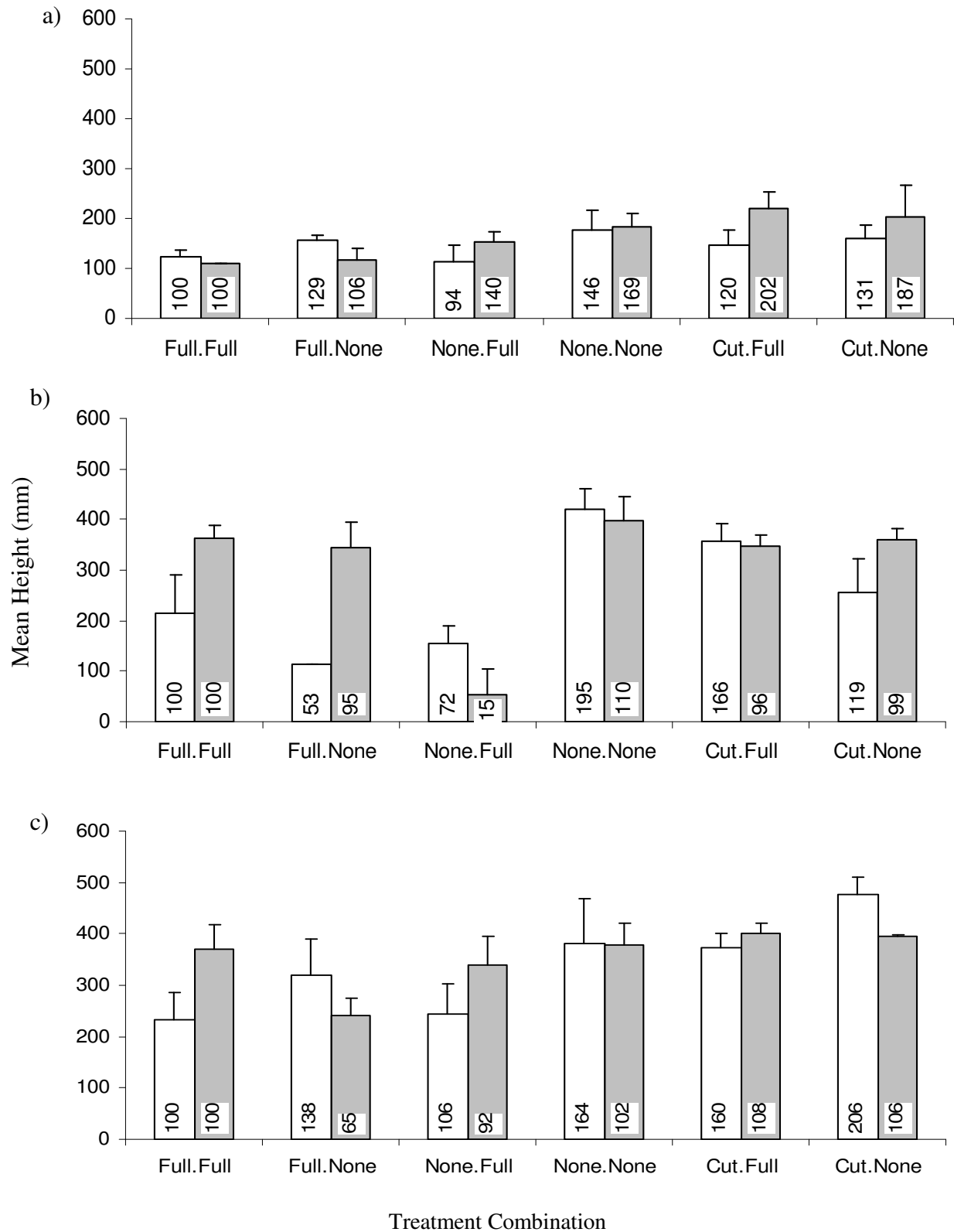APPENDIX TWO

FULL RESULTS OF DATA ANALYSES FOR ABOVE AND BELOW GROUND INTERACTIONS BETWEEN THREE GRASS SPECIES AND THE SURROUNDING SWARD ON THREE DIFFERENT SOIL LEVELS

Table 1: Shallow soil – means for dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions.

Species	Belowground	Aboveground					
		Full		None		Cut	
Eragrostis racemosa	Full	7.00 ± 1.18		7.40 ± 1.22		7.95 ± 1.85	
	None	8.70 ± 1.05		9.47 ± 1.85		13.00 ± 2.58	
Panicum maximum	Full	6.65 ± 1.73		7.73 ± 0.70		10.90 ± 1.65	
	None	12.10 ± 0.55		10.40 ± 1.72		10.90 ± 3.63	
Themeda triandra	Full	8.85 ± 1.77		12.65 ± 1.27		15.55 ± 2.90	
	None	12.35 ± 1.15		14.10 ± 1.22		16.47 ± 1.55	
	Grand mean	10.68 ± 0.49					

	Aboveground			Belowground		Mean
	Full	None	Cut	Full	None	
Eragrostis racemosa	7.85 ± 0.80	8.43 ± 1.07	10.47 ± 1.75	7.45 ± 0.77	10.39 ± 1.16	8.92 ± 0.75
Panicum maximum	9.38 ± 1.33	9.07 ± 0.95	10.90 ± 1.52	8.43 ± 1.25	11.13 ± 0.65	9.78 ± 0.73
Themeda triandra	10.60 ± 1.18	13.38 ± 0.90	16.01 ± 1.70	12.35 ± 1.12	14.31 ± 1.24	13.33 ± 0.84

Belowground	Aboveground			Mean
	Full	None	Cut	
Full	7.5 ± 0.88	9.26 ± 0.93	11.47 ± 1.49	9.41 ± 0.86
None	11.05 ± 0.71	11.32 ± 1.02	13.46 ± 1.49	11.94 ± 0.8
Mean	9.28 [a] ± 0.66	10.29 [a] ± 0.70	12.46 ± 1.04	

Table 2: Shallow soil – means for number of tillers (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions.

Species	Belowground	Aboveground								
		Full			None			Cut		
Eragrostis racemosa	Full	39.30	±	8.01	50.80	±	11.48	45.50	±	7.22
	None	61.20	±	7.85	64.30	±	4.65	56.55	±	17.34
Panicum maximum	Full	7.50	±	1.19	6.30	±	1.26	22.80	±	8.29
	None	14.00	±	1.08	12.20	±	3.94	11.80	±	2.39
Themeda triandra	Full	67.00	±	16.19	90.50	±	19.47	123.50	±	6.64
	None	65.80	±	10.04	88.80	±	15.02	112.00	±	22.57
	Grand mean	52.20	±	4.67						

	Aboveground									Belowground						Mean		
	Full			None			Cut			Full			None					
Eragrostis racemosa	50.2 ab	±	6.65	57.5 a	±	6.57	51 ac	±	8.94	45.20	±	4.96	60.70	±	6.21	52.9	±	4.17
Panicum maximum	10.7 d	±	1.44	9.3 d	±	2.32	17.2 d	±	4.50	12.20	±	3.52	12.70	±	1.46	12.4	±	1.83
Themeda triandra	66.4 bc	±	8.82	89.60	±	11.39	117.80	±	10.03	93.70	±	10.54	88.80	±	9.87	91.2	±	7.1

	Aboveground									Mean		
Belowground	Full			None			Cut					
Full	37.9	±	9.14	49.2	±	12.36	63.9	±	13.57	50.3	±	8.41
None	47	±	8.04	55.1	±	11.25	60.1	±	14.43	54.1	±	7.83
Mean	42.5 a	±	6.03	52.5 ab	±	8.15	62 b	±	9.70			

Table 3: Medium soil - means for dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions (Analyses performed on log transformed data).

Species	Belowground	Aboveground								
		Full			None			Cut		
Eragrostis racemosa	Full	7.60	±	0.42	8.40	±	1.57	7.53	±	1.06
	None	10.20	±	1.31	17.00	±	3.13	18.73	±	2.81
Panicum maximum	Full	8.75	±	2.65	8.87	±	1.79	20.45	±	8.75
	None	17.85	±	1.89	16.55	±	1.39	20.15	±	3.42
Themeda triandra	Full	17.05	±	1.34	19.45	±	3.06	24.55	±	2.65
	None	27.13	±	1.16	26.30	±	2.33	25.10	±	1.21
	Grand mean	16.76	±	0.98						

	Aboveground									Belowground									Mean		
	Full			None			Cut			Full			None						Mean		
Eragrostis racemosa	8.90	±	0.80	12.70	±	2.29	13.13	±	2.55	7.84	±	0.60	15.31	±	1.71				11.58	±	1.16
Panicum maximum	13.30	±	1.91	12.71	±	1.77	20.30	±	4.35	12.69	±	3.31	18.18	±	1.25				15.44	±	1.78
Themeda triandra	22.09	±	2.39	22.88	±	2.20	24.83	±	1.35	20.35	±	1.64	26.18	±	1.10				23.26	±	1.15

Belowground	Aboveground									Mean		
	Full			None			Cut			Mean		
Full	11.13	±	1.45	12.24	±	1.97	17.51	±	3.58	13.63	±	1.82
None	18.39	±	2.21	19.95	±	1.84	21.33	±	1.59	19.89	±	1.36
Mean	14.76 [a]	±	1.45	16.09 [ab]	±	1.53	19.42 [b]	±	1.94			

Table 4: Medium soil – means for number of tillers (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions (Analyses performed on log transformed data).

