SEEDLING ESTABLISHMENT OF *THEMEDA TRIANDRA* FORSSK. IN THE MONTANE GRASSLANDS OF NATAL

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Declaration

I hereby certify that the research work reported in this dissertation is the result of my own original investigation except where acknowledged.

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Abstract

Soil erosion and vegetation destruction have reached serious proportions in disturbed areas of the montane grasslands of the Natal Drakensberg. Little is known of the inherent ability of indigenous grasses to produce viable seed and establish seedlings for rehabilitation programmes. This study examined the effects of fire and small-scale disturbance on the seedling dynamics of the dominant grass, *Themeda triandra* Forssk.

Annual seed production of *T. triandra* increased with length of burning rotation, ranging from 21 seeds m^{-2} in the annual winter burn to 485 seeds m^{-2} in the five-year burn. High predation of seeds (70-98%) and low viability (37% in 15 month-old seeds) contributed to the poor representation of *T. triandra* in the seed bank when compared to the above-ground vegetation.

Seedling densities and survival were monitored by mapping quadrats at six-weekly intervals from November 1986 to September 1989. Highest establishment of *T. triandra* was recorded in the biennial spring burn treatment (<184 seedlings m^{-2}). Microclimatic studies of the seedling environment demonstrated that increases in photosynthetically active radiation following burning, and high soil moisture associated with accumulation of litter, favour seedling establishment.

The main constraint to seedling establishment was high mortality in winter which resulted in a 1% survival of seedlings of *T. triandra* during the three-year study. This indicates that in the fire-climax grasslands of the study, seedlings contribute little to the population structure. The most significant factor contributing to low survivorship is intraspecific competition between seedlings. Spacing of seedlings in rehabilitation programmes is therefore a critical factor in optimizing seedling establishment.

Analysis of the fate of seeds of *T. triandra* between their production and establishment, showed that the main constraints for seedling establishment were predation, low viability and poor germination. A population model, based on transitions between seeds, seedlings and mature tufts, predicts that a biennial spring burn is the optimal treatment for maximising both seedling establishment and vegetative growth.

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Chapter 1
Introduction

1.1 Background to the study

South Africa has developed international standing with respect to its establishment and scientific management of protected areas, such as national parks, wilderness areas and nature reserves (Botha & Huntley 1989). However, recent political and social changes in South Africa require a wider understanding of environmental problems facing the country. In rural areas, soil erosion and vegetation destruction have reached serious proportions due to population pressures, socio-economic conditions and traditional grazing patterns which conflict with limited land resources (Cooper 1991) (Plate 1 & 2). The real challenge in the next decade is to examine alternatives to improve production as a sustainable option for land use. Rehabilitation ecology is one of the options to be considered to bring already degraded land back into production.

With the rapidly changing political environment in South Africa there is also increased pressure to allow grazing by domestic stock on traditionally conserved areas. One of the most strategically important wilderness areas in South Africa, under such pressure, is the Natal Drakensberg mountain range. The Natal Drakensberg is the highest mountain range in South Africa giving rise to many of the major rivers that are so important to the economy of the country. The upper reaches of the catchments which feed these rivers largely fall under the control of the Natal Parks Board. This conserved area, known as the Natal Drakensberg Park, comprises 79.6% (270 321 ha) of the Natal Drakensberg mountain range. The prime objective in managing these catchments is to maintain a sustained yield of water with the lowest possible levels of silt and other contaminants, while conservation of the flora and fauna and recreation are compatible supplementary

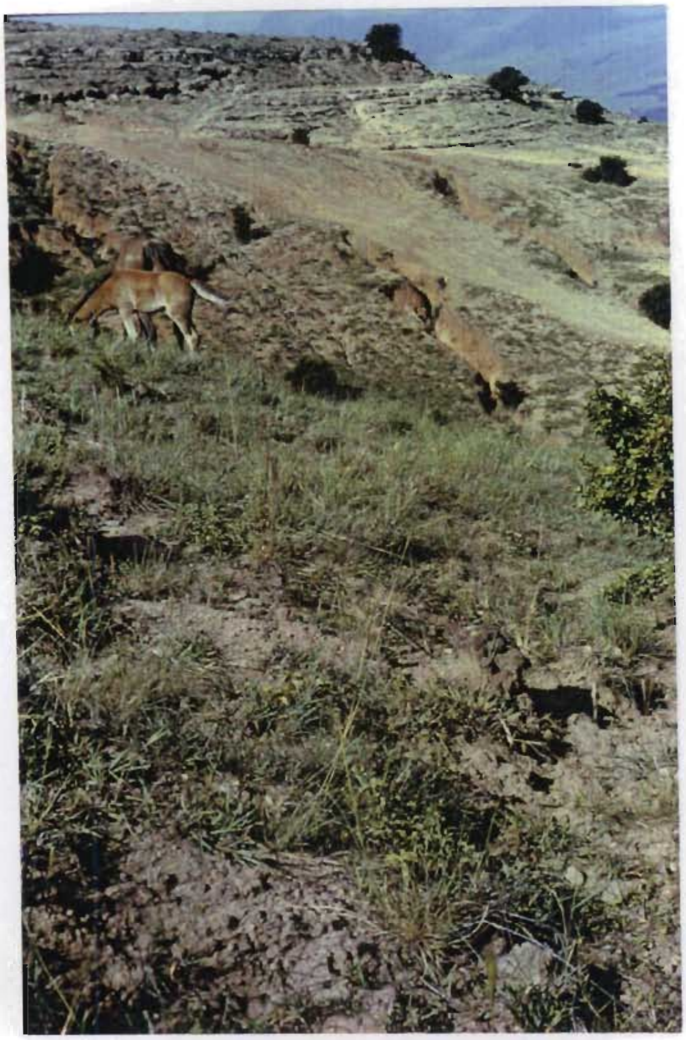


Plate 1. Extensive soil erosion resulting from overgrazing in rural areas of KwaZulu.

Plate 2. Deep donga erosion in the foothills of the Drakensberg.

objectives (Bainbridge 1987). Of the remaining 20.4%, a small portion, 3%, is in private ownership and 17.4% comprises the most western portion of KwaZulu, a dependent state. In KwaZulu, the main objectives of the montane areas in the Drakensberg are to provide year-round grazing to subsistence graziers and, to a limited extent, to provide a source of food and medicinal plants.

The dominant vegetation of the Natal Drakensberg below *ca.* 2 000 m is perennial, seasonal grassland (Plate 3). In summer, this grassland, particularly if burnt, is a vivid green colour, whereas in autumn and winter it has a reddish-brown colour. Most of the grasses are tufted with a high basal cover of nearly 50% (Killick 1990). *Themeda triandra* Forssk. is the main species and is associated with other grasses, such as *Tristachya leucothrix* Nees, *Heteropogon contortus* (L.) Roem. and Schult., *Trachypogon spicatus* (L.f.) Kuntze, *Monocymbium ceresiiforme* (Nees) Stapf, *Alloteropsis semialata* (R.Br.) Hitchc. and *Elionurus muticus* (Spreng.) Kunth. Forbs are commonly mixed with the grasses, but seldom make a significant contribution to basal cover (Tainton 1981).

One of the main factors affecting growth and reproduction of these grasses is fire (Plate 4). Lightning induced fires are a natural phenomenon in the Drakensberg. The highest lightning ground-strikes recorded in South Africa (>9.0 strikes km^{-1} annum^{-1}) occur in the Drakensberg (Edwards 1984). Fires caused by lightning generally occur in late spring or summer, but rarely result in burns more than a few hectares. Besides natural fires, anthropogenic fires have occurred for many millennia in the grasslands (Tainton & Mentis 1984). There is archaeological evidence that in the Drakensberg primitive man used fire for domestic purposes since at least the terminal Middle Stone Age (50 000 BP) (Carter 1978). Subsequently, Late Stone Age San hunter-gatherers used fire more extensively to attract game by burning away old grass to induce flushes of new green

Plate 3. *Themeda triandra*-dominated grassland on the Little Berg.

Plate 4. Controlled burning in the Drakensberg.

shoots. By the early eighteenth century Bantu-speaking people practised burning to temporarily improve grazing and aid hunting (Hall & Vogel 1980). The grasslands are particularly susceptible to anthropogenic fires in the dry winter season. White settlers of the early 19th century burned extensively from mid-August to early spring to promote early growth for grazing by sheep and cattle (Nänni 1969). Fire can therefore be regarded as a central component in the grasslands and not as an extraneous factor (van Wilgen, Everson CS & Trollope 1990).

Fire regimes in the grassland areas are determined principally by climate and available fuel, and to a slightly lesser extent by people's objectives in setting fires. With increased knowledge of the ecological effects of fire in South African ecosystems (Scott 1984), burning policies now have a more scientific basis. In the Drakensberg catchment areas, management prescriptions are based on the effect of fire on the vegetative biology of the key species (Everson CS, Everson TM & Tainton 1985). Current prescriptions support burning between May (early winter), after the first frosts, and mid-September (early spring), before significant growth has taken place. However, a significant gap in the burning policy is that it is based only on the vegetative response of grasses to fire. Little is known of the effect of fire on the inherent ability of local indigenous grasses to produce viable seed and establish seedlings. It is essential to examine the entire life history of individual species (sexual and vegetative) to understand the factors that limit their occurrence within the grassland community.

Although sexual reproduction generally plays a minor role in regeneration of perennial grasslands (Liebenberg 1955; Briske & Wilson 1977), it may be important following disturbance. After the disturbance of the vegetation (e.g. burning during the active growth period, overgrazing and path erosion), secondary or regeneration succession takes place. The ability of an existing species to become re-established after disturbance will depend on its tolerance to changed site conditions, and avoidance mechanisms such as seed dormancy and a persistent seed bank (van Aandel & van den Bergh 1987). An understanding of the ecological processes that occur can give managers the option of actively restoring the grassland.

Killick's (1963) viewpoint of succession in the Drakensberg strongly reflects the elements of the classical Clementsian model (Clements 1936). Killick speculates that in the early stages of natural succession in grasslands of the Drakensberg, the dominant grasses are *Rendlia altera* (Rendle) Chiov., *Sporobolus centrifugus* (Trin.) Nees, *Eragrostis capensis* (Thunb.) Trin., and *Monocymbium ceresiiforme*. Next in the succession are *Themeda triandra* and its associated grasses *Trachypogon spicatus, Tristachya leucothrix, Harpochloa falx* (L.f.) Kuntze and *Heteropogon contortus*. Although these grasslands occupy areas that are climatically suited to the advancement of plant succession beyond the grassland stage, they are prevented from this by recurrent grass fires or grazing (Tainton 1981). The potential climax vegetation of the grassland is related to altitude and related temperature changes. Three vegetation zones are recognized on the basis of their climax vegetation: the montane belt (1 250-1 800 m), the subalpine belt (1 800-2 500 m) and the alpine belt (2 500-3 350 m). The climax vegetation of these respective zones are *Podocarpus latifolius* forest, *Passerina-Erica-Widdringtonia* fynbos and *Erica-Helichrysum* heath.

The *Themeda*-dominated grasslands of the subalpine belt are highly stable under good management (i.e. a regular burning regime in the dormant season). If, however, the grasslands are disturbed, changes in species composition can occur. For example, if these grasslands are protected from fire, they are extensively replaced by *Elionurus muticus*

(Granger 1976). Once *T. triandra* is displaced from the sward, it is difficult, if not impossible, to re-establish (Tainton 1981). Reasons for *T. triandra* not re-establishing itself are unclear. However, Tainton (1981) postulated that the original large scale establishment of *T. triandra* was due to a particular set of weather patterns that no longer occur in southern Africa. An interesting feature of these grasslands is that no annual grass species occur in the sward. The absence of early successional annual grasses that can exploit changed habitats and modify the physical environment for later successional species, may contribute to the inability of climax grasses such as *T. triandra* to re-establish after disturbance.

Despite its significance for conservation and agriculture, few studies have been undertaken to determine the importance of sexual reproduction in the regeneration of *T. triandra*. One reason for this may be that seedlings are insignificant in size compared to vegetative tufts and therefore more difficult to study in dense grassland. Another reason may be that seedlings of grass species are extremely difficult to identify. Although monitoring seedling numbers over time forms the basis of seedling population studies, the task is incomplete unless all the processes involved (e.g. seed production, predation, dormancy, germination etc.) are examined.

The present study is a unique long-term examination of all the processes of seedling population dynamics of *T. triandra* in the montane grasslands of South Africa. The main objective of this study was to determine the role of seed biology in the establishment of *T. triandra* under the different disturbance regimes that occur in this environment. In order to determine whether sexual reproduction in *T. triandra* is an effective regenerative strategy in montane grasslands, a number of hypotheses were developed and tested in this study. These hypotheses relate to the different phases of seedling establishment including seed production, dispersal, dormancy, predation, size of seed bank and the availability of a favourable site.

1.2 Seed production

- *Hypothesis 1*: **Regular burning increases seed production of *T. triandra* because flowering is prolific in biennially burnt grasslands.**

The number of seeds produced by a species determines the size of its potential seedling population. Plant size within a species is a critical factor affecting seed production (Marshall, Levin & Fowler 1985). Fire stimulates the development of new tillers and subsequent size of the plant (Everson CS, Everson TM & Tainton 1985). Grassland with a regular burning frequency will therefore be more productive. Without fire the sward becomes rank and the number of reproductive tillers declines. Different fire regimes may also affect seed production since burning at different times of the year greatly affects the frequency of flowering of grass species (Killick 1963).

1.3 Dispersal

- *Hypothesis 2*: ***Themeda triandra* has a low probability of colonizing eroded sites because it has poor dispersal ability.**

Recruitment from seed in disturbed areas is only effective if the seed can reach areas of potential colonization. Wind dispersed seeds typically fall near their source and most fall within a distance equivalent to a few plant heights (Levin & Kerster 1974; Cook 1980). Seeds of *T. triandra* are relatively large in comparison to other grasses and possess an awn. The role of the awn in seed dispersal has been subject to much debate. One view is that the awn orientates the seed during fall from the parent plant increasing chances that it will land with the callused end embedded in the soil (Peart 1981). Alternatively, awns curl and twist with alternating wet and dry conditions and push the seed into the soil (Pentz 1955).

1.4 Dormancy

• *Hypothesis 3*: ***Themeda triandra*** **seeds have a dormancy mechanism which enables the species to survive the cold, dry winter season. Dormancy decreases with increasing age of the seed which ensures the germination of seedlings when favourable climatic conditions occur.**

The dispersal phase of plants is usually dormant. Harper (1977) describes three states of dormancy. Dormancy is sometimes innate (the seed is viable but germination is prevented by some property of the embryo), enforced (environmental unsuitability), or induced (the dormancy state changes as a result of some after-ripening experience). In environments with extremely cold winters such as the Drakensberg, dormancy of *T. triandra* seeds is likely to be enforced.

1.5 Predation

• *Hypothesis 4*: **Predation reduces the potential seedling population of *T. triandra* in montane grasslands.**

Seeds with long dormancy periods are highly susceptible to predation (Hacker 1989). Since seeds of *T. triandra* have a dormancy period of approximately 12 months (West 1951), they are exposed to predators for long time periods and therefore have a high probability of being preyed upon. Poor dispersal ability will also increase predation since most seeds fall in close proximity to one another and therefore have a high probability of being found by predators. Another factor that may increase the probability of predation is the large amount of nutritional endosperm in seeds of *T. triandra* (Gibbs Russell *et al.* 1990).

1.6 Seed bank

- *Hypothesis 5*: **In grasslands with a regular burning regime there is no persistent seed bank. However, density of seeds in the soil increases with time after fire.**

The composition of the seed bank is an indication of the regeneration potential of the vegetation. Persistence of seeds in the seed bank is determined by environmental factors (e.g. fire) as well as processes such as germination, viability, decomposition and predation. In the regularly burnt grasslands of the Natal Drakensberg, fire may destroy seeds, resulting in a short-lived or transient seed bank. Conversely, protection from fire will enable seeds that are susceptible to fire damage to accumulate in the soil and form a persistent seed bank.

1.7 Availability of a favourable environment

Hypothesis 6: **Recruitment from seed is unimportant in the population dynamics of stable grassland because disturbance is required to provide openings for seedling establishment.**

Grass seedlings in dense vegetation are exposed to severe competition from surrounding plants. This competition is most likely to be for light, water and nutrients. By contrast, newly emerged vegetative tillers derive support from the parent plant. Hence, vegetative tillers have a competitive advantage over the seedlings in undisturbed grasslands. However, since vegetative tufts of *T. triandra* do not spread rapidly, disturbance may provide a greater opportunity for regeneration from seed. In disturbed areas, reduced competition for nutrients (Sharitz & McCormick 1973), greater light intensity (Grime 1979) and absence of neighbours (Harper 1977) create different microclimates that may favour seedling establishment.

1.8 Overview of experimental design

To test the above hypotheses, a number of experiments were initiated. A conceptual model (Fig. 1.1) depicts how the various components of the life cycle of a grass plant are interrelated. This was used to plan the different phases of the study. Each phase or life cycle component is generally dealt with in a separate chapter in the thesis. This allows easier reference for particular life cycle components.

The conceptual model begins and ends with the adult plant. The adult plant produces seed (Chapter 4) which may be either dispersed into the system (Chapter 4), or preyed upon and lost from the system (Chapter 5). Dispersed seeds enter the soil seed bank (Chapter 5) where they may germinate (Chapter 4). Establishment and survival of these seedlings (Chapter 6) is dependent on the environmental heterogeneity in the different burning treatments. The environment immediately surrounding the seedling (Chapter 7) determines which seeds are recruited into the seedling population. In their subsequent growth, seedlings will be faced with competition from each other and from adult plants (Chapter 8). Those seedlings that survive will develop into adult plants which complete the life cycle when they reach reproductive maturity.

These elements of the seedling life cycle are used to develop a deterministic model which predicts the relative importance of transitions between the life-cycle events in *T. triandra*. The model will provide the basis for informed management of the grass community by predicting opportunities for seedling establishment.

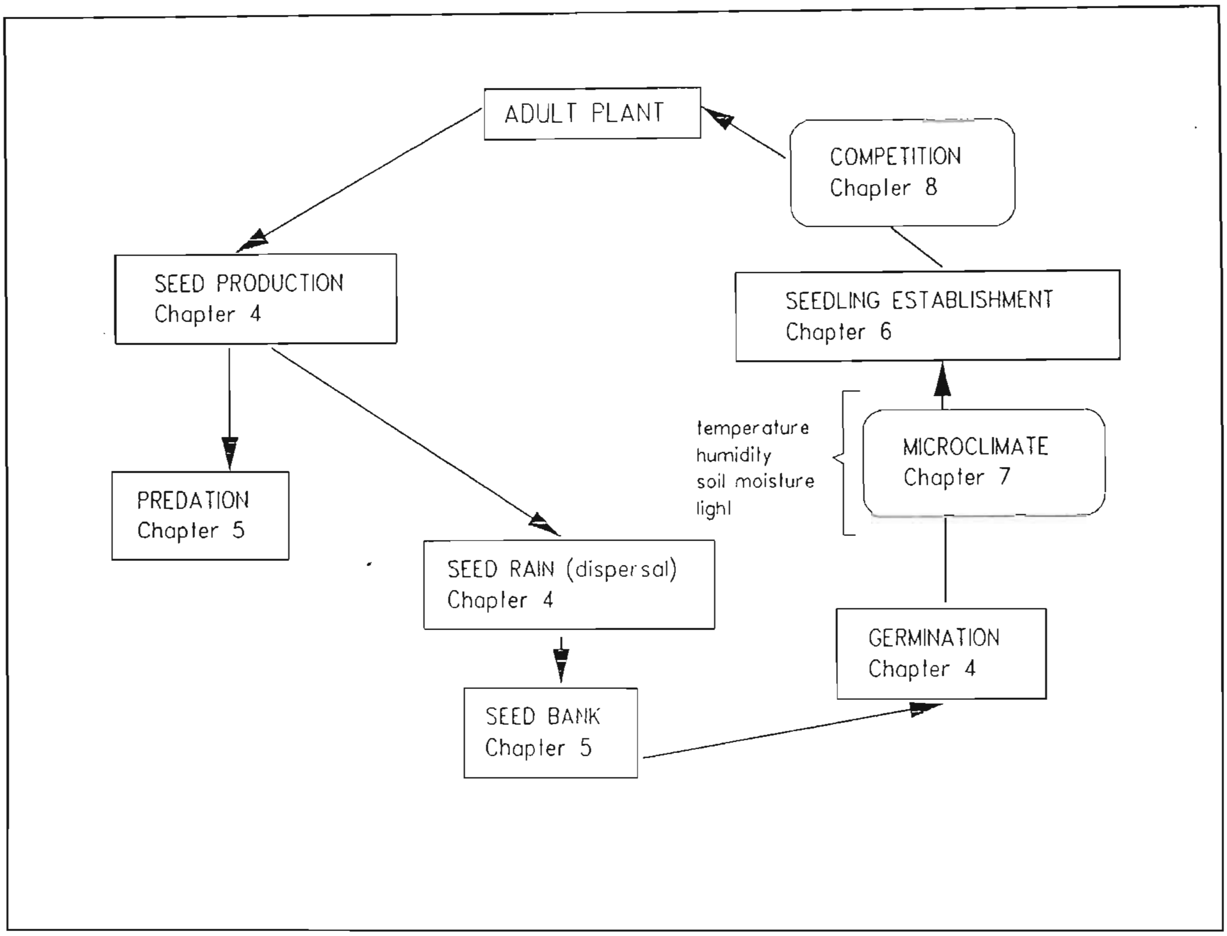


Figure 1.1 Schematic diagram of the experiments conducted and the association between them. The chapter of the thesis dealing with each section is indicated

Chapter 2
Literature review

Disturbance is a change in conditions which interferes with the normal functioning of a given biological system (van Andel & van den Bergh 1987). According to this definition fire is no longer a disturbance factor in biomes where plant life-forms cope with fire through various adaptive traits. However, since different fire regimes may cause changes in the life-history characteristics of plant species, fire is regarded as a disturbance factor in this study.

To determine a community's response to disturbance it is necessary to examine the life histories of the component species. A plant's life-history consists of all the stages through which it passes from birth to death. In perennial grasses there are two distinct reproductive processes: (1) vegetative reproduction in which new individuals are initiated in the axils of leaves at the base of the parent plant, and (2) sexual reproduction in which individuals are produced from seed. The life-history phase that enables a plant to persist through disturbance is successful seedling establishment.

Habitats with a high risk of disturbance have a large seed pool which permits populations to re-establish themselves rapidly (Baskin & Baskin 1985). For example, high seed production is typical of annual grasses where grazing is a recurring disturbance (Maranon & Bartolome 1989). The seed reserves provide a buffer against fluctuations in the environment. By contrast, in stable environments that rely mainly on vegetative regeneration, seed production is characteristically low (Rabinowitz & Rapp 1980).

The variability in seed production of grassland species may also be related to the successional stage which the species occupies. Annual species occurring in the early stages of succession typically produce many small seeds to reach suitable habitats, while later successional species produce fewer, larger seeds (Solbrig 1979). Age of plants of species which characterise a particular seral stage may also influence seed yield. For example, in heath vegetation, seed output varies with stand age (Mallik, Hobbs & Legg 1984). Since fire is an integral part of montane grasslands in South Africa, different fire regimes may also be expected to affect production of seed by grasses.

Although seed yield ultimately influences the number of seedlings that establish, dispersal can also play a critical role in determining population size. The seed dispersal phase of the life history of a plant provides many advantages including: (1) movement of seed away from the parent plant where predation rates may be highest, and where parent-offspring competition is severe; (2) placement of seeds in suitable germination microsites, the presence of which may be unpredictable in both time and space; and (3) movement of seeds to recently disturbed sites (Collins & Uno 1985).

Many grass seeds bear elaborate appendages, such as hygroscopically active awns, that are believed to be adaptations for wind or animal dispersal (Chippindall 1955). However, Rabinowitz & Rapp (1981) reported that awns are unable to impart movement over horizontal distance. Awns of the grasses, *Aristida vagans* and *Microlaena stipoides* serve to orientate the seed during its fall to promote establishment of seedlings in the immediate vicinity of the parent plant (Peart 1981). In a similar manner the awn of a seed of *T. triandra* acts as a flight, tending to make the seed fall callus downwards so that it easily lodges in the soil (Lock & Milburn 1970). With this poor dispersal mechanism, it is likely that most seeds of *T. triandra* will fall in the immediate neighbourhood of the parent plant. The arrangement of individuals will be of critical importance in determining the interactions and dynamics of the population (Fowler 1984).

Delays in germination enable seeds to be dispersed in space and time, and spread the risk of failure over several periods of potential growth (Harper 1977). Many plants have a seasonal period of dormancy which minimizes germination in periods of low survival probability (Christensen & Muller 1974). The duration of the dormant phase of the life cycle depends on the adaptive response to the seasonal environment. For example, in cold environments an increase in temperature may trigger the end of winter dormancy, while in dry regions the first rains may break dormancy (Harper 1977). In the Natal Drakensberg, a distinct dry season and a harsh winter are likely to initiate dormancy. During the dormant phase seeds may become incorporated into the soil seed bank.

The importance of the soil seed bank in the dynamics of plant populations has been widely recognized (Harper 1977; Silvertown 1987; Rabinowitz 1981; Antlfinger 1989). Seed banks that store viable seed in the soil for several years can buffer a population from extinction and preserve the representation of a plant species within a community (Anderson 1989; Kalisz 1991). Besides enabling plants to survive periodic disturbances, buried seeds enable plants to exploit gaps in closed vegetation (Donelan & Thompson 1980; Archibold 1981; Rabinowitz 1981). Low numbers of viable buried seed may indicate that the vegetation is highly dependent on vegetative propagation, or that other factors, such as predation and decay, deplete the seed bank (Baker 1989). Inadequate sampling techniques may also account for low numbers of seeds recorded in seed banks (Simpson, Leck & Parker 1989).

A common problem encountered in seed bank studies is standardizing techniques that can account for the great spatial and temporal heterogeneity found in seed banks (Thompson & Grime 1979; Schenkeveld & Verkaar 1984; Coffin & Lauenroth 1989). The high degree of spatial aggregation of seeds in the soil has prompted various studies on sampling adequacy (Froud-Williams, Chancellor & Drennan 1984; Forcella 1984;

Benoit, Kenkel & Cavers 1989). The consensus is that a large number of small sampling units are more appropriate than a small number of large sampling units (Kropac 1966). Ultimately however, in most seed bank studies, the sampling cost, and the available resources (time, space and labour) dictate sample size (Benoit, Kenkel & Cavers 1989).

A common sampling technique used to quantify the size of the seed bank is the emergence technique. The size of the seed bank is determined indirectly by counting numbers of seedlings emerging from incubated moistened soil samples. The main disadvantage of this technique is that it reveals only a portion of the germinable seeds present (van Tooren 1988). Since many plant species produce seeds that remain dormant in the soil for several years (Kalisz 1991), an alternative approach is to directly count the numbers of seeds using the flotation technique (Kropac 1966). However, the reliability of separating seeds from the soil by flotation is affected by variable seed densities.

One of the difficulties in comparing seed bank studies is that data have been collected and presented in many forms (Simpson, Leck & Parker 1989). In some instances, the number of seeds per unit volume of soil is recorded (Abrams 1988), while in others the number of seeds per square meter is recorded (Pavone & Reader 1982). Another difficulty is the variability in the size of the seed banks. Even within grasslands the seed bank is variable. For example, Rabinowitz (1981) recorded 6 000 seeds m^{-2} in prairies, while Williams (1984) recorded 12 000 seeds m^{-2} in long-term pasture and Maranon & Bartolome (1989) recorded 15 980 to 40 730 seeds m^{-2} in open annual grassland.

There is often little correlation between seed populations and existing grassland vegetation at a site (Major & Pyott 1966; Thompson & Grime 1979). Graham & Hutchings (1988) showed that few grass seeds retain their viability for long periods resulting in their poor representation in the seed bank. One would expect species in grassland with a high frequency of disturbance to have a persistent seed bank. However, in disturbed savanna grassland in South Africa, grazing reduced the seed output of *T. triandra* so that its density in the seed bank was significantly lower than its abundance in the vegetation (O'Connor 1991). Disturbances such as drought reduce the seed supply of dominant tallgrasses in prairies so that the seed bank does not reflect the above-ground vegetation (Weaver & Mueller 1942). Williams (1984) attributes other factors to differences in species composition between the vegetation and seed bank; the dense canopy and absence of bare areas in grassland preventing seeds from finding a safe site, losses of seeds in the seed bank through germination, and losses by seed predation.

Seed predation is potentially a major ecological and evolutionary force affecting seed populations (Janzen 1971; Schupp 1988). Predation has been shown to destroy almost the whole seed output of many species. For example, in heathland 95% of seeds were lost to predators (Anderson 1989), in savanna grasslands Capon & O'Connor (1990) recorded up to 87% predation, while Bond (1984) reported 81.7 % predation in *Protea* species in fynbos. In particular, seeds with long dormancy periods are highly susceptible to predation (Hacker 1989).

However, large seed losses by predation do not necessarily have a significant impact on populations (Harper 1977; Collins & Uno 1985; Janzen 1971; Anderson 1989). Recruitment in stable populations of long-lived perennials is limited by the availability of safe sites rather than by seed supply (Miles 1972; Putwain, Machin & Harper 1968; Peart 1989). Therefore, even if predation is high, its effect on seedling establishment is negligible if safe sites for establishment are scarce.

Competition between individuals for safe sites (Putwain, Machin & Harper 1968; Burdon, Marshall & Brown 1983; Gross 1980; Peart 1989) may also account for the lack of relationship between the vegetation and the seed bank. In undisturbed natural communities, survivors have successfully competed over many years with individuals for the available resources and may no longer be represented in the seed bank. Undisturbed communities therefore create few opportunities for new competitors. By contrast, disturbance generally provides a major opportunity for seedling regeneration (Antos & Zobel 1986; Goldberg & Gross 1988). Habitat disturbance reduces the number of competitors (Harper 1977), increases light availability (Grime 1979; De Hullu & Gimingham 1984; Goldberg 1987) and reduces competition for nutrients (Sharitz & McCormick 1973).

In many tropical and subtropical grassland ecosystems fire is the major disturbance factor (Lock & Milburn 1970). For example, fire, with drought and grazing are typical disturbance factors in most North American prairies (Abrams 1988) and Australian grasslands (Moore 1970). Within South African grassland ecosystems, which are subjected to frequent burning, fire is considered to be an important selective agent in the evolution of life history traits of the biota (Phillips 1930; West 1971). Seedling establishment is promoted through the removal of the canopy and the subsequent increase in light. After fire, the blackened and unshaded soil is warmer in comparison to unburnt areas and favours seed germination (Daubenmire 1968; Lock & Milburn 1970).

Disturbed areas are, however, not always suitable for plant growth (Bayer 1955; Graham & Hutchings 1988; Carson & Pickett 1990). Seedlings which establish in bared areas or gaps are at least temporarily exposed to extremes in the microclimate (Williams & Ashton 1987) and to higher levels of predation (Verkaar, Schenkeveld & Huurnik 1986;

Sork 1987; Schupp 1988). Some seedlings require shelter from direct sunlight (Thomas & Wein 1985), while absence of litter in disturbed areas may increase evaporation from the soil surface and reduce seedling survival (Chambers, MacMahon & Brown 1990). By contrast, in established areas, vegetation cover can affect seed germination by reducing temperature and humidity fluctuations and producing a favourable microclimate for germination (Davis, Borchert & Odion 1989).

The success of revegetation of disturbed areas depends on the severity of disturbance (Archibold 1980). For example, Abrams (1988) recorded lower seed density in prairie disturbed regularly by fire than in undisturbed prairie. In severely disturbed forests affected by volcanic ash on Mount. St. Helens, Antos & Zobel (1986) recorded no seedling establishment of herbs or shrubs in the first year and only 35 m^{-2} by the fourth year. In the montane grasslands of South Africa which are subjected to various intensities of disturbance (i.e. different frequencies and season of burning), the success of seedling establishment is unknown (Everson CS 1985).

Many plants in fire-prone environments exhibit seasonal dormancy (Daubenmire 1968). Perennial grasses, particularly those in the summer rainfall areas of South Africa, become dormant during the winter and most of the aerial parts of the plant die back to ground level (Frost 1984). For approximately six months of the year these grasslands are low in available nutrients and not suitable for grazing until the following growing season. For grass species such as *T. triandra*, the regular removal of this dead material is essential to its persistence, since *T. triandra* cannot produce new tillers from heavily shaded basal nodes (Everson CS, Everson TM & Tainton 1988). Burning to remove the dead material has therefore been a traditional tool for improving forage quality and palatability in South African grasslands (Thompson 1936; Mentis & Tainton 1984).

Historically, autecological studies of grasslands in southern Africa have largely concentrated on the vegetative growth of *T. triandra* to increase production (Tainton & Booysen 1965; Dankwerts, Aucamp & Du Toit 1984). In particular, research has focused on the effect of fire on tiller dynamics (Tainton, Groves & Nash 1977; Everson CS, Everson TM & Tainton 1985). In spite of the importance of *T. triandra* in agriculture, there has been little research on its seedling dynamics. This study attempts to expand the knowledge of grass seedling dynamics in South African mountain ecosystems.

Chapter 3
Study area

3.1 Locality

The Drakensberg Mountains in Natal form a continuous crescent-shaped escarpment situated between 160 and 240 km inland of the east coast of South Africa varying in altitude between 1 380 m and 3 350 m a.m.s.l. The escarpment creates a natural boundary between the province of Natal, South Africa, and Lesotho (between latitudes 28° 30′S and 30° 30′S, and longitudes 28° 30′E and 29° 30′E). Cathedral Peak Forestry Research Station (Fig. 3.1), where this research was carried out, lies in the northern part of the crescent (29° 00′S, 29° 15′E).

3.2 Topography

The Drakensberg escarpment owes its presence to the continental uplifting that took place during the late Pliocene. The subsequent headward erosion of numerous major eastward-flowing drainage channels resulted in the formation of the basaltic lava cliffs of the main range, and a broken plateau lying below (1 800-2 500 m). This plateau, known locally as the Little Berg, is dissected by deep ravines and swift flowing streams and ends abruptly in conspicuous Clarens sandstone cliffs. The spurs are capped with basalt and project almost at right angles to the escarpment (Patridge & Maud 1987). At the heads of these spurs lie the catchments that feed the main rivers.