Species	Belowground	Aboveground								
		Full			**None**			**Cut**		
Eragrostis racemosa	**Full**	35.7	±	2.56	35.5	±	11.59	41.5	±	6.40
	None	55.7	±	7.39	71.0	±	11.91	44.5	±	16.33
Panicum maximum	**Full**	5.0	±	1.08	11.7	±	0.58	20.50	±	2.02
	None	7.0	±	0.71	13.0	±	2.80	7.0	±	2.80
Themeda triandra	**Full**	78.2	±	5.45	97.2	±	14.77	122.2	±	25.85
	None	104.7	±	7.52	107.7	±	9.29	84.2	±	3.54
	Grand mean	115.10	±	12.33						

	Aboveground									Belowground						Mean		
	Full			**None**			**Cut**			**Full**			**None**			**Mean**		
Eragrostis racemosa	45.8	±	5.23	53.3	±	10.21	43.0	±	8.14	37.6	±	4.15	57.1	±	4.86	47.3^a	±	4.57
Panicum maximum	6.0	±	0.71	12.3	±	1.44	13.7	±	3.01	12.4	±	2.14	9.0	±	1.48	10.7^b	±	1.31
Themeda triandra	91.5	±	6.46	102.5	±	8.32	103.2	±	14.05	99.2	±	10.20	98.9	±	4.92	99.1^c	±	5.81

Belowground	Aboveground									Mean		
	Full			**None**			**Cut**			**Mean**		
Full	39.7 ^{de}	±	15.54	48.1 ^{abce}	±	12.38	61.4 ^{ac}	±	15.48	49.7	±	8.87
None	55.8 ^{cde}	±	13.24	63.9 ^{c}	±	12.64	45.2 ^{bd}	±	10.80	55.0	±	8.4
Mean	47.7	±	7.49	56.0	±	8.74	53.3	±	9.38			

Table 5: Deep soil - means for dry biomass (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions (Analyses performed on log transformed data).

Species	Belowground	Aboveground		
		Full	None	Cut
Eragrostis racemosa	Full	5.20 ± 0.59	5.40 ± 0.83	9.30 ± 3.46
	None	9.20 ± 0.82	9.60 ± 2.95	17.30 ± 1.73
Panicum maximum	Full	8.90 ± 5.12	14.50 ± 2.10	25.10 ± 6.41
	None	31.60 ± 1.36	41.77 ± 5.13	48.20 ± 11.16
Themeda triandra	Full	15.80 ± 6.02	15.90 ± 1.56	43.00 ± 17.08
	None	23.30 ± 4.33	22.50 ± 1.00	36.90 ± 3.62
	Grand mean	21.30 ± 1.96		

	Aboveground			Belowground		Mean
	Full	None	Cut	Full	None	
Eragrostis racemosa	7.20 ± 0.89	7.50 ± 1.50	13.30 ± 2.06	6.70 ± 0.89	12.00 ± 1.51	9.4 ± 1.08
Panicum maximum	20.20 ± 5.01	28.10 ± 5.82	36.60 ± 7.38	16.20 ± 3.07	40.50 ± 4.63	28.3 ± 3.66
Themeda triandra	19.60 ± 3.72	19.20 ± 1.51	39.90 ± 7.90	24.80 ± 6.34	27.50 ± 2.63	26.2 ± 3.35

Belowground	Aboveground			Mean
	Full	None	Cut	
Full	10 ± 2.39	12 ± 1.65	25.8 ± 6.68	15.9 ± 3.19
None	21.4 ± 3.44	24.6 ± 4.39	34.1 ± 5.46	26.7 ± 3.31
Mean	15.7 ± 2.37	18.3 ± 2.63	30 ± 4.2	

Table 6: Deep soil - means for number of tillers (a) Species.Aboveground.Belowground (b) Species.Aboveground and Species.Belowground and (c) Aboveground.Belowground interactions (Analyses performed on log transformed data).

Species	Belowground	Aboveground Full			None			Cut		
Eragrostis racemosa	Full	31.50	±	3.38	41.00	±	3.76	56.10	±	4.95
	None	53.30	±	7.98	56.70	±	18.10	71.00	±	6.78
Panicum maximum	Full	4.70	±	1.04	18.00	±	6.76	20.20	±	5.09
	None	13.30	±	4.64	14.00	±	2.29	26.00	±	3.14
Themeda triandra	Full	94.00	±	33.73	98.70	±	12.83	159.70	±	19.78
	None	106.00	±	20.03	106.70	±	14.63	146.70	±	16.24
	Grand mean	62.10	±	5.93						

	Aboveground Full			None			Cut			Belowground Full			None			Mean		
Eragrostis racemosa	42.40	±	5.74	48.80	±	8.18	63.50	±	4.87	42.90	±	3.35	60.30	±	6.21	51.6	±	4.09
Panicum maximum	9.00	±	2.86	16.00	±	3.29	23.10	±	2.97	14.30	±	3.25	17.80	±	2.60	6	±	2.05
Themeda triandra	100.00	±	18.30	102.00	±	8.84	153.20	±	11.72	117.40	±	15.71	119.80	±	10.57	118.6	±	9.22

Belowground	Aboveground Full			None			Cut					
Full	43.4	±	15.54	52.6	±	10.69	78.7	±	19.83	58.2	±	10.94
None	5.5	±	13.24	59.1	±	13.42	81.2	±	15.24	65.9	±	9.86
Mean	50.4 [a]	±	10.00	55.8 [a]	±	8.32	79.90	±	12.00			
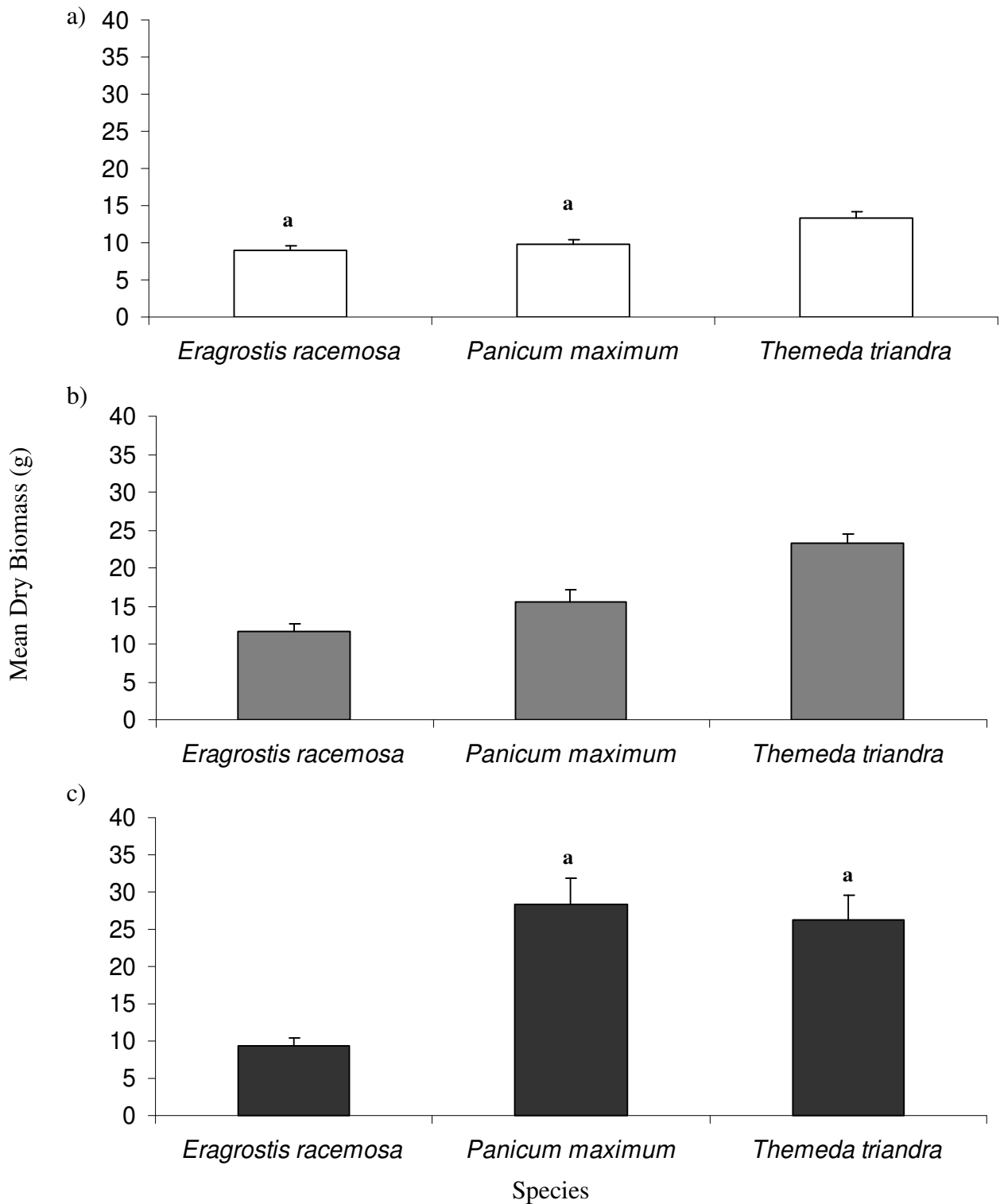
Figure 1: Means for species dry biomass across shallow (a), medium (b) and deep (c) soil. Analyses for medium and deep soil performed on log transformed data. Treatments with letters in common are not different (P < 0.05, shallow soil $LSD_{biomass}$ = 2.047).
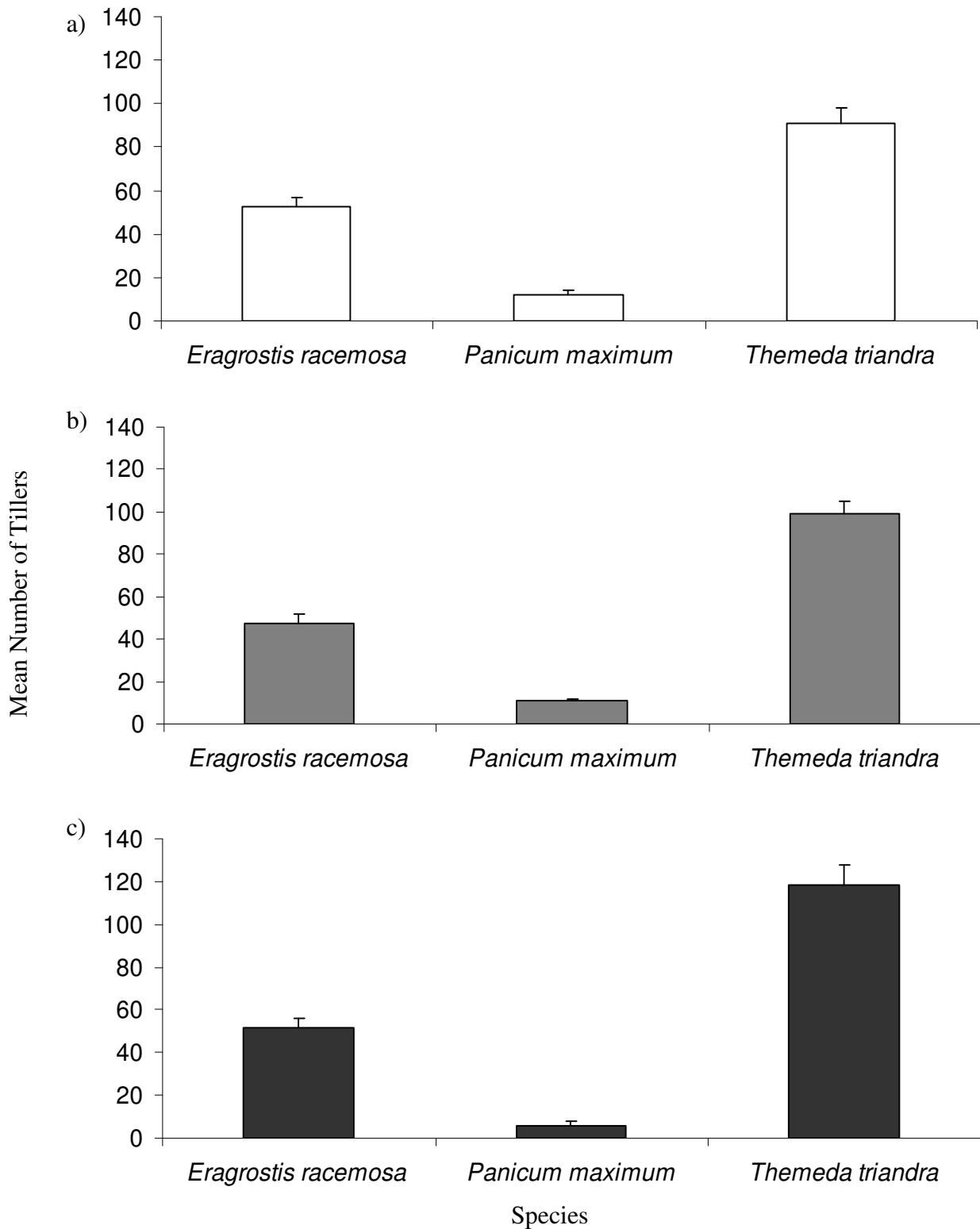
Figure 2: Means for species for number of tillers across shallow (a), medium (b) and deep (c) soil. Analyses for medium and deep soil performed on log transformed data.
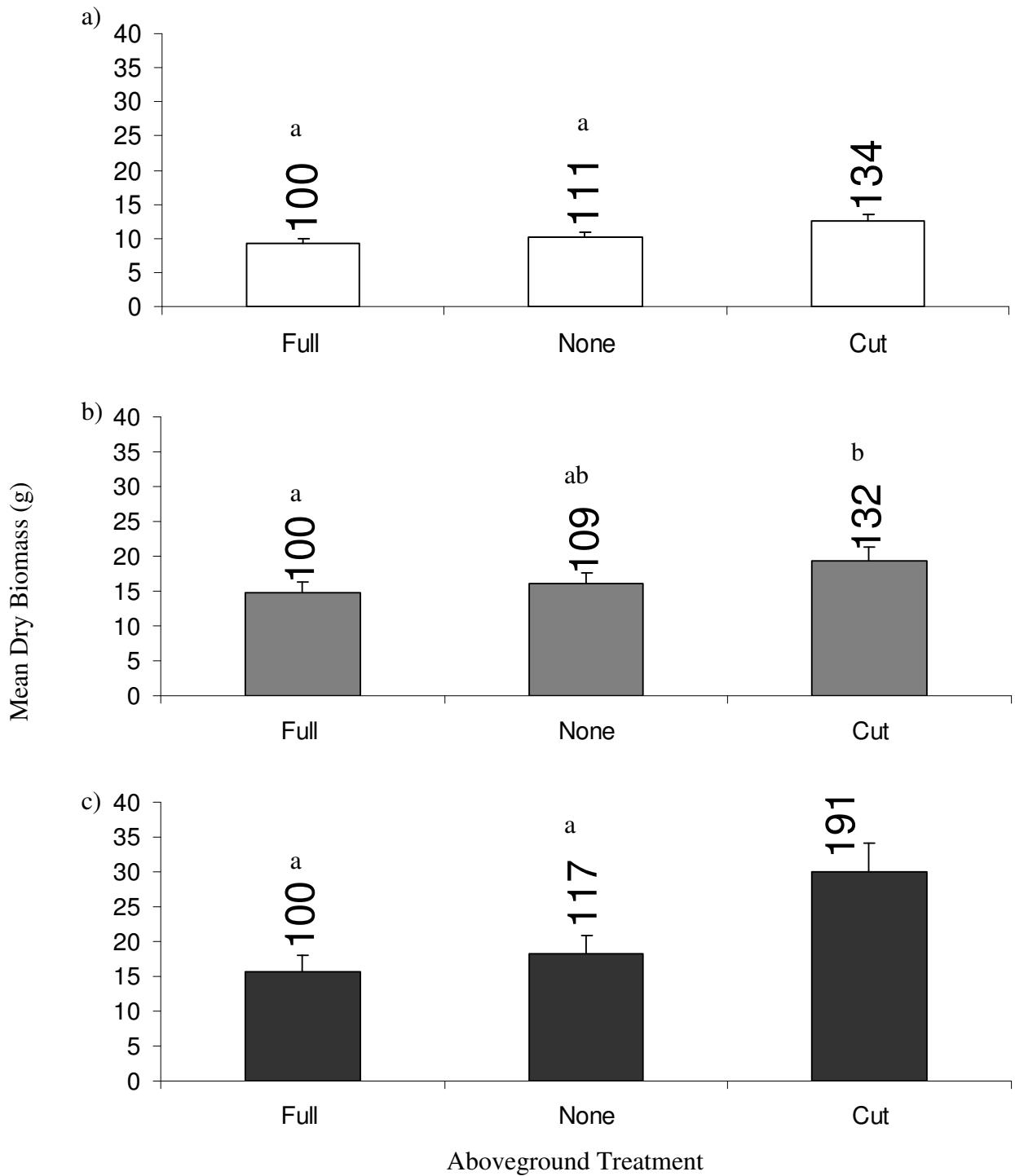
Figure 3: Means for dry biomass under three aboveground treatments showing results of means comparisons (LSD) using untransformed data for shallow soil and log transformed data for medium and deep soils. Treatments with letters in common are not different (P < 0.05, shallow soil LSD = 2.047).