3.3 Geology and soil

The geology of the Drakensberg is simple because the rocks lie almost horizontally (Patridge & Maud 1987). The Drakensberg forms part of the Karoo System, which comprises several sedimentary series overlaid by a basaltic cap. Only the two youngest

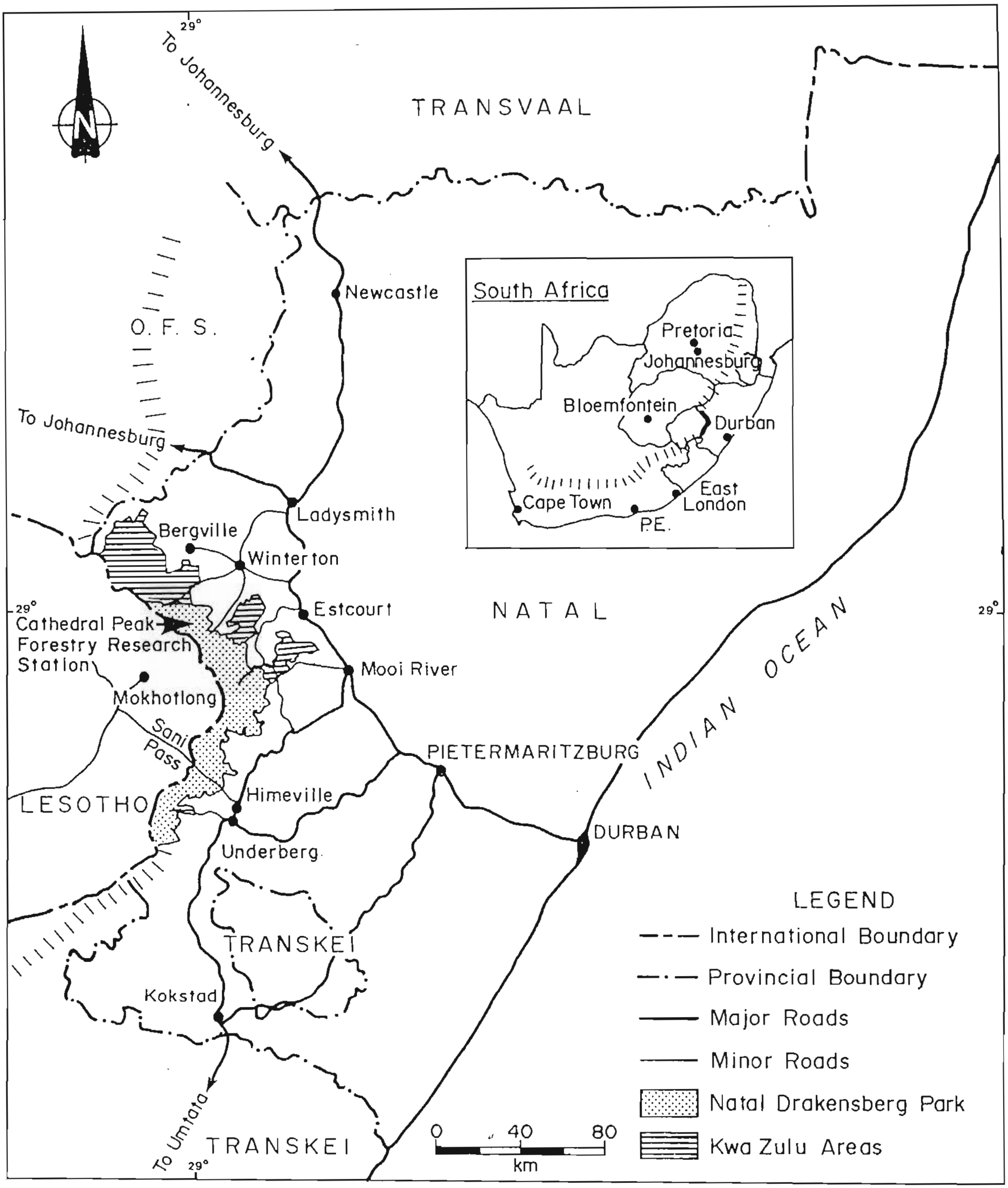


Figure 3.1 The locality of the Cathedral Peak Forestry Research Station in the Natal Drakensberg Park.

series are represented in the Cathedral Peak area, namely the Beaufort Series and the Stormberg Series (Patridge & Maud 1987). These consist of Molteno beds, Red beds, Clarens sandstone and Drakensberg lavas (Patridge & Maud 1987). This system coincides with the late Triassic period and is between 180 and 200 million years old.

Soils on the Little Berg were classified by van der Merwe (1941) as Lateritic Red and Yellow Earths. They are of residual and colluvial origin and derived from basalt. Characteristically they are acidic, highly leached and structureless. Their low fertility is a result of the high annual precipitation and long exposure to weathering. The topsoils are of friable consistence and well suited for rapid infiltration and storage of water. The high water holding capacity of the soils of the Little Berg may be important in seedling establishment because it allows seedlings to survive dry periods (Granger 1976). By contrast, the subsoils have a very high clay content and poor infiltration. If, for any reason, the soil is bared, the A horizon is rapidly removed by wind or water erosion. Removal of the A horizon results in the development of permanent erosion scars. Revegetation does not take place on bared B horizons naturally, unless some A horizon material is transported by colluvial action (Bainbridge 1979). The organic content of the top soil is high (6% to 10%), considering the frequency of fire in the region (Everson CS 1985). This high organic matter content, in association with the presence of colloidal iron and aluminium, increases the water holding capacity of the soil.

3.4 Climate

The Cathedral Peak area lies in the summer rainfall zone of South Africa and has wet, humid summers and dry, cold winters. The climatic data were obtained from a meteorological station at 1 817 m on the Little Berg. Although total annual rainfall is important in the growth of vegetation, the distribution of rainfall, and especially the length of the dry season are limiting factors in this region. The conditions are particularly dry between April and October (Fig. 3.2).

Air temperatures are never excessively high at Cathedral Peak. The highest temperatures (<35°C) are usually recorded in November before the rainy season properly sets in (Nänni 1969). The mean maximum temperature for the study period 1987-1991 ranged between 19.7°C (June 1991) and 30.8°C (November 1990). Monthly means of minimum temperature ranged from 3.0°C in July 1987, the coldest month, to 12.3°C in February, the hottest month. The mean annual temperature was 13.8°C (period of record 1949 to 1991). Despite longer average daylight hours in summer (14 hours) than in winter (11 hours), the total number of daily sunshine hours in summer is 2.5-3.5 hours less than in winter. This is due to the characteristically cloudy and rainy conditions that reduce sunshine during the summer months (Granger 1976).

Winter frosts are an important factor in the Drakensberg since they kill off the above-ground parts of the grasses. This causes the herbage to dry out and increases the susceptibility of the vegetation to fires (Everson TM, Everson CS, Dicks & Poulter 1988). Frost occurs in the Drakensberg from late April to early September, but is almost a daily occurrence in winter (June and July). The average annual number of frost nights (minimum temperature <0°C) for the period 1987-1991 was 25. Frost is an important factor preventing revegetation of bare ground. One of the most conspicuous features of a frosty night in the Drakensberg is the formation of needle-ice (Plate 5). The heaving effect of ice crystals in frozen soils lifts up the soil particles on ice pedicles (Granger 1976). The powdery soil that remains after thawing is easily eroded by both wind and water erosion. Frost readily erodes exposed soils, roadsides and paths.

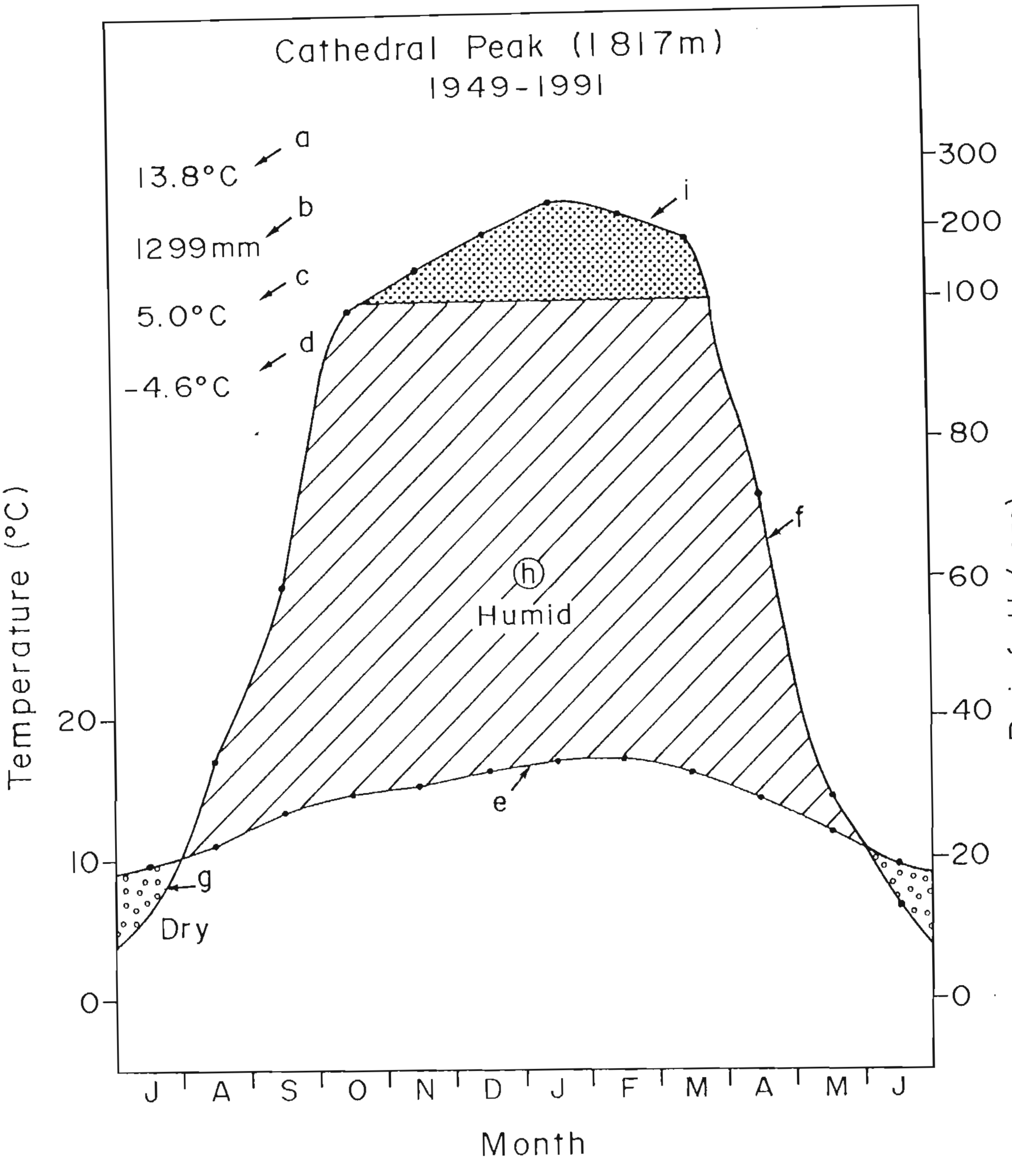


Figure 3.2 A climatic diagram for Cathedral Peak (1949-1991). The symbols of the diagram have the following meanings: a, mean annual temperature; b, mean annual rainfall; c, mean daily minimum temperature of coldest month; d, lowest absolute minimum temperature; e, mean monthly temperature; f, mean monthly rainfall; g, drought period; h, humid period; i, mean monthly rainfall exceeding 100 mm with scale reduced to a tenth.

Rainfall is the most important feature contributing to natural soil erosion. The precipitous walls of the escarpment and its adjoining slopes, together with the high mean annual rainfall (1 299 mm for the period 1949-1991) makes the area susceptible to accelerated soil erosion. Approximately 85% of the rain falls during the summer months October to March. During high intensity summer thunderstorms, 100 mm of rain may fall within an hour (King 1982). Loss of the soil mantle and underlying weathered material results in increased streamflow during summer.

Snow falls mainly in July although it has been recorded in every month of the year at Cathedral Peak (Granger 1976). The average number of snow falls per annum on the Little Berg plateau during the study period was four. Falls are seldom heavy and melt within a few days.

Wind is an important climatic variable in the Drakensberg because it is prevalent during the dry season when fire hazard is at a maximum (Everson TM, van Wilgen & Everson CS 1988). Persistent winds can also restrict growth of plants and cause soil erosion (Watts 1971). Throughout the year the winds blow from the west to northwest, responding to high pressure circulation over the Lesotho plateau. Below the escarpment topographically-induced wind systems and gradient winds of the Indian Ocean prevail. Föhne or Berg winds are a characteristic feature of the Drakensberg (Killick 1963), occurring in late winter and early spring (August and September). These winds, which are hot and dry, have been recorded at Cathedral Peak at speeds of up to 100 km h^{-1}. Extreme fire hazard conditions are strongly associated with Berg winds.

3.5 Role of fire

Fire is a natural ecological factor in the grasslands of the Drakensberg. After the first winter frosts in May, the aboveground herbage dries out, increasing the flammability of the fuel (Everson TM, van Wilgen & Everson CS 1988). The burning policy of the Drakensberg is based on comprehensive research by Nänni (1979), Edwards (1984) and Everson CS (1985). Climatic factors are the main natural constraints to managers of large areas in the Drakensberg. The ideal burning period for soil protection is August and September, as this will result in the shortest period of exposure of the soil surface that is unprotected by vegetation. However, this is the time of highest fire danger as hot dry Berg winds peak in frequency and intensity during August and September. One option is to burn early in the season so that the grasslands green up by October, forming a protective cover over the soil before the heavy summer rains. However, burning at this time exposes the soil to wind erosion, as there is little or no cover during the winter months. In contrast, grasslands burnt in October (spring) only recover by the end of November, exposing the soils to the storms of October and November. Therefore, differences in season of burn result in exposure to erosive forces at different times of the year. If the grassland is burnt once growth is initiated in summer (November-December), subsequent growth is markedly reduced. The optimum time for burning is mid-August, when the effects of erosion are minimized. Taking these constraints into account, Everson CS & Tainton (1984) recommend that the grassland catchments are burnt biennially, with the burning season being rotated between three periods:

(1) May (early winter),

(2) June-July (winter) and

(3) August-mid-September (early spring).

3.6 Vegetation

The vegetation of the Drakensberg has been extensively studied and described in detail (West 1951; Killick 1963; Edwards 1967; Hilliard & Burtt 1987). Grassland covers the greater part of the Drakensberg. Shrub and tree species, such as *Protea*, may invade the grassland, and closed shrubland is often found along the streams and on the cliffs and rock outcrops. Forest patches and tree clumps are confined to gullies, rock-falls and other sheltered places below 1 950 m (Hilliard & Burtt 1987).

The climax plant communities of the Drakensberg are associated with three distinct altitudinal zones; the river valleys (1 250-1 800 m), the Little Berg (1 800-2 500 m) and the summit plateau (2 500-3 350 m) (Fig. 3.3). The corresponding vegetation belts are:

(1) **The Montane Belt:** *Podocarpus latifolius* forest (1 250-1 800 m). The montane belt extends from the valley floors to the lowermost basalt cliffs at the edge of the Little Berg. *Themeda triandra* grassland occupies the greater part of this belt. The main woody communities are *Protea* savanna and *Leucosidea-Buddleia* scrub occurring on valley slopes, and *Podocarpus latifolius* forest which is confined to sheltered gorges.

(2) **The Subalpine Belt:** *Passerina - Erica - Widdringtonia* fynbos (1 800-2 500 m). Ericoid shrubs, that are mostly evergreen with small leaves, are characteristic of fynbos. This belt extends from the edge of the Little Berg to just below the summit of the Drakensberg. Besides the grassland and shrubland communities present in the montane belt, temperate grasslands occur on south-facing aspects.

(3) **The Alpine Belt:** *Erica-Helichrysum* heath (2 500-3 350 m). This belt occupies a narrow strip at the edge of the Drakensberg escarpment and consists of *Festuca-Merxmuellera-Pentaschistis* grassland interspersed with low woody species of *Erica* and *Helichrysum*.

The study site, situated at 1 890 m, falls into the subalpine belt. Grassland, which was classified by Acocks (1979) as Highland Sourveld, is the dominant vegetation type.

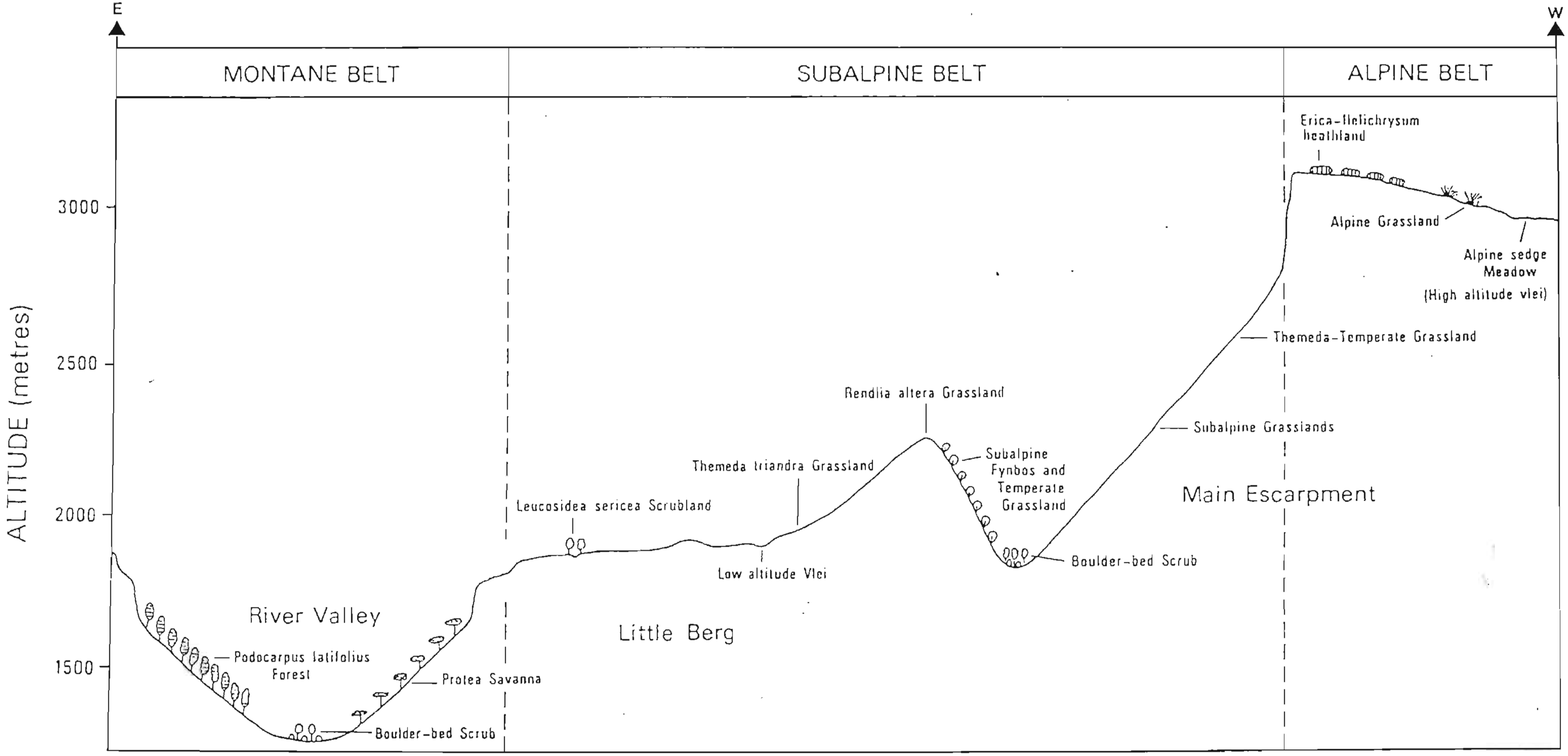


Figure 3.3 Profile through the Drakensberg area showing the vegetation belts and their dominant vegetation communities (from Killick 1963).

This comprises a short dense grassland (0.5-1.0 m) dominated by *Themeda triandra, Tristachya leucothrix* and *Alloteropsis semialata*. Nearly all the Drakensberg grasses are tufted in habit and when closely packed give the appearance of a continuous cover, but after burning, the bare ground between tufts is clearly visible (Hilliard & Burtt 1987). It is these bare patches that may be important habitats for seedling establishment.

Associated with the grasses are a variety of non-woody herbs and sedges. Most of these plants have underground storage organs that permit perennation through the cold dry winters and give protection against fire (Hilliard & Burtt 1987).

3.7 Study site

The Cathedral Peak Research Station is the main centre for hydrological research in the summer rainfall region of southern Africa. It was established in 1935 to examine the influences of various management practices on the vegetation and water yield of the local mountain catchments. The fifteen research catchments (numbered I to XV) are situated at the head of three isolated Little Berg spurs (Nänni 1956). Each of these catchments receives a specific treatment (eg. afforestation, protection from fire, etc.). The majority of catchments outside the research area are burnt biennially in spring. Most of the experiments in the present study were carried out on Brotherton Spur, a flat ridge situated between two catchments at an altitude of 1 890 m.

A burning trial was established on Brotherton Spur in 1980 to measure and predict changes in the vegetation that occur with different burning treatments (Plate 6). The trial was designed to examine the long-term effects of frequencies and seasons of burning on species composition and fire behaviour (Granger 1979). Twenty-one treatments are represented in the trial. The experiment is a randomized block design comprising 12 treatments replicated three times and nine demonstration treatments.

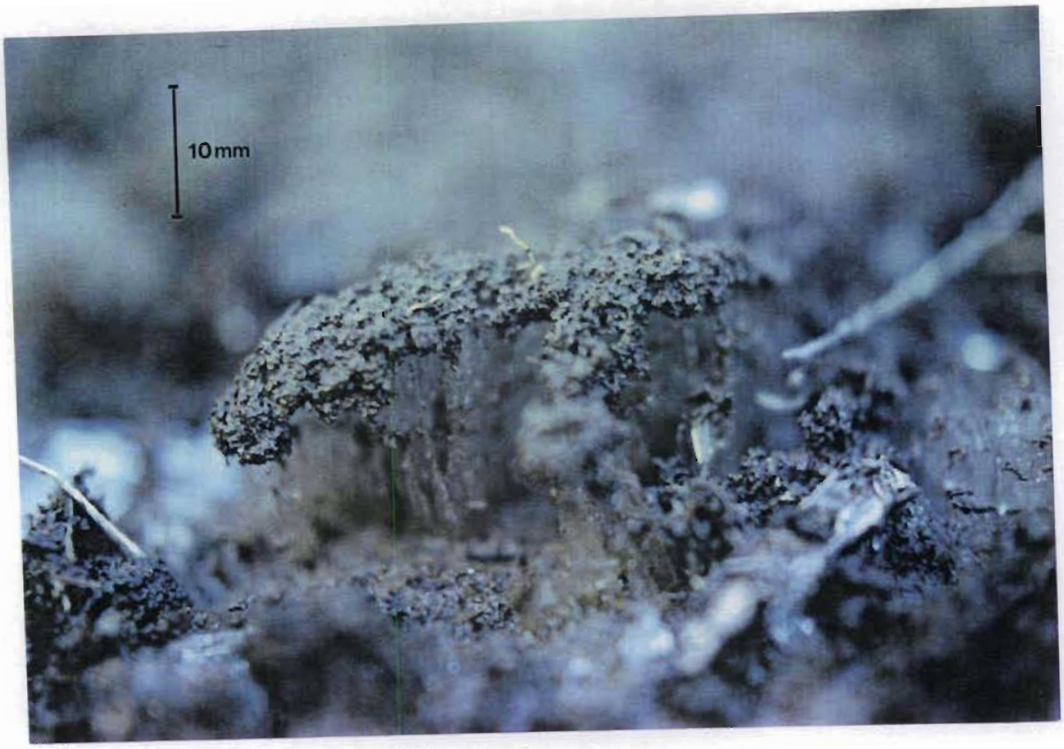


Plate 5. Needle ice formation on the Little Berg (1 800 m)

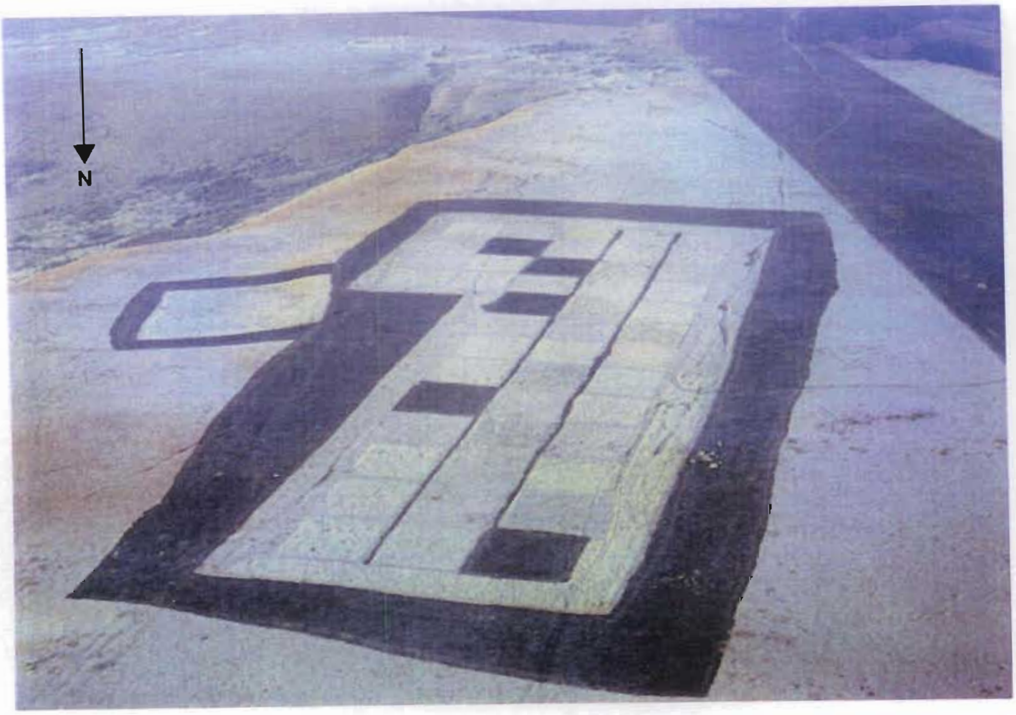


Plate 6. The Brotherton burning trial on the Little Berg. The photograph taken in winter (July 1993) shows the recently burnt firebreaks (represented by black strips) and the annual winter burns (represented by black blocks).

Each plot measures 25 X 25 metres with a 4-m wide space between plots for fire protection. The present study was conducted either on selected treatments within this trial, or in the surrounding grassland that has a thirty-year history of biennial spring burning. The burning treatments selected were an annual winter burn to represent the firebreaks which are burnt every year, a biennial spring burn which is the present burning prescription for the area, a biennial summer burn which is practised by rural farmers but has been shown to be detrimental to the vegetative re-establishment of grasses (Everson CS, Everson TM & Tainton 1985), and a five-year burn to encourage the growth of woody species.

The present study was initiated six years after commencement of the burning trial. It coincided with the sixth treatment of the one-year burn, the third treatment of both the two-year burns and the second year after one treatment of the five-year burn.

3.8 Summary

The Drakensberg mountain range forms the highest water-yielding catchments in the country (Schulze 1980). The area is characterized by steep slopes, highly dissected terrain and a severe climate consisting of periodic strong winds, high intensity rainfall, frost and snow. These features coupled with the high mean annual rainfall and fire, make the area susceptible to soil erosion. Once areas are bared of vegetation, natural re-establishment is exceptionally slow. Little is known about the ability of grass plants to survive this environment through seedling establishment. During the dry period water stress is likely to be high and therefore unfavourable for seedling establishment. Fire is frequent during the dry season, but also occurs in the rainy season. Variation in local microclimate conditions arising from different burning regimes, may play an important role in the survival of grass seedlings.

Chapter 4
The seed biology of *Themeda triandra* in montane grasslands

4.1 Natural history of *Themeda triandra*

The most dominant grass species of the study area, with respect to basal cover, is *T. triandra* (Killick 1963). *Themeda triandra* is a palatable, perennial grass associated with natural grassland in optimum grazing condition. With good management the dominance of *T. triandra* is maintained, and the grassland can be regarded as being in a steady or stable state. To achieve this, a regular burning regime in the dormant period is required (Tainton & Mentis 1984). Fire also appears to favour sexual reproduction in *T. triandra* since it flowers prolifically in the second year after burning, but declines as the interval between burning increases (personal observation). However, Everson CS, Everson TM & Tainton (1985) showed that most of the tillers of *T. triandra* remain vegetative until death. While the effects of frequency and season of burn on vegetative growth of *T. triandra* have been studied in detail (Everson CS, Everson TM & Tainton 1985), little is known about their effect on grass seedling dynamics.

Knowledge of grass seedling dynamics is becoming increasingly important with the growing emphasis on land management and diminishing native grass resources. In Australia, where <1% of natural grassland remains, attempts are being made to reintroduce native species, such as *T. triandra*, since they are more resistant to drought than introduced species, and have the ability to grow on soils of low fertility (Hagon, Groves & Chan 1975). Besides managing indigenous grass populations for genetic material in grassland restoration programmes, emphasis is on maximising germination and seedling establishment of *T. triandra* to meet an anticipated commercial market for revegetation purposes (Sindel & Groves 1990). In South Africa, the restoration of native species to degraded grasslands is highly desirable to increase productivity for subsistence and commercial farming activities.

The potential of re-establishment of *T. triandra* from seed will largely depend on its seed biology characteristics, particularly seed production, dispersal and germination. The objectives of this part of the study were:

(1) to determine the effect of different burning regimes on seed production of *T. triandra*, to test the hypothesis that, in the fire-prone environment of the Natal Drakensberg, regular burning increases seed production;

(2) to determine the dispersal attributes of seed of *T. triandra*, to test the hypothesis that *T. triandra* has a low probability of colonizing disturbed sites because it has a poor dispersal ability; and

(3) to determine the germination characteristics of *T. triandra*, to test the hypothesis that *T. triandra* seeds have a dormancy mechanism to survive the harsh winter season.

The experiments designed to test these hypotheses were intended to indicate aspects of the seed biology of *T. triandra* that can be manipulated for grassland restoration programmes.

4.2 Methods

4.2.1 Seed production

In the Drakensberg, *T. triandra* flowers from November and sets seed in December. The seed matures from the apex of the inflorescence downwards, and is dispersed over a short period of a few days. Three 1 m^2 plots were marked out in each of the burning treatments (annual winter, biennial summer, biennial spring and five-year burn). In December inflorescences bearing mature seeds were collected from all sites. Filled and empty (sterile) seeds were hand sorted and the number of filled seeds counted. Data were analyzed by one-way ANOVA and differences between means were determined by a Tukey Multiple Range test (Zar 1984).

4.2.2 Dispersal

Before seed dispersal, six tufts of *T. triandra*, 200 mm in diameter, were located and isolated by clearing all surrounding plants within a radius of approximately 2 m^2. All the vegetation within a 4-m radius of the cleared area was clipped to remove any reproductive culms. The total cleared radius of six metres ensured that seeds dispersed came from the selected tuft and not the surrounding vegetation. The net effect of these removals could increase the efficiency of wind as a dispersal agent. Dispersal traps were therefore placed at four radiating compass points around each isolated plant to detect whether the pattern of seed dispersal was associated with the direction of the prevailing winds.

Seed dispersal was measured in the field in 1989 and 1990 using sticky traps. The sticky trap used in 1989 was not successful in capturing seeds because the adhesive, a gum substance (Foster-Heunneke & Graham 1987), lost its stickiness after two days in the field. Additional problems are mentioned here to make other researchers aware of the potential disadvantages of this technique. The gum was extremely messy and difficult to apply in the field, especially if conditions were windy. Alternatively, prior preparation was not possible because the boards stuck to each other during transportation up the mountain pass to the study site.

The study was repeated in 1990 using sticky "Fascal" vinyl sheets (Haddons Pty (Ltd), Pietermaritzburg) instead of the gum. The vinyl sheets are similar to stick-on labels, and comprise an adhesive sheet overlaid with a plastic material that can be peeled off when required. This enabled the traps to be prepared in the laboratory before transportation to the study site. Traps were prepared by pinning the vinyl sheeting on 96 pieces of hardboard (250 X 200 mm). Sixteen traps, four at each of the four radiating compass points, were placed on the soil surface around each plant. The traps were exposed for two weeks and examined every second day for seeds.

Dispersal was also measured in the laboratory to examine the effect of a constant wind on distance of dispersal. Six 200 mm diameter potted plants of *T. triandra* were used. The plants, bearing ripe seeds, were positioned at the head of sticky boards placed next to each other. The boards formed a rectangle of 800 mm by 1.75 m. Pot heights were adjusted to 600 mm to correspond to the natural plant height in the field. A fan, providing a constant wind of 4 m s^{-1}, simulated maximum wind speed likely to occur at the height of the grass sward at the time of seed set. The number of seeds and distance of dispersal were recorded.

4.2.3 Germination

Freshly matured seeds of *T. triandra* were harvested by hand from plants growing at 1 800 m. Since seeds of *T. triandra* have a dormancy period of up to 12 months (Martin 1975), the seeds were stored in paper packets at room temperature (23-27°C) for 12 months. A series of germination tests was carried out on this seed to examine the effects of temperature, light and burial on germination. Germination tests were carried out in growth chambers at a 12-h photoperiod or in continuous darkness. Constant temperatures were 5, 25, 35, 40°C, and alternating temperature regimes were 5/16, 5/30°C, respectively. These thermoperiods were chosen to represent the fluctuations that are likely to occur under field conditions, and high temperatures that have been shown to stimulate germination of coastal plants of *T. triandra* (KM Adams, personal communication).

A second series of tests was carried out on seed that was buried approximately 20 mm deep in gauze bags for one to five months. Seeds were then incubated at 25°C, the average maximum summer temperature recorded in the study period.

In all tests seeds were incubated in 150 mm plastic Petri dishes on filter paper saturated with distilled water and kept moistened throughout the experiment. Fungicide powder was applied to the seeds to prevent fungal growth inhibiting germination. Germination (i.e. emergence of the radical) was recorded daily and germinated seeds were removed. Nine replicates of 50 seeds were used for each treatment and the results are presented as the total percentage of seeds that had germinated. Final germination percentages were determined after 21 days when no further germination occurred. Differences between treatments were examined using one-way ANOVA, and a Tukey Multiple Range test was used to compare the mean percentage germination per treatment (Zar 1984).

4.3 Results

4.3.1 Seed production

One-way ANOVA indicated no significant difference in total seed production between the three years of the study (Table 4.1). Burning frequency, however, had a significant effect ($P<0.05$) on seed production with the number of seeds increasing with longer burning rotations, irrespective of season of burn. For example, seed production was lowest in the annual winter burn plots where only 2 to 38 seeds m^{-2} $annum^{-1}$ were produced from 1987 to 1989. Seed production was higher in both the biennially burnt plots with a mean of 153 seeds m^{-2} $annum^{-1}$ in the biennial summer burn (1987-1989), and 267 seeds m^{-2} $annum^{-1}$ in the biennial spring burn (1987-1989). Highest seed production was recorded in the five-year spring burn where mean annual seed production for the study period was 485 seeds m^{-2}. In this treatment seed production was variable with the number of seeds approximately doubling from 1987 to 1988, but then decreasing in the fourth year of no burning. In the biennial summer burn seed production progressively decreased from 1987 to 1989.

Table 4.1 Mean annual seed production of *Themeda triandra* in different burning treatments. (b) = burn.

Year	Treatment burn	Nº of seeds m^{-2}	S.E.
1987	Annual winter (b)	2	0.8
	Biennial summer	250	113.5
	Biennial spring	268	44.8
	Five-year	411	67.9
1988	Annual winter (b)	22	4.6
	Biennial summer (b)	157	41.5
	Biennial spring (b)	259	53.4
	Five-year	757	165.4
1989	Annual winter (b)	38	17.7
	Biennial summer	52	36.5
	Biennial spring	274	29.0
	Five-year	287	94.8

4.3.2 Dispersal

The number of seeds captured by the traps set in the field declined with increasing distance from the parent plant. Most seeds (94.2%) fell within a 0.5 m radius of the parent plant. There was no evidence of a wind-related pattern of dispersal. In the laboratory experiment, all seeds dispersed from the plants were captured on the sticky boards. Even under the extremely windy conditions simulated in the laboratory (4 m s^{-1}), most seeds (83.6%) fell within a one meter radius of the plant, while no seeds fell beyond 1.75 m (Table 4.2).

4.3.3 Germination

Germination was low in all temperature and light treatments ranging from 0 to 36.9% (Table 4.3). While treatment had a significant effect on germination ($F = 21.6, P < 0.001$), no single treatment was significantly higher than all the others. The three most favourable treatments were: an alternating dark/light regime at 35°C (36.9%), burial for five months (29.8%) and continuous dark at 25°C (28.0%). In the burial treatments the percentage germination increased from 14.2% in seeds buried for one month to 29.8% in seeds buried for five months. The treatments that had significantly lower germination (0.0-2.2%) were ambient light, continuous light at 40°C and continuous dark at 5°C.

4.4 Discussion

The number of seeds that an individual produces relates to the stage in the succession in which the species occurs. Early successional species (annuals) produce many seeds, increasing their chances of reaching suitable microsites (Stebbins 1970, Solbrig 1979). Species in successionally advanced or stable communities have a low reproductive effort and produce fewer and larger seeds (Roos & Quinn 1977). For example, in savanna grassland in South Africa O'Connor (1991) showed that, the reproductive output of *Aristida bipartita*, an early successional species, was >10 000 seeds m^{-2}. By comparison, that of *T. triandra*, a later successional species, was <400 seeds m^{-2}. In the montane grasslands of this study, annual seed production was low (2-757 m^{-2}) and was consistent with its successional status as a fire-climax species.

Seed production of *T. triandra* differed significantly between treatments. These differences are related to the morphological adaptations of *T. triandra* to fire. This species survives fire by producing an underground rhizome close to the soil surface. The rhizome bears tiller initials, some of which may develop into tillers in the absence of defoliation (Tainton & Mentis 1984). However, removal of a portion of the aerial growth invariably stimulates tiller development so that the plant recovers rapidly after such treatment (Booysen, Tainton & Scott 1963). Resistance to fire is also maintained by the development of the meristematic apex close to the soil surface during the vegetative stages of tiller development. However, when the tiller reaches reproductive

Table 4.2 Dispersal distance of *Themeda triandra* seeds under natural and laboratory (wind speed 4 m s^{-1}) conditions. Values in brackets represent the standard error of the mean.