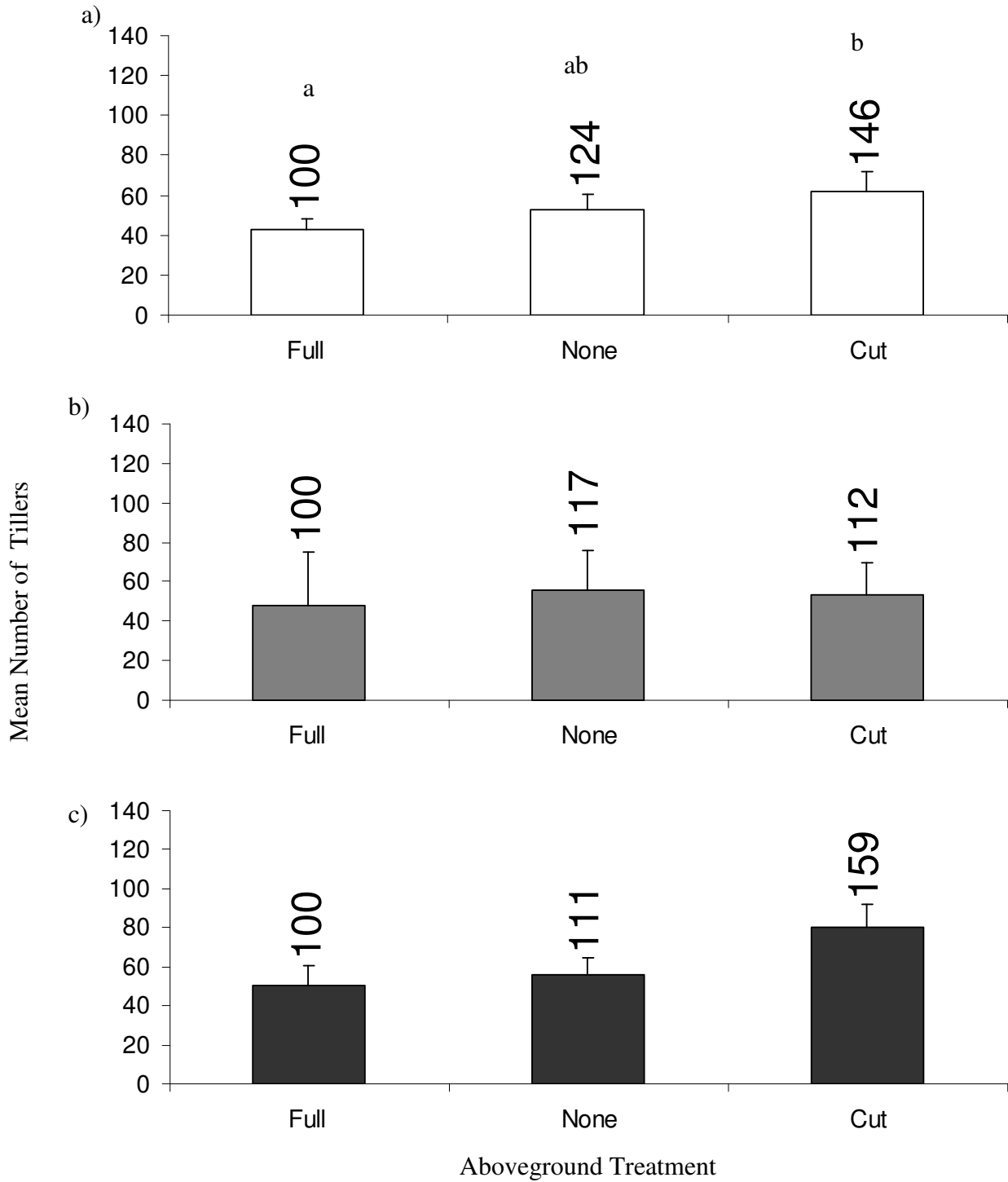
Figure 4: Means for number of tillers under three aboveground treatments showing results of means comparisons (LSD) using untransformed data for shallow soil and log transformed data for medium and deep soils. Treatments with letters in common are not different (P < 0.05, shallow soil LSD = 12.79).
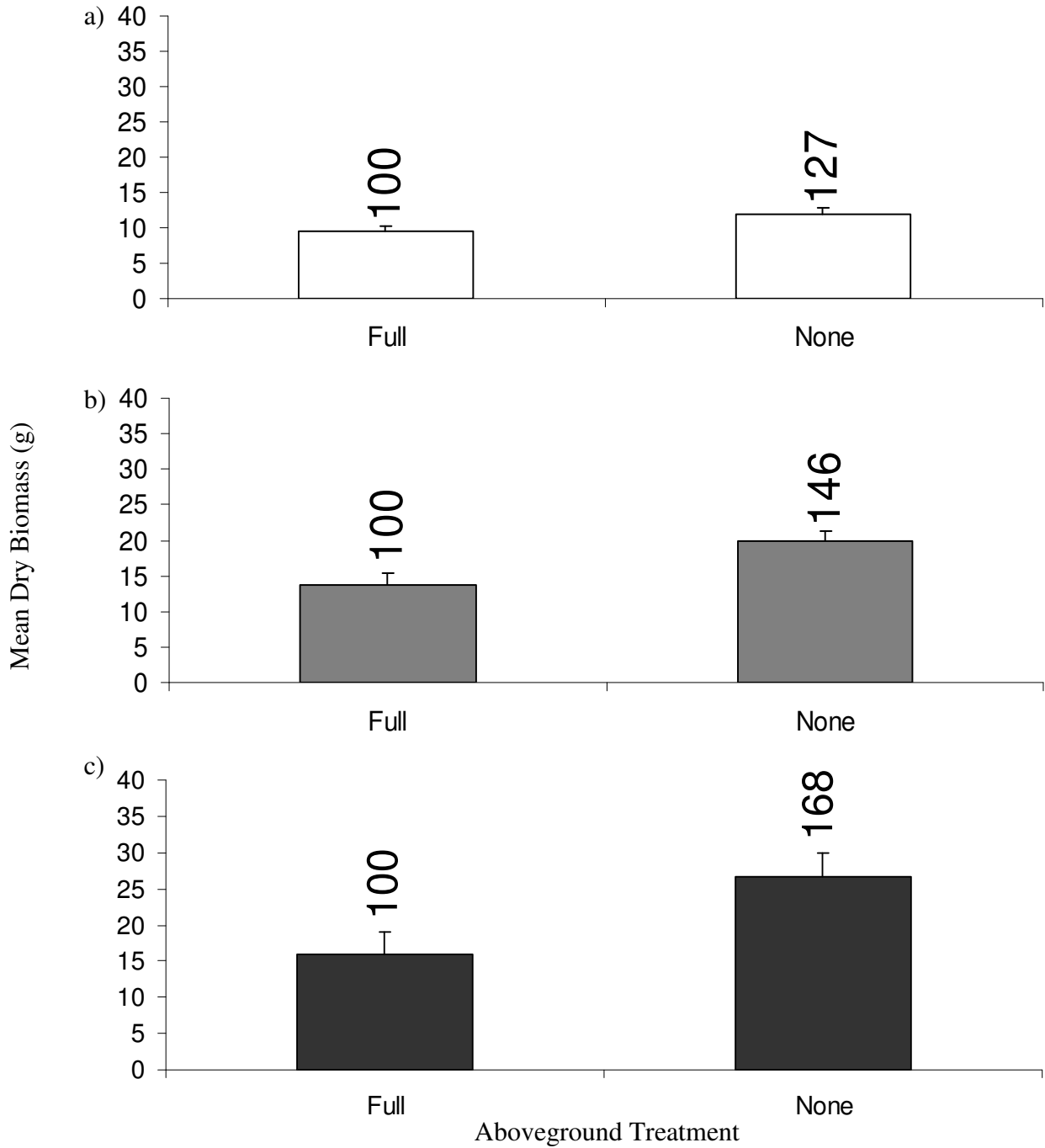
Figure 5: Means for aboveground dry biomass under two belowground treatments on (a) shallow, (b) medium and (c) deep soils and showing percentage yield relative to the control above bars. Analyses for medium and deep soil performed on log transformed data.
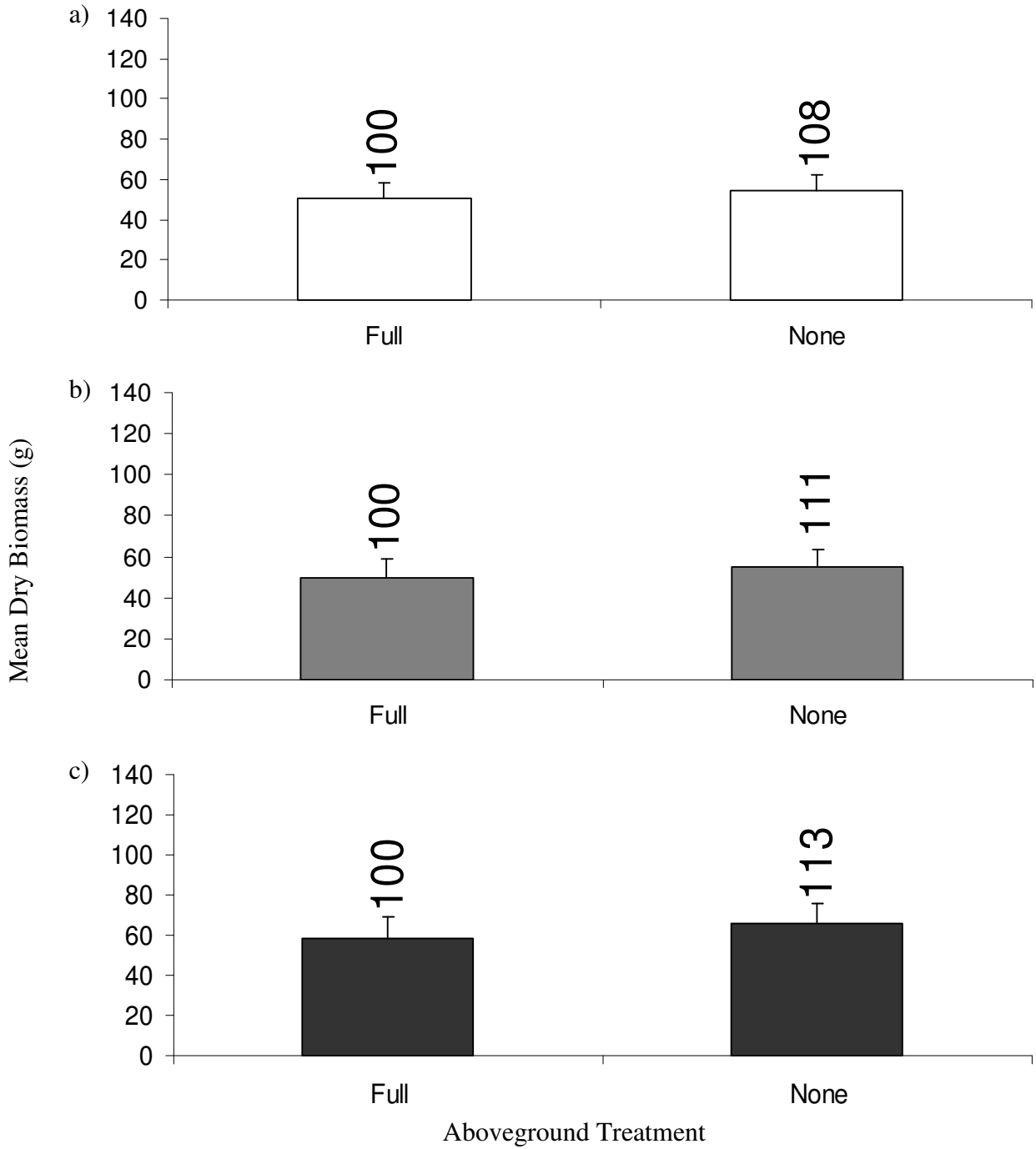
Figure 6: Means for number of tillers under two belowground treatments on (a) shallow, (b) medium and (c) deep soils and showing percentage yield relative to the control above bars. Analyses for medium and deep soil performed on log transformed data.
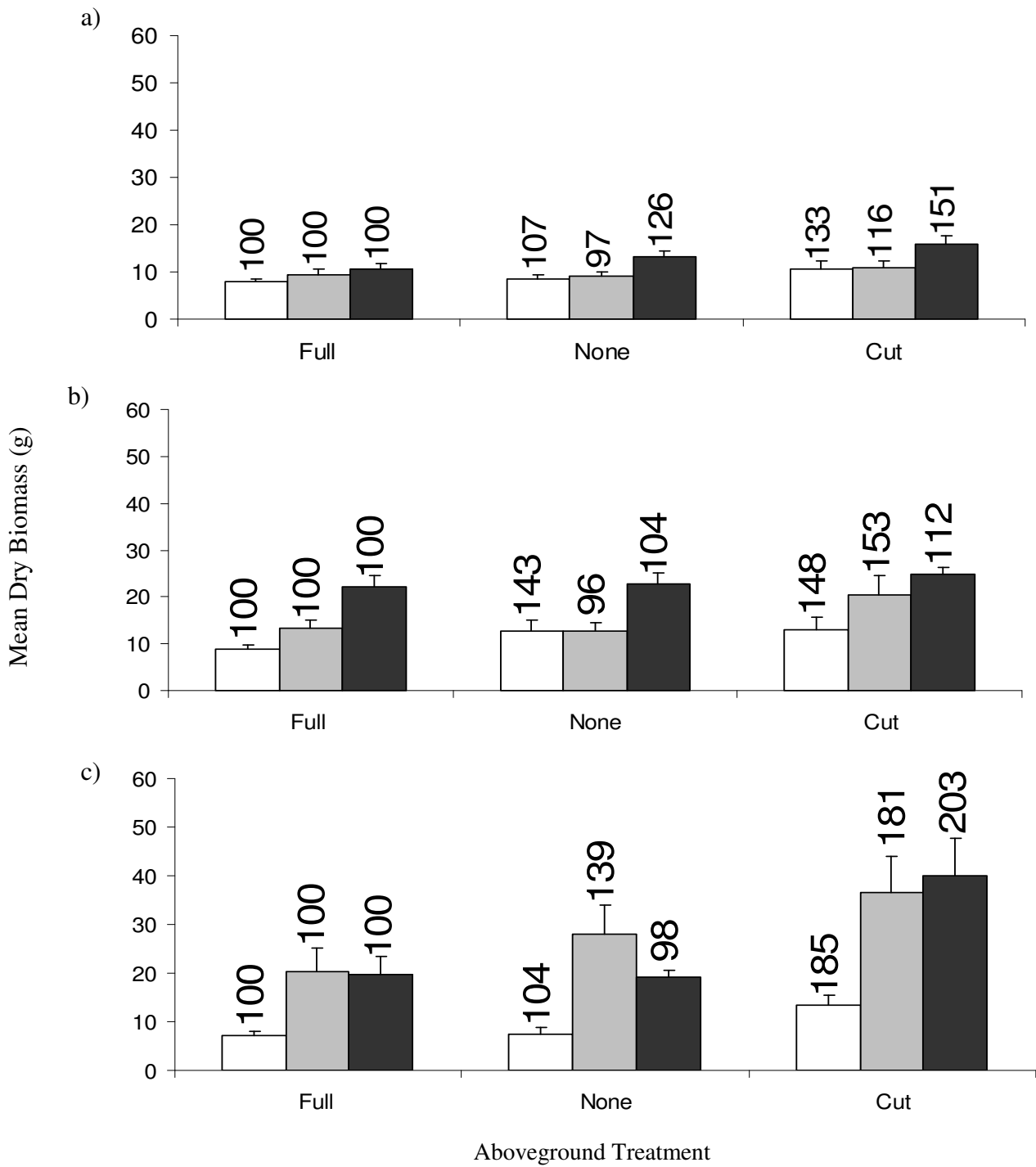
Figure 7: Mean dry biomass for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under three aboveground treatments on (a) shallow, (b) medium and (c) deep soils showing percentage yield relative to the control. Analyses for medium and deep soil performed on log transformed data.
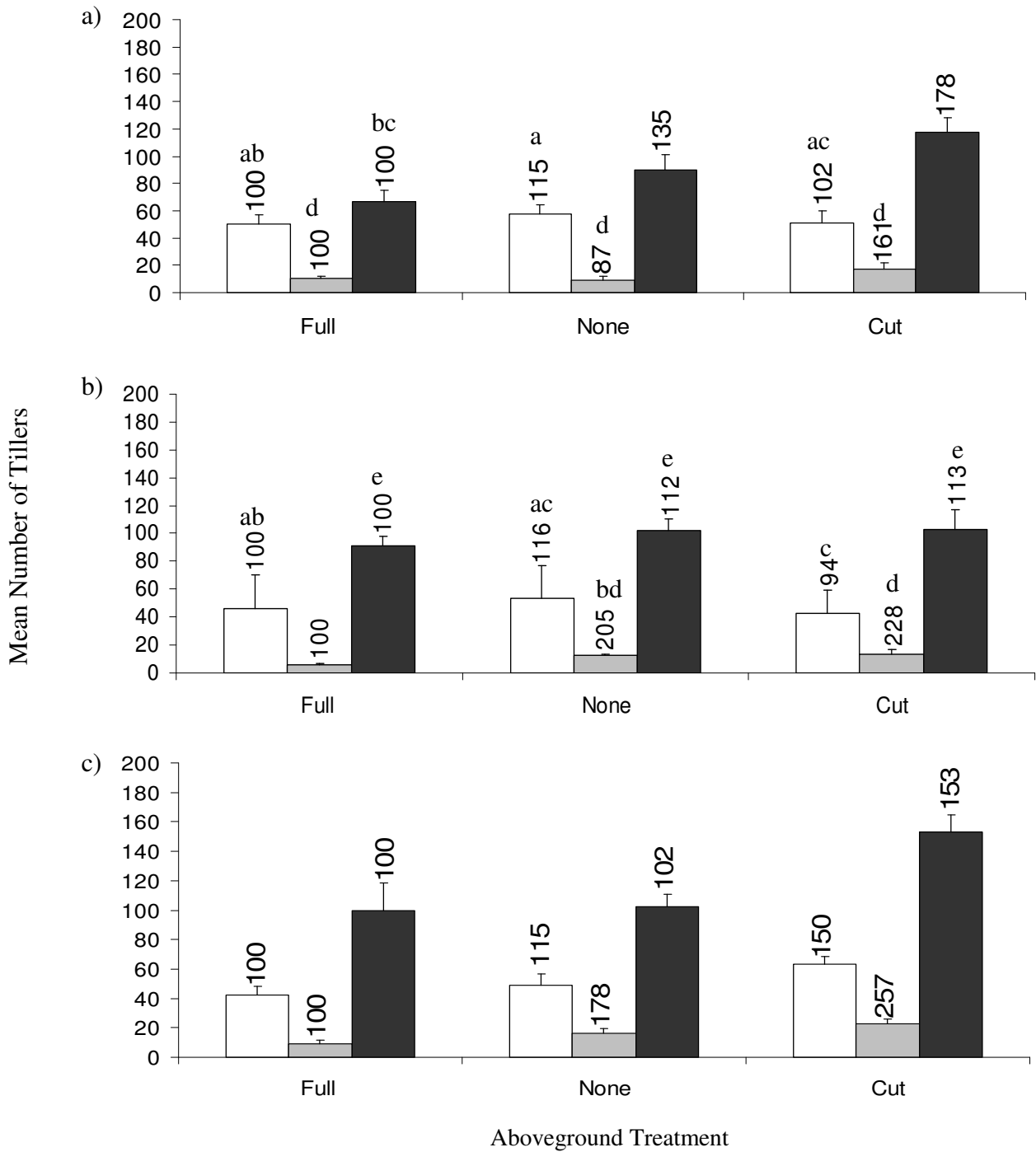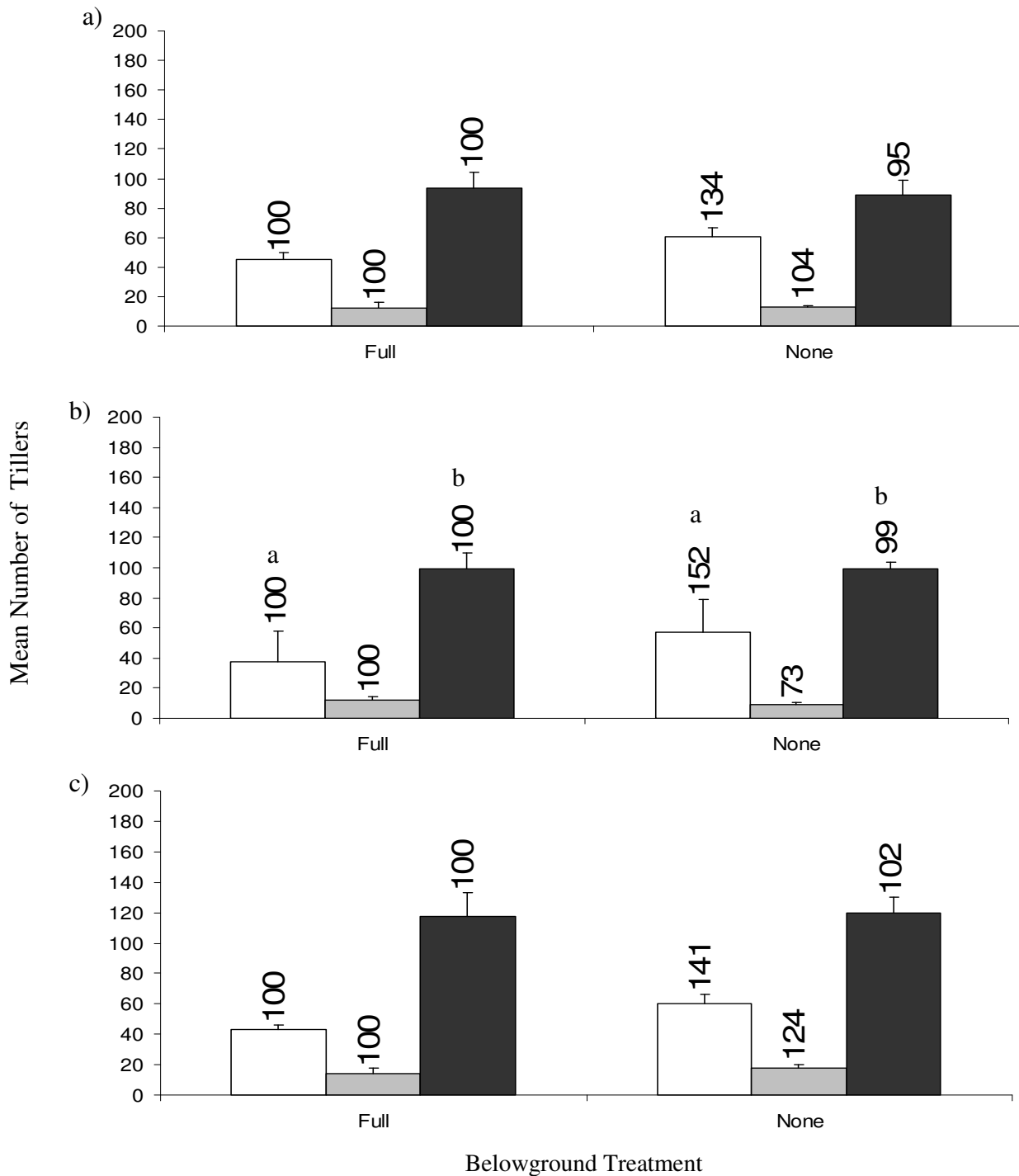
Figure 8: Mean number of tillers for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under three aboveground treatments on (a) shallow, (b) medium and (c) deep soils showing percentage yield relative to the control. Analyses for medium and deep soil performed on log transformed data. Treatments with letters in common are not different (P < 0.05, shallow soil LSD = 22.15).
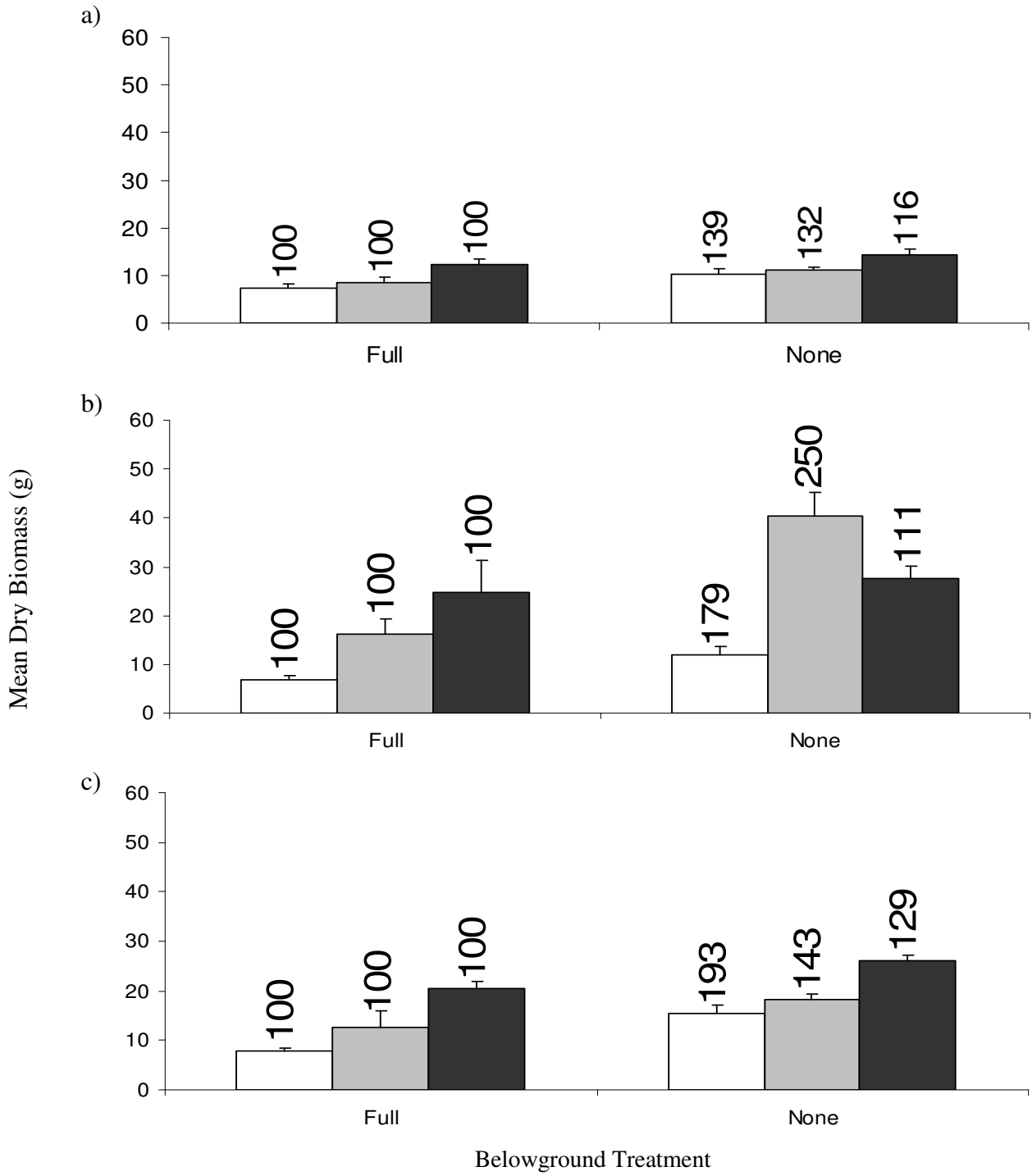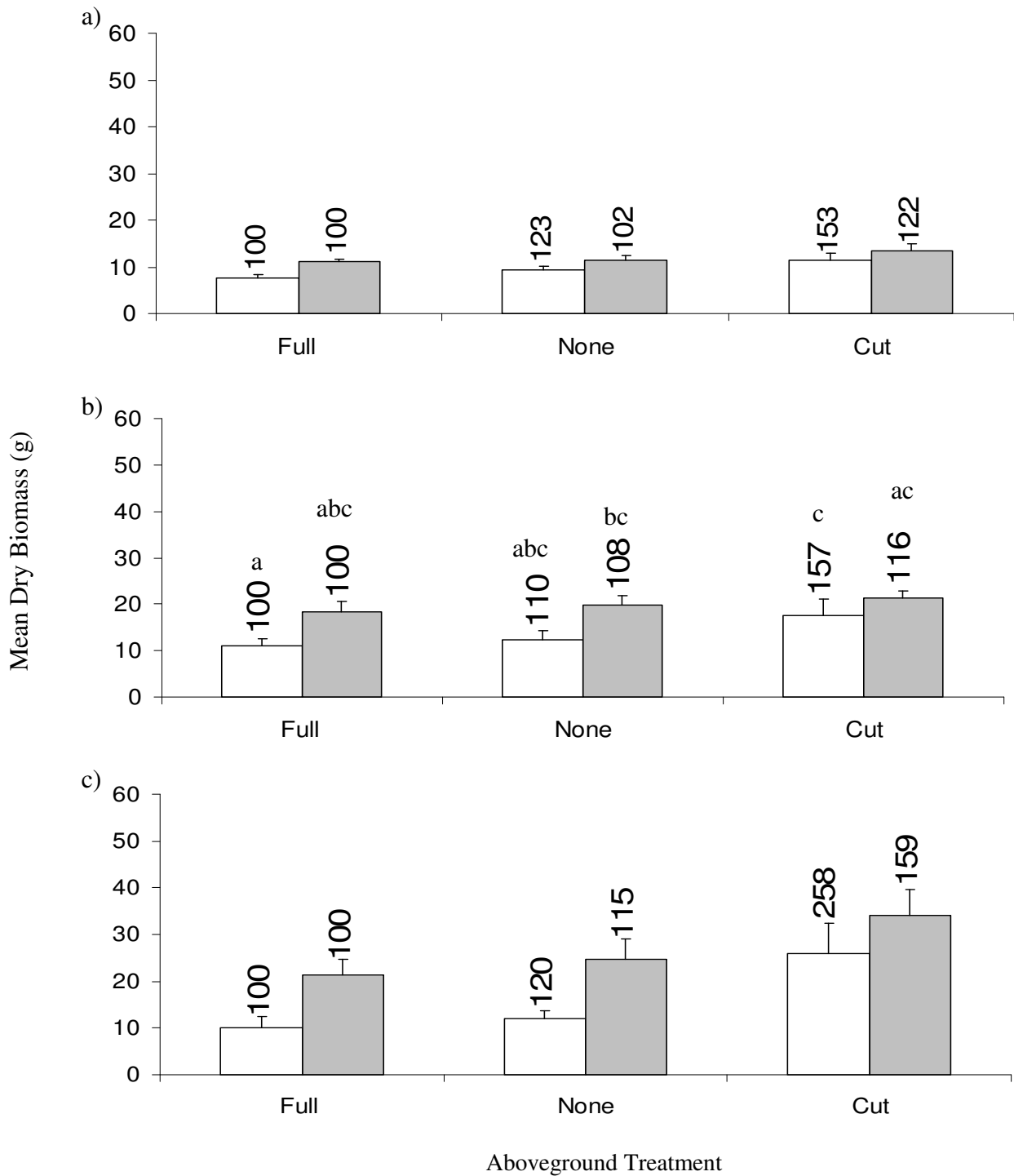
Figure 9: Mean dry biomass for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under two belowground treatments showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data.