	Natural			Laboratory		
Distance (m)	**Mean # of seeds**		**Total (%)**	**Mean # of seeds**		**Total (%)**
0.00 - 0.25	6.7	(0.19)	58.0	4.3	(0.54)	10.2
0.25 - 0.50	4.2	(0.95)	36.2	15.3	(1.91)	36.2
0.50 - 0.75	0.5	(0.22)	4.4	9.7	(1.19)	23.0
0.75 - 1.00	0.2	(0.16)	1.4	6.0	(0.47)	14.2
1.00 - 1.25	0.0	(0.0)	0.0	4.3	(0.54)	10.2
1.25 - 1.50	0.0	(0.0)	0.0	2.3	(0.27)	5.5
1.50 - 1.75	0.0	(0.0)	0.0	0.3	(0.27)	0.7

Table 4.3 Percentage germination of *Themeda triandra* seeds in different burning treatments (values are the means of 9 replicates of 50 seeds).

Treatment	Mean % germination	S.E.
Ambient dark	10.2	2.0
Ambient light	00.0	0.0
Dark 5°C	00.0	0.0
Dark 25°C	28.0	2.6
Light 40°C	02.2	0.7
5°C/16°C dark/light	04.9	1.3
5°C/30°C dark/light	22.2	3.3
35°C/35°C dark/light	36.9	4.0
Buried 1 month	14.2	3.5
Buried 2 months	15.6	1.9
Buried 3 months	16.0	2.3
Buried 4 months	19.5	3.8
Buried 5 months	29.8	2.8

maturity, the meristem is elevated above the soil surface and is extremely vulnerable to any form of defoliation.

The low number of seeds recorded in the annual winter burn shows that burning every year in winter significantly reduced seed production. *Themeda triandra* reaches reproductive maturity in the second year of life (Everson CS, Everson TM & Tainton 1985). Burning every year therefore prevents vegetative tillers from achieving reproductive maturity. In the biennial summer (January) and spring (September) burns, the grassland is only burnt every two years, enabling the development of reproductive tillers. The differences in seed production between these two treatments suggests that besides frequency of fire, season of burn greatly affects seed production.

The low numbers of seeds in the biennial summer burn is related to the detrimental effect of burning during the growing season. The apical buds of *T. triandra* are elevated early in the season and remain sensitive to damage until the buds develop into mature inflorescences (Tainton & Booysen 1963). Grass plants fail to flower and produce seed if the sward is burnt during stem elongation (Tainton 1981). Burning in summer will therefore destroy the buds and reduce flowering. In addition, summer burning can result in heat injury to the meristematic region of *T. triandra*, resulting in the loss of whole tufts (Everson CS, Everson TM & Tainton 1985).

Spring burning is applied before the initiation of tiller growth, while the apical buds are situated close to the ground. Since the buds are not damaged by the fire, they can grow to maturity to produce inflorescences in their second year. One would therefore expect low seed production in the first season immediately after the burn before the reproductive tillers mature. However, seed production varied little between years in the biennial spring burn, implying that some reproductive tillers do survive the fire and can produce seeds even in the first season after the burn.

The initial high seed production recorded in the five-year burn corresponds to the second and third year of the treatment in which the grassland is two and three years old. Large numbers of seeds in the third year after a spring burn are attributed to many tillers achieving reproductive maturity without fire. However, with continued protection from fire, the accumulation of litter at the base of the plants decreases the light penetration at the soil surface. Such excessive base shading promotes tiller development from elevated nodes (Tainton 1981). As this pattern of aerial tillering is at the expense of basal tillering, shading eventually leads to low tiller densities. The subsequent decrease in seed production in the fourth year of the treatment (1989) is attributed to shading and death of tillers and subsequent loss in reproductive potential.

Seed output is also determined by the relative abundance of a species (Mallik, Hobbs & Legg 1984). In the grasslands of the Natal Drakensberg, the relative species composition is controlled by fire. Burning out-of-season (summer) destroys whole tufts of *T. triandra* (Everson CS & Tainton 1984). The low seed production in the summer burn treatment is therefore directly related to low abundance of *T. triandra*. By contrast, the high relative frequency of *T. triandra* in the biennial spring burn treatment (Chapter 6) contributes to the high number of seeds produced by this species. Since this is the prescribed treatment for the conserved areas of the Natal Drakensberg, abundance of seed in these areas is therefore not considered a limiting factor for seedling establishment.

However, in disturbed areas, enhanced seed input from surrounding areas may be necessary in promoting re-establishment of the vegetation. An important factor in determining the success of seedling establishment in secondary succession is the possession of an effective dispersal mechanism (Archibold 1980). Many grass seeds bear awns which aid seed dispersal (Acocks 1990). Although seeds of *T. triandra* possess an awn, 84% of seeds fell within one meter of the parent plant. Since the effect of the simulated windy conditions on horizontal distance of seed dispersal was negligible, it is concluded that the awn of *T. triandra* is not an effective dispersal mechanism. *Themeda triandra* is therefore typical of most wind dispersed plants where most seeds fall near the parent plant (Levin & Kerster 1974; Cook 1980). Since seeds of *T. triandra* can travel only short distances, seed dispersal may be adequate only in providing a seed source for small-scale disturbances in close proximity to the adult plants. However, the inability for widespread dispersal prevents *T. triandra* from being successful in the re-establishment of larger disturbed areas. The results therefore support the hypothesis that *T. triandra* has a low probability of colonizing a disturbed site because it has poor dispersal ability.

Indigenous grass seeds generally have to pass through a period of dormancy before full germination potential is realized (Liebenberg 1955). For example, Erasmus & van Staden (1983) showed that the grass *Setaria chevalieri* required an after-ripening period before maximum germination was achieved. West (1951) has shown that the seeds of *T. triandra* require an after-ripening period in dry storage of approximately 12 months before full germination potential is realized. Martin (1975) found that this is due to embryo dormancy and mechanically resistant glumes that are involved in the timing of natural germination that occurs approximately 12 months after dispersal. In the present study germination increased from 14% to 30% in seeds buried for one month and five months, respectively. Dormancy in the mountain environment will enable the seeds to avoid germination in the cold, dry winter season and enhance the survivorship after germination the following spring.

One way to promote the succession of *T. triandra* into degraded areas is to maximize opportunities for seedling establishment. A knowledge of the essential germination requirements of *T. triandra* is necessary for the success of rehabilitation programmes of disturbed areas. Since *T. triandra* grows in fire-prone environments, burning may stimulate germination of seeds. Recently, plant-derived smoke has been shown to increase germination of seed of *T. triandra* from 6.0% to 35.8% (Baxter, van Staden, Granger & Brown 1994). This may account for the high germination of *T. triandra* (191 seedlings m^{-2}) observed in an area burnt out by a wild fire, when compared to only 0.2 seedlings m^{-2} in an adjacent unburnt area (Trollope 1984). By contrast, Zacharias, Tainton & Oberholster (1988) found that germination of *T. triandra* seeds exposed to a single fire treatment was lower (24%) than unburnt seeds (63%). Since the seeds in this experiment were placed in a germination cabinet immediately after the fire, it is not known how long they were subjected to smoke. This also precluded the effect of favourable changes in the microclimate following fire from being determined. In the present study, establishment of up to 160 seedlings m^{-2} in recently burnt biennial spring grassland (Fig. 6.3, p.79) indicates that burning stimulates germination. Increased light intensity following the removal of the above-ground biomass by fire may also stimulate germination. However, low germination (0.0-2.2%) recorded in seeds exposed to ambient light and continuous light at 40°C indicate that other factors must stimulate germination. Seeds subjected to high temperatures (35°C) in an alternating dark/light regime had the highest germination (37%). This phenomenon, whereby high temperatures promote germination of seeds in subalpine regions of the Drakensberg, is unusual. However, such high temperatures (36.8°C) were recorded on blackened soil exposed by burning during the micrometeorological study (Chapter 7).

In summary, the hypothesis, that seed production increases with time since fire, was too simplistic since seed production did not increase directly with fire interval. Burning every year significantly reduced seed production and, although seed production increased with a fire interval of two to three years, longer burning intervals reduced seed production. Since different burning regimes greatly affected seed production, strategies for controlling seedling populations through fire management can be effective. The optimum burning regime for increasing seed production of *T. triandra* is a biennial burn applied every second year in spring. Since *T. triandra* has poor dispersal ability, active harvesting of seed will be essential for re-introducing this species to areas where it has disappeared. Another constraint to successful seedling establishment of *T. triandra* is its poor germination. While smoke induces a positive germination response, the percentage germination of seeds remains low for cost-effective restoration programmes. Further research on optimising germination of *T. triandra*, or alternatively planting seedlings into disturbance patches, is therefore required.

Chapter 5
The effect of different burning regimes on the seed bank of montane grasslands

5.1 Introduction

The success of grassland restoration programmes depends primarily on the seed biology of a species. However, where grasslands are severely disturbed, such seed sources may not be readily available. For example, in overgrazed grasslands of the Drakensberg, there has been loss of important forage species such as *Themeda triandra* and invasion of unpalatable weedy herbaceous species with numerous small, light seeds such as *Felicia muricata* (Thumb.) Nees (personal observation). Once the dominant species have been removed from the system there is a limited source of reproductive and vegetative propagules. Vegetative establishment of *T. triandra* on extensive bared patches is therefore an extremely slow process. The ability of seeds to remain viable in the soil will ultimately determine the potential of a community to maintain itself and respond to change. An understanding of the seed bank dynamics of a community is therefore important in the determination of the composition of the plant association after disturbance (Cowling, Pierce & Moll 1986; Houle & Phillips 1988; Hartnett & Richardson 1989; Putwain & Gillham 1990).

In the Drakensberg, fire is likely to be the most important factor modifying the abundance and diversity of species in the seed bank. Seeds of some species may be sensitive to fire while others have burial mechanisms that enable them to escape the direct effect of fire. In sites frequently subjected to fire, such as the annually burnt firebreaks, it is probable that fire destroys most seeds, reducing their rates of accumulation in the seed bank. In the prescribed management burns, which are burnt biennially in spring, seeds may accumulate in the second year and enter the seed bank.

It follows that in fire exclusion areas, there is a strong likelihood of high numbers of seeds entering the seed pool. This study examines the hypothesis that frequent burning prevents seeds from being incorporated into the seed bank while protection from fire is favourable for the accumulation of seeds in the seed bank. To test this hypothesis, seed populations beneath three burning regimes (annual winter burn, biennial spring burn and fire exclusion) were observed.

Besides fire, seed predation is an important factor controlling the size of the seed bank. High levels of seed predation in grasslands (70-87%) have been reported by Verkaar, Schenkeveld & Huurnink (1986), van Tooren (1988) and Capon & O'Connor (1990). The main predators, ants and rodents, reduce the number of seeds entering the seed pool. Seeds are exposed on the soil surface and are susceptible to predation during the period between seed dispersal and seed burial. Most of the seeds produced by *T. triandra* are dispersed in December and January and commence germinating in the following November. They may therefore be exposed to predation for up to eleven months depending on how soon they become buried in the soil. Thus, seed predators can reduce the size of the seed bank in montane grasslands. This hypothesis was tested experimentally by measuring the intensity of seed predation in an open habitat (annual winter burn) and a closed habitat (biennial spring burn).

Although seed predation may be severe, the overall impact on seedling populations may be minimal (Collins & Uno 1985, Janzen 1986). For example, if seeds are not viable, predation will have little impact on seedling recruitment since the seeds would not have germinated anyway. The viability of *T. triandra* is therefore an important factor that must be taken into account before assessing the impact of predation on the seed bank.

Seed banks may be either transient, with seeds that germinate within a year of initial dispersal, or persistent, with seeds that remain in the soil for more than one year

(Simpson, Leck & Parker 1989). Species, which comprise the transient seed bank, are unlikely to be successful in colonizing bared areas since their presence is dependent on seed rain from the above-ground vegetation. By contrast, the persistent seed bank maintains a reservoir for the genetic diversity of a species enabling its population to escape the effects of fluctuating and unpredictable environmental conditions (Williams 1985, Grime 1979, Kalisz 1991). Most grasslands that comprise perennial species have a transient seed bank (Coffin & Lauenroth 1989) and few grass seeds become incorporated into the seed bank (Williams 1984). The poor correlation between the seed bank and the composition of the above-ground vegetation of chalk grassland (Graham & Hutchings 1988), limestone grassland (Ryser & Gigon 1985) and tall grass prairies (Rabinowitz 1981) is characteristic of transient seed banks. The high probability of predation and fire reducing the number of seeds in the soil suggests that, in the perennial grasslands of this study, there will be poor correlation between the above- and below-ground species composition.

The objectives of this study were therefore to; 1) determine the viability of *T. triandra*, 2) evaluate the effects of burning regime on buried seed populations, 3) evaluate the effect of predation on grass seed in the different burning regimes and 4) evaluate the relationship between the seed bank and plant community composition.

5.2 Methods

5.2.1 Viability of *Themeda triandra*

Seed banks can only function if their seeds retain their viability. Seeds of *T. triandra* were harvested in December 1988 and stored in paper bags at room temperature. Viability tests were carried out on selected age classes (0, 5, 11, 15 and 40 months). One hundred and eighty filled caryopses from each age class were dissected from their protective glumes and one half of each seed immersed in a 1% aqueous solution of tetrazolium salt for 24 hours (Hacker 1989). Viable seeds stained dark pink.

Viability of *T. triandra* seeds of different age classes were compared using a χ^2 test for a 2 X 5 contingency table. Pairwise comparisons were tested statistically by means of a Fisher Exact Probability test (Zar 1984).

5.2.2 Seed bank composition

Although a fire exclusion treatment was represented within the Brotherton burning trial, this treatment was only seven years old at the commencement of the present study. This period was considered too short to adequately determine the effect of fire exclusion on the seed bank. A catchment protected from fire for 38 years and invaded by woody shrubs was therefore selected as the fire exclusion treatment. This was compared to the annual winter burn surrounding the catchment, and the biennial spring burn of the adjacent catchment. All three treatments had been applied over the past 38 years and were located in close proximity to one another (within 25 m). They occurred on similar slopes (21-22° slope angles) and a northeast aspect (62-83°).

Soil-core samples were taken on two occasions to determine if seeds with different dormancy requirements were represented in the seed bank. The first samples were taken prior to spring germination (August 1987) so that seeds requiring a cold treatment to break dormancy had received this under natural conditions during winter. The second set of samples were collected in autumn (March 1988), when dissemination of seeds of all species was over, so that seeds with no dormancy requirement were represented. Seeds from the latter sample were also likely to represent species with a high temperature requirement since seeds had persisted in the soil through the hot summer months from December to March.

The germination method was used to quantify the seed bank of the grassland community in this study. While this method may underestimate the seed bank, it is generally justified as providing an estimate of the readily germinable portion of seeds in the soil Gross (1990). Fifty soil core samples, 60 mm in diameter and 170 mm deep (surface area = 0.003 m^2), were taken in each of the three burning regimes on the two sampling occasions. Each soil sample was air-dried, sieved (3.36 mm mesh) to remove plant material that might reproduce vegetatively, and spread over a tray of sterile soil. All sample trays and nine control trays with only sterile soil were randomly placed in a shade tunnel (60% full sunlight) and watered daily. At daily intervals trays were rotated randomly to minimize positional effects in the tunnel. Seedlings, which emerged, were recorded at weekly intervals and removed after identification. The samples were stirred after six months to stimulate further germination (Thompson & Grime 1979). Stirring inverts the soil profile so that seeds on the surface with a burial requirement are accounted for. The experiment was terminated after twelve months when no further germination occurred.

For each core the number of individuals per species was recorded and their density (mean number of seedlings m^{-2}) was calculated. All species recorded were categorized as either herbs, sedges or grasses since the relative frequency of each of these groups indicates the potential agricultural production of the community. Comparisons between the three burning regimes were made by testing statistically the number of core samples in which these groups were present versus the number absent by means of a χ^2 test for 3 X 2 contingency tables (Siegel & Castellan 1988). A similar approach was used to test for differences between the number of samples in which grasses, sedges and forbs were present and absent within a burning regime.

Differences in individual species presence or absence in soil samples and their densities were examined for several species which appear ecologically important in these grasslands. These species are *T. triandra*, because of differences in its frequency of occurrence between the seed bank and the above-ground vegetation; *Stiburus alopecuroides*, because its seedlings are abundant in the field, *Hypoxis rigidula* Bak.and *Oxalis obliquifolia* Steud., because they appear to be early successional species in disturbed areas and *Eragrostis curvula* (Schrad) Nees (variety Ermelo), the dominant grass in the seed bank. Although *E. curvula* is an indigenous species in southern Africa, this particular variety has been introduced in the area for reclamation purposes. A χ^2 analysis for 2 X 3 contingency tables was used to test for differences in occurrence of each species between burning regimes. Differences between burn treatments in numbers of individuals germinating per soil sample were examined using Kruskal-Wallis One-Way Analysis of Variance tests (Siegel & Castellan 1988).

To test for clumping of seeds in the soil, a Poisson distribution was fitted to the data for each treatment and to all treatments combined. The Kolmogorov-Smirnov test was used to determine significance departures from the expected distribution (Siegel & Castellan 1988). A χ^2 analysis was used to test whether differences in the relative frequency of soil cores with no seeds and those with seeds for the two seasons and the three burning treatments were significant. Analysis of χ^2 was also used to test whether the effect of treatments was the same in both seasons.

5.2.3 Above-ground species composition

The relative frequency of the above-ground species in each of the burning treatments was estimated using the descending point technique (Levy & Madden 1933). A Levy bridge, comprising 10 pointed rods spaced 150 mm apart, was randomly placed within each plot 20 times. At every location each rod was lowered and the species nearest to the lowered point recorded and identified. Two hundred observations were made at each site and the frequency of each plant species was expressed as a proportion of the total number of observations for the sample site. The number of plant species in the above-ground vegetation were compared to the number of species represented in the seed bank in all treatments. To make the above- and below-ground species composition data comparable, the soil seed bank data were converted to percentage species composition.

The association between the above-ground vegetation and the seed bank was examined by determining the number of species present only in the above-ground vegetation, the number of species found only in the seed bank, and comparing the number of species common to both. Differences in the numbers of grass and forb species present in the above-ground vegetation and in the buried seed bank within each burning regime were tested using Fisher Exact Probability tests (Siegel & Castellan 1988). Data of the numbers of species of grasses and of forbs occurring in the above-ground vegetation and in the seed bank between the three burning regimes were analyzed using χ^2 values from 2 X 3 contingency tables. The number of different sedge (Cyperaceae) species recorded was too low to be included in the analyses.

5.2.4 Seed predation

Predation on *T. triandra* seed was examined in two natural grassland sites which had received 38 years of annual winter and biennial spring burning treatments. The sites were situated adjacent to each other on a flat spur at an altitude of 1 800 m. Predation was measured during three months: November, prior to seed dispersal; December, when seed dispersal was still taking place; and January, after seed dispersal.

The awns were removed from the 1 500 sample seeds to facilitate handling, and to enable experimental seeds to be distinguished from naturally dispersed seeds. During November, December and January, 20 replicates of 10 seeds were placed at random intervals along two 50 meter transects in each of the burning treatments. The seeds were placed directly on the soil to represent as natural conditions as possible. Although windy conditions occurred during the study, the grass canopy provided protection against the wind and no seeds were disturbed at the soil surface. Tagged wires were placed next to each site to enable relocation of the seeds. The seeds were monitored daily for up to five days.

5.3 Results

5.3.1 Viability of *Themeda triandra*

Viability of freshly harvested seed of *T. triandra* was high (90.0%) with no significant deterioration detected after five months (80.8%). However, viability decreased significantly after 10 months to 60.0% ($P < < 0.001$) and again after 15 months to 37.1% ($P < < 0.001$). Forty month-old seed was significantly less viable (18.8%) than 15 month-old seed ($P < 0.005$).

5.3.2 Seed bank composition

The most striking differences in the seed bank come from a comparison of autumn and spring samples (Table 5.1). The density of seedlings recorded in the autumn sample (49.50 - 110.70 m^{-2}) was significantly lower ($P < < 0.001$) than those in the spring sample (1 555.40 - 1 732.20 m^{-2}). This was largely due to the absence of sedges and the poor representation of grasses in the autumn sample. Grasses germinated in only 2.0% of the 150 soil samples collected in autumn in comparison to 43.3% in the spring samples. Forbs germinated more frequently in both the autumn and spring samples than did grasses and sedges ($P < < 0.001$) but occurred in only 10.7% of the autumn cores when compared to the spring cores (88.7%).

Table 5.1 Species density (plants m^{-2}) in the seed bank of the annual winter burn, biennial spring burn and fire exclusion plot in spring and autumn. sd=standard deviation of 50 samples.

SPRING	Annual winter burn		Biennial spring burn		Fire exclusion	
SPECIES	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**
GRASSES						
Eragrostis curvula	35.40	127.50	183.82	437.20	572.70	734.40
Eragrostis capensis	42.40	35.40	14.14	69.27	14.10	69.30
Harpochloa falx	07.10	49.50	0.00	0.00	7.10	49.50
Stiburus alopecuroides	14.10	69.30	14.14	69.27	49.50	300.00
Themeda triandra	7.10	49.50	0.00	0.00	21.20	84.00
Tristachya leucothrix	-	-	7.07	49.49	-	-
GRASSES TOTAL	**106.10**	-	**219.17**	-	**664.60**	-
SEDGES						
Bulbostylus humilis	84.80	260.30	28.28	95.90	56.60	178.30
Cyperus semitrifidus	452.50	640.40	134.33	272.81	70.70	173.20
Cyperus spp.	21.20	84.00	7.07	49.49	14.210	99.00
SEDGES TOTAL	**558.50**	-	**169.68**	-	**141.40**	-
FORBS						
Anthospermum natalensis	56.60	311.11	7.07	49.49	-	-
Buddleia salvifolia	-	-	-	-	14.10	69.30
Erica woodii	-	-	7.07	49.49	-	-
Helichrysum spp.	629.20	506.30	650.44	506.68	841.30	853.90
Hesperantha baurii	-	-	56.56	178.30	-	-
Hypoxis rigidula	134.30	307.30	63.63	196.06	28.30	119.10
Oxalis obliquifolia	42.40	137.90	35.35	106.05	35.40	145.80
Rhodohypoxis baurii	-	-	7.07	49.49	-	-
Sebaea natalensis	28.30	119.10	-	-	-	-
Senecio spp.	-	-	7.07	49.49	7.10	49.50
FORBS TOTAL	**890.80**	-	**841.33**	-	**926.20**	-
SPRING TOTAL	**1555.40**	-	**1230.18**	-	**1732.20**	-
AUTUMN						
GRASSES	7.10	49.50	0.00	0.00	14.10	69.30
Themeda triandra						
GRASSES TOTAL	**7.10**	-	**0.00**	-	**14.10**	-
FORBS						
Helichrysum spp.	7.10	49.50	7.10	49.50	21.20	84.00
Hypoxis rigidula	14.10	69.30	28.30	196.00	0.00	0.00
Oxalis obliquifolia	28.30	119.10	14.10	69.30	35.40	176.80
FORBS TOTAL	**49.50**	-	**49.50**	-	**96.60**	-
AUTUMN TOTAL	**56.60**	-	**49.50**	-	**110.70**	-

The number of soil samples in which grasses germinated differed significantly between burning regimes with most grasses germinating from soil samples taken from the fire exclusion treatment (Table 5.2, $\chi^2 = 23.2$, $P<0.001$). No significant differences were detectable between the burning regimes in the number of soil samples in which sedges and forbs germinated. However, significant differences occurred within all burning regimes between the numbers of soil samples in which grasses, sedges and forbs germinated. Forbs were recorded more frequently than grasses or sedges ($P<<0.001$ in each case). Forbs were excluded from the data set and a second χ^2 analysis performed on numbers of soil samples in which grasses and sedges germinated in the three burning regimes. This revealed no significant difference between grasses and sedges in the biennial spring burn. However, a significantly greater number of samples had sedges germinating in them than grasses in the annual winter burn ($\chi^2 = 6.3$, $P<0.02$) while the converse occurred for samples taken from the fire exclusion site ($\chi^2 = 16.0$, $P<0.001$).

Table 5.2 Number of cores in which grasses, sedges and forbs were recorded in the annual winter burn, biennial spring burn and fire-exclusion treatment.

Treatment	Grasses	Sedges	Forbs
Annual winter	12	24	43
Biennial spring	18	17	45
Fire-exclusion	35	15	45

The seed bank of these grasslands was characterized by a small number of species, more or less equally abundant, and a high number of *Helichrysum* spp. (Table 5.3). Differences between burn treatments are predominantly due to two species, *Eragrostis curvula* ($\chi^2 = 35.1$, $P<<0.001$) and *Cyperus semitrifidus* ($\chi^2 = 8.5$, $P<0.02$). There were no significant differences in the percentage species composition of *T. triandra*, *Stiburus*

Table 5.3 Percentage composition of the seed bank (n=50) and vegetation (n=200) in different burning treatments.

	Annual winter burn		Biennial spring burn		Fire exclusion	
SPECIES	canopy	soil	canopy	soil	canopy	soil
GRASSES						
Alloteropsis semialata	5.0	-	6.5	-	14.7	-
Andropogon apendiculatus	0.2	-	1.4	-	1.1	-
Aristida monticola	-	-	-	-	0.5	-
Cymbopogon validus	-	-	-	-	0.3	-
Digitaria monodactyla	-	-	0.1	-	-	-
Diheteropogon filifolius	3.7	-	2.7	-	0.4	0.4
Diheteropogon amplectans	2.3	-	1.7	-	1.2	-
Elionurus muticus	0.6	-	0.6	-	1.2	-
Eragrostis curvula	-	2.3	0.2	15.0	-	32.7
Eragrostis racemosa	2.7	-	0.4	-	-	-
Eragrostis capensis	0.4	2.7	0.5	1.2	-	-
Festuca costata	0.3	-	0.7	-	-	-
Harpochloa falx	3.0	0.5	6.6	-	16.7	0.4
Helictotrichon turgidulum	-	-	-	-	0.1	-
Heteropogon contortus	6.0	-	3.4	-	0.9	-
Koeleria cristata	2.0	-	3.5	-	3.7	-
Loudetia simplex	-	-	0.1	-	-	-
Microchloa caffra	1.0	-	0.8	-	0.2	-
Monocymbium ceresiiforme	0.5	-	0.4	-	-	0.8
Panicum natalense	0.5	-	0.4	-	0.1	-
Rendlia altera	3.0	-	4.6	-	0.6	-
Stiburus alopecuroides	0.3	1.0	-	1.2	-	2.9
Themeda triandra	29.2	0.5	25.5	-	18.9	1.2
Trachypogon spicatus	6.4	-	7.9	-	2.1	-
Tristachya leucothrix	8.1	-	12.8	0.6	17.9	-
GRASSES TOTAL	**75.2**	**7.0**	**80.8**	**18.0**	**80.6**	**38.4**
SEDGES						
Bulbostylus humilis	4.5	5.4	1.2	2.3	0.3	3.3
Cyperus semitrifidus	6.0	29.0	3.2	10.9	1.0	4.1
Cyperus spp.	2.3	1.4	0.8	0.6	-	0.8
SEDGES TOTAL	**12.8**	**35.8**	**5.2**	**13.8**	**1.3**	**8.2**
FORBS						
Acalypha punctata	-	-	-	-	0.5	-
Anthospermum natalensis	1.3	3.6	1.3	0.6	-	-
Buddleia salvifolia	-	-	-	-	-	0.8
Craterocapsa montana	0.5	-	-	0.6	-	-
Erica woodii	-	-	-	0.6	1.3	-
Haplocarpha scaposa	0.5	-	0.7	-	0.3	-
Helichrysum spp.	1.3	40.5	0.5	52.9	3.6	48.6
Hesperantha baurii	0.4	-	0.3	4.6	-	-
Hypoxis rigidula	3.0	8.6	3.3	4.8	3.5	1.6
Oxalis obliquifolia	2.4	2.7	7.9	2.9	4.3	2.0
Rabdosia calycina	0.3	-	-	-	-	-
Rhodohypoxis baurii	-	-	-	0.6	1.1	-
Sebaea natalensis	-	1.8	-	-	-	-
Senecio spp.	2.3	-	-	0.6	3.5	0.4
FORBS TOTAL	**12.0**	**57.2**	**14.0**	**68.2**	**18.1**	**53.4**

alopecuroides (Hack.) Stapf, *Hypoxis rigidula* Baker, *Oxalis obliquifolia* Steud. ex Rich. and *Helichrysum* Mill. spp. in the seed bank (Table 5.3).

Fitting a Poisson distribution to the seed bank data showed that in each treatment there was a tendency towards clumping. Clumping of seeds was significant in the combined treatments ($P < 0.01$) with over-representation of the samples containing no seedlings and of the samples containing more than seven seedlings. This accounts for the high variability in the soil samples as is indicated by the large standard deviations listed in Table 5.1. Season of burn had a significant effect on the proportion of soil samples containing no seeds ($\chi^2 = 5.28$, $P < 0.05$), there being more seeds in spring than autumn. There was some indication of this seasonal effect being greater in fire-exclusion plots, but numbers were too small to allow for a proper statistical test.

5.3.3 Above-ground species composition and its comparison to the seed bank

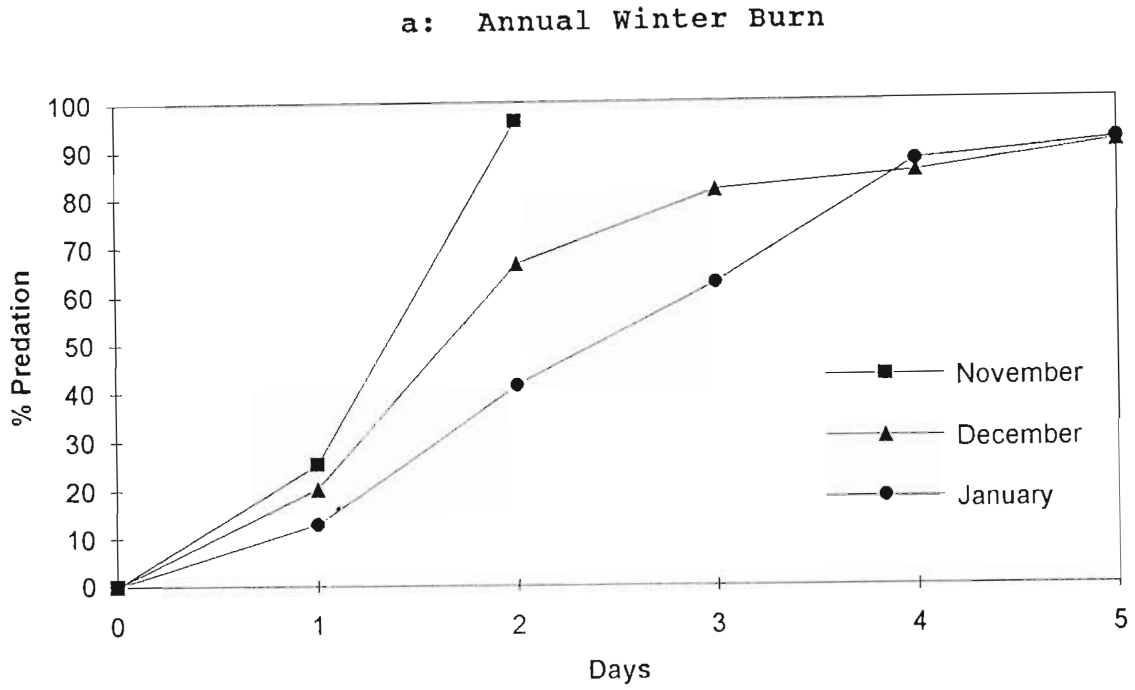
Combining the three burning treatments gave a total of forty-two species in the above-ground vegetation and the seed bank. These comprised 25 grass, 3 sedge and 14 forb species (Table 5.3). Thirty-nine species were recorded in the above-ground vegetation, while only 21 species germinated from the soil samples. A maximum of 21 species was recorded in the above-ground vegetation that were not represented in the buried seed bank. By contrast, only three species were unique to the seed bank flora. Although grasses dominated the above-ground vegetation (75% relative frequency), they were poorly represented in the buried seed bank (<15%). Herbaceous species were significantly more abundant in the buried seed bank than in the above-ground vegetation ($\chi^2 = 83.6$, $P < 0.0001$). With the exception of *Eragrostis curvula*, all species represented in the seed bank and in the above-ground vegetation are native to the area.

No significant differences were detected in the number of species of forbs and grasses in the annual winter and fire-exclusion treatment. However, significant differences in the number of species of forbs and grasses ($\chi^2 = 8.7, P<0.01$) were found within the biennial spring burn treatment (Table 5.3). Between treatment differences were not significant for the three groups of species.

5.3.4 Seed predation

Predation on seeds of *T. triandra* was high with a minimum of 70% of seeds being removed in December, the time of natural seed dispersal (Fig. 5.1). Most severe predation (98%) was recorded in November, the month prior to natural seed release. No significant differences in the level of predation between the annual winter and biennial spring burn treatments were detected.

The main predators of grass seeds are ants (*Camponotus* and *Myrmicaria* spp.) and, to a lesser extent, small rodents such as the three-striped mouse, *Rhabdomys pumilo* (Sparrman). The presence of empty seed husks from which the endosperm had been removed was evidence of rodent predation. During the study, foraging ants were observed transporting seeds from the study site to their nest approximately 14 meters away. On one occasion an individual ant transported a seed from the seed pile for approximately three meters, passed the seed to another individual and returned to the seed pile for another seed. The same seed was passed on four times over the whole route and, in 30 minutes, seven *T. triandra* seeds were taken down into the nest. On the first day of the trial there was a low number of samples in all treatments with no seeds remaining (Fig. 5.2). This indicates that it takes at least a day for the seed pile to be discovered. However, once a seed pile was located there was a high probability of it being removed entirely within three days. For example, on the second and third day of the trial there was a high frequency of no seeds remaining in a seed pile (Fig. 5.2). The only exception occurred in December of the biennial spring burn treatment when the



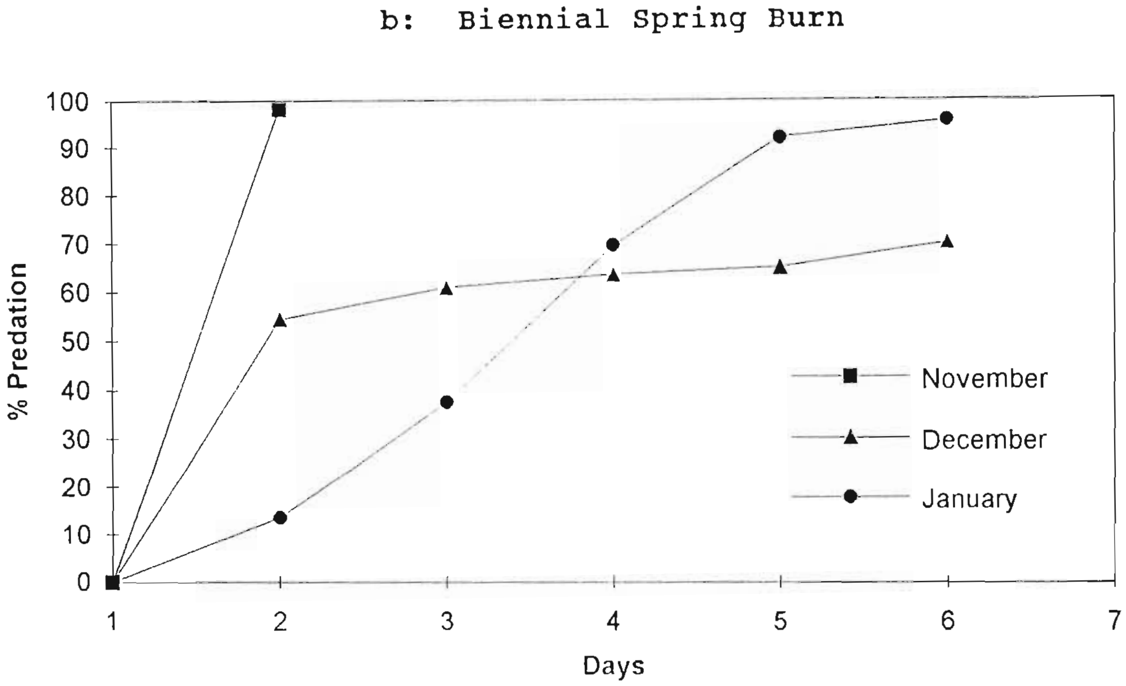


Figure 5.1. Percentage predation of seeds of *Themeda triandra* from an annual winter and a biennial spring burn during the months of the summer of 1989.

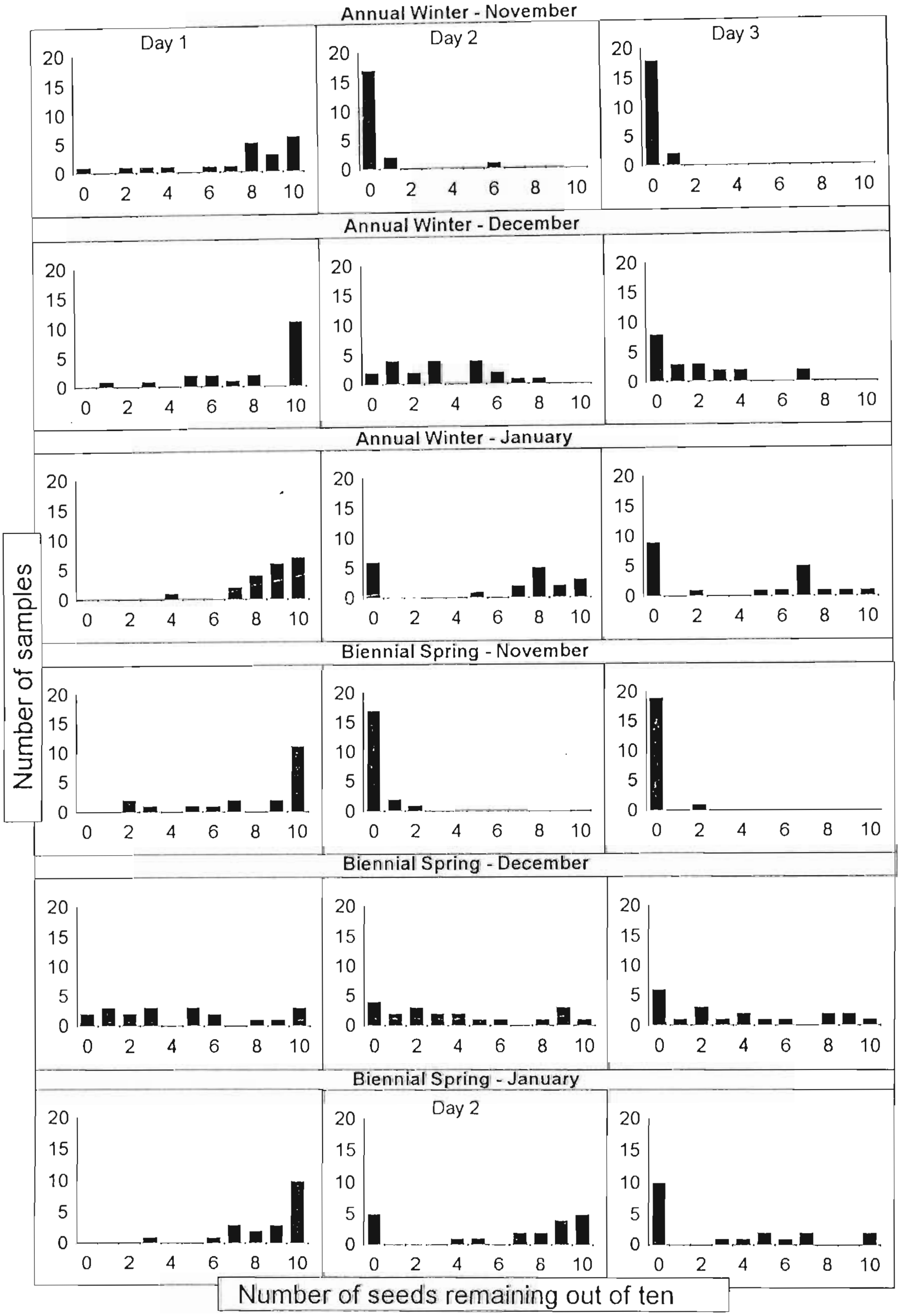


Figure 5.2 Daily frequency distributions of the number of seeds remaining after predation in annual winter and biennial spring burn treatments.

frequency of removal of seeds from each pile was constant over the first three days. Since this was the time of natural seed dispersal, it is likely that the probability of location of the experimental seed was reduced by the abundance of natural seed.

5.4 Discussion

One way to determine the importance of recruitment of *T. triandra* seeds in the stabilization of disturbed areas is to analyze the seed bank. The seed bank can be an important indication of potential community regeneration (Williams 1985; Houle & Phillips 1988). Communities with a persistent seed bank are more likely to be successful in re-establishment after disturbance. In desert grassland, Henderson, Peterson & Redak (1988) recorded a persistent seed bank of 8 068 seeds m^{-2} dominated by *Sporobolus cryptandrus* and early successional annuals. High seed densities of annual fescues and forbs (12 227 m^{-2}) recorded in mixed grass prairie indicate that the seed bank can be a key factor in regeneration (Major & Pyott 1966). The low numbers of grasses and forbs recorded in the seed bank of this study ($<$1 732 m^{-2}) are characteristic of a transient seed bank. Poor representation of *T. triandra* in the seed bank ($<$21 m^{-2}) indicates that the seed bank will not be a major source of seeds of this species in the re-establishment of disturbed grassland.

One of the reasons for lack of persistence of seeds in the soil may be low viability. For example, in *T. triandra* there was a significant decrease in viability after 15 months (37.1%). This indicates a low probability of viable seeds remaining in the soil from previous years. Since viability of *T. triandra* seeds decreased exponentially, one would expect the autumn sample, comprising three month-old seed, to have more seeds than the spring sample in which the seeds were eight months old. However, there were no differences in the number of *T. triandra* seeds between the samples (Table 5.1). This indicates that other factors such as dormancy may determine the germinable size of the seed bank.

The marked seasonal differences in the total size of the seed bank, ranging from <57 m^{-2} in the autumn sample to 1 732 m^{-2} in the spring sample, indicates that environmental conditions may control dormancy. The very low densities of germinated seed recorded in the autumn sample can be attributed to the stratification requirement of some species. Seeds with a stratification requirement will not germinate until they have been exposed to low temperatures for an extended period. This phenomenon is of ecological importance as it protects the seed from early germination in the winter months in response to an unseasonal warm period (Salisbury & Ross 1969). In this study, seeds in the autumn sample having a stratification requirement, would fail to germinate as they were collected before the first frosts. The higher density of germinated seeds recorded in the spring sample (1 732 m^{-2}) indicates that the germination requirements were fulfilled. These seasonal differences increase survival by enabling the species to be dispersed in time as well as space (Antlfinger 1989; Burrows 1989).

Another factor which affects the size of the seed bank is severity of disturbance (Moore & Wein 1977). In this study the seed bank with the highest density (1 732 seeds m^{-2}) was recorded in the grassland protected from fire. Prevention of fire therefore allows a build-up of seeds in the soil. Increased seed densities with longer burning regimes have also been found by Abrams (1988) in tallgrass prairie and Zammit & Zelder (1988) in mixed chaparral. The hypothesis, that frequent burning prevents seeds from being incorporated into the seed bank, was not supported by this study since the seed bank density was higher in the annual winter burn than in the biennial spring burn.

The poor representation of grasses in the seed bank (7-38%) contrasts with their dominance in the above-ground vegetation (75-81%). The low density of *T. triandra* in the seed bank (<21.2 m^{-2}, Table 5.1) suggests that there was little correlation between the seed bank and the relative frequency of individuals of *T. triandra* in the area from which the soil samples were taken. Species richness in the seed bank was approximately half that of the above-ground vegetation with only one third of the grasses represented in the seed bank. This indicates that, following disturbance, the seed bank would contribute little to re-establishment of grasses. The absence of native pioneer grass species in the seed bank may be indicative of the low level of disturbance and the length of time that these fire-climax grasslands have persisted.

Several factors may contribute to the low numbers of *T. triandra* seeds present in the seed bank, the most significant being predation. Seeds of *T. triandra* are relatively large (5-7 mm long, 1-2 mm wide) and have a nutritious endosperm that attracts predators and increases their chances of being preyed upon (Gibbs Russell *et al.* 1990). Although clumping of seeds in the experiment may over-estimate predation, under natural conditions seeds fall close to each other because of lack of dispersal mechanisms. Poor dispersal will therefore increase the probability of being located by predators.

One of the distinctive characteristics of the seed banks in this study was the absence of weedy species. This may account for the small seed bank of these grasslands when compared to other studies where weedy species make up the largest component of seeds recovered (Kropac 1966; D'Angela, Facelli & Jacobo 1988; Rice 1989). The lack of weeds in these grasslands may be due to the low level of soil disturbance in these areas. Although it is possible that weedy species were not detected in this study because of certain germination requirements, weeds are specifically adapted to colonise disturbed sites (Cavers & Benoit 1989). Such conditions were created by transferring the seeds to trays and stirring the soil. These procedures, together with the favourable germination conditions in the experiment, should have promoted the germination of these species but did not.

The species most common in the seed bank were early successional sedge and forb species which could play an important role in colonizing disturbed sites. The most abundant forbs in all treatments were *Helichrysum* spp. Species of *Helichrysum*, although largely perennial, are usually the first forbs to colonise bare ground on eroded slopes or overgrazed grassland. *Helichrysum* species have several characteristics that are typical of early successional pioneer species. They produce large quantities of very small seeds (<1 mm long) which are widely dispersed by wind. These seeds have a dry papery texture when compared to seeds of *T. triandra* and are more likely to escape predation and become incorporated into the seed bank.

Seeds of the dominant sedge species, *Cyperus semitrifidus*, are also small and papery in texture. This species dominated the seed bank of the annual winter burn, but was less abundant in the fire exclusion treatment where succession was more advanced. *Cyperus semitrifidus* appears to be a short-lived early successional species that appears soon after disturbance.

Although *Eragrostis curvula* is indigenous to the area, a cultivated pasture variety was introduced in the last 20 years for erosion control of paths and road verges. More recently during the last eight years, this cultivar has been used extensively for the rehabilitation of two disturbed catchments which are 195 ha and 139 ha in extent respectively and situated approximately three kilometres from the study site. It is probable that this seed source contributed *E. curvula* to the seed bank of the site protected from fire (Table 5.3). *Eragrostis curvula* has limited grazing value, but establishes readily and is a prolific seeder (van Oudtshoorn 1992). It may compete successfully with the later successional native species for limited resources in disturbed and protected areas. As *E. curvula* is an early successional species it has the potential to influence the dynamics of the vegetation. In order to determine whether the accumulation of *E. curvula* seed is potentially a problem in the grassland, the competitive interaction between the Ermelo variety and the dominant native grass, *T. triandra*, should be experimentally determined.

Since the native grass species did not form a persistent seed bank in the natural grassland during the year of the study, there is unlikely to be a build-up of soil seed reserves over time. It is evident that seed banks of montane grasslands have little potential for the recruitment of *T. triandra*. The main implication of this study is that the seed bank will play a limited role in the restoration of the grasslands in degraded areas.

Chapter 6
Seedling establishment in montane grasslands

6.1 Introduction

The response of plant populations to disturbance depends on the magnitude of the disturbance and on the biological attributes of the plant species (Snaydon 1987). One of the reasons that seedlings have been generally neglected in population studies of grasses in South Africa is that they are believed to contribute very little to maintaining the total size of the ramet population (Everson CS 1985). By contrast, vegetative tufts of *T. triandra* grow more or less indefinitely through continual tiller production, resulting in high basal cover. As tufts reach a particular size they fragment into smaller tufts which themselves slowly expand (Acocks 1990). Although this growth pattern does not allow rapid vegetative spread, the dominance of *T. triandra* is maintained with annual winter and biennial spring burning regimes (Everson CS, Everson TM & Tainton 1985). Disturbance, such as summer burning, results in a loss of *T. triandra* from the sward. Outside the conserved areas of the Drakensberg, the disturbance factor mostly responsible for the deterioration of the grassland is the communal grazing system. In sensitive areas of the Drakensberg (e.g. the access slopes onto the Little Berg), this traditional grazing system causes the vegetation to be overgrazed to virtually no cover (Acocks 1990). One of the options for increasing the carrying capacity of degraded grassland is to restore highly productive native grasses, such as *T. triandra*, to their previous position of dominance.

Since seeds typically enable plants to survive adverse environmental conditions, the question arises as to the ability of seedlings of *T. triandra* to re-establish in disturbed environments. Besides overgrazing and fire, disturbances which commonly occur in the

Drakensberg include baboon foraging activities and erosion caused by factors such as vehicle tracks, hiking trails and landslides. Such disturbances may change the relative effectiveness of different forms of regeneration. For example, regeneration of the herb *Rubus fructicosus* in shade of British woodlands is nearly exclusively vegetative, but in clearings there are high rates of seed production (Grime 1979).

Different disturbance regimes in the Drakensberg may favour seedling establishment of the dominant grasses. Following disturbance, vegetation cover can be restored either by the survival and regrowth of plants initially present, or by the establishment of seedlings (Antos & Zobel 1986). Since *T. triandra* has no means of extensive vegetative spread, regrowth from plants surrounding a disturbed area is likely to be slow. In South African savanna grasslands, O'Connor (1991) found that low rainfall and overgrazing resulted in poor seedling recruitment of *T. triandra*. In the Drakensberg little is known of the inherent ability of indigenous grasses to establish seedlings, or of the response of seedlings to changing environmental conditions. The specific aims of this section of the study are to (1) document the distribution, establishment and survivorship of naturally occurring grass seedlings, (2) determine whether grass seedling establishment varies with different disturbance regimes and (3) determine the efficiency of the sexual reproductive strategy of the dominant grass, *T. triandra*.

6.2 Study site

Study sites were located in the Brotherton burning trial described previously (Chapter 3). The programme for the treatments and times of assessment since the initiation of the experiment in 1980 is shown in Table 6.1.

Table 6.1 Schedule of treatments (month of application) between 1980 and 1989. A = first census (followed by assessments at 6 weekly intervals to September 1989), b=plot burnt, v=vegetation removed, s=soil (A horizon) and vegetation removed.

Treatment	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989
Annual Winter burn	Oct/b	Jul/b	Jul/b	Jul/b	Jul/b	Jul/b	Jul/b A	Jul/b	Jul/b	Jul/b
Biennial Summer burn	Oct/b	-	Jan/b	-	Jan/b	-	Jan/b A	-	Jan/b	-
Biennial Spring burn	Oct/b	-	Oct/b	-	Oct/b	-	Oct/b A	-	Oct/b	-
Five-year burn	Oct/b	-	-	-	-	Oct/b	- A	-	-	-
Disturbed-no veg.	Oct/b	-	Oct/b	-	Oct/b	-	Sep/v A	-	-	-
Disturbed-no veg. & A hor.	Oct/b	-	Oct/b	-	Oct/b	-	Sep/s A	-	-	-

Weather data recorded from a meteorological station on the Little Berg indicated that climatic conditions during the experimental period from 1986 to 1989 were typical of the regional climate. For example, annual rainfall ranged from 1 001 mm to 1 322 mm, close to the long-term mean of 1 299 mm (1941-1991). The mean temperature of the hottest month, January, was only 0.2°C lower than the long-term mean of 16.5°C. July was the coldest month (mean maximum 16.9°C, mean minimum 5.4°C), with the mean temperature being 1.1°C lower than the long-term mean.

6.3 Methods

6.3.1 Seedling establishment

Seedling establishment was monitored in the four burning treatments, two artificially disturbed sites and small-scale naturally disturbed sites. The artificially disturbed treatments were created in a biennial spring burn plot within the Brotherton trial. These represented two levels of disturbance: (a) severe erosion was simulated by removing the vegetation and the A horizon of the soil with a sharp spade, and (b) less severe erosion was simulated by leaving the soil intact, but killing all the above- and below-ground vegetation. This was achieved by placing black plastic over the plots two months before the commencement of the experiment. This technique successfully removes the vegetation without physically disturbing the soil layer (Frasier, Cox & Woolhiser 1987). The artificially disturbed 1 m^2 plots were replicated three times.

Naturally disturbed baboon foraging sites were located at the same altitude as the burning trial on an adjacent spur. Bare patches develop in the grassland when baboons move rocks in search of insects upon which to feed (Plate 7). Fifty bare patches, resulting from rocks being overturned, were marked with numbered stakes. Since the patches were approximately circular in shape, the radius was measured and used to calculate the area of each site. The number of seedlings that established in the patches was recorded at six-weekly intervals throughout the growing season of 1989.

Nine 0.25 m^2 quadrats were randomly marked with four permanent corner stakes in each of the four burning treatments. On each eight-weekly sampling occasion a grid, subdivided into four cells of equal size (0.0625 m^2) with cross wires, was fitted over the stakes. A pantograph (Plate 8) was then used to trace the basal area of all the established perennial grasses, forbs and sedges within each cell, in addition to the position of all grass seedlings. Different species were allocated different colours for easy identification. This mapping procedure was carried out in the 36 plots of the burning treatments, and the six artificially disturbed plots. At the commencement of the study I planned to repeat this mapping technique at monthly intervals. However, this goal was unrealistic since the first mapping operation alone took six weeks to complete. Subsequent data collection was therefore limited to mapping only the precise location, number and survival of newly emerging grass seedlings. Each of these seedling assessments took approximately two weeks to complete. Data collection commenced in November 1986, after a flush of germination, and continued at 6-weekly intervals until September 1989.

Plate 7. Bare patch in the grassland created by baboons overturning rocks to forage

Plate 8. Mapping vegetation using a pantograph

Mapping the tagged seedlings at different census dates gave a measure of the seedling population flux. At each census, records were also made of death and flowering of the plants. Seedlings were marked with fireproof tags for accurate relocation and identification. Mapping the total basal area of all the vegetation in the plots was repeated after two years in 1988.

One method to determine patterns of seedling establishment is to plot the number of seedlings against a time axis. Graphical representations of seedling numbers of the most dominant seedlings, *T. triandra* and *Stiburus alopecuroides*, were used to illustrate the total change in population numbers over 35 months. Differences in the densities of seedlings of these two species in the four burn treatments and two artificially disturbed treatments were tested using a Kruskal-Wallis test (Siegal & Castellan 1988). Nonparametric multiple comparisons indicated which treatments were significantly different (Zar 1984). The Kolmogorov-Smirnov Two Sample test compared the differences between the cumulative proportional frequencies of *T. triandra* and *S. alopecuroides* over all treatments (Campbell 1981).

6.3.2 Life tables and survivorship

One limitation of examining total seedling numbers is that actual births and deaths are not depicted. Alternatively, a life-table provides a concise summary of the patterns of death and survivorship at different ages within a population (Deevey 1947). While this is a valuable tool for examining the demographic structure of a population, it does not consider overlapping generations. Cohort life-tables follow the fate of a particular cohort from its recruitment until the death of the last member (Moore & Chapman 1986). They therefore illustrate the age-specific mortality risk experienced by the cohort. While cohort life-tables are not practical for long-lived individuals, they were suitable for the short-lived seedlings in this study.

To examine the survival of seedlings in the present study, cohort life tables were constructed for seedlings of *T. triandra* in the biennial spring and biennial summer burns, and for seedlings of *S. alopecuroides* in the biennial summer and five-year burn treatments. Seedling numbers were too low in the other treatments to be included in the cohort analyses. Since most germination occurred between late November and January, seedlings establishing during this period were treated as belonging to one cohort. In case of individuals living longer than the proposed three-year study, a final census was done four years after the commencement of the study. The cohort life-table consists of a series of columns headed by the following standard notations:

N_x - the number surviving to the beginning of the next time interval,

l_x - survivorship, the probability of an individual recorded at the first census surviving until the start of each recording period. The survivorship function $l(0)=1$ is rescaled so that $l(0) = 1\ 000$ and interpreted as the number of survivors out of an initial cohort of 1 000, rather than as a probability,

d_x - the number dying during each time interval (determined by subtracting the number still surviving at each time interval from the number surviving at each preceding time),

q_x - the age specific mortality rate for the population at different dates is calculated by dividing the number dying during the time interval (d_x) by the number surviving to the start of the time interval (N_x),

L_x - stationary population ($l_x + l_{x+1} /2$),

e_x - mean life expectation ($\sum_{x}^{\infty} L_x/l_x$).

6.3.3 Leslie matrix models

Transition matrix models (Leslie 1945) were developed to predict the distribution of age classes of seedlings of *T. triandra* and *S. alopecuroides* receiving different treatments. The general form of the model is represented by the matrix equation:

$$\underset{\mathrm{A}}{\begin{vmatrix} F_0 & F_1 & F_2 \;.....\; F_n \\ P_0 & 0 & 0 \;.......0 \\ 0 & P_1 & 0 \;.......0 \\ 0 & 0 & P_2 \;.......0 \\ - & - & P_{n+1} \;.....0 \end{vmatrix}} \times \underset{\mathbf{a}_t}{\begin{vmatrix} N_{t0} \\ N_{t1} \\ N_{t2} \\ - \\ N_{tn} \end{vmatrix}} = \underset{\mathbf{a}_{t+1}}{\begin{vmatrix} N_{t+1,0} \\ N_{t+1,1} \\ N_{t+1,2} \\ - \\ N_{t+1,n} \end{vmatrix}}$$

$$\mathrm{A} \times \mathbf{a}_t = \mathbf{a}_{t+1}$$

The transition matrix (**A**) represents different age classes of seedlings with specific fecundity rates representing tiller production (F). Transition probabilities of seedlings surviving from one age class to the next (P) can be estimated from survivorship of tagged seedlings (l_x in Table 6.5, p.81). For example, in the biennial spring burn P_0 for *T. triandra* is 208.7/1 000 = 0.21. The number of seedlings present in each age class of the cohort (N_x in Table 6.5, p.81) can be represented as a vector ($\mathbf{a}_t$). In this study there were four age classes corresponding to the annual census taken each spring for four years. The product of multiplication of the matrix and the column vector ($\mathbf{a}_t$) is the column vector ($\mathbf{a}_{t+1}$), representing the population structure after one year.

It was not possible to predict absolute changes in population numbers since no tagged seedlings reached reproductive maturity within the four-year study period. However, it was possible to simulate relative trends in population structure with realistic estimates of fecundity from independent field observations. The maximum likelihood of fecundity was obtained from a competition experiment in which the mean fecundity of seedlings with reduced competition was four tillers per seedling (Chapter 8). Proportional increases in fecundity were estimated as eight and sixteen tillers per seedling for the third and fourth age classes respectively. Low fecundity was simulated by substituting 0, 0.5, 1 and 2 tillers per seedling for each year of the study. The transition matrices and vectors (Table 6.6) were therefore based on actual mortality rates and both real and simulated fecundity rates. Each iteration of the model represented a period of one year.

6.3.4 Percentage species composition of vegetation

In the stable environment of the fire-climax grassland community in this study one would expect seedlings to be representative of the above-ground species composition. The relative frequency of species in each of the burning treatments was objectively quantified using the descending point technique described in Chapter 5. The results provide an estimate of the proportional species composition in percent.

6.3.5 Environmental variables

Seedling dynamics may be influenced by external factors such as climate. Correlation analysis was used to examine the relationship between seedling establishment and the climatic variables, rainfall and minimum temperature. The climatic data were obtained from a meteorological station situated on the Little Berg, approximately three kilometres from the study site.

6.4 Results

6.4.1 Seedling establishment

The average density of all grass seedlings (summed over the whole germination period for each year) varied significantly between the different treatments (Fig. 6.1). Annual establishment was lowest in the annual winter burn treatment (<1.3 seedlings m^{-2} annum $^{-1}$) (Table 6.2). The maximum numbers of seedlings recorded in the biennial burns were higher with 51 seedlings m^{-2} annum^{-1} establishing in the summer burn, and 184 seedlings m^{-2} annum^{-1} in the spring burn. In both treatments seedling establishment was highest in the second and fourth years of the study (1987 and 1989), which coincided with the inter-burn years (Fig. 6.1). The highest annual seedling establishment was recorded in the five-year burn (211 m^{-2} in 1987). However, this high value was not maintained in the following years and seedling establishment declined steadily to 0.4 m^{-2} in 1989. The density of seedlings emerging on the artificially disturbed site with no A horizon was lower (<7.6 seedlings m^{-2}) than the site with no vegetation (<33.6 m^{-2}). Low seedling establishment (4.1 m^{-2}) was also recorded in the small patches ($\bar{x}=0.02$ m^2) of the baboon foraging site (Table 6.2).

Table 6.2 Mean seedling densities per square metre (± S.E.) for all grass species combined. nd = no data, b = burn.

Treatment	**1986**	**1987**	**1988**	**1989**
Annual winter burn	0.0 ± 0.0 b	0.9 ± 0.8 b	1.3 ± 1.0 b	0.4 ± 0.4 b
Biennial summer burn	3.6 ± 1.8 b	50.7 ± 24.4	8.0 ± 4.1 b	24.4 ± 16.0
Biennial spring burn	23.1 ± 7.6 b	184.4 ± 58.3	50.7 ± 19.4 b	132.0 ± 64.0
Five-year burn	76.0 ± 56.5	211.1 ± 102.0	18.7 ± 9.5	0.4 ± 0.4
Disturbed-no vegetation	0.0 ± 0.0	33.6 ± 4.9	3.0 ± 2.1	7.3 ± 1.9
Disturbed-no A horizon	0.0 ± 0.0	7.6 ± 0.3	0.3 ± 0.3	0.7 ± 0.5
Disturbed by baboons	nd	nd	nd	4.1 ± 2.0

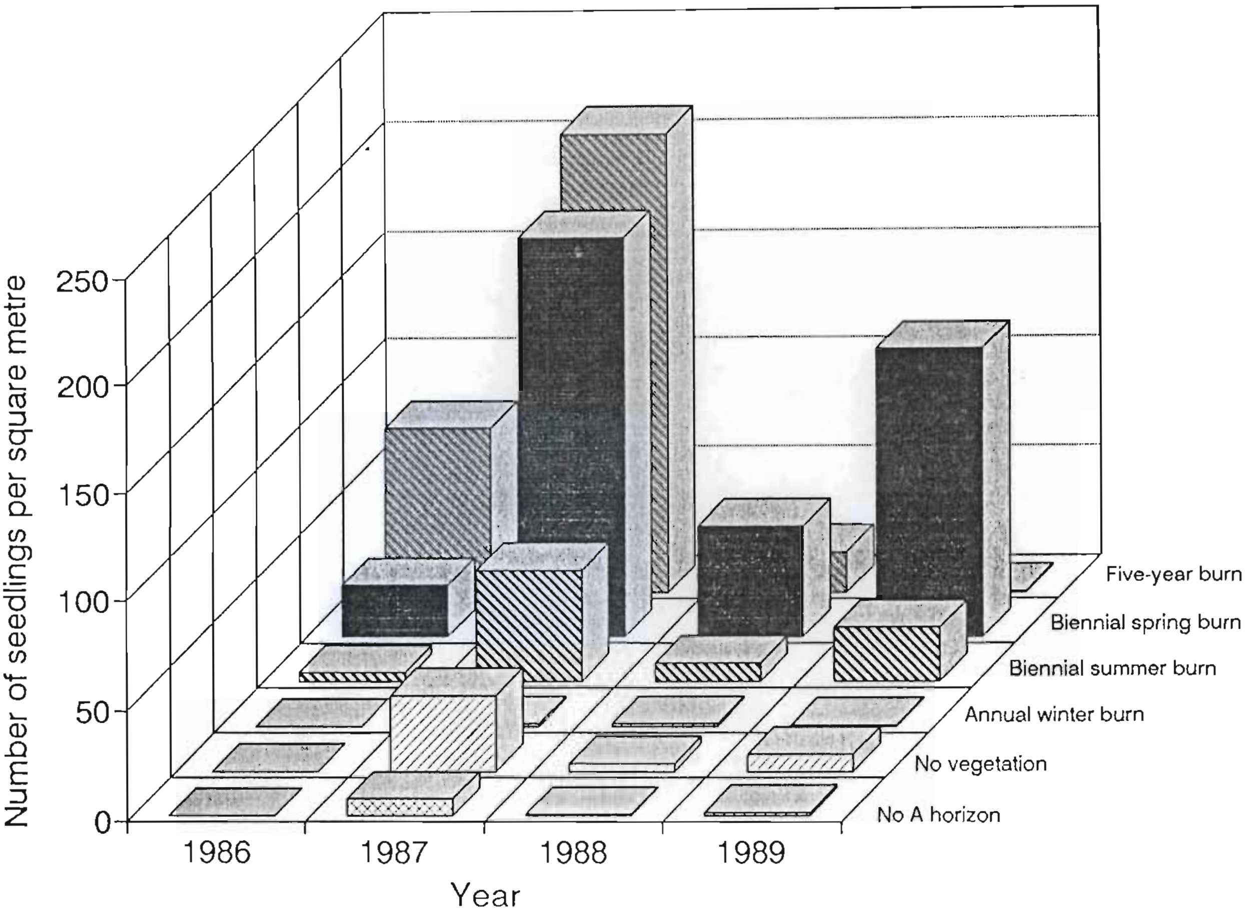


Figure 6.1 Annual establishment of all grass seedlings in the different treatments.

Grasses were poorly represented in the artificially disturbed sites in comparison to sedges and herbs (Table 6.3, $P<0.001$). Although high numbers of annual sedges (<186 m^{-2}) and herbs (<146 m^{-2}) invaded the cleared sites, the species were short-lived (3-4 months) and contributed little to basal cover (<1%). Even after three years there was no observable recovery of vegetation on the severely disturbed site. By contrast, on the site with only vegetation removed, encroaching neighbouring plants revegetated approximately 5% of the area after 34 months.

In the small patches in the baboon foraging site (mean size 0.02 m^2), regeneration of *T. triandra* from seeds was lower (4.1 ± 2.0 seedlings m^{-2}) than in the larger artificially disturbed sites (9 ± 1.2 seedlings m^{-2}).

Table 6.3 Annual seedling establishment (seedlings m^{-2}) of sedges, herbs and grasses in the artificially disturbed sites.

Treatment	Plant type	1987	1988	1989
A horizon & vegetation removed	sedge	50.0	40.7	185.7
	herb	68.7	45.0	31.0
	grass	10.7	17.0	28.3
Only vegetation removed	sedge	76.7	108.7	18.3
	herb	145.7	152.7	98.3
	grass	78.0	42.3	50.0

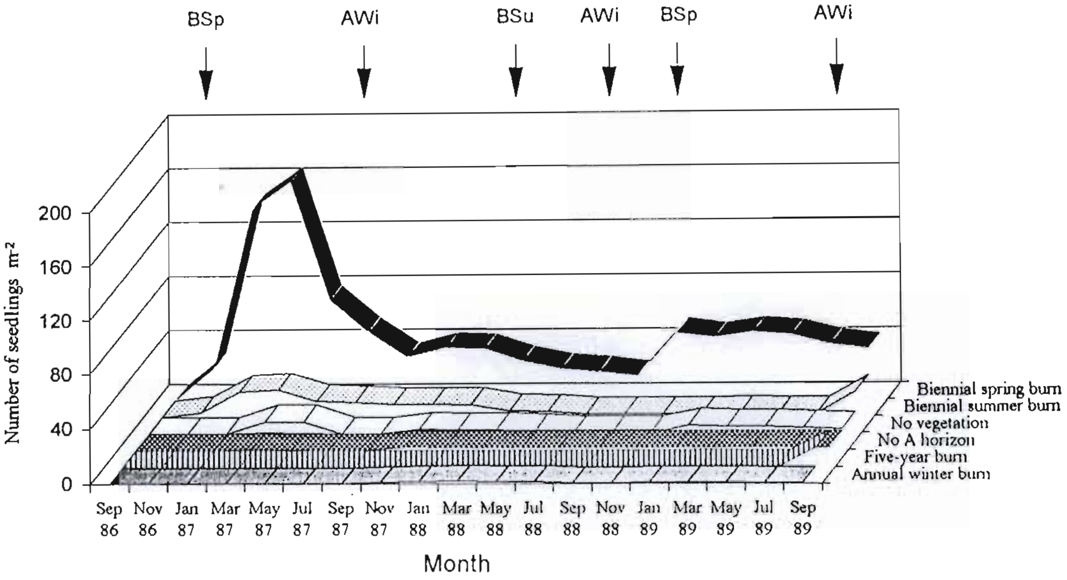
By monitoring the number of births and deaths of individual seedlings at each site, it was possible to determine the general change in population numbers over three years. There was a significant difference (Kruskal-Wallis test, $P<0.001$) between the density of seedlings of *T. triandra* in the biennial spring burn and the other five treatments (Table 6.4). In the biennial spring burn, numbers were initially high after the treatment burn in October 1986 (160.4 m^{-2} in March 1987), but decreased sharply to 30.7 m^{-2} in September 1987 (Fig. 6.2a). Seedling numbers increased again after the second treatment burn in October 1988, but numbers were lower (48.9 seedlings m^{-2}) than after the previous burn treatment. The lowest numbers of seedlings were recorded in the annual winter burn (< 1 seedling m^{-2}). In the five-year burn the only establishment (13.8 seedlings m^{-2}) took place in September 1989. No significant differences were detected between the annual winter and five-year burn. By contrast the summer burn had significantly higher seedling establishment (22.6 m^{-2}) than the annual winter burn (Kolmogorov-Smirnov test, $P < 0.0001$).

Seeds of *Stiburus alopecuroides* germinated from January to March. Seedling establishment of *S. alopecuroides* was significantly higher ($P < 0.001$) in the five-year burn than in the other treatments (Table 6.4). The low seedling numbers in the biennial summer burn treatment (18.4 seedlings m^{-2}) did not differ significantly to the annual winter burn and the two disturbed sites where no seedlings of *S. alopecuroides* established.

Table 6.4 Average density (seedlings m^{-2}) of *T. triandra* and *S. alopecuroides* for the different treatments (Kruskal-Wallis test, $P < 0.0001$). Values sharing the same letter across a row are not significantly different at the 1% level.

	Treatment					
Species	AWi	BSu	BSp	Five-year	No soil	No veg.
T. triandra	1.3 (a)	22.6 (a)	107.2 (b)	0.2 (a)	1.5 (a)	2.9 (a)
S. alopecuroides	0.0 (a)	18.4 (a)	76.4 (b)	208.8 (c)	0.0 (a)	0.0 (a)

By contrast, the number of seedlings decreased progressively in the five-year burn from 228 seedlings m^{-2} in 1987 to 40 seedlings m^{-2} in June 1989 (Fig. 6.2b). This indicates that more frequent burning may be necessary to maintain high levels of seed germination and establishment. Numbers of seedlings were low in the first two years of the biennial a: *Themeda triandra*



b: *Stiburus alopecuroides*

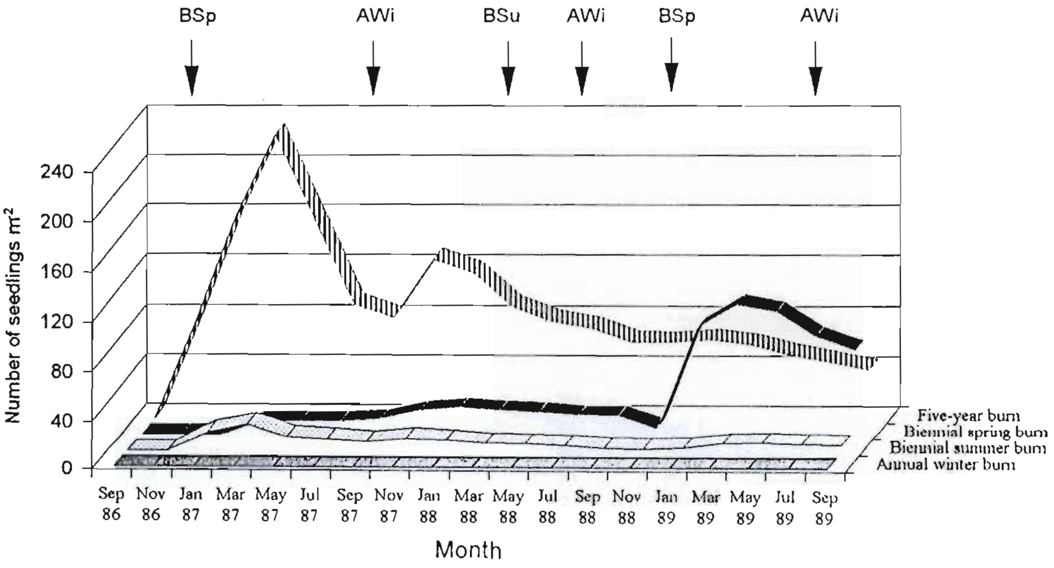


Figure 6.2 Monthly totals of seedlings of (a) *T. triandra* and (b) *S. alopecuroides* in different treatments. Arrows indicate time of burn.

spring burn ($<$22.7 seedlings m^{-2}), but increased to 104.9 seedlings m^{-2} in the third year ($P<0.001$) (Fig. 6.2b).