Figure 10: Mean number of tillers for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under two belowground treatments showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data. Treatments with letters in common are not different (P < 0.05).
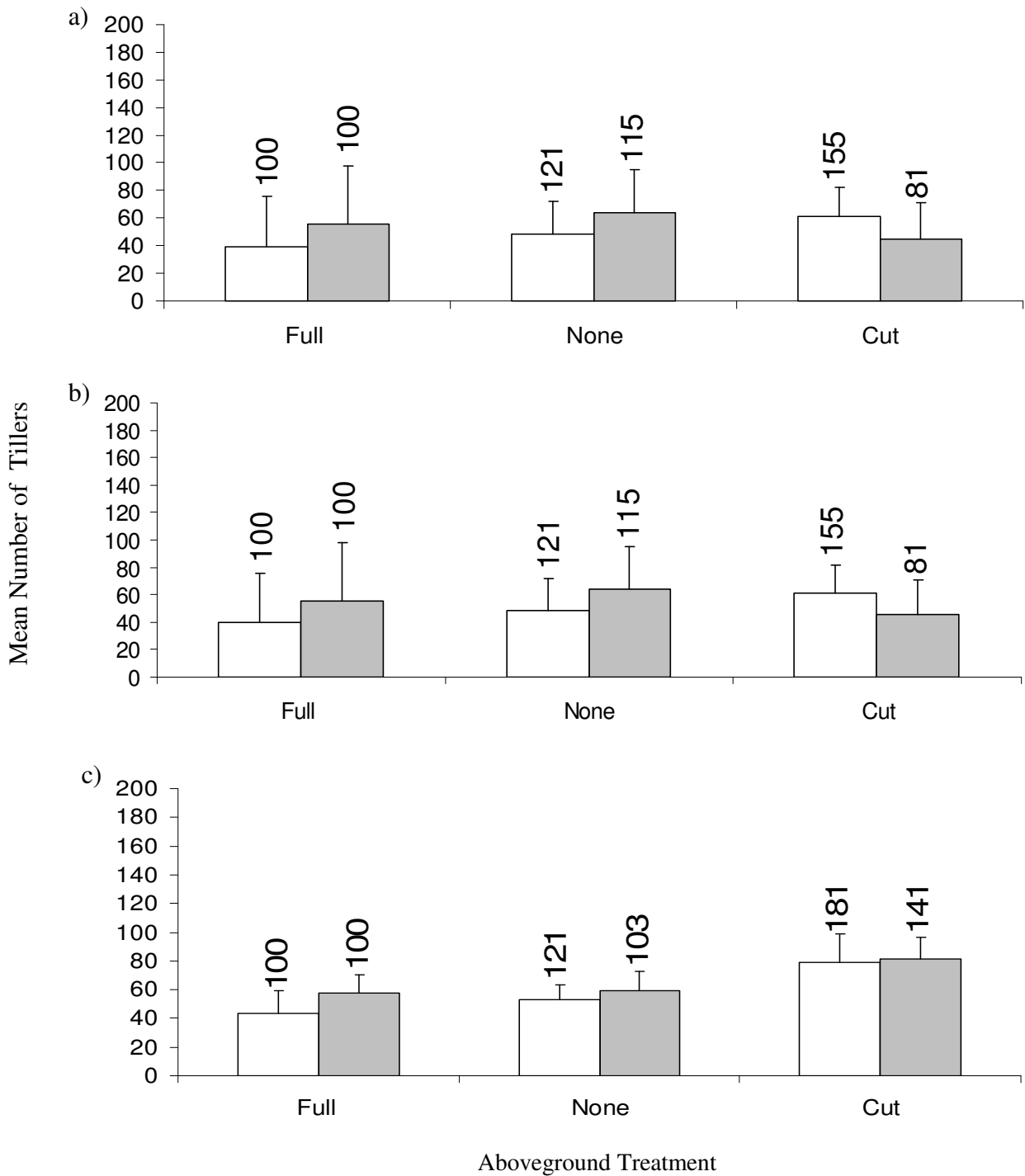
Figure 11: Mean dry biomass for full (open) and no belowground competition (grey) under three aboveground treatments showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data. Treatments with letters in common are not different (P < 0.05).