Numbers of seedlings of the two dominant grasses, *T. triandra* and *Stiburus alopecuroides* (Fig. 6.2), showed similar patterns of establishment. Each species was characterized by a flush of germination in summer (November to January) followed by heavy mortality in the first winter. The main difference between the population flux of these species was the higher number of seedlings of *S. alopecuroides* (80.9 seedlings m^{-2}) that survived the winter period when compared to *T. triandra* (30.7 seedlings m^{-2}).

Seedling growth of both *T. triandra* and *S. alopecuroides* in the natural vegetation was stunted when compared to that of vegetative daughter tillers. After initial germination and growth to approximately 100 mm, it was not possible to distinguish between one-year old and three-year old seedlings. Dead seedlings had a brown, withered appearance but no visible damage by herbivory.

6.4.2 Life tables and survivorship

Life tables for both *T. triandra* and *S. alopecuroides* were characterized by high mortality (q_x) during the initial establishment phase (Table 6.5). Survival of *T. triandra* was low in the biennial spring burn where only 6 seedlings of the original cohort of 321 survived to the end of the study period. The mean expectation of life (e_x) in 1986 was 0.74, suggesting that after germination, seedlings in the first year of establishment could expect to live for only nine months. However, those individuals that survived the first nine months had a longer life expectancy of approximately 16 months ($e_x=1.35$).

The smaller cohort of seedlings in the biennial summer burn (42) was also characterised by initial high mortality. Approximately half the seedlings died during the period of active growth (Table 6.5). The summer burn in January 1988 had a catastrophic effect on the 20 remaining individuals as all died. This high mortality shows the severity of this treatment on survival of this species. A similar pattern occurred in the same treatment for *Stiburus alopecuroides*. Mortality (q_x) was 81.3% in the cohort of seedlings established in 1986.

Table 6.5 Life tables for cohorts of seedlings of *T. triandra* and *S. alopecuroides* established in 1986.

(a) *T. triandra* Biennial spring burn.

Year	N_x	l_x	d_x	q_x	L_x	e_x
1986	321	1000.0	791.3	.7913	604.4	0.74
1987	67	208.7	186.9	.8955	115.3	0.69
1988	7	21.8	3.1	.1429	20.2	1.35
1989	6	18.7	-	-	9.3	-

(b) *T. triandra* Biennial summer burn.

Year	N_x	l_x	d_x	q_x	L_x	e_x
1986	42	1000.0	523.8	.5238	731.1	0.97
1987	20	476.2	476.2	1.000	238.1	0.50
1988	0	0	-	-	0	-

(c) *S. alopecuroides* Biennial summer burn.

Year	N_x	l_x	d_x	q_x	L_x	e_x
1986	56	1000.0	714.3	.7143	642.9	0.88
1987	16	285.7	232.1	.8125	169.6	0.82
1988	3	53.6	17.9	.3333	45.7	1.19
1989	2	35.7	-	-	17.9	-

(d) *S. alopecuroides* Biennial five-year burn.

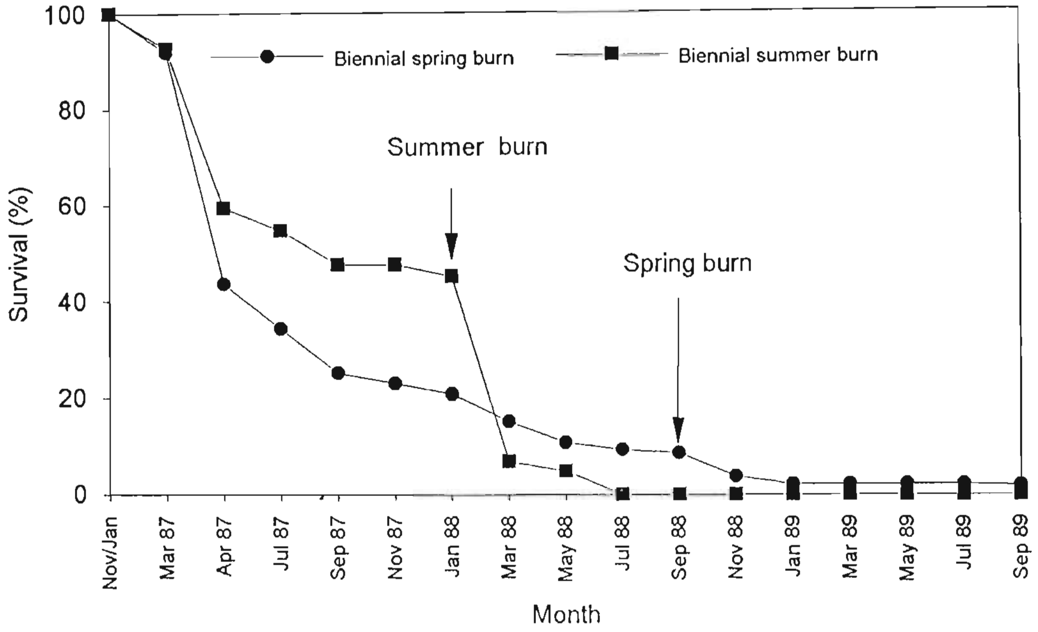
Year	N_x	l_x	d_x	q_x	L_x	e_x
1986	354	1000.0	692.1	.6921	654.0	1.07
1987	109	307.9	135.6	.4404	240.1	3.82
1988	61	172.3	81.9	.4754	131.3	1.02
1989	32	90.4	-	-	45.2	-

Life table analysis of *S. alopecuroides* in the five-year burn shows high mortality (69.2%) at the beginning of the establishment phase. Fluctuating mortality followed with only 32 of the original cohort of 354 seedlings remaining at the end of the 34-month study.

The data in the life tables were summarized to produce survivorship curves. The pattern of survivorship was a Deevey Type IV curve for both *T. triandra* (Fig. 6.3a) and *S. alopecuroides* (Fig. 6.3b). This is characteristic of a population where there is a high mortality in the juvenile stage, and the probability of death decreases with time (Solbrig & Solbrig 1979). Few individuals of the initial cohort of *T. triandra* seedlings survived the three-year observation period. The survivorship curve of *T. triandra* in the biennial spring burn treatment (Fig. 6.3a) shows that the highest mortality risk (approximately 60%) occurred in the first winter following establishment. Only 43.6% of the initial population survived the frosts in May 1987. During winter (June/July) seedlings continued to die with 25.2% surviving to September 1987. Survivorship then declined linearly to 8.7% in September 1988. The biennial spring treatment burn was applied in this month after which survival decreased to 3.7%. By September 1989 only 1.9% of the original population remained alive. This represents a 1% probability of survival of the original cohort of seedlings over three years. Seasonal mortality in the first winter (May-July) was the main constraint to seedling survival.

Seedlings of *T. triandra* exhibited a similar pattern of survivorship in the biennial summer burn (Fig 6.3a). However, initial mortality was lower with 59.4% of the seedlings surviving the first of the winter frosts of May 1987. Survivorship continued to decrease steadily during winter until commencement of the growing season in September when there was little change. Following the treatment burn in January, survivorship decreased sharply from 45.2% to 7.0%. The seedlings that survived the burn died the following winter.

a: Survivorship -*Themeda triandra*



b: Survivorship - *Stiburus alopecuroides*

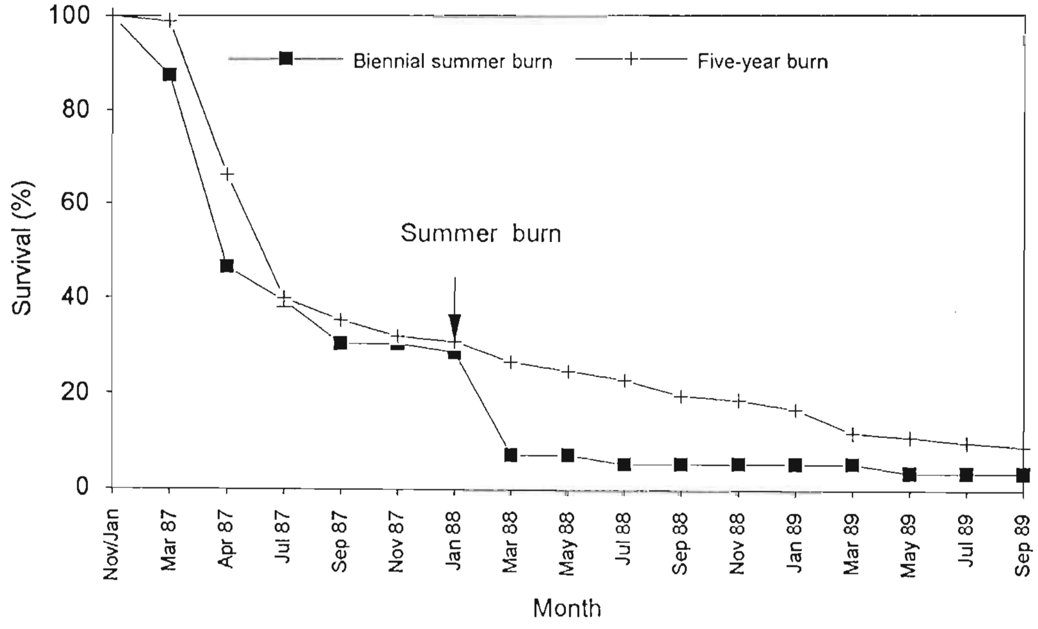


Figure 6.3. Survivorship curves of *Themeda triandra* and *Stiburus alopecuroides* in various burn treatments.

Survivorship of *S. alopecuroides* in the five-year burn and the biennial summer burn (Fig. 6.3b) followed a pattern similar to that of *T. triandra* with highest mortality during the first winter season. By September 1987 survivorship decreased to 30.3% in the biennial summer burn and to 35.3% in the five-year burn. Thereafter, in the five-year burn seedlings died at a constant rate throughout the study period until only 9.0% of the original cohort remained after 34 months. By contrast, in the summer treatment, survivorship decreased sharply from 28.6% in January 1988 after the treatment burn, to 7.1% in March 1988. By September 1989, only 3.6% of the initial seedling cohort remained alive. The comparison of mean values of survival of the dominant grasses, *T. triandra* and *S. alopecuroides,* showed significant treatment effects ($F=5.32, P<<0.001$) but no significant differences with respect to species or year. For the total number of seedlings establishing there was a significant difference in both species ($F=5.3$, $P<<0.001$) and treatment ($F=16.2$, $P<<0.001$).

6.4.3 Leslie matrix models

The models, based on the transition matrices at both high and low fecundity rates (Table 6.6), predict that the numbers of *T. triandra* seedlings in the 0-1 year age class will increase exponentially with biennial spring burning (Fig. 6.4a). However, the number of seedlings in the older age classes will decline with no survivors after three years. By contrast, the model predicts that at low fecundity rates seedling numbers of all age classes will decrease exponentially with biennial summer burning (Fig. 6.4b). However, if fecundity is high (e.g. because of decreased competition from nearest neighbours), this downward trend is reversed. Therefore, the effects of reduced competition on seedling reproduction (Chapter 8) will override the detrimental effects of summer burning. Exponential increase in 0-1 year-old seedlings is also predicted for *Stiburus alopecuroides* in both the biennial summer (Fig. 6.4c) and five-year burn (Fig. 6.4d) treatments. Seedlings in the older age classes will not survive beyond two years in the biennial

Table 6.6 Transition matrices (A) and vectors (a_t) used to derive predicted patterns of population growth of *T. triandra* and *S. alopecuroides* in different burn treatments in Fig. 6.4.

(a) *T. triandra* - Biennial spring burn

low fecundity

$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 0.5 & 1 & 2 & 321 \\ 1\text{-}2 & 0.21 & 0 & 0 & 0 & 67 \\ 2\text{-}3 & 0 & 0.02 & 0 & 0 & 7 \\ 3\text{-}4 & 0 & 0 & 0.19 & 0 & 8 \\ \hline & & A & & & a_t \end{array}$$

high fecundity

$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 4 & 8 & 16 & 321 \\ 1\text{-}2 & 0.21 & 0 & 0 & 0 & 67 \\ 2\text{-}3 & 0 & 0.02 & 0 & 0 & 7 \\ 3\text{-}4 & 0 & 0 & 0.19 & 0 & 8 \\ \hline & & A & & & a_t \end{array}$$

(b) *T. triandra* - Biennial summer burn

low fecundity

$$\begin{array}{l|ccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 0.5 & 1 & 42 \\ 1\text{-}2 & 0.48 & 0 & 0 & 20 \\ 2\text{-}3 & 0 & 0 & 0 & 0 \\ \hline & & A & & a_t \end{array}$$

high fecundity

$$\begin{array}{l|ccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 4 & 1 & 42 \\ 1\text{-}2 & 0.48 & 0 & 0 & 20 \\ 2\text{-}3 & 0 & 0 & 0 & 0 \\ \hline & & A & & a_t \end{array}$$

(c) *S. alopecuroides* - Biennial summer burn

low fecundity

$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 0.5 & 1 & 2 & 56 \\ 1\text{-}2 & 0.29 & 0 & 0 & 0 & 16 \\ 2\text{-}3 & 0 & 0.05 & 0 & 0 & 3 \\ 3\text{-}4 & 0 & 0 & 0.4 & 0 & 2 \\ \hline & & A & & & a_t \end{array}$$

high fecundity

$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 4 & 8 & 16 & 56 \\ 1\text{-}2 & 0.29 & 0 & 0 & 0 & 16 \\ 2\text{-}3 & 0 & 0.05 & 0 & 0 & 3 \\ 3\text{-}4 & 0 & 0 & 0.04 & 0 & 2 \\ \hline & & A & & & a_t \end{array}$$

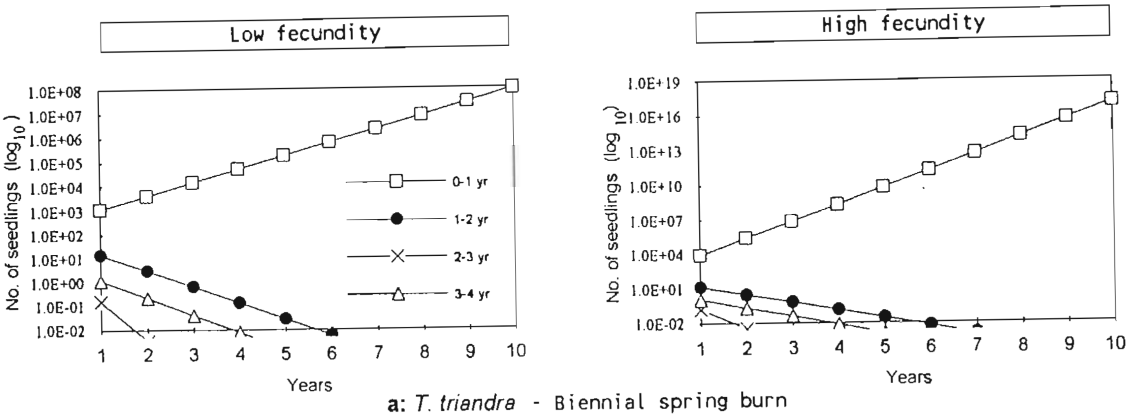
(d) *S. alopecuroides* - Five-year burn

low fecundity

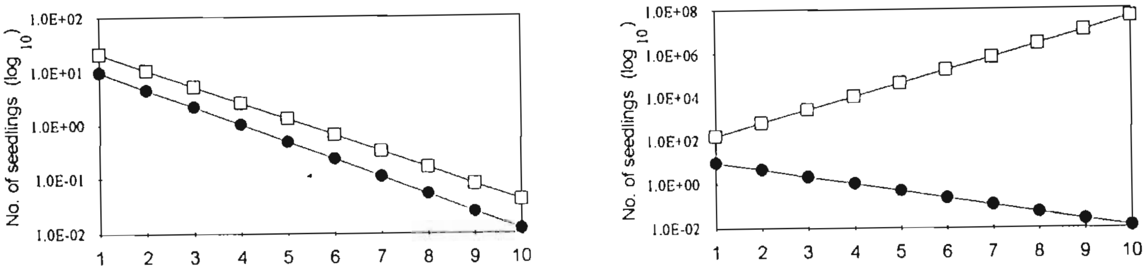
$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 0.5 & 1 & 2 & 354 \\ 1\text{-}2 & 0.31 & 0 & 0 & 0 & 109 \\ 2\text{-}3 & 0 & 0.17 & 0 & 0 & 61 \\ 3\text{-}4 & 0 & 0 & 0.09 & 0 & 32 \\ \hline & & A & & & a_t \end{array}$$

high fecundity

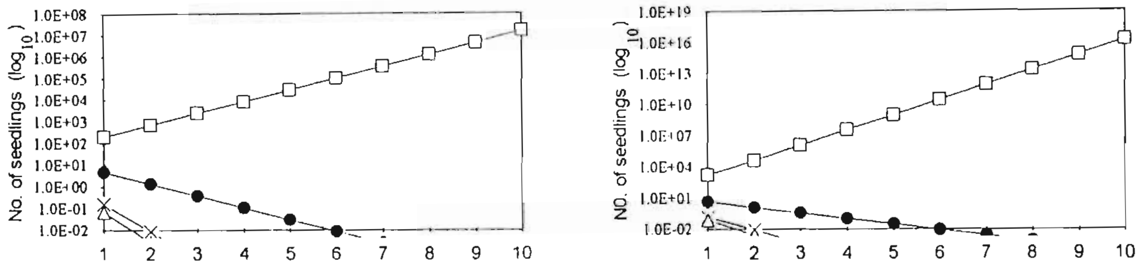
$$\begin{array}{l|cccc|c} \text{Age class (yrs)} & 0\text{-}1 & 1\text{-}2 & 2\text{-}3 & 3\text{-}4 & \text{Present State} \\ \hline 0\text{-}1 & 0 & 4 & 8 & 16 & 354 \\ 1\text{-}2 & 0.31 & 0 & 0 & 0 & 109 \\ 2\text{-}3 & 0 & 0.17 & 0 & 0 & 61 \\ 3\text{-}4 & 0 & 0 & 0.09 & 0 & 32 \\ \hline & & A & & & a_t \end{array}$$



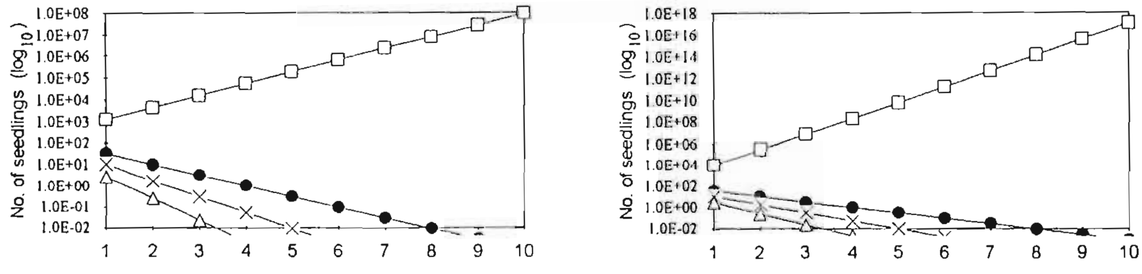
a: *T. triandra* - Biennial spring burn



b: *T. triandra* - Biennial summer burn



c: *S. alopecuroides* - Biennial summer burn



d: *S. alopecuroides* - Five-year burn

Figure 6.4. Predicted changes in numbers of seedlings of four age classes of *T. triandra* and *S. alopecuoides* when subjected to different burning treatments.

summer burn, and four years in the five-year burn.

Although the model predicts an exponential increase in numbers of one-year old seedlings of *T. triandra* and *S. alopecuroides,* it is unlikely that such high numbers will be realized. At some stage the effects of neighbours will adversely affect the population. The low number of older seedlings suggests that seedlings will contribute little to the overall population structure of montane grasslands.

6.4.4 Percentage species composition of vegetation

Thirty-six species, of which 14 were grasses, were recorded in the above-ground vegetation (Table 6.7). Except for the biennial summer burn, the relative frequency of plant species (expressed as a proportion of 200 Levy bridge observations), was dominated by *Themeda triandra* (26.0-30.2%). The highest relative frequency of *T. triandra* was recorded in the annual winter burn. *Tristachya leucothrix* was co-dominant with *T. triandra* in the annual winter (15.2%), biennial spring (15.5%) and five-year (19.8%) burn. In the summer burn the species with the highest relative frequencies were *Harpochloa falx* (18.8%), which is unpalatable to animals when mature, and *Tristachya leucothrix* (16.5%), which has variable palatability. The relative frequency of *Stiburus alopecuroides* was variable ranging from 1.0% in the biennial summer burn to 12.7% in the five-year burn.

All species of grass seedlings recorded in the burning treatments were present in the above ground vegetation. However, seedling establishment was characterised by low species richness with only two species, *T. triandra* and *S. alopecuroides*, having seedlings in sufficient numbers to analyse statistically. The other six species recorded (*Koelaria cristata* (L.) Pers., *Trachypogon spicatus*, *Heteropogon contortus*, *Harpochloa falx*, *Microchloa caffra* Nees, and *Panicum ecklonii* Nees), had densities of less than three

Table 6.7 Relative species composition (%) of the above-ground vegetation in the annual winter, biennial summer, biennial spring and five-year burning treatments.

Species	Annual winter	Biennial summer	Biennial spring	Five-yr burn
Grasses				
Andropogon appendiculatus	0.00	0.33	0.17	0.00
Digitaria flaccida	0.00	0.00	0.33	0.83
Diheteropogon amplectans	1.33	2.83	2.33	3.00
Eragrostis racemosa	0.50	0.00	0.17	0.00
Harpochloa falx	5.67	18.83	7.33	6.50
Heteropogon contortus	8.33	3.33	6.17	2.83
Koeleria cristata	4.83	5.50	3.33	4.83
Microchloa caffra	0.00	0.33	0.00	0.00
Monocymbium ceresiiforme	0.50	0.00	0.00	0.00
Panicum ecklonii	1.00	0.00	0.00	1.83
Stiburus alopecuroides	4.83	1.00	7.83	12.67
Themeda triandra	30.17	10.17	26.67	26.00
Trachypogon spicatus	6.17	4.50	6.50	3.33
Tristachya leucothrix	15.17	16.50	15.50	19.83
Sedges				
Bulbostylis oritrephes	0.00	6.33	9.17	5.67
Cyprus spp.	9.00	0.00	0.00	0.00
Scleria sp.	0.00	0.17	0.00	0.00
Herbs				
Acalypha punctata	4.50	4.50	0.00	0.00
Anthospermum herbaceum	0.67	1.83	0.50	0.33
Commelina africana	0.00	0.00	1.00	0.50
Craterocapsa montana	0.17	0.17	0.00	0.33
Erica woodii	0.00	0.00	0.50	0.00
Haplocarpha scaposa	0.00	0.50	0.00	0.00
Hebenstretia dentata	0.00	0.17	0.00	0.33
Helichrysum adenocarpum	0.33	3.33	0.17	0.00
Helichrysum adscendens	0.33	0.30	0.33	0.17
Helichrysum aureo-nitens	0.00	0.67	0.00	0.33
Helichrysum aureum	0.00	0.00	0.00	0.00
Helichrysum miconiifolium	1.83	1.83	0.33	0.17
Hesperantha baurii	0.00	0.00	0.17	0.00
Hypoxis filiformis	1.50	2.83	2.33	1.33
Oxalis obliquifolia	6.00	10.17	7.67	6.67
Satyrium longicauda	0.17	0.00	0.00	0.00
Senecio adnatus	0.00	0.33	0.33	0.00
Senecio ingeliensis	0.00	0.17	0.00	0.00
unidentified forb	1.33	3.00	1.00	2.50
TOTAL	100.00	100.00	100.00	100.00

seedlings m^{-2}. No seedlings of *T. leucothrix*, the co-dominant species with *T. triandra*, were recorded in any of the burning treatments.

6.4.5 Environmental variables

Correlations between number of seedlings and weather data showed no significant association between rainfall and seedling establishment ($r = 0.33$) and minimum temperature and seedling establishment ($r = 0.27$). However, broad weather patterns may not be sufficient to indicate such associations. On the basis of these results, a study was initiated to determine the microclimatic variation of the seedling environment in the different treatments (Chapter 7).

6.5 Discussion

The montane grasslands of the Natal Drakensberg are characterized by a seasonal pattern of seedling emergence. Germination commences in late spring (November) which is characterized by warmer temperatures and the onset of the rainy season. After the initial flush, germination is staggered from November through to March, a strategy that should optimize seedling survival in an unpredictable environment. Since germination commences in November, before adult plants shed their seeds (late December), newly produced seeds must remain dormant in the soil throughout the dry, cold winter. While seeds of montane grasslands require a period of exposure to low temperature for germination, differences in mean seedling densities between treatments suggest that other factors must influence establishment (Table 6.2).

The number of seedlings establishing ultimately depends on the number of seed produced. The number of seeds produced by *T. triandra* in each burning treatment generally increased from one-year old to five-year old grassland (Chapter 4). Except for the five-year burn in 1988 and 1989, seedling densities showed similar patterns of increase from one- to five-year old grassland. Therefore, availability of seed is an important factor determining the success of seedling re-establishment programmes.

One factor that may influence the seedling recruitment of a species is the abundance of that species in the community. Seedling establishment in this study was dominated by the most abundant grass species, *T. triandra*. Similarly, the abundance of seedlings of *S. alopecuroides* in the five-year burn corresponded to the high relative abundance of this species in the above-ground vegetation.

However, high abundance of a species is not always associated with high seedling densities. Although the annual winter burn treatment had the highest frequency of *T. triandra* in the above-ground vegetation it had the lowest annual seedling establishment. Similarly, the high frequency of *Tristachya leucothrix* in the vegetation was not reflected in the seedling population. This suggests that establishment of seedlings must depend on other factors besides abundance of parents in the vegetation. One such factor may be disturbance since this determines the characteristics of the seedling environment and consequently influences establishment.

Establishment of alpine grass and forb seedlings in Montana, USA is determined by the severity, type, size and frequency of disturbance (Chambers, MacMahon & Brown 1990). In the montane grasslands of the Drakensberg, the low establishment of seedlings of *T. triandra* in the annual winter burn is related to frequency of disturbance. In grasslands burnt every year, reproductive tillers fail to develop, and few seeds are produced. By contrast, fire stimulates vegetative reproduction of tillers, accounting for the high relative frequency of *T. triandra* in grassland burnt every year. The low seedling recruitment in the annual winter burn treatment also indicates that there is little input of seed from the surrounding vegetation. This is probably due to the poor seed dispersal of *T. triandra*.

The low establishment of seedlings of *Tristachya leucothrix* is due to type and severity of disturbance. Insect herbivory of the florets of this species resulted in severe damage to the seeds. Approximately 1 000 seeds of this species collected for germination studies, failed to germinate because of damage by insects. Subsequent examination of plants in the field confirmed the widespread destruction of seeds while still on the plant. The absence of *T. leucothrix* seedlings in these grasslands appears to be due to the low probability of healthy seeds entering the seed pool.

The low numbers of seedlings of *T. triandra* in the biennial summer burn (Fig. 6.1) indicate that burning every second year can be detrimental to the establishment of seedlings. Here the season of burn, rather than frequency of burn, is the controlling factor. The summer burn is carried out in January during the critical growth period of tillers. Burning at this time destroys the apical meristem, resulting in the death of the plant and a reduction of the frequency of *T. triandra*. Low seedling numbers of *T. triandra* are therefore related to low abundance of mature tufts of *T. triandra* in this treatment.

Except for the annual winter burn, all burning treatments had highest seedling establishment in the growing season immediately following the burn (Fig. 6.1). Similar increases in seedling establishment of *T. triandra* after burns were recorded by Lock & Milburn (1970) in grasslands in Uganda. The trend of high seedling establishment after fire may be related to smoke-induced germination (Baxter, van Staden, Granger & Brown 1994). Alternatively, changes in the grassland microclimate after fire may enhance seedling establishment. For example, species with a light requirement for germination will be stimulated by the decrease in litter shading the soil and the removal of the plant cover. The initial high establishment in the five-year burn may be attributed to a favourable moist environment below the canopy. However, with continued absence of fire, the canopy becomes dense and moribund and reduces light reaching the soil surface. The lack of light was evident in the spindly appearance of the seedlings in this treatment.

Seedling densities in the five-year burn (211 m^{-2} in 1987) and the biennial spring burn (184 m $^{-2}$ in 1987) compare favourably to other studies. For example, in Australia, Hacker (1989) recorded very low establishment of Buffel grass, *Cenchrus ciliaris*, (<0.4 m^{-2}), while Gross & Smith (1991) recorded an annual seedling establishment of <44 m^{-2} for *Panicum dichotomiflorum* in Ohio, the United States. Anderson (1989) considers that an annual seedling establishment of 40 m^{-2} is sufficient for conserving the genetic variability of a population. However, this genetic diversity will not be maintained unless seedlings survive to reproductive maturity.

In grasslands of the Drakensberg, low survivorship of seedlings of *T. triandra* and *Stiburus alopecuroides* ensures that seedlings contribute little to the grassland population dynamics. In all burning treatments, young seedlings less than one-year old suffered the heaviest mortality risk, most dying in the first six months after germination. However, probability of death decreased for seedlings that survived the first winter. Seedlings are vulnerable to the dry, cold conditions in winter. By comparison, new tillers on established plants derive support from the parent. Everson CS, Everson, TM & Tainton (1985) found that approximately 77% of tagged vegetative tillers of *T. triandra* in a biennial spring burn survived the first winter.

Timing of germination may be a critical factor determining the survival of seedlings. Seedlings that germinate early in the season will be larger and will have more reserves for winter than seedlings that germinate later. For example, in semi-arid rangelands of the western United States, survival of the perennial grass *Agropyron desertorum* (Fisch.

ex Link) was enhanced by early emergence (Salihi & Norton 1987). In the grasslands of this study, seedlings germinating both early and late in the season had a high mortality risk, suggesting that the staggered germination pattern was not effective in promoting survival of seedlings.

The exponential increase in one-year old seedlings predicted by the Leslie matrix model was not demonstrated in the field. One reason for this is that the model assumes that mortality and fecundity will not change with time. The low survivorship of seedlings in the field may be related to density-dependent factors such as overcrowding from neighbours. This implies that competition may be a limiting factor in the successful establishment of seedlings. The predicted decline in older seedlings has important implications for rehabilitation programmes. The success of such programmes will depend on increasing survival of the older age-classes of seedlings. While the absolute numbers of seedlings predicted by the models must be treated with caution, the predictions of the overall trend in population structure are important. They demonstrate that a biennial spring burning regime would be most suitable for promoting establishment of *T. triandra* seedlings, while the five-year burning regime is favourable for establishment of seedlings of *Stiburus alopecuroides*.

Besides fire, other factors may be important in regulating seedling numbers. Sarukhan & Harper (1973) showed that in populations of *Ranunculus repens* in grazed pasture in Britain, the seasonal mortality risk occurred in the period of most active growth, not during the harsher climatic seasons. Similarly, Sharitz & McCormick (1973) found that *Minuartia uniflora* growing in the south-eastern United States had high mortality during the seedling establishment phase of its life cycle. Seedling losses in the present study were frequently preceded by a period of high seedling recruitment. The association between mortality and high seedling densities gives some evidence for the occurrence of density-dependent regulation in these grasslands. Competition between individual seedlings, or between individuals and mature tufts for limited resources may contribute to the initial high mortality. Harper & White (1974) showed that density stress may have a profound influence on the size of an individual. In the present study, the stunted growth of seedlings and their inability to reach reproductive maturity is evidence of density stress. Many seedlings observed in this study were clumped and occurred in local patches of high seedling densities. Some of these patches may subsequently prove unfavourable for seedling survival, resulting in high seedling losses. There was no evidence of physical damage to the seedlings of *T. triandra* and *Stiburus alopecuroides* by insects or animals, showing that grazing was not detrimental to seedling survival.

Marked seasonal patterns of emergence suggest that climatic conditions are likely to influence emergence (Froud-Williams, Chancellor & Drennan 1984). In chalk grasslands in England the amount of precipitation was highly correlated with mortality of seedlings (Schenkeld & Verkaar 1984). In the montane grasslands of this study, there was no correlation between total number of seedlings and rainfall, and number of seedlings and minimum temperature. However, frost may be a limiting factor in seedling survival. Frost heave during winter occurs as a result of water in the soil surface layer freezing and forming vertical ice needles (Killick 1963). The ice crystals lift soil surface particles (Plate 5, p.31) resulting in movement of the surface layer, upper roots and seedlings. Exposure of roots above the soil surface results in desiccation and death of seedlings. This phenomenon, in which ice needles heave the surface soil and kill seedlings, has been observed in afro-alpine environments (Hedberg 1964). Death of seedlings by frost heave was frequently observed in the sub-alpine grasslands of this study.

By contrast, seedling regeneration in arctic tundra is enhanced in areas frequently disturbed by frost activity, erosion, animals and fire (Gartner, Chapin & Shaver, 1986).

Genetic variability within a species enhances its ability to cope with a range of environmental conditions (Ernst 1987). Gaps in the vegetation are important as entry points for new genotypes and species (Silvertown & Smith 1988). Some species have the variability to cope with extreme environmental disturbance. For example, De Hullu & Gimingham (1984) reported that seedling establishment of *Calluna* in Scottish heathland was most successful in bare patches. Williams & Ashton (1987) also recorded substantial establishment of shrub seedlings on bare ground in grassy communities in Australia. Similarly, Metcalfe, Ellison & Bertness (1986) showed that seedling success of *Spartina alterniflora* Loisel. was higher in bare patches than in vegetated areas of New England salt marsh. Factors favouring seedling establishment in disturbed environments include reduced competition for nutrients (Sharitz & McCormick 1973), greater light intensity (Grime 1979) and absence of neighbours and interspecific competition (Harper 1977). Disturbed areas are, however, not always suitable for plant growth (Bayer 1955). Seedlings in bared areas or gaps are exposed to extremes in microclimate (Williams & Ashton 1987; von Maltitz 1990). Some seeds require shelter from direct sunlight (Thomas & Wein 1985), while reduced litter layers in disturbed areas may alter the size and composition of the seedling community (Fowler 1988).

The low seedling establishment of *T. triandra* in the artificially disturbed sites (<9 m^{-2}) suggests that in bare areas this species will contribute little to a post-disturbance community. However, the slow encroachment of grass tillers from the surrounding vegetation indicates that ultimately, colonization by vegetative spread of tillers is more successful than that by seed in bare areas. The success of this regeneration will depend on the size of the bare area. Goldberg & Gross (1988) found that small gaps were not successfully invaded by successional species reproducing from seed, but that the peripheral vegetation encroached upon the gaps vegetatively.

An interesting aspect of the recovery of the disturbed sites was the absence of alien invasive plants. Disturbed sites are usually characterized by high numbers of weedy species (Rice 1989). The absence of aliens in these grasslands is probably due to distance from seed source, absence of seeds of weeds in the seed bank, and the colder climate associated with the high altitude of the study area.

Archibold (1980) outlined three factors that are important in determining secondary succession on disturbed sites. These are firstly the ability of the residual flora to tolerate changed microclimate, secondly the regrowth from buried viable propagules and thirdly the effective dispersal from neighbouring species. The poor establishment of the climax species in the disturbed sites suggests that these grasses cannot tolerate the change in the environment. Other studies have shown that later successional species are not successful in colonizing disturbed areas. In disturbed gravel sites in Alaska, legumes are among the first colonizers. They improve the physical environment and facilitate colonization of later successional species (Bishop & Chapin 1989). Also, Yeaton, Frost & Frost (1986) found that the early successional species on disturbances caused by warthog excavations of savanna grassland were mostly non-grasses and potential nitrogen fixers. Although the soils of the Drakensberg are low in nitrogen (approximately 0.55%) no legumes established during the 34-month study period. In the cleared sites, annual sedges and *Oxalis obliquifolia* were among the first plants to establish. The high densities recorded indicate that these species are more resistant to changes in microclimate than the fire-climax species. They have a strong competitive advantage at the early stage of succession as they produce large numbers of seeds that germinate rapidly and are readily dispersed. Although these species contributed little to basal cover, they are important pioneers in the secondary succession of bared areas.

Patterns of succession in grassland may reflect fluctuation, a reversible change in dominance within a stable species assemblage, or succession, a directional change in composition (Rabotnov 1974). The pattern of seedling dynamics in the cleared sites shows a directional change in composition from annual sedges and herbs to a few climax grasses. This is typical of other studies of disturbed sites where early successional species are mainly annuals with a large reproductive effort, and later species are often perennials with a smaller reproductive effort (Hancock & Pritts 1987). In some studies secondary succession is by weedy invaders that require physical disturbance of the soil to germinate (Brown 1987). In this study revegetation was only by species already present in the surrounding undisturbed vegetation.

The results of this study show that in biennial spring and five-year burns, sexual reproduction is effective in the production of seedlings. However, most of the seedlings in this study survived for very short periods, and had little impact upon population processes. High mortality of seedlings is therefore the key constraint to potentially higher seedling establishment. The high mortality risk and low reproductive rate of seedlings implies that the grass seedling population would quickly decline. However, in reality the vegetative tufts ensure a continual input of seeds, some of which germinate and survive for periods up to three years. To maximize opportunities for the establishment of *T. triandra* in bared areas, factors that will increase survival (e.g. favourable microclimate) need to be determined to ensure the success of grassland restoration programmes.

Chapter 7
The effect of disturbance factors on the grassland microclimate

7.1 Introduction

Within any area of general climatic uniformity, local conditions of temperature, light, humidity and moisture vary greatly. It is these factors which play an important role in the production and survival of plants (Tainton 1981). Seedlings in particular are sensitive to changes in microclimate as they are unable to tolerate environmental fluctuations as easily as mature plants (Taylor & Tisheng 1988). Microclimatic factors that favour seedling establishment are of direct concern in grassland restoration programmes.

Fire is one of the main disturbance factors that influences the grassland microclimate since burning changes the vegetation suddenly and drastically. The extent to which fire influences the microclimate depends on the intensity of the fire, the nature of the vegetation and the frequency of fire occurrence (Cass, Savage & Wallis 1984). Changes in microclimate associated with different disturbance treatments may be responsible for the differences in seedling establishment observed in Chapter 6.

A critical microclimatic factor determining the seedling dynamics of plant populations is soil moisture (Fowler 1988; Frasier, Cox & Woolhiser 1987). Changes brought about by burning may influence soil water dynamics. For example, removal of the litter layer by fire will expose the soil and reduce soil water storage capacity (Cass, Savage & Wallis 1984). Burning at different times of the year will affect the recovery of the vegetation and subsequent exposure of the soil to rainfall.

The ability of a plant to take up water is determined by conditions prevailing in the soil and atmosphere (vapour pressure deficit). Solar radiation provides the main energy input to plants and soil, and drives processes such as transpiration (Cooper 1970). Fire changes the radiation balance of a community by increasing the penetration of light and changing the reflectance of the soil surface (Kelly 1989). Such changes in the microclimate may increase the water stress of plant seedlings and influence their survival.

Another important effect of burning is the increase in temperature at the soil surface after fire. Tothill (1969) found that higher ambient temperatures after burning favoured germination of *Heteropogon contortus* seed in Australian grassland when compared to unburnt situations. Trollope (1984) recorded higher seedling establishment of *T. triandra* in burnt savanna grassland when compared to unburnt areas. Since mowing of the unburnt area failed to stimulate germination of *T. triandra*, he attributed the germination in the burnt areas to stimulation by heat.

A knowledge of the microclimatic factors that favour both germination and seedling establishment can indicate ways to maximise opportunities for seedling establishment in re-establishment programmes. The aim of this aspect of the study was to determine the microclimatic responses of soil moisture, light, temperature and vapour pressure deficit in *Themeda*-grassland subjected to different disturbance regimes.

7.2 Study area and methods

Five treatments, located within the Brotherton burning trial, were selected for the microclimate studies: an annual winter, biennial summer, biennial spring, five-year burn, and a disturbed site with the A horizon removed. The sites were in close proximity to one another (extreme sites were 80 m apart), so that climatic differences between sites were negligible. The programme for the treatment burns during the microclimate study is shown in Table 7.1.

Table 7.1 Schedule of treatment burns (month of application) for 1990 and 1991.

Treatment	1990	1991
Annual winter burn	July	July
Biennial summer burn	January	-
Biennial spring burn	October	-
Five-year burn	-	-
Disturbance (no A-horizon)	-	-

In each of the sites the following microclimate factors were measured:

(1) Photosynthetically-active radiation (PAR)(μmoles s^{-1} m^{-2}) was determined with a line quantum sensor (Licor, Lincoln, Nebraska) placed at the soil surface. Incoming solar radiation (W m^{-2}) was measured at a nearby meteorological station with a solarimeter (Kipp and Zonn, Delft, Holland).

(2) Soil moisture in the top 100 mm of soil was measured gravimetrically. Three soil samples were collected in each of the treatments at midday and oven dried at 104°C to constant weight.

(3) Temperature and relative humidity were measured at the soil surface with an aspirated psychrometer (Delta-T, Cambridge, England) protected by a radiation shield. These values were used to calculate vapour pressure deficit (kPa).

Readings of these microclimatic parameters were taken once a month on a clear day from July 1990 to June 1991. Readings were logged on to a Campbell 21 data logger (Campbell Scientific Inc. Logan, Utah) at hourly intervals between 07h00 and 17h00. Transporting the sensors between sites took 15 minutes. This time was considered too great to enable replication since differences between plots over long time intervals could be incorrectly attributed to treatment effects.

To enable comparisons between treatments, the monthly curve of soil moisture and the diurnal curves of temperature, PAR and vapour pressure deficit were plotted. Monthly rainfall and mean temperature from July 1990 to June 1991 were obtained from a nearby meteorological station (within 2 km) at the same altitude as the study site and presented as a climatic diagram (Fig. 7.1).

7.3 Results

Before inferences can be drawn from the association between microclimatic variables and patterns of seedling establishment, it is necessary to examine the general climatic conditions during this study. Comparison between the climatic diagram for the 12-month study period from July 1990 to June 1991 (Fig. 7.1), and the long-term climatic diagram from 1949-1991 (Fig. 3.2, p.25), shows that the first part of summer was exceptionally dry. Rainfall in September was only 7 mm, well below the long-term average of 59 mm for that month. Temperatures were generally higher with the mean annual temperature of 15.4°C being 1.6°C higher than the long-term average of 13.8°C (Fig. 3.2, p.25). The low rainfall and high temperatures are indicative of the drought conditions that prevailed during this study.

7.3.1 Radiation

Maximum incoming solar radiation (Fig. 7.2) steadily increased from 603 W m^{-2} in winter (July) to 1 136 W m^{-2} in summer (December). With the exception of December 1990 which was cloudy in the afternoon, the bell-shaped curves of solar radiation depict the clear days on which the microclimate measurements were taken.

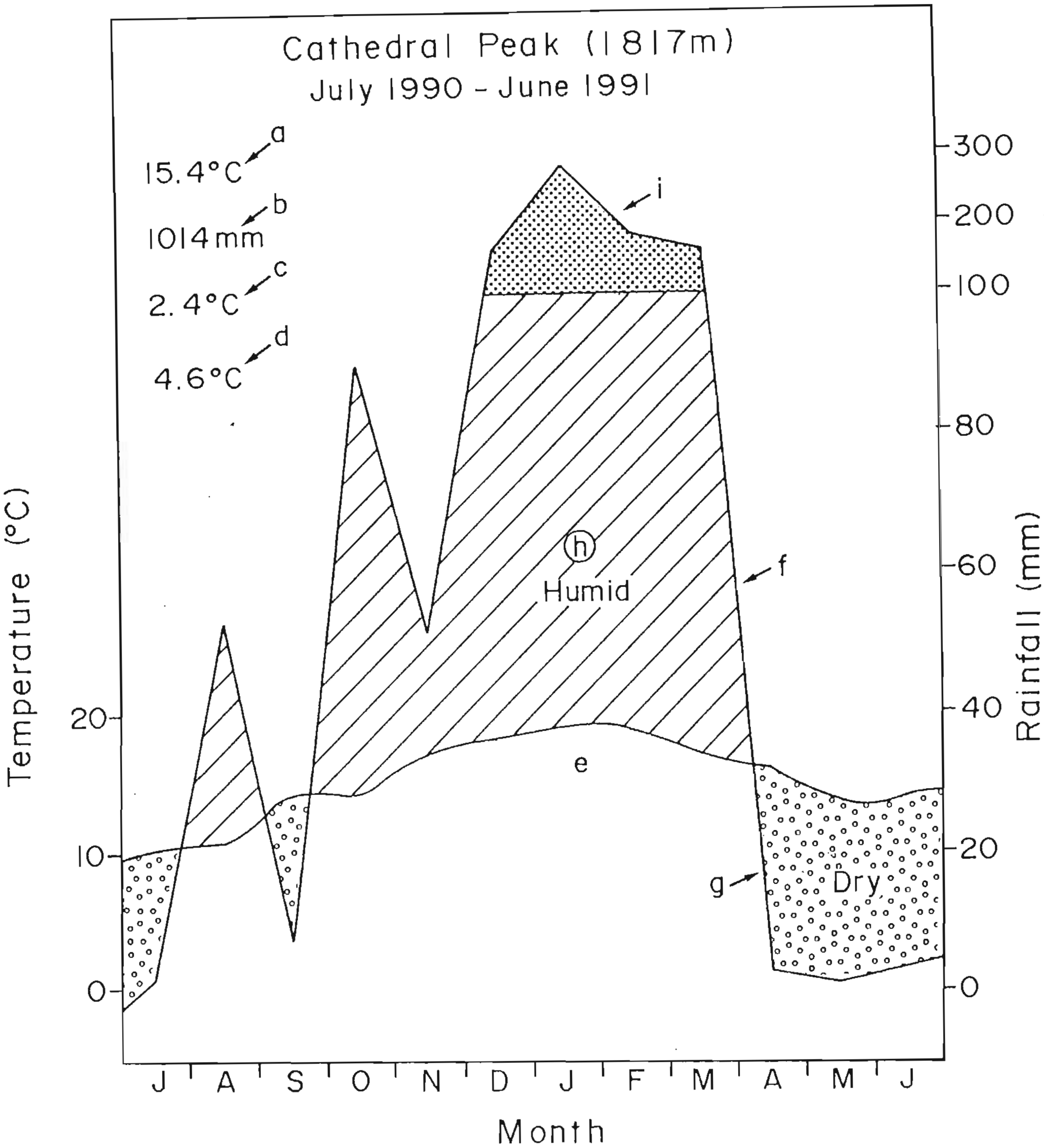


Figure 7.1 A climatic diagram for Cathedral Peak for the duration of the microclimate study. The symbols of the diagram have the following meanings: a, mean annual temperature; b, mean annual rainfall; c, mean daily minimum temperature of coldest month; d, lowest absolute minimum temperature; e, mean monthly temperature; f, mean monthly rainfall; g, drought period; h, humid period; i, mean monthly rainfall exceeding 100 mm with scale reduced to a tenth.

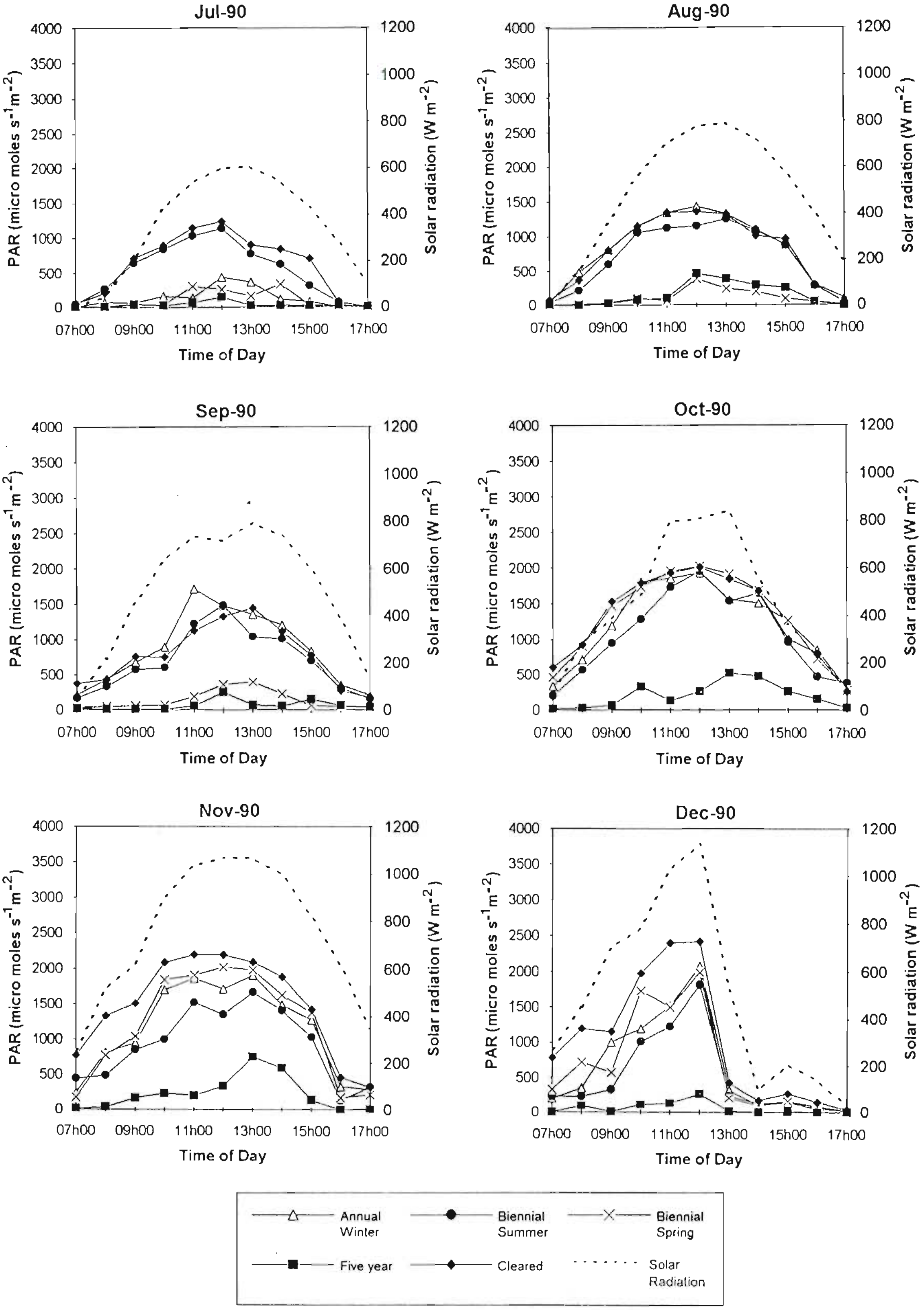


Figure 7.2 Daily trends in PAR and solar radiation in five disturbance treatments on selected days from July 1990 to December 1990.

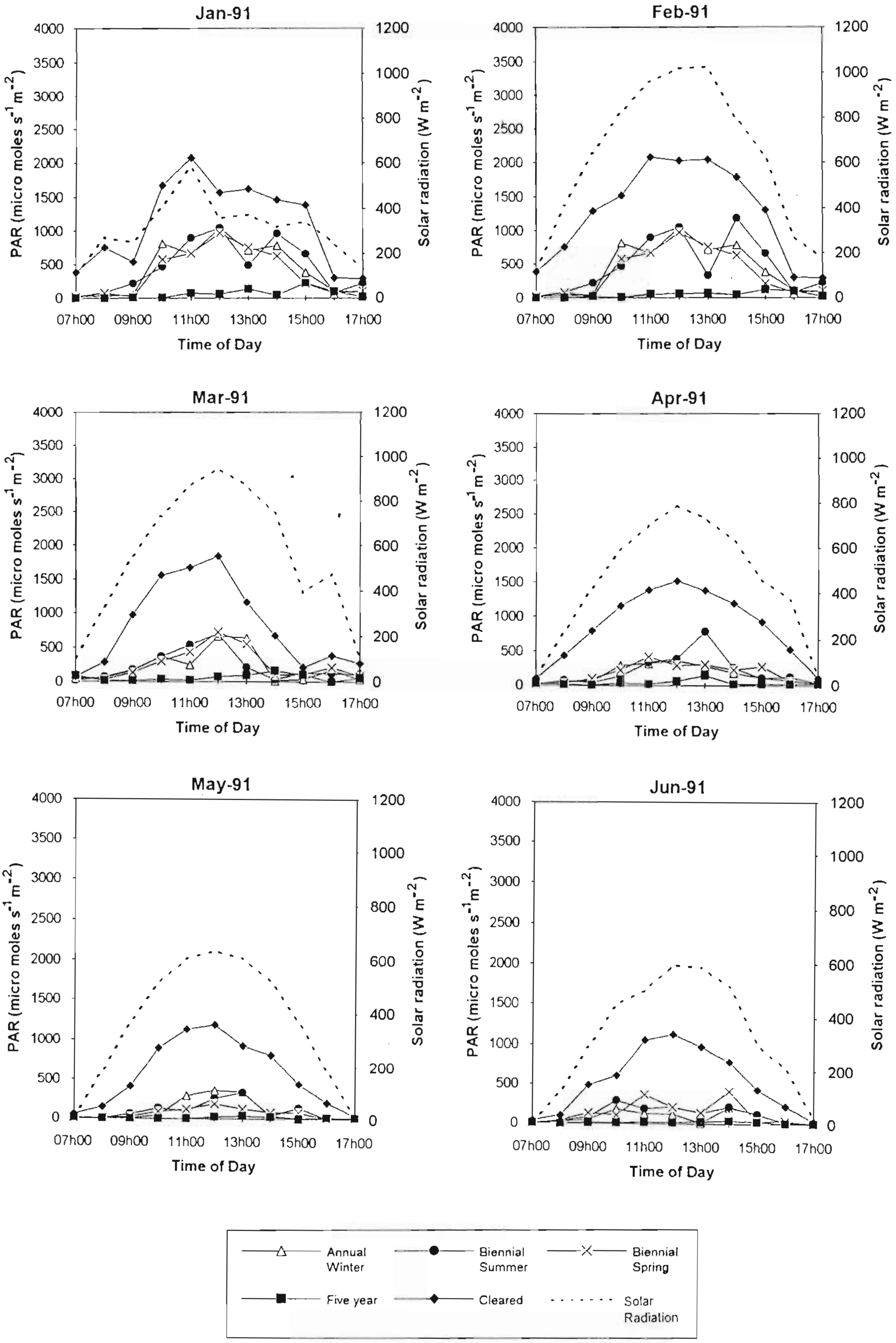


Figure 7.2 cont. Daily trends in PAR and solar radiation in five disturbance treatments on selected days from January 1991 to June 1991.

The effect of burning on PAR is clearly illustrated in the annual winter burn treatment (Fig. 7.2) where maximum radiation intensity increased from 430 μmoles s^{-1} m^{-2} prior to the burn (July), to 1 479 μmoles s^{-1} m^{-2} in August (three days after the burn). The application of the biennial spring burn in October also resulted in a sharp increase in PAR from a maximum of 394 μmoles s^{-1} m^{-2} in September to a maximum of 2 021 μmoles s^{-1} m^{-2} immediately after the burn (Fig. 7.2). As the canopy developed, PAR decreased in both treatments to <1 000 μmoles s^{-1} m^{-2} at midday (January). In the cleared site the high radiation continued into the summer months reaching a maximum of 2 419 μmoles s^{-1} m^{-2} in February. The dense canopy of the five-year burn had a significant effect on reducing light penetration at the soil surface. Maximum light recorded in November was <751 μmoles s^{-1} m^{-2}.

7.3.2 Soil moisture

As the study area lies in the summer rainfall zone of southern Africa, plants are most likely to experience maximum soil moisture stress at the end of the winter season. This was apparent in the annual winter burn, the biennial summer burn and the cleared site where soil moisture in July (mid-winter) was <42% (Fig. 7.3). This value is below the permanent wilting point of 43% of these soils (Everson CS 1979). In spite of only 0.6 mm rainfall in July (Fig. 7.1), soil moisture was above permanent wilting point in the biennial spring burn (62.2%) and the five-year burn (64.9%) treatments.

Under normal climatic conditions soil moisture increases with the onset of the spring rains in September providing moisture for germinating seedlings. However, the low rainfall recorded in September (Fig. 7.1) indicates that dry conditions can occur during the rainy season. The belated spring rains resulted in low soil moisture (<50%) during summer (November). However, such low values were not apparent in the five-year grassland where the moribund material acted as a mulch and a soil moisture of 91% was recorded. Surprisingly, throughout the study period, there was no significant difference in soil moisture between the cleared site and the other treatments (Fig. 7.3).

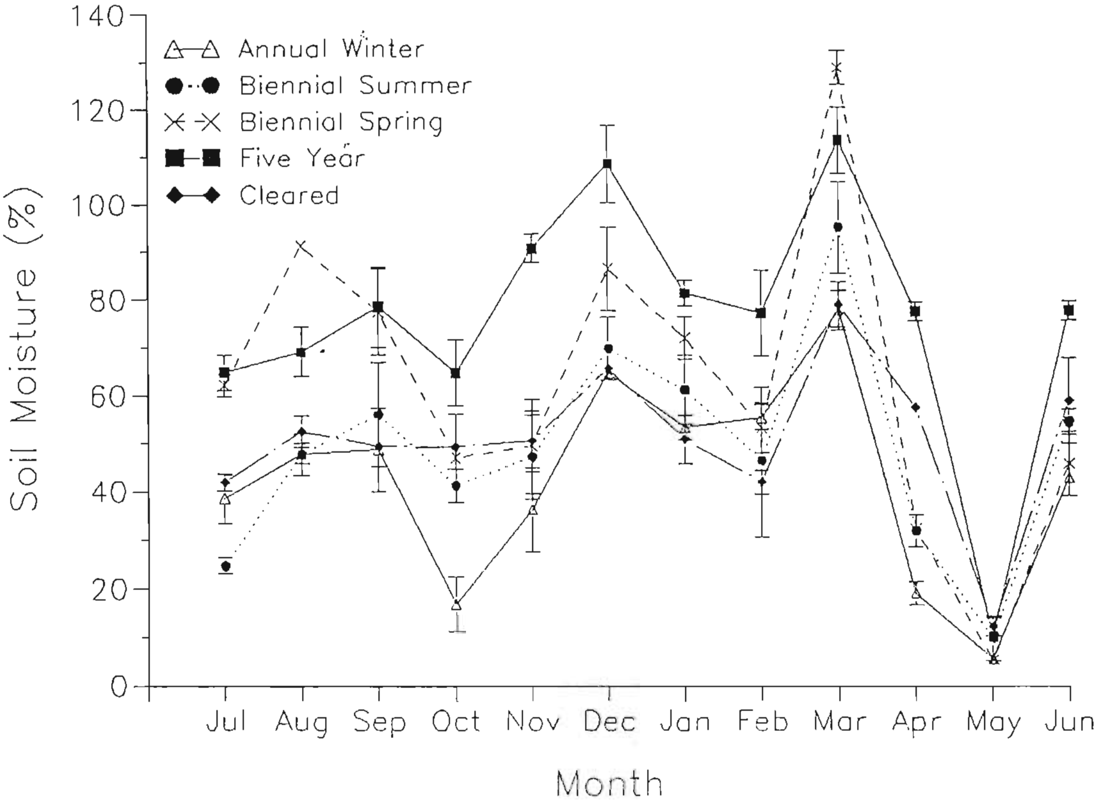


Figure 7.3 Monthly trends in soil moisture in different treatments from July 1990 to June 1991.

7.3.3 Vapour pressure deficit

Throughout the study period there was little difference in vapour pressure deficit between treatments (Fig. 7.4). Although there was a tendency for stress to be greater in the disturbed site and lower in the five-year burn treatment, these differences were variable. Plants are likely to experience high water stress at the end of winter because of low rainfall, the effect of hot, dry Berg winds in August/September and high radiation interception (Granger 1976). The high values of vapour pressure deficit recorded for all treatments from July to September (± 2.4-3.9 kPa) were therefore expected. While maximum vapour pressure decreased slightly to ± 2.8 kPa in October in response to 90 mm rainfall (Fig. 7.1), exceptionally high values (± 3.7 kPa) were recorded in November. Such severe drought in mid-summer, the growing season, can critically affect survival of seedlings. The arrival of the rains in December 1990 (169.6 mm) coincided with a sharp decrease in the vapour pressure deficit to 1.5 kPa.

7.3.4 Temperature

The diurnal fluctuations in temperature exhibited remarkably little variation between treatments (Fig. 7.5). The pattern of high temperatures occurring in summer (November-January), and low temperatures in winter (May-July) is evident. The coldest day during the study period was 14 August 1990 where air temperatures at the soil surface ranged from -2.54°C at 07h00 when frost was present on the ground to 23.81°C at 12h00. Such cold temperatures contribute to the high mortality of seedlings observed at this time of the year (Fig. 6.3, p.83). Winter day-time temperatures were relatively warm. Such warm conditions, associated with no rain and high radiation levels, are likely to enhance plant water stress. During the hottest day in the study (19 November 1990), temperatures ranged from 20.34°C at 07h00 to 36.80°C at 12h00 (Fig. 7.5). Since rainfall was <50 mm, seedlings would be subject to extreme stress during this period.

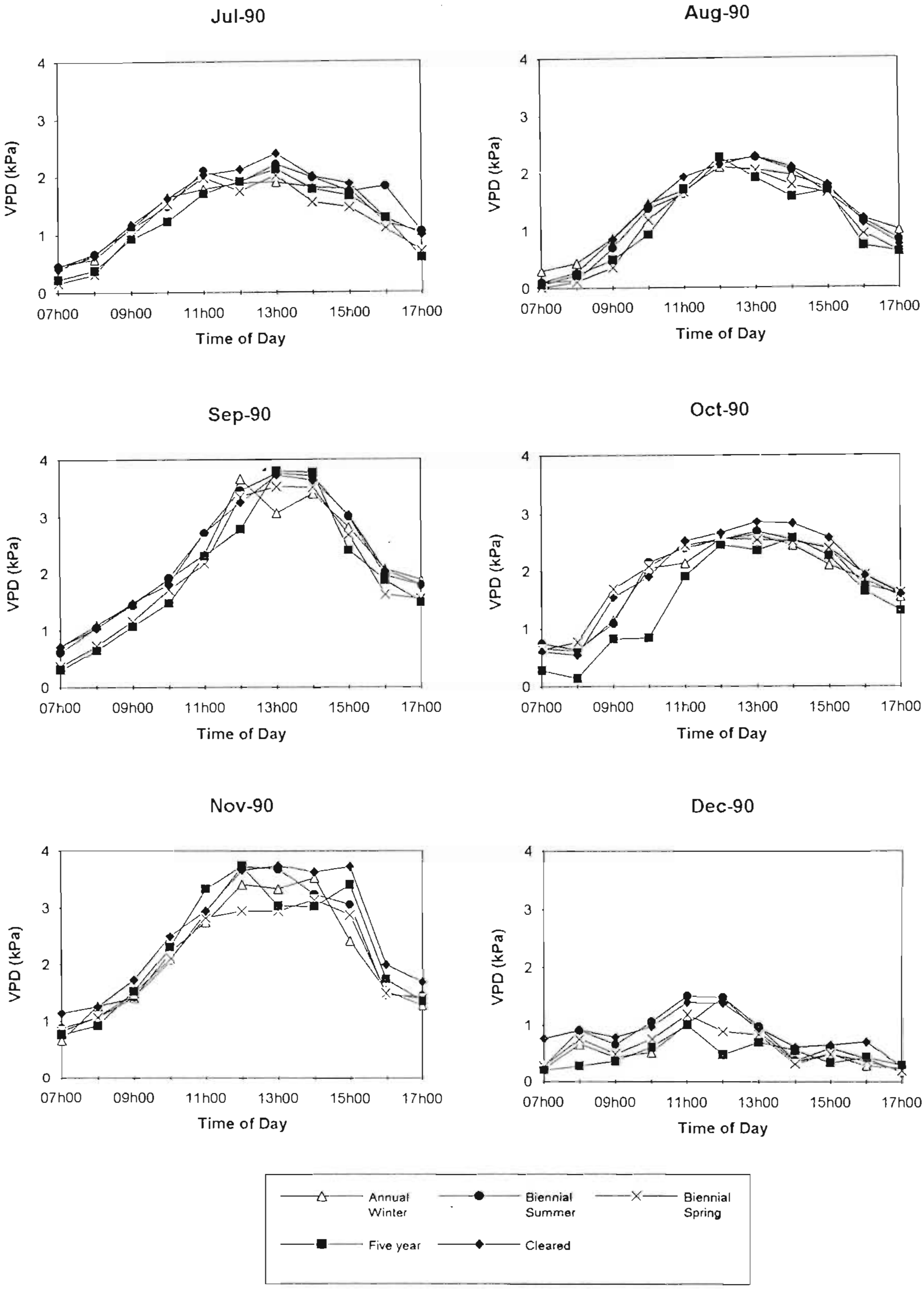


Figure 7.4 Daily trends in vapour pressure deficit in five disturbance treatments on selected days from July 1990 to December 1990.

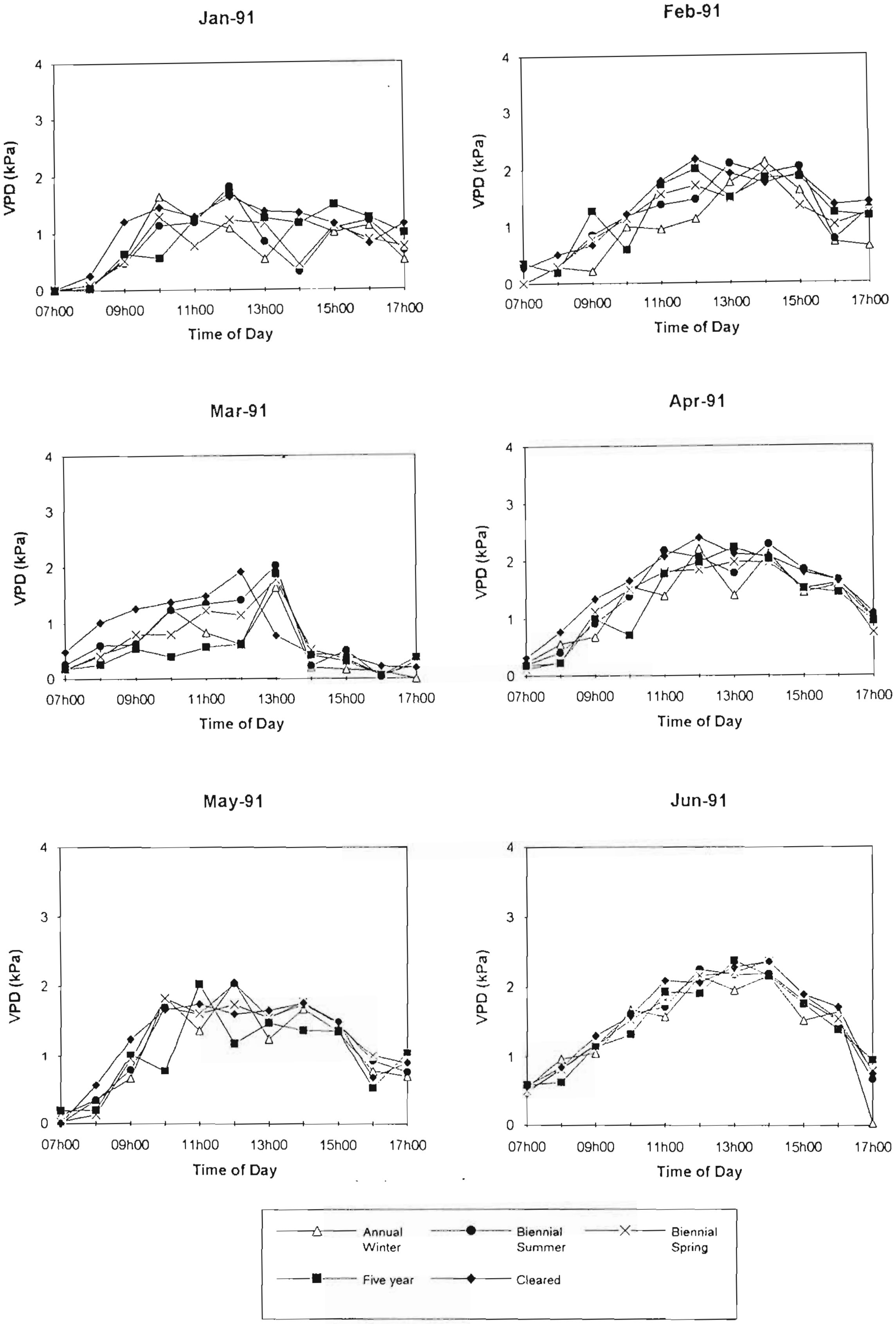


Figure 7.4 cont. Daily trends in vapour pressure deficit in five disturbance treatments on selected days from January 1991 to June 1991.

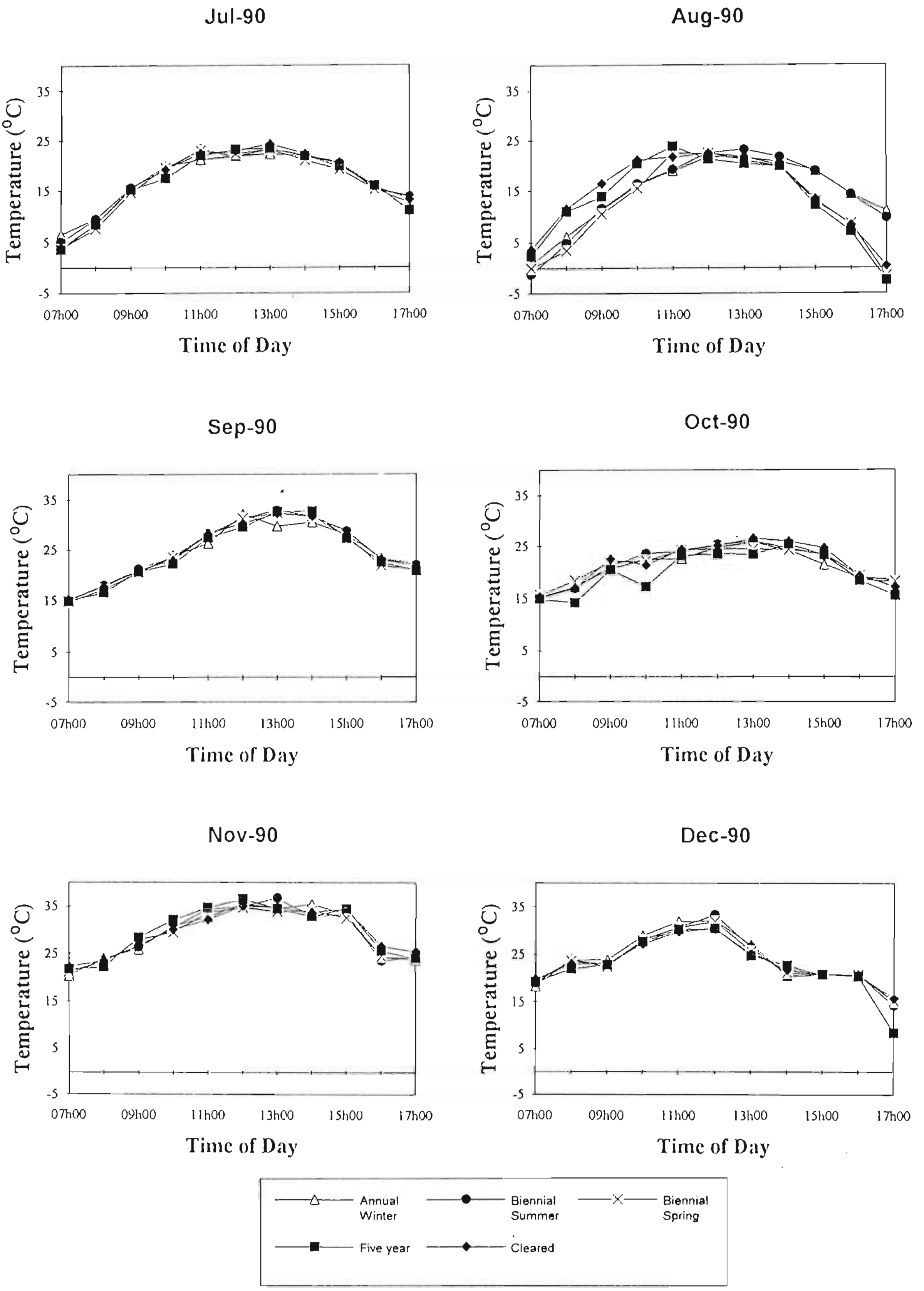


Figure 7.5 Daily trends in temperature in five disturbance treatments on selected days from July 1990 to December 1990.