Figure 12: Mean number of tillers for full (open) and no belowground competition (grey) under three aboveground treatments showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data.
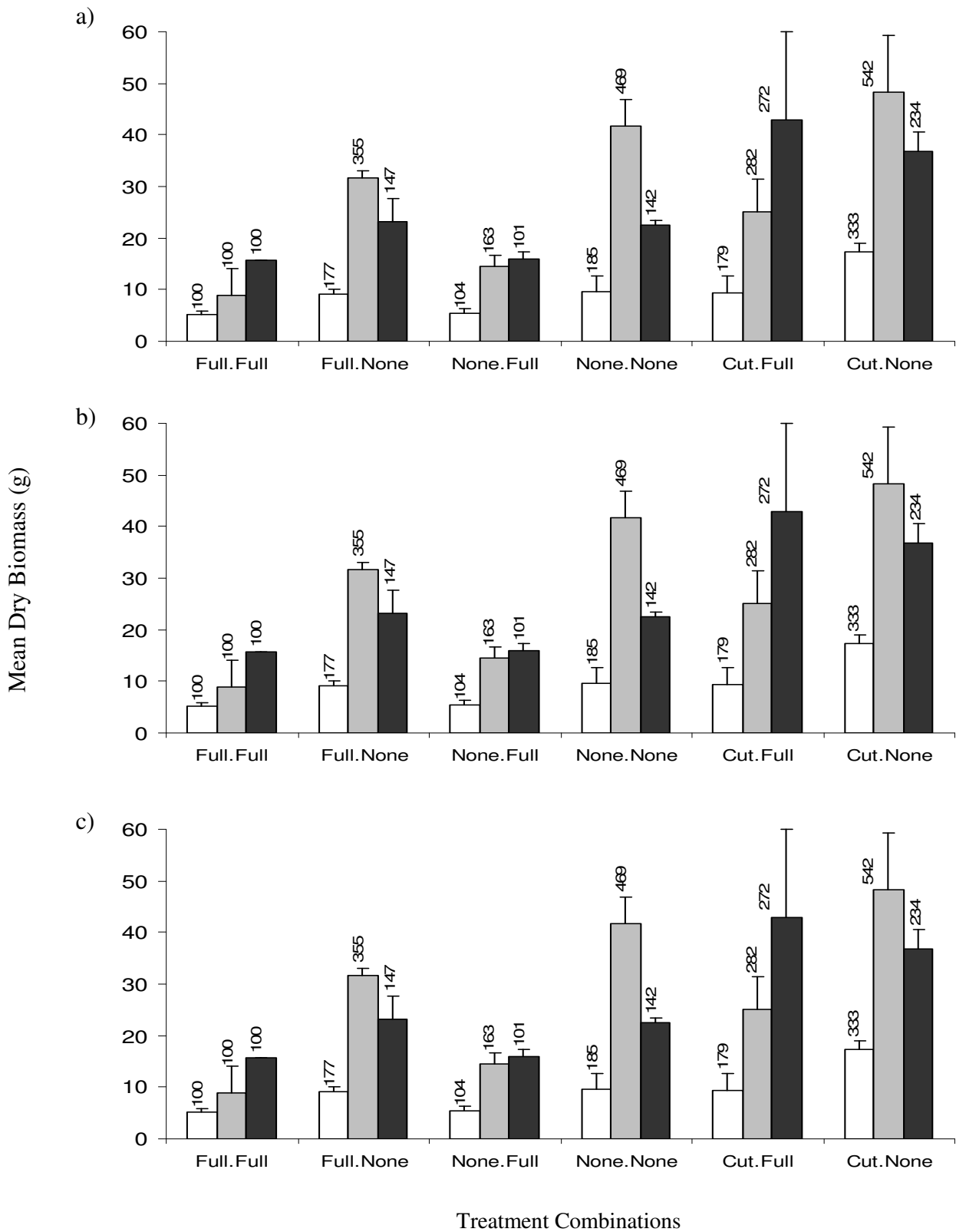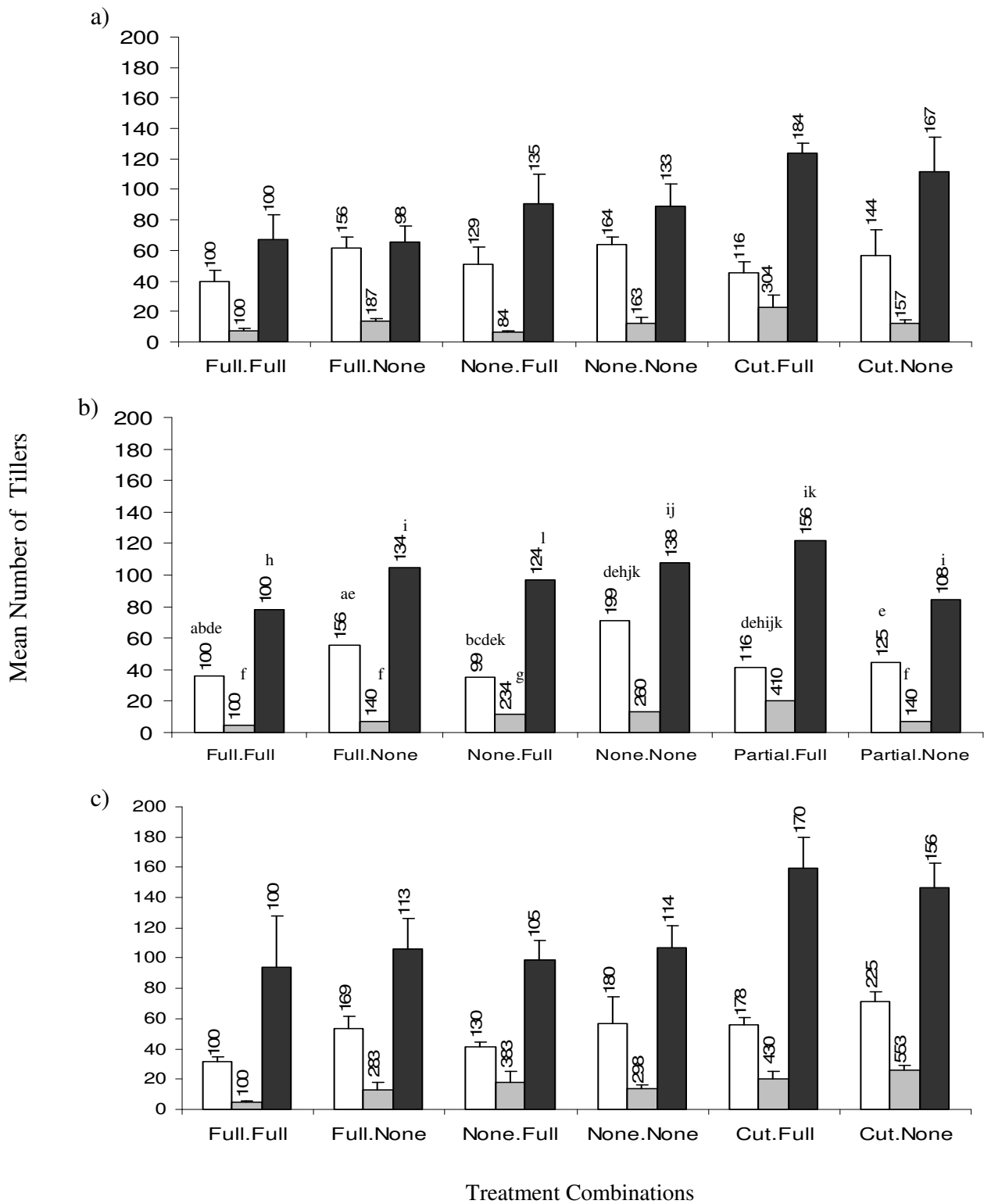
Figure 13: Mean dry biomass for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under six aboveground and belowground treatment combinations showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data.
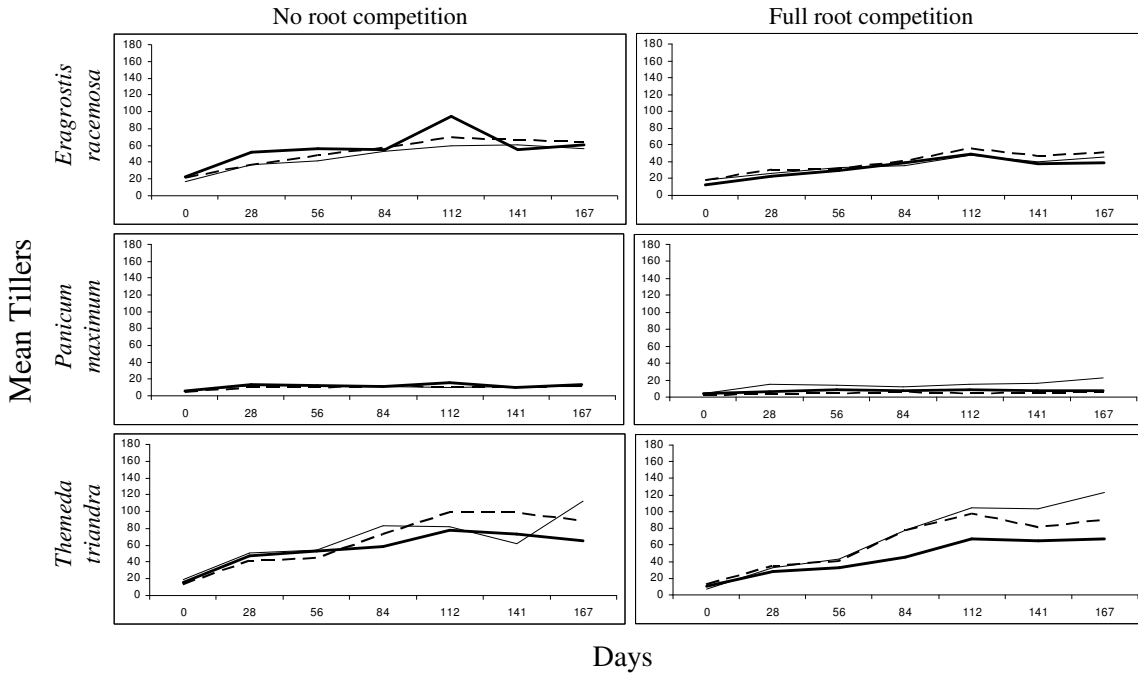
Figure 14: Mean number of tillers for *E. racemosa* (open), *P. maximum* (grey) and *T. triandra* (black) under six aboveground and belowground treatment combinations showing percentage yield relative to the control on (a) shallow, (b) medium and (c) deep soils. Analyses for medium and deep soil performed on log transformed data.