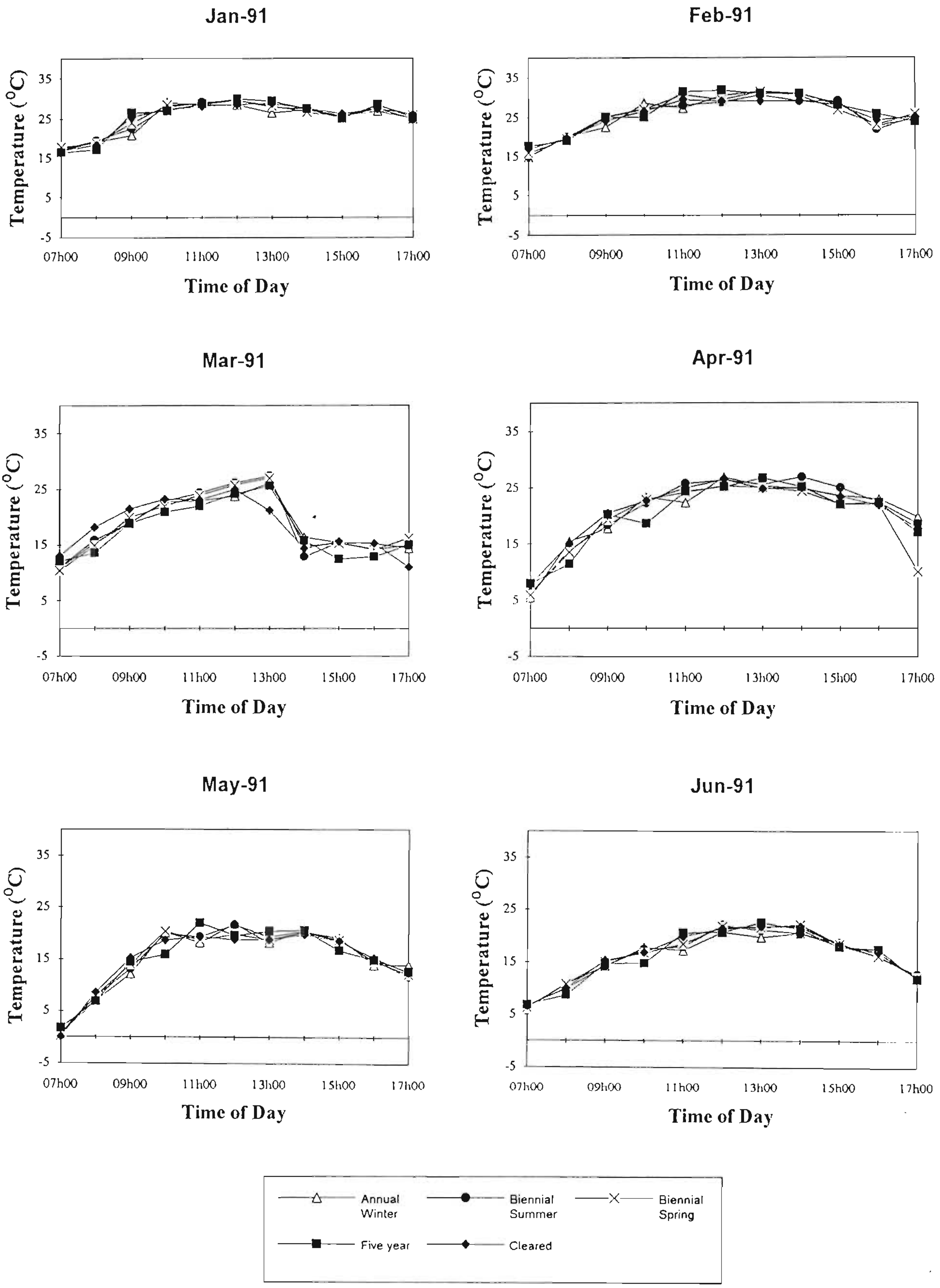


Figure 7.5 cont. Daily trends in temperature in five disturbance treatments on selected days from January 1991 to June 1991.

7.4 Discussion

An important factor in the process of secondary succession is the ability of the residual flora to tolerate changed microclimate (Archibold 1980). A knowledge of the microclimatic factors that influence seedling establishment will therefore be necessary in grassland rehabilitaiton programmes. The nature of the micro-environment is largely dependent on its plant cover and structure, which can be manipulated by man (Edwards, Booysen & Mappledoram 1972). In particular, the application of different burning regimes can alter the grass microclimate and influence seedling establishment. The microclimates created in the different burning treatments and in the denuded site of this study are related to observed patterns of seedling establishment.

In the grasslands of this study, high light levels following burning coincided with high establishment of seedlings. However, continued high light intensities are detrimental to seedling survival. The poor seedling establishment in the denuded site is attributed to the high values of PAR recorded throughout the year. This indicates that a canopy cover is necessary during colonization to protect young seedlings from high levels of PAR. Conversely, insufficient irradiance can have a negative effect upon colonization of seedlings (Goldberg 1987). In the five-year burn treatment, light intensity below the canopy was significantly lower than in the other treatments. This corresponded to an exponential decrease in seedling establishment in the years following the treatment burn. Continuous low light is therefore detrimental to seedling establishment.

Successful establishment from seed requires adequate soil moisture for seedling development. Fowler (1988) reported that shortage of water was the main cause of seedling death in *Aristida*-grassland since most grass seedlings dried out without visible damage. In the present study, the main cause of death is also likely to be due to desiccation since no physical damage to the dead seedlings was observed. During winter, soil moisture was recorded below permanent wilting point in the three treatments with the lowest seedling establishment, namely the cleared site, the annual winter burn and the biennial summer burn treatments. This indicates that soil water availability is a significant factor determining seedling establishment.

The water retention properties of a soil depend on the amount of organic matter present. The soils of the Drakensberg have a high organic content and soil moisture in excess of 100% is common (Everson CS 1979). The high soil moisture (128.8%) recorded in the biennial spring burn of March 1991 demonstrates the ability of the soil to act as a sponge and retain water. In years of normal rainfall this may provide sufficient moisture for survival of the seedlings until the spring rains. However, the effect of the drought was apparent in this study with moisture falling below the permanent wilting point in the rainy season (November). Such dry conditions would have a catastrophic effect on seedling survival. Hagon & Groves (1977) showed that organic mulches may benefit seedling establishment by decreasing soil water loss. This appeared to be the case in the five-year burn where the accumulation of moribund material resulted in cool, moist conditions even in the dry months.

One of the factors determining the ability of a seedling to survive inadequate soil moisture is the development of a root system capable of supporting the plant through later periods of water stress (Frasier, Cox & Woolhiser 1987). The seedlings of *T. triandra* observed in this study had poorly developed root systems. Since most of their roots occurred in the top 100 mm of soil they were susceptible to moisture stress during the dry season.

Vapour pressure deficit is a measure of the atmospheric moisture stress that the seedlings are subjected to. While there was a trend for lower vapour pressure deficit in the five-year burn when compared to the other sites, between site differences were generally variable. The most significant observation in this study was that the high deficits recorded in the dry winter period persisted into summer. Although such severe drought conditions may be atypical of the normal summer rainy season in the Drakensberg, hot periods of 2-3 weeks duration without rain can occur in mid-summer (J.E. Granger, personal communication). Thus seedlings may be subjected to high stress in the active period of growth, summer.

In mountains where temperatures are generally low, plants can thrive only in the zone close to the ground level where the soil acts as a heat reservoir and provides the necessary microclimate (Geiger 1957). The high number of seedlings establishing after a burn (Chapter 6) may be due to the increase in temperature at the soil surface. Daubenmire (1968) reported that after a fire the blackened and unshaded soil is warmer than soil in unburned areas. However, in the present study, the winter burn in July, the spring burn in September and the summer burn in January had no noticeable effect on air temperature at the soil surface. Therefore temperature patterns in the different treatments may not be related to seedling establishment. The absence of significant differences between the surface air temperature at the denuded site and that of soil covered with vegetation was surprising since cooler temperatures would be expected beneath the plant canopy. One of the reasons for this may be that turbulent mixing of the air at the soil surface reduces between site differences in air temperature. Alternatively, the small size of the bare patches of this study may not be sufficient to detect temperature differences. The extensive bare areas in degraded grassland, at times in excess of half a hectare, would be subject to greater exposure.

Williams & Ashton (1987) showed that disturbances in sub-alpine grasslands create microsites suitable for the establishment of shrub seedlings. Other studies have also shown that disturbance in grasslands is important for seedling recruitment (Gross & Werner 1982, Rapp & Rabinowitz 1985, Silvertown & Tremlett 1989). By contrast, areas lacking cover are fully exposed to sun, wind and rain and only hardy pioneer plants may be able to withstand these extreme conditions. In the cleared sites of this study, vegetation, top-soil, litter and mulch were absent. The low number of grass seedlings recorded at these sites indicates that denuded sites do not create a favourable microclimate for grass seedlings. One of the reasons for this may be frost activity which has been attributed to high seedling mortality in other alpine ecosystems (Bliss 1985). In this study frost activity was frequently observed particularly in the cleared areas. The lifting of the seedlings out of the soil exposes the roots resulting in desiccation of the seedling.

While the microclimate characteristics of the different treatments apply only to the year of the study, certain trends are apparent which should be taken into account in rehabilitation programmes. The most important factor influencing survival of seedlings is soil moisture. The high soil moisture recorded in the five-year burn during the drought is attributed to the thick layer of litter which accumulated in the absence of fire. Since a similar effect can be created by mulching, this is recommended for grass seedling re-establishment in the Drakensberg. Hagon & Groves (1977) showed that in Australia, re-establishment of *T. triandra* could be improved by mulching to prevent moisture loss and raise soil temperatures. The second most important factor influencing seedling establishment is light. Although increased light following burning favours seedling establishment, the continuous high light intensities recorded in the cleared sites were detrimental to seedling establishment. If mulching is applied in rehabilitation programmes it is necessary to determine the density of mulch that would allow sufficient light for germinating seedlings. Although no single treatment could be related to the complex seedling dynamics in these grasslands, the results contribute to a greater understanding of the microclimatic factors which are important in seedling establishment.

Chapter 8
Competitive interactions in *Themeda triandra* grassland

8.1 Introduction

The main constraint to successful establishment of grass seedlings in the Drakensberg is the high mortality of seedlings (Chapter 6). Proximity of seedlings to each other and the spatial arrangement of neighbours can affect the performance and life history characteristics of individuals in a population (Moore & Chapman 1986). In the dense grassland of the Drakensberg, inter and intraspecific competition for limited resources is likely to be an important factor contributing to mortality of grass seedlings. Since *T. triandra* dominates in both biomass and abundance in these grasslands, intraspecific interactions are most likely to affect size and reproductive potential of individuals of this species.

Adult plants in these grasslands are mainly perennial tufted species that are well adapted to present climatic conditions. Unlike pioneer species, they depend on vegetative tiller production rather than seed production for survival. Tufted grasses do not die after reaching a certain size but have the ability to continue growing more or less indefinitely (Acocks 1990). This growth habit has led to the belief that individual grass tufts may be hundreds of years old and co-exist with one another (Rattray 1960). Plants with a large biomass have a competitive advantage for limited resources and inhibit the development of other species (Peart 1989). *Themeda triandra*, by virtue of its high basal cover and large biomass, appears to be a vigorous competitor in regularly burnt grassland. However, its inability to survive severe disturbance implies that this competitive advantage is not maintained when the dynamic equilibrium of the climax grassland is upset.

When there is a short-term change in resources, such as increase in light intensity after fire, the competitive ability of a plant determines whether it will increase or decrease in abundance. The competitive superiority of *T. triandra* is not maintained with different burning regimes. For example, burning in summer destroys the vegetative tufts of *T. triandra*, resulting in gaps in the vegetation (Everson CS, Everson TM & Tainton 1985). A knowledge of how the surrounding species react to these local extinctions will indicate which species are likely to be most successful in rehabilitation programmes. It will also show whether secondary succession of disturbed sites can be speeded up by reseeding with indigenous species. The competitive interactions of the *T. triandra* plants in this study were examined to provide evidence for the acceptance or falsification of the following hypotheses:

- *Hypothesis 1*: **Intraspecific interactions reduce the growth, reproductive potential and survival of seedlings of *T. triandra*.**

Seed dispersal typically reduces competition between individuals since seeds are transported away from the parent plant. In *T. triandra*, however, the seed dispersal mechanism is poorly developed and most seeds fall in close proximity to the parent plant (Chapter 4). High mortality and failure of seedlings growing close to each other to reproduce suggests that intraspecific competition maintains seedlings as minor contributors to the structure of the grassland community.

- *Hypothesis 2*: **Intraspecific interactions between tufts of *T. triandra* reduces the size and reproductive potential of adult plants.**

In the dense grasslands of the study area, where mature tufts of *T. triandra* occupy similar niches, it is unlikely that plants can avoid competition. Intraspecific competition between individuals will therefore determine the potential size of tufts.

- *Hypothesis 3*: **Interspecific interactions that affect plant performance (e.g. reproductive potential) depend on fire regime.**

The growing zones of grass plants are situated at or immediately below the surface of the soil, and are therefore protected from fire. If fire or defoliation does not take place, the accumulation of organic material shades the base of the grass plant resulting in aerial tiller development at the expense of basal tiller development. These aerial tillers do not develop their own root system and eventually die. Excessive base shading therefore leads to low tiller densities and contributes to reduced productivity (Everson CS, Everson TM & Tainton 1988). Different grass species react to defoliation in different ways depending on the position of the growing zone. For example, regular burning favours species such as *T. triandra* which produce tillers either at the soil surface or above the ground. Increased light after fire stimulates the growth of new shoots, giving this species a competitive advantage over those that require low light levels for tiller initiation (e.g. *Tristachya leucothrix*).

8.2 Study area

In addition to the annual winter, biennial summer, biennial spring and five-year burn treatments, cleared treatments were established for the competitive exclusion experiments. These experiments, which required disturbance of the vegetation, were conducted in the immediate vicinity of the Brotherton burning trial in vegetation that had been burnt biennially in spring for at least 30 years.

8.3 Methods

8.3.1 Intraspecific competition of seedlings

Competition between *T. triandra* seedlings was determined by comparing the growth of seedlings in dense and sparse conditions. Since high mortalities occurred during experimental planting of seedlings in the field, an *in situ* approach was used. Twenty-five seedlings of *T. triandra* were randomly selected and tagged in each of two sites located within five metres of each other in a biennial summer burn treatment. A small patch of crowded seedlings was located in a 100 mm gap between two grass tufts. This represented the high density site and was equivalent to approximately 100 seedlings m^{-2}. Such patches of clumped seedlings occurred regularly in the grassland, and did not appear to be associated with gaps of specific sizes during the mapping of seedlings (Chapter 6). The low density site was represented by approximately 30 seedlings m^{-2}. Growth of each plant was determined by measuring the length of the longest leaf at weekly intervals and by counting the number of tillers per seedling at the end of the growing season. Since plants typically start dying back in late summer, measurements were obtained only from plant tissue that was green.

Growth of seedlings at the two sites was compared using the Wilcoxon-Mann-Whitney test (Siegel & Castellan 1988). Correlation analysis was used to examine whether growth was associated with either rainfall or maximum temperature (Zar 1984). The null hypothesis, that there was no difference in survival between the low and high density populations of seedlings, was tested by χ^2 analysis. The Wilcoxon-Mann-Whitney test was also used to compare differences in tiller numbers between the seedlings growing at the two sites.

8.3.2 Intraspecific competition of adult plants

8.3.2.1 *Nearest neighbour technique*

The effect of intraspecific competition on the growth and reproduction of adult plants was measured in the field using the nearest-neighbour technique of Pielou (1962). In this method the distance between a randomly chosen individual and its nearest neighbour is recorded and the size (circumference) of each tuft measured and summed for the two tufts. Measurements are made only if there is no individual of another species between the intraspecific pair of individuals under consideration. Twenty-five tufts of *T. triandra* were randomly selected and the shortest distance to the nearest neighbour measured. The circumference (mm) of each individual was measured, and the above-ground biomass was harvested from each plant at the end of the experiment. Harvested plant material was dried at 60°C to constant weight and weighed to the nearest gram. Reproductive potential was measured as the total number of flowering culms on each plant and its neighbour. Inflorescences are borne at the end of the flowering culm and bear groups of spikelets containing seeds. The number of spikelets per inflorescence was also counted. Regression lines were plotted between the variables measured (distance, circumference, number of tillers, number of inflorescences, number of spikelets and mass). The intensity of competition between intraspecific pairs of plants of *T. triandra* was determined by comparing correlation coefficients for each regression line. If competition is occurring, a significant and positive correlation will occur between distance and the sums of other parameters (e.g. distance versus sum of numbers of inflorescences).

Principal Components Analysis (PCA) is an alternative approach to examining relationships between plant variables for detecting patterns within the data that may be related to competitive interactions. PCA is an ordination technique for projecting a multi-dimensional group of points into a space of fewer dimensions so that similar samples are grouped together (Gauch 1982). In this study, PCA was performed on the nearest neighbour data set to determine whether the plants fall naturally into a number of distinct groups. The PCA from the statistical graphics system, Statgraphics (Version 5) produced by Statistical Graphics Corporation (1991), was used for the analysis.

8.3.2.2 *Isolation technique*

Competition between individuals was examined following deliberate removal of nearest neighbours. Fifty, even-sized tufts of *T. triandra*, approximately 200 mm in circumference, were selected at the time of flowering in December 1988. The size (circumference of the tuft), number of inflorescences and number of spikelets of each were measured. Half of the plants served as a control while the other half were isolated by clearing vegetation from a square meter around each tuft. A year later (December 1989), the measurements were repeated on the same plants. Intensity of competiton was tested using regression analyses of size of plants and number of inflorescences and spikelets for the control and cleared plots in 1988 and 1989. *T*-values were used to test the significance of the differences between the slopes and means of the regression equations for the control and cleared plots. Principal Components Analysis was applied to the experimental isolation data set to establish whether plants form homogenous groups on the basis of proximity of neighbours.

8.3.3 Interspecific competition under different burning regimes

A mapping technique was used to examine the effect of interspecific competition on basal cover of the dominant plants in four burning treatments. Nine quarter-square-metre plots were marked in each burning treatment; the annual winter burn, the biennial summer burn, the biennial spring burn and the five-year burn. The presence of every plant (grasses, herbs and sedges) in the plot and the basal area of every tuft of every species were mapped at a scale of 4:1 by the pantograph method described in Chapter 6. Total basal cover was mapped initially in 1986 to coincide with the scheduled treatment burns of all the sites (with the exception of the five-year burn which was two years old). The removal of the above-ground biomass by fire greatly facilitated mapping and increased the accuracy of the technique. Mapping took longer in the five-year burn due to the two years of accumulation of biomass in this treatment. The second mapping was carried out in 1988 and was again timed to coincide with scheduled burns. At this stage the vegetation in the five-year burn was four years old, so that the accumulated biomass and moribund material made it more difficult to map tuft boundaries precisely. A Calcomp 23180 digitiser (California Computer Products, Anaheim California) was used to measure the mapped area of each plant, of each species, in the nine replicates of the four burning treatments for both 1986 and 1988. The effect of burning treatment on the basal area of each species was compared with ANOVA after applying a ln(x+1) transformation to the raw data. The differences between treatments were determined by a Tukey Multiple Range test.

The dynamic nature of the grasses can be determined by counting the number of plants of the dominant species, *T. triandra, Tristachya leucothrix* and *Stiburus alopecuroides* that changed in size over two years. If the proportion of plants increasing is equal to the proportion decreasing then the community is in a state of dynamic equilibrium. If, however, the majority of plants are either decreasing or increasing in size, it is likely that a directional change is taking place and the community is not in equilibrium. A χ^2 analysis with three degrees of freedom was used to test whether the numbers increasing and decreasing were the same for all treatments. To test whether the proportion of the total number of plants increasing in size in two specific treatments was significant, the following formula (G.P.Y. Clarke, personal communication) was applied:

$$u = \frac{P_1 - P_2}{\sqrt{\frac{P_1(1-P_1)}{n_1} + \frac{P_2(1-P_2)}{n_2}}}$$

where u (standardized normal deviate) was significant at 5% if >1.96 and 1% if >2.54. P_1 and P_2 were the proportions increasing (i.e. the number of plants increasing divided by the total number of plants), and n_1 and n_2 were the total number of plants in each treatment.

In the mountainous terrain of the Drakensberg, soil exposed to high intensity storms increases runoff and sediment production. The reciprocal of basal cover, bare area, is an important indicator of the potential for soil erosion. The effects of the four burning treatments on the area of bare soil were determined using ANOVA techniques after $\ln(x+1)$ transformation. A Tukey Multiple Range test was used to determine which treatments were different.

8.4 Results

8.4.1 Intraspecific competition of seedlings

Throughout the growing season seedlings in the low density population were significantly taller than those in the high density population ($z = 5.11$, $P<0.001$) (Fig. 8.1). At the end of the season (mid-March), the mean maximum height reached in the high density site was 62 mm, approximately half that of the seedlings in the low density site (118 mm). Thus intraspecific competition reduced growth of seedlings of *T. triandra* by 52.5%. Besides being stunted, the seedlings in the high density population were frail when compared to the robust, sturdy seedlings in the low density population. At the end of the growing season, six out of a total of 25 seedlings had died in the low density plot and 11 out of 25 in the high density plot. These differences, however, were not significant.

Extension growth of the longest leaf increased steadily in both the low and high density seedling populations until mid-January (Fig. 8.1). Senescence at this time resulted in a steady decline in the amount of living leaf material. Both sites showed a second growth flush between February and mid-March, after which all growth ceased with the advent of the first frosts. There was no correlation between this growth pattern and rainfall. However, there was a positive correlation between maximum temperature and growth ($r=0.65$).

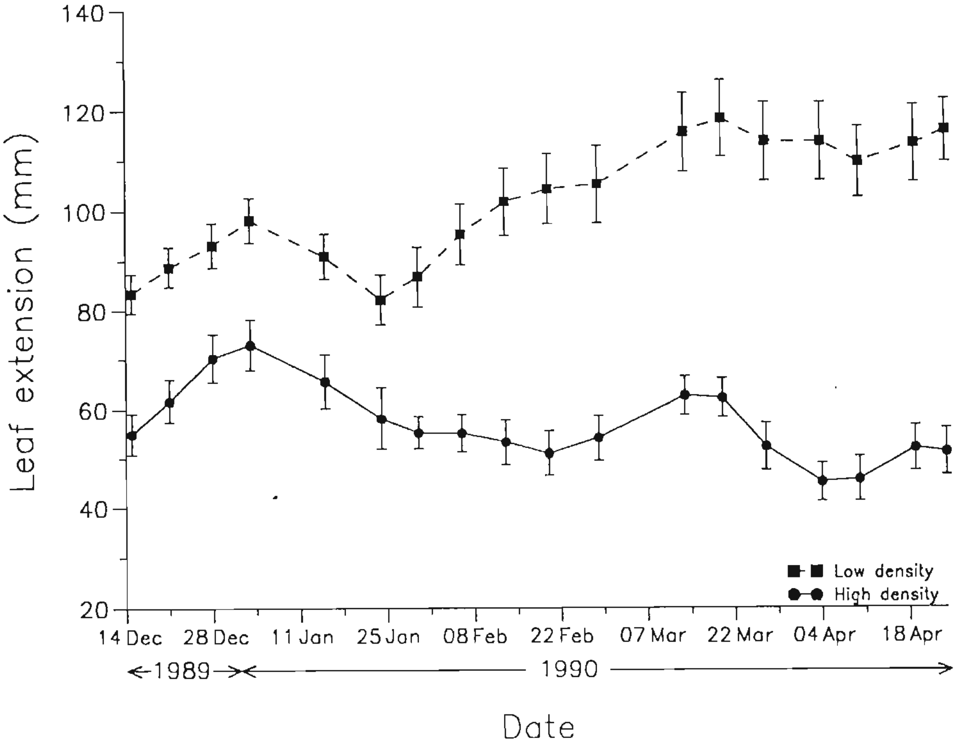


Figure 8.1 Mean growth of seedlings of *T. triandra* in a low and a high density site. Vertical bars represent the standard error of the mean.

Tiller production by the 25 seedlings differed markedly between the low and high density sites. In the high density plot, no new tillers were produced during the four-month monitoring period while in the low density plot there was a cumulative gain of 104 tillers ($\overline{x}$ = 5.16±0.7). Comparison of the average ranks of the samples led to a rejection of the null hypothesis that the samples have the same distribution (z = -5.67, $P<0.001$). Intraspecific competition between seedlings of *T. triandra* therefore significantly reduced tiller number.

8.4.2 Intraspecific competition of adult plants

8.4.2.1 *Nearest neighbour*

Pielou (1960) suggested that under competitive conditions a positive relationship would be detected between the distance from a plant to its nearest neighbour and the sum of the performance of both plants. However, no such relationship was found between distance and size of adjacent plants of *T. triandra* in this study. Similarly, no such relationship was found between distance and number of inflorescences, distance and number of spikelets, and distance and dry weight. Graphical representation of the PCA on the nearest neighbour samples (Fig. 8.2) indicates a lack of homogeneous groupings based on size. Over 90% of the variation among plants is accounted for by the first principal component which is circumference. The coefficient of the vector for distance is very small (0.005), indicating that distance between plants does not account for differences among plants in their size and flowering habits.

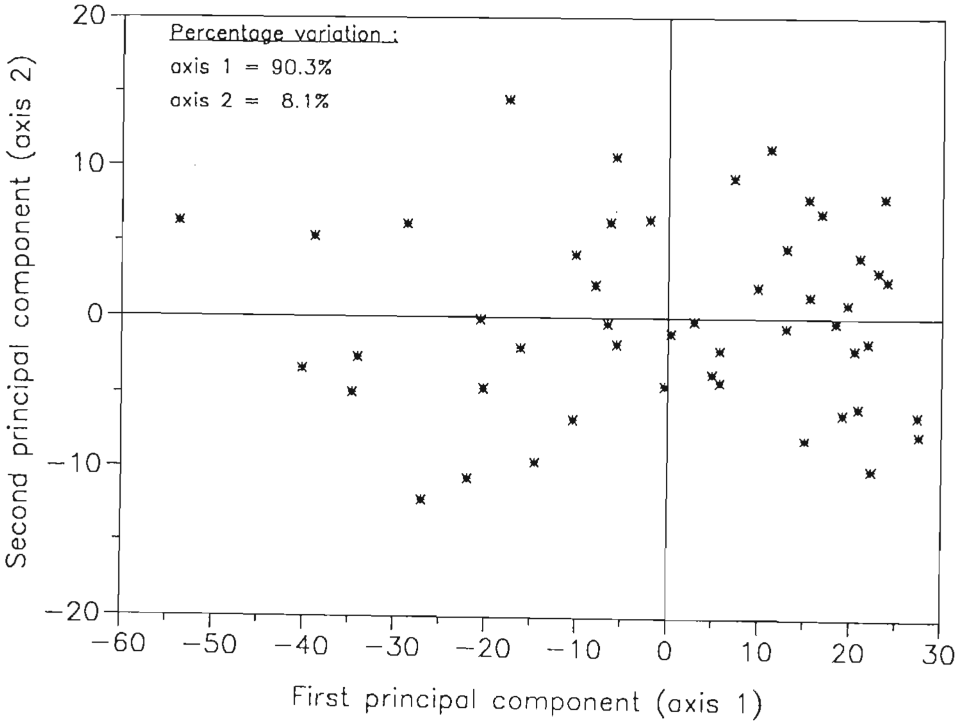


Figure 8.2 Principal components analysis of the nearest neighbour data.

8.4.2.2 *Isolation technique*

The regression of circumference against number of inflorescences (Fig. 8.3) shows that at the commencement of the experiment in 1988, there was no difference between the control and cleared plots. After one year there was no significant difference in size of plants in the control plot. By contrast, all plants in the cleared sites increased significantly in size ($P<0.001$). At the end of the experiment the circumference of plants in the cleared sites ($\overline{x}$ = 401±13.4 mm) was approximately twice that of the control plants ($\overline{x}$ = 199±8.7 mm, Table 8.1).

The number of inflorescences produced by plants in the control site was not related to size of tuft. For example, in 1988 the number of inflorescences produced on tufts of equivalent size (200 mm circumference) varied between four and thirty-two per plant (Fig. 8.3). However, after one year there was a significant correlation (r = 0.60, $P<0.001$) between size of plant and number of inflorescences in the cleared sites. Again, the number of reproductive tillers (inflorescences) was not proportional to the increase in circumference. The number of inflorescences on large plants (*ca.* 400 mm in circumference) ranged from 24 to 76. The regression coefficients of the 1989 control plot show that for every increase in circumference of 1 mm, there is a corresponding increase of 0.07 inflorescences (Table 8.1). This can be compared to the cleared plot where an increase of 0.25 inflorescences per mm increase in circumference can be expected (Table 8.1). The regression of change in size against change in the number of inflorescences (Fig. 8.4) indicates that bigger plants have a greater change in the proportion of inflorescences than do smaller plants.

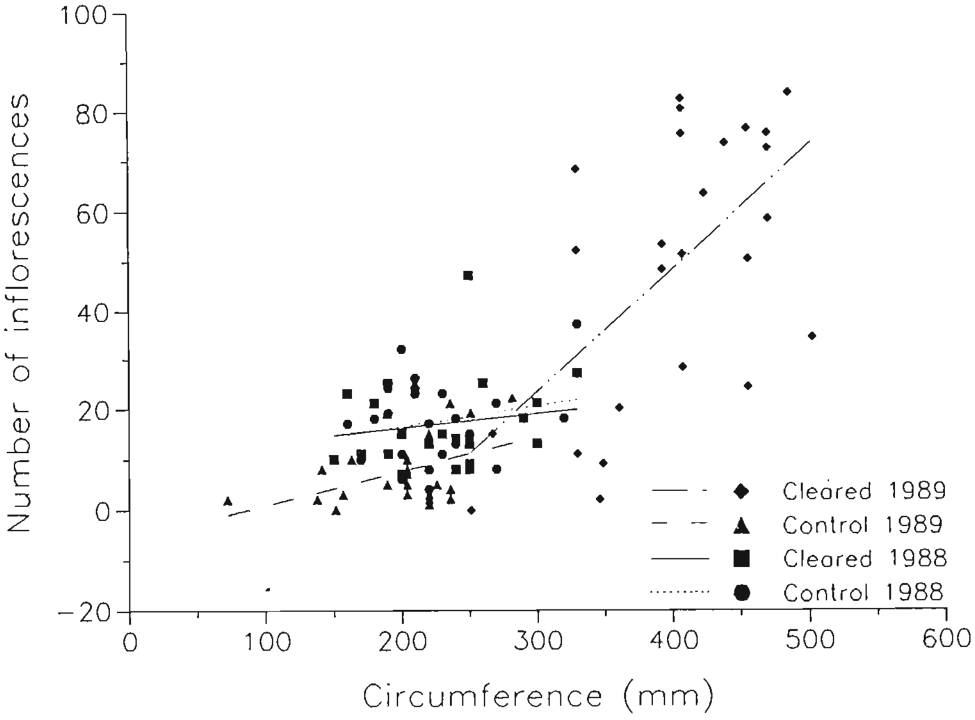


Figure 8.3 Regressions of circumference against number of inflorescences in the control and cleared sites in 1988 and 1989.

Table 8.1 A summary of linear regression analyses of the effect of size (circumference) on the number of inflorescences and spikelets of *T. triandra* in the cleared and control site in 1988 and 1989 (n=25)

Site	Yr	Regression variables	Mean	Slope	*F* ratio	Sig.
Cleared	88	Circum. vs number inflor.	222.56	0.0277	0.4661	NS
Cleared	89	Circum. vs number inflor.	401.00	0.2452	0.0016	***
Control	88	Circum. vs number inflor.	222.28	0.0402	0.3141	NS
Control	89	Circum. vs number inflor.	199.00	0.0676	0.0275	*
Cleared	-	Change in circum. vs chg. inflor.	175.40	0.2067	0.0776	*
Control	-	Change in circum. vs chg. inflor.	-23.80	0.0560	0.1144	NS
Cleared	88	Inflorescences vs number spikelets	16.76	1.7263	0.0001	***
Cleared	89	Inflorescences vs number spikelets	48.08	2.3611	0.0001	***
Control	88	Inflorescences vs number spikelets	17.28	2.0748	0.0001	***
Control	89	Inflorescences vs number spikelets	7.56	2.2639	0.0001	***

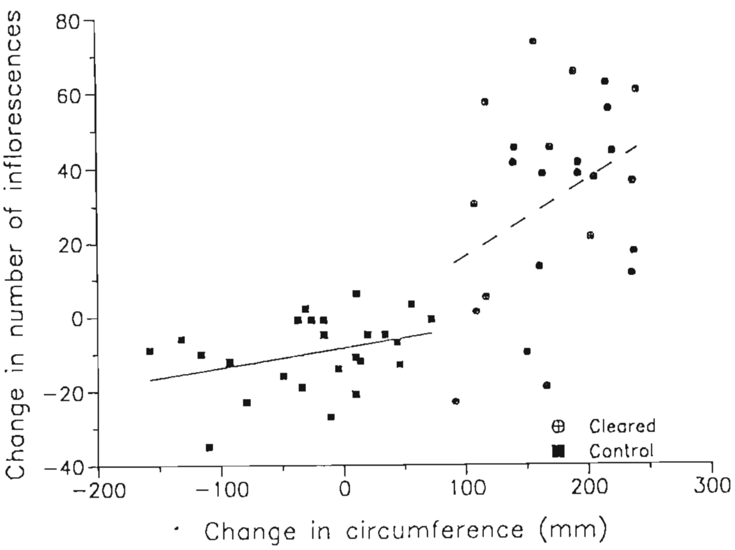


Figure 8.4. Regressions of change in circumference against change in the number of inflorescences in the cleared and control site.

There was a significant correlation between the number of inflorescences and spikelets for the control (r = 0.92) and cleared (r = 0.88) plot in 1988, and for the control (r = 0.98) and cleared plot (r = 0.90) in 1989 (Fig. 8.5). Therefore, the number of spikelets produced per inflorescence is independent of treatment.

The PCA plot of the experimental isolation data exhibits two distinct units, namely the control and cleared plots (Fig. 8.6). The samples from these plots differ markedly in size (the first principal component) and flowering habits (the second principal component). The scores of the cleared plants are clumped indicating that their size and flowering habit are less variable than in the control plants. By contrast, the wide dispersion of points along the second principal component axis in the control plants shows the high variability in flowering characteristics (production of inflorescences and spikelets).