No root competition   Full root competition

Eragrostis racemosa

Panicum maximum

Themeda triandra

Mean Tillers

Days

Figure 12: Change in mean tiller number over time for three aboveground treatments under two belowground treatments, on the shallow soil level.
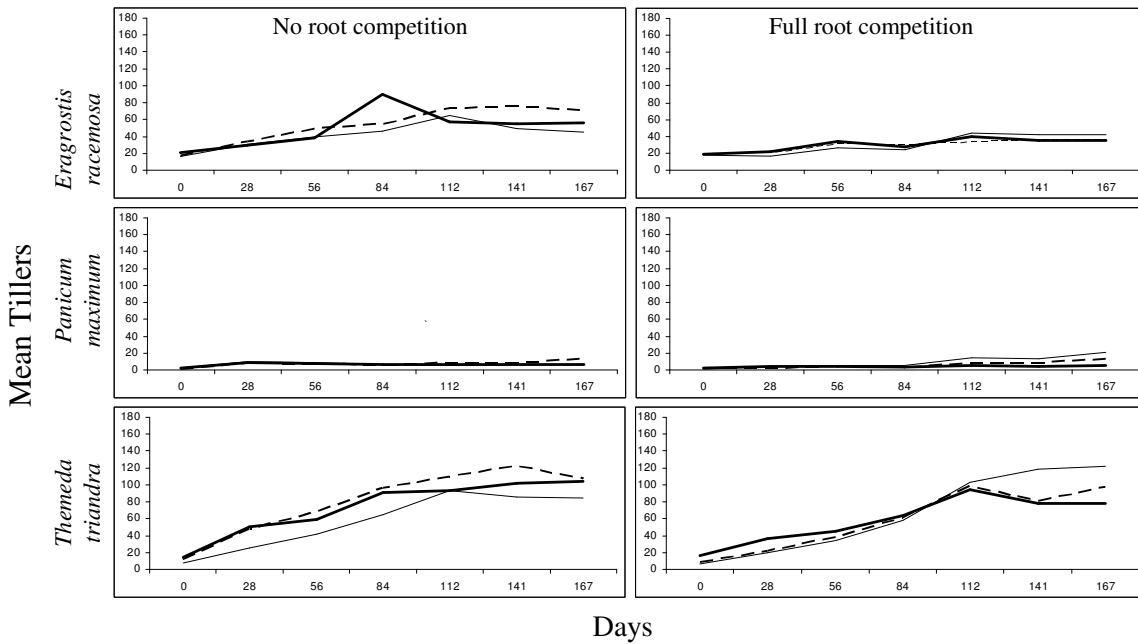
No root competition   Full root competition

Eragrostis racemosa

Panicum maximum

Themeda triandra

Mean Tillers

Days

Figure 13: Change in mean tiller number over time for three aboveground treatments under two belowground treatments on medium soil level.
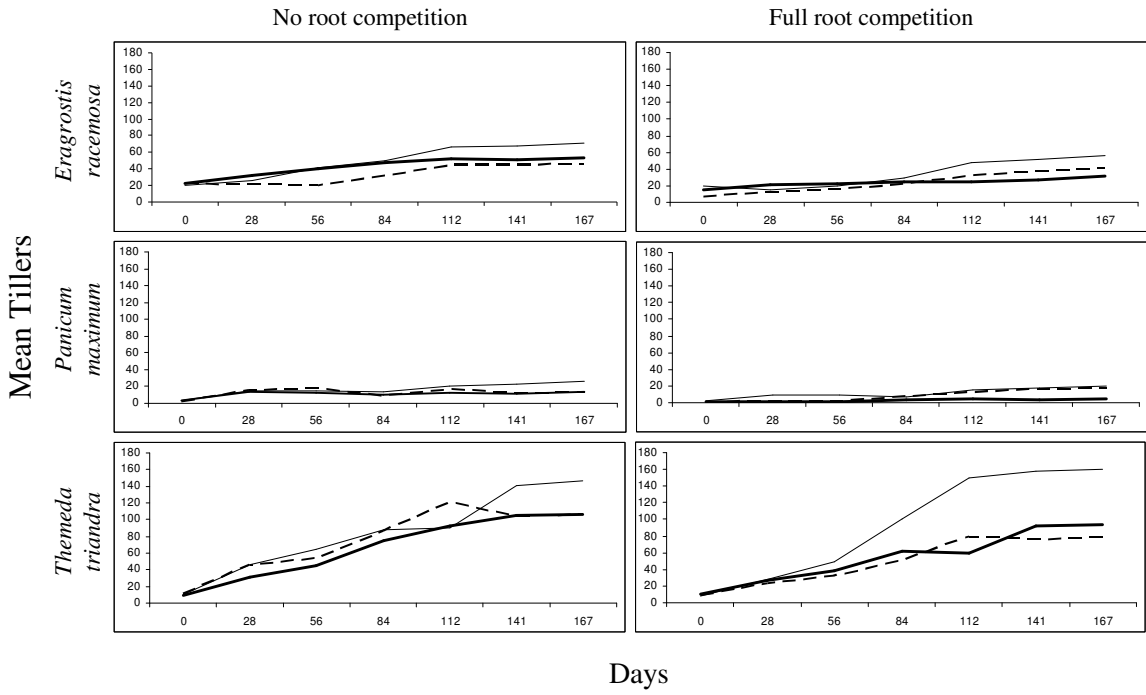
Figure 14: Change in mean tiller number over time for three aboveground treatments under two belowground treatments on the deep soil level.
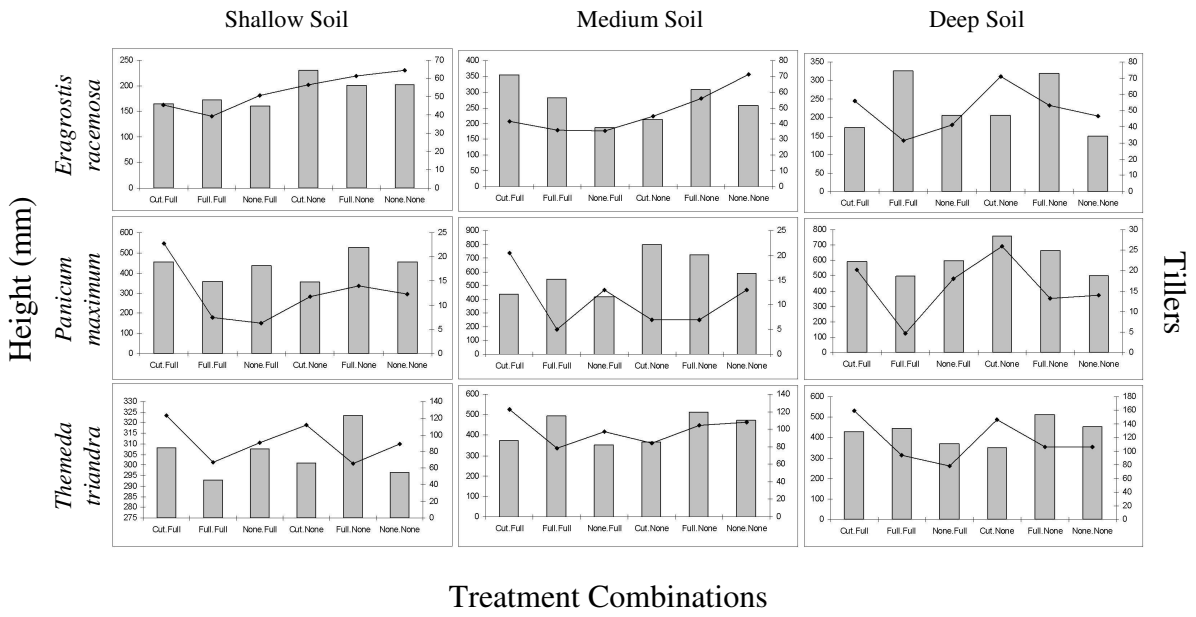
Figure 13: Mean grass height (bars) against tiller number (line) for combinations of Aboveground.Belowground Treatments after 167 days growth.