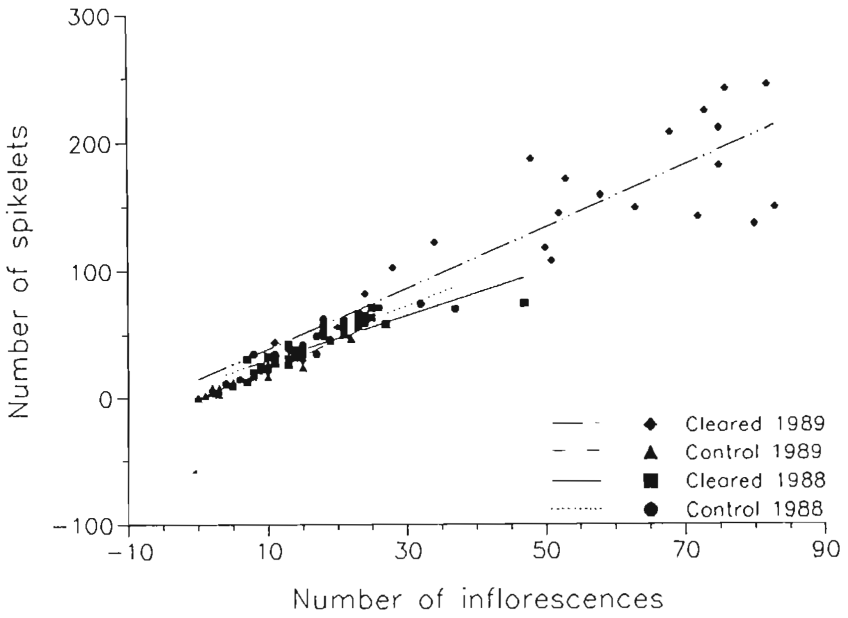


Figure 8.5 Regression of the number of inflorescences against spikelets in the control and cleared sites in 1988 and 989.

8.4.3 Vegetative basal cover

Mapping the vegetation in the four burning treatments showed that the competitive ability of different species changed with burning treatment. The extent of change in basal cover shows the dynamic nature of these grasslands.

An example of the maps for each treatment for 1986 and 1988 are presented in Figs. 8.7-8.10 to illustrate the extent of these fluctuations. In some cases, whole tufts disappeared within two years. For example, in the summer burn treatment, a large tuft of *Tristachya leucothrix* (area = 1 052 mm^2) situated at the bottom left of the plot (Fig 8.7a), was completely destroyed by this treatment (Fig. 8.7b). In the same treatment, four tufts of *Koelaria cristata* (total basal area = 1 332 mm^2) situated at the bottom right of the plot were also destroyed. The dominance of wiry species that tiller below the ground (e.g.

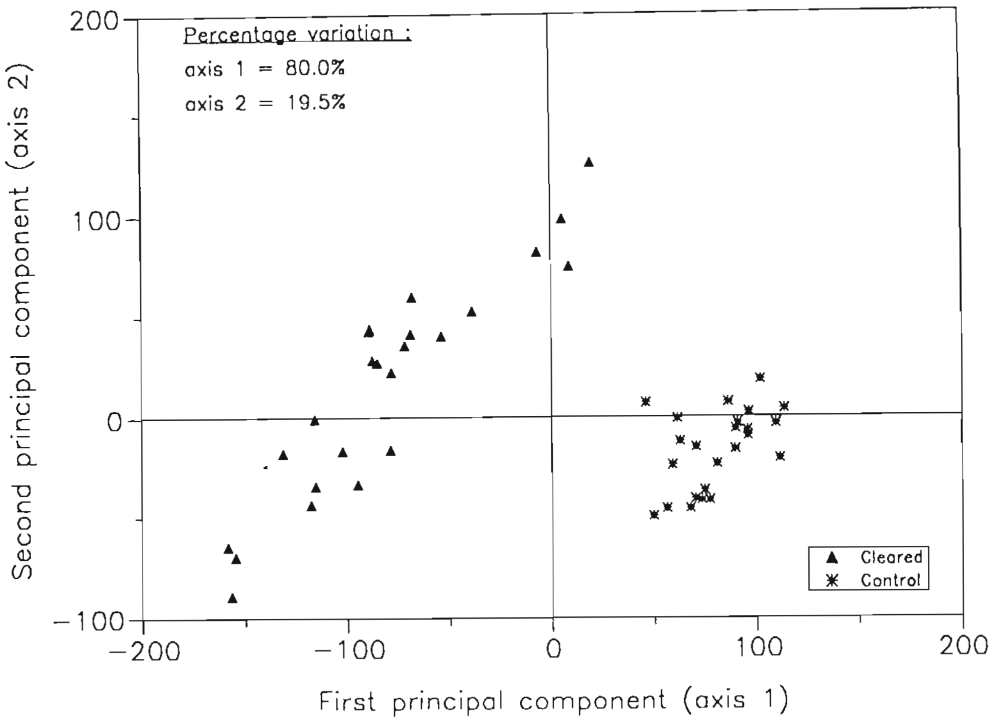


Figure 8.6 Scatterplot of the first two principal components (size and flowering habit) of *T. triandra* in the control and cleared sites.

Harpochloa falx) is typical of this treatment. Another feature of summer burning that is clearly visible in these maps is the absence of large tufts of *T. triandra*.

Lack of species diversity characterized the five-year burn treatment, with only two species, *Tristachya leucothrix* and *T. triandra* dominating in basal area (Fig. 8.8 a,b). Large bare areas between the plants are evident. Although there was a low number of tufts in this treatment, their basal area was generally high. Changes in the shape of tufts between 1986 and 1988 are clearly visible.

By contrast, at least five species were present in the annual winter burn, with the dominant species being *T. triandra* and *Heteropogon contortus* (Fig. 8.9 a,b). While one might expect major changes in the basal area of plants subjected to a severe treatment such as the summer burn, the degree of change in tuft size in the regularly burnt grassland was unexpected. In both the annual winter (Fig. 8.9 a,b) and biennial spring burn treatments (Fig. 8.10 a,b) tufts changed size and shape markedly over two years. The typical growth habit of *T. triandra* is evident in the map of the biennial spring burn treatment (Fig. 8.10 a,b). The large central tuft of *T. triandra* in the plot of 1986 had broken up into two smaller tufts by 1988.

The percentage basal area of the seven most abundant grass species (*T. triandra, Tristachya leucothrix, Stiburus alopecuroides, Heteropogon contortus, Diheteropogon amplectans, Koelaria cristata* and *Harpochloa falx*) was significantly different between the four burning treatments (Fig. 8.11). For example, in 1986 the basal area of *Themeda triandra* was high in the annual winter (62.5%), biennial spring (50.5%) and five-year burn (36.1%) treatments. By contrast, *T. triandra* contributed <11.5% of the total basal area in the biennial summer burn treatment. The species that dominated this treatment were *K. cristata, T. leucothrix* and *H. falx*, with basal covers ranging from 25.2-28.9%. These three species, which have a low grazing value, contributed <16% basal cover in the annual winter and biennial spring burn treatments. Among the most striking changes that occurred in the summer burn was the disappearance of *S. alopecuroides*. This species was most abundant in the five-year burn where it contributed 28.4% of the basal cover. The results of the ANOVA indicate a significant effect of treatment on the mean basal cover of *S. alopecuroides, T. triandra* and *K. cristata* ($P<0.01$).

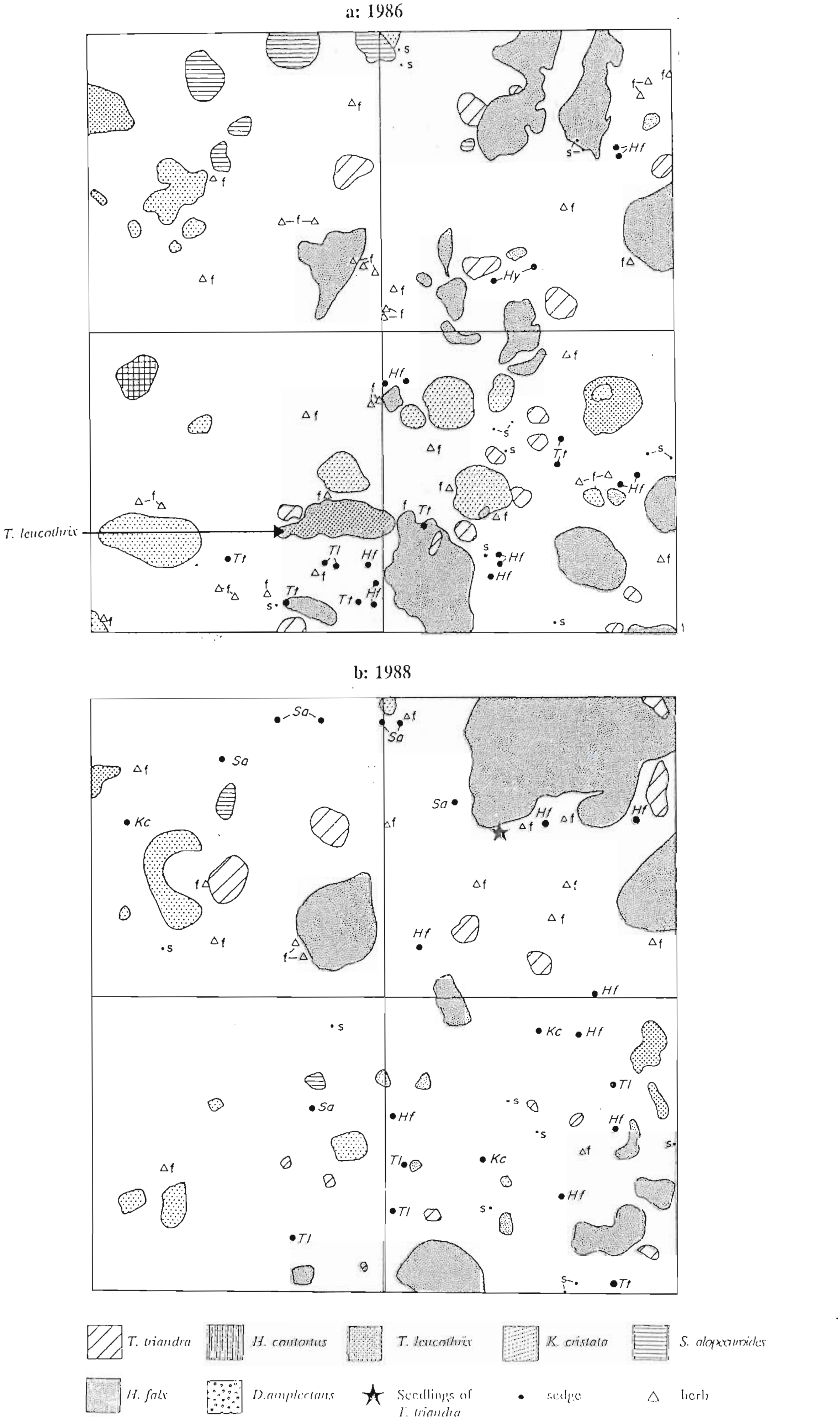


Figure 8.7 Typical map of the basal area of the vegetation in the biennial summer burn in 1986 and 1988. Scale 1:5.

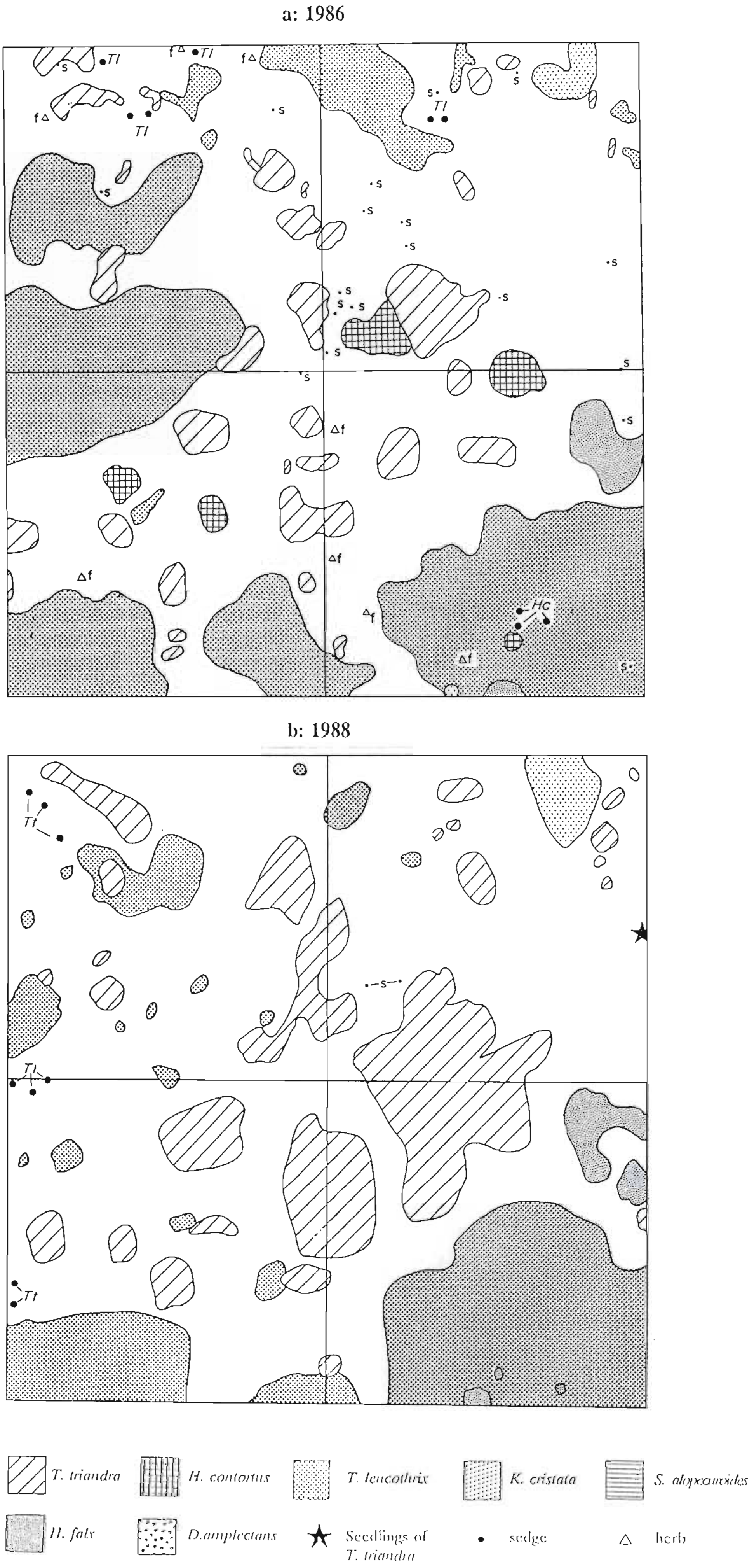


Figure 8.8 Typical map of the basal area of the vegetation in the five-year burn in 1986 and 1988.

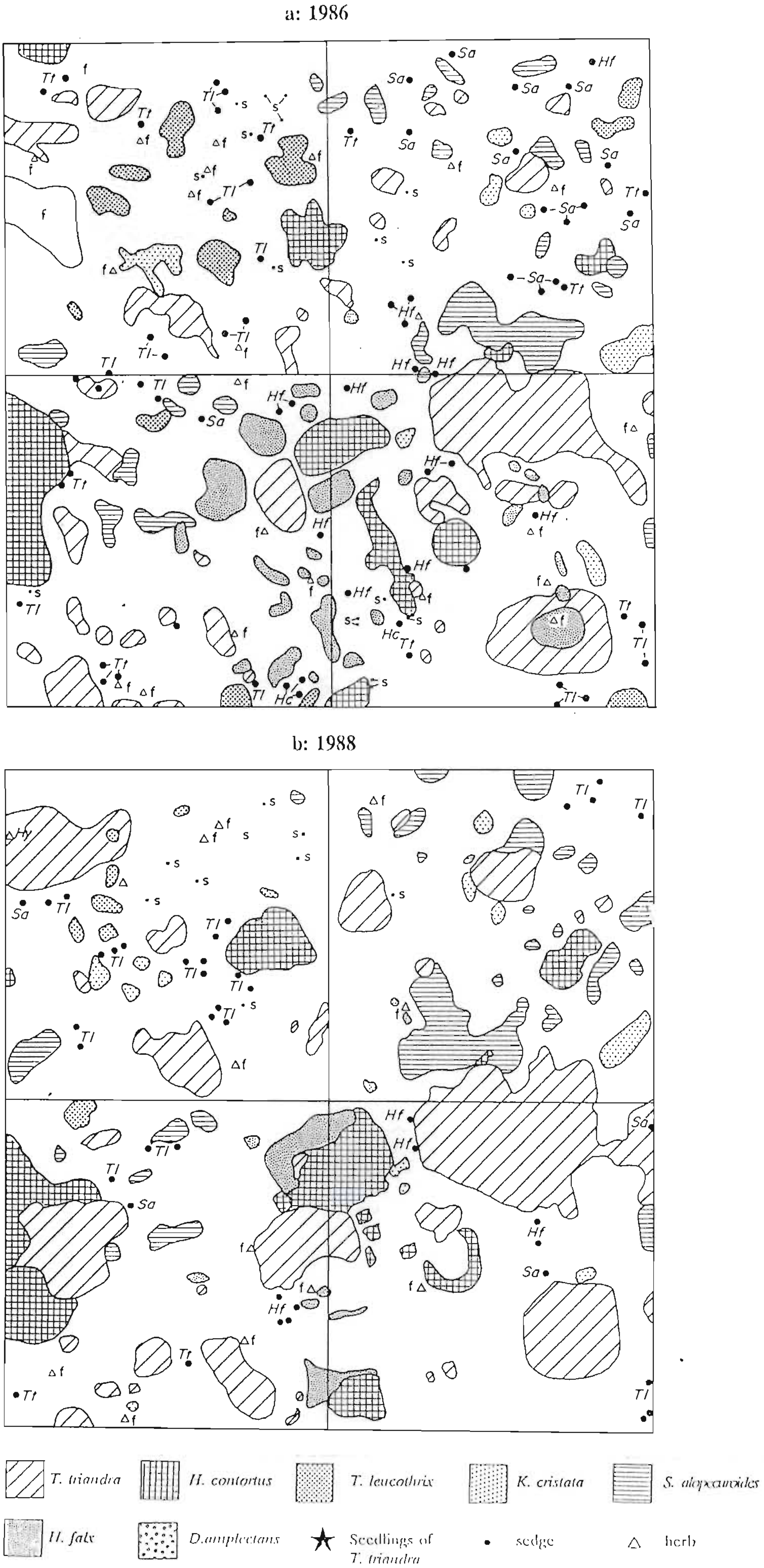


Figure 8.9 Typical map of the basal area of the vegetation in the annual winter burn in 1986 and 1988. Scale 1:5.

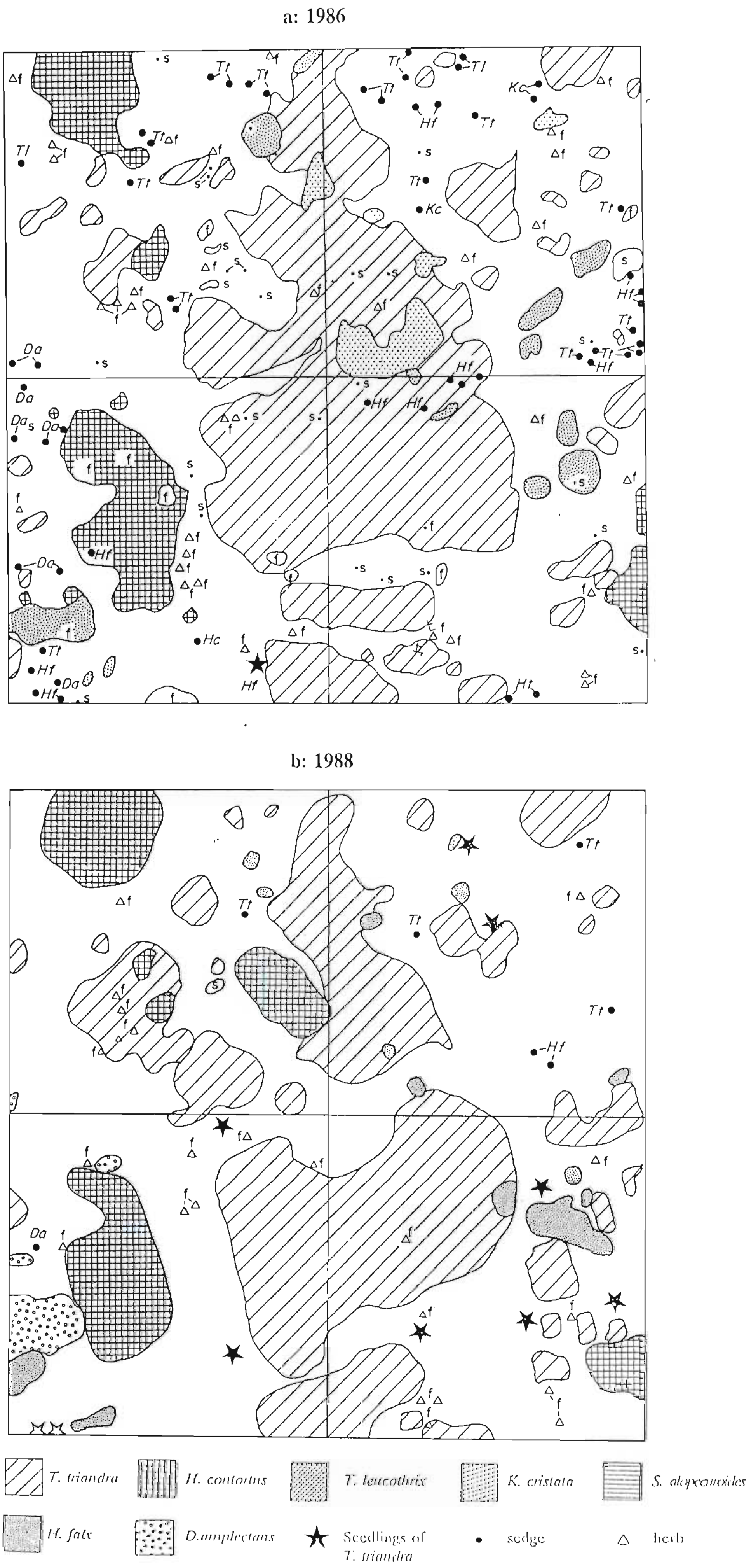


Figure 8.10 Typical map of the basal area of the vegetation in the biennial spring burn in 1986 and 1988. Scale 1:5.

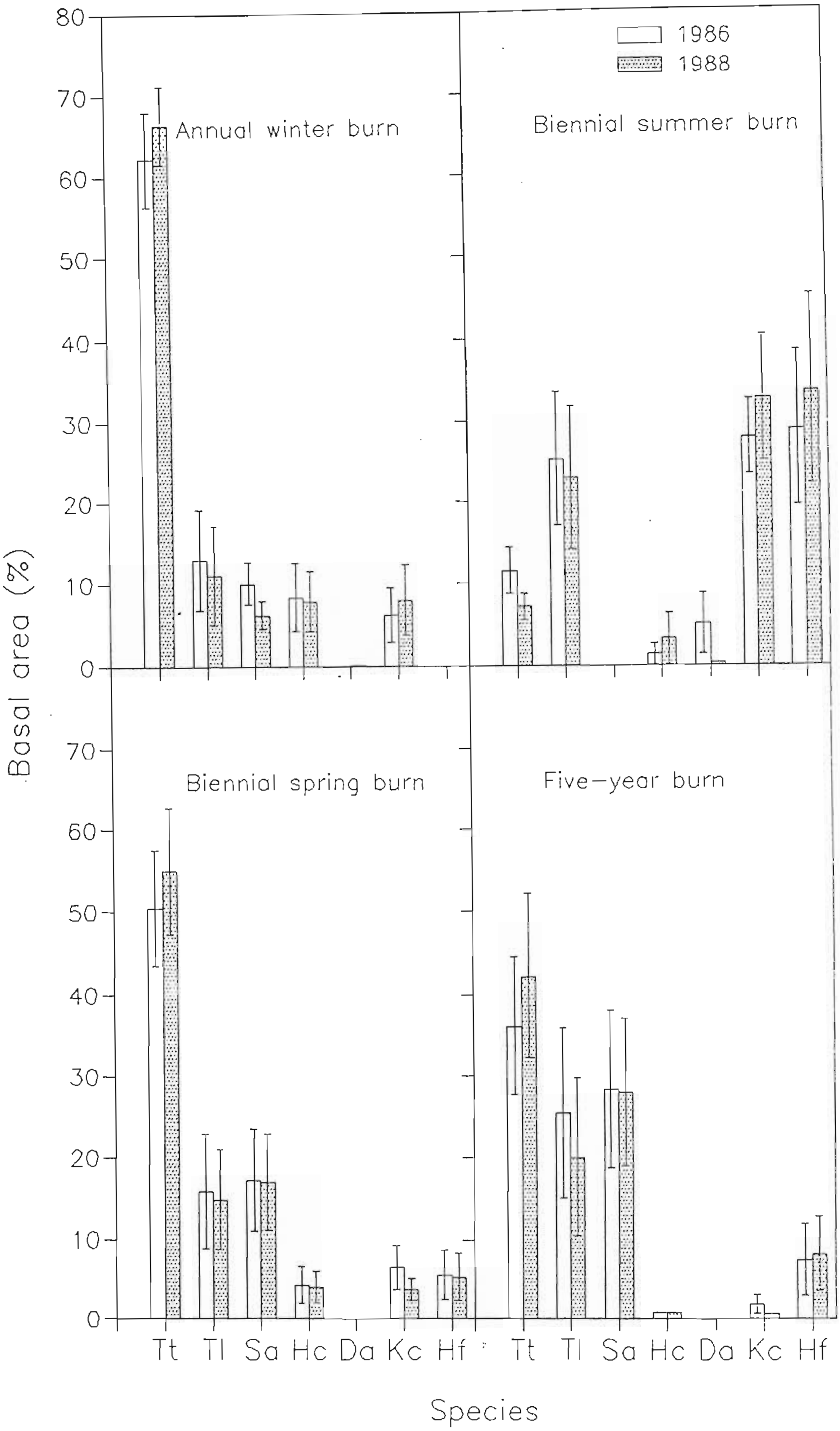


Figure 8.11 Percentage basal area of the seven most dominant species in four burning treatments in 1986 and 1988. Vertical bars represent standard errors. Tt - *Themeda triandra*, Tl - *Tristachya leucothrix*, Sa - *Stiburus alopecuroides*, Hc - *Heteropogon contortus*, Da - *Diheteropogon amplectans*, Kc - *Koelaria cristata*, Hf - *Harpochloa falx*.

The dynamic nature of the grasses is shown by the changes in size and number of plants of the dominant species, *T. triandra, Tristachya leucothrix* and *Stiburus alopecuroides* over two years (Table 8.2). The proportion of *T. triandra* plants that increased in basal cover was significantly different between treatments ($\chi^2 = 24.00$, $P<0.001$). In the annual winter, biennial spring and five-year burns, the *T. triandra* plants were in equilibrium with equal numbers ($P = 0.47$-0.51) increasing and decreasing in area (Table 8.2). By contrast, in the biennial summer burn most of the *T. triandra* plants (72%) significantly increased in area ($P<0.001$). There were, however, approximately half the number of *T. triandra* plants in this treatment when compared to the other treatments.

In all treatments the total number of plants of *Tristachya leucothrix* was low (25-55) when compared to *T. triandra* (125-300). Treatment had a significant effect ($\chi^2 = 10.26$, $P<0.05$) on the proportion of *T. leucothrix* plants that increased in basal area. In the annual winter, biennial summer and five-year burns more than half the plants ($P = 0.54$-0.73) increased in size. The greatest difference in the proportion of *T. leucothrix* plants increasing was between the biennial summer and biennial spring burn treatments ($u = 3.54$, $P<0.001$).

The total number of plants of *Stiburus alopecuroides* was low (<91) in all treatments, particularly the biennial summer burn where it was absent. There was no significant difference in the proportion of *S. alopecuroides* plants that increased in the three treatments where it occurred.

Percentage bare area differed significantly between treatments ($P < 0.01$, Table 8.3). In the annual winter burn there was no significant difference in bare area between years (81.8-82.1%). By contrast, the biennial summer burn resulted in a significant increase of 5.6% bare area between 1986 and 1988. The biennial spring burn reduced the extent of bare area between 1986 and 1988 (85.0 to 78.9%), while the five year burn resulted in the greatest reduction of bare area (7.8%).

Table 8.2 The effect of different burn treatments on the number of plants of *T. triandra*, *T. leucothrix* and *S. alopecuroides* that increased (+) and decreased (-) in basal area over two years. *P* = proportion of plants that increase in size, NP = not present.

	Annual winter	**Biennial summer**	**Biennial spring**	**Five-yr**
T. triandra				
+	145	90	142	105
-	155.	35	134	119
Total	300	125	276	224
P	0.48	0.72	0.51	0.47
T. leucothrix				
+	16	33	16	30
-	09	12	24	25
Total	25	45	40	55
P	0.64	0.73	0.40	0.54
S. alopecuroides				
+	59	NP	36	20
-	32	NP	30	26
Total	91	NP	66	46
P	0.65	NP	0.38	0.43

Table 8.3 Mean percentage bare area in the four burning treatments. Values in brackets represent ± S.E.

Treatment	1986	1988
Annual winter burn	81.8 (±3.0)	82.1 (±1.9)
Biennial summer burn	85.0 (±1.4)	90.6 (±1.9)
Biennial spring burn	85.0 (±2.9)	78.9 (±2.9)
Five-year burn	74.5 (±2.4)	66.7 (±3.2)

8.5 Discussion

Seedlings responded negatively to high numbers of neighbouring seedlings where the mean growth was reduced by 52.5% and no new tillers were produced. Although the higher seedling survival recorded in the low density sites was not significant, it is likely that if monitoring had continued through the winter period, more deaths would have been recorded in the frail seedlings of the high density plot. The detrimental effect of neighbours on seedling growth is in contrast to the situation in more xeric environments. Fowler (1988) observed that in arid zones, seedlings of *Aristida longiseta* with neighbours had higher rates of survival than seedlings with no neighbours. This implies that in dry zones the effects of aggregation in favourable microclimates outweigh the effects of competition. By contrast, in the moist environment of the Drakensberg, the comparatively poor performance of seedlings of *T. triandra* in the high density site indicates that neighbours have a negative effect on seedlings. Therefore, seedlings that establish in gaps will have a competitive advantage. The lack of correlation between seedling growth and rainfall indicates that moisture is not a limiting resource for competition in this environment.

Following germination in December, seedlings have approximately three months of growth before the onset of senescence in March. Smaller sized seedlings are therefore unlikely to catch up in size before the first frosts. These seedlings will have lower carbohydrate reserves to tide themselves over the winter season. High mortality of seedlings in winter is thus a result of competition between closely growing individuals and subsequent poor growth.

Unlike seedlings which are independent, and likely to suffer direct competition with neighbouring plants, new tillers have access to limiting nutrients through the parent. The occurrence of tillering and formation of independent tufts with their own root system has been shown to reduce competition (Scandrett & Gimingham 1989). In the grasslands of the Drakensberg, the lack of correlation between distance and size of individual tufts of *T. triandra* suggests that competition is not occurring. However, the increase in circumference and reproductive potential of tufts of *T. triandra* following removal of nearest neighbours is evidence that competitive interference does exist between plants. The most likely explanation for these contradicting results is that the nearest neighbour technique is not suitable for detecting competitive relationships in communities where individuals grow very close to each other. In the dense grasslands of this study, nearest neighbour distances were small, ranging from 20-110 mm. By contrast, Yeaton & Cody (1979) used this technique successfully in succulent plants where distances were up to 11 m. The presence of numerous neighbours may also account for the failure of nearest neighbour analysis to detect negative correlations between distance and sum of sizes of neighbours (Fowler 1984). This is likely to be the case in the present study where a cental tuft was surrounded by up to eight neighbouring individuals.

The small distances between tufts indicates that plants are competing primarily for space. However, examination of the percentage bare area in plots subjected to different burning treatments shows that the amount of space available for growth is high. Managers of the Drakensberg catchments aim to produce high quality water by reducing the amount of bare ground exposed to soil erosion. This study suggests that a biennial summer burn will result in increased runoff since this treatment had the highest amount of bare ground. The treatment with the lowest amount of bare ground was the five-year burn. Although this is the most favourable treatment for reducing runoff and sediment production, the low species diversity in this treatment may not fit with management objectives of maintaining high species diversity in the Drakensberg.

While above-ground space may not be a limiting resource for growth, below-ground competition may be a factor determining tuft size. Roux (1969) suggested that the competitive advantage of *T. triandra* is a result of its deep root system which enables it to survive in an environment where little nitrogen is available. However, examination of the root profile of the grassland (Fig. 8.12) indicates that the roots of *T. triandra* do not penetrate deeper than those of other grassland species. Since the competitive superiority of *T. triandra* is only maintained with certain burning regimes, it is likely that its specific response to fire is an important factor contributing to successful species interactions.

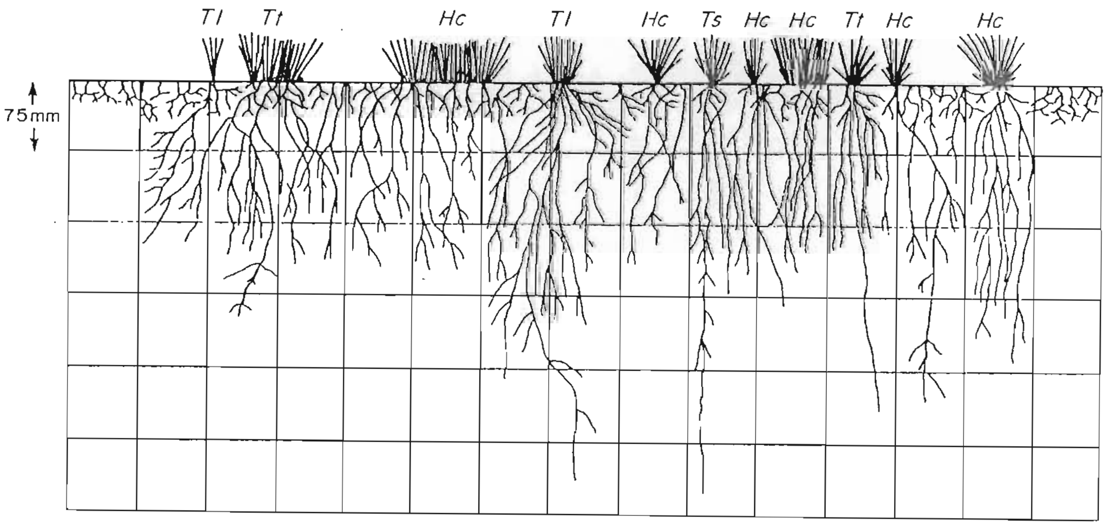


Figure 8.12 Profile of below-ground biomass in the study area. *Tl - Tristachya leucothrix, Ts - Trachypogon spicatus, Hc - Heteropogon contortus, Tt - Themeda triandra* (after Hardy 1983).

The most favourable burning treatment for stability in the grassland community is the biennial spring burn. In this treatment, the three dominant species are in a state of equilibrium with the proportion of plants increasing being approximately equal to the proportion decreasing. While *T. triandra* is also close to equilibrium in the annual winter burn, there is a greater proportion of unpalatable species such as *Tristachya leucothrix* and *Stiburus alopecuroides* increasing in size. A similar trend was apparent in the five-year burn with the exception of *S. alopecuroides* which had a greater number of plants decreasing in size. The five-year burn was characterized by a dominance of large tufts, with few smaller-sized plants occurring. This may be due to the increased litter and aerial cover in this treatment shading out smaller plants.

The high number of *T. triandra* tufts that increased in size in the severe summer burn treatment was unexpected. Although this implies an increase in *T. triandra*, this treatment had only half the number of *T. triandra* plants when compared to the other treatments, severity of treatment having caused loss of half the plants. This reduced the competition from neighbours and may account for the unexpected increase in size in many of the surviving plants. The disappearance of *Stiburus alopecuroides* from the summer burn plots and the increase in basal cover of unpalatable species such as *Tristachya leucothrix,* indicates a directional change in species composition which is likely to be irreversible. Summer burning, commonly practised by subsistence farmers, should therefore be discouraged to prevent further loss of valuable fodder species.

In the event of a local extinction of a tuft or species, it is important for managers to know which species will establish. Gaps created in the summer burn were filled by two species already present in the vegetation, *Koelaria cristata* and *Harpochloa falx*. *Koeleria cristata* produces little biomass and because of its hairiness it is relatively unacceptable to domestic grazing animals (Tainton, Bransby & Booysen 1976). Likewise *H. falx* is a wiry grass with low palatability when mature. Increases in these species are likely to lead to greater grazing pressure on the remaining palatable species, and a subsequent decrease in the productivity of these grazing systems. Re-establishment of productive native grasses such as *T. triandra* may be necessary to improve agricultural production in these systems.

The main conclusion that can be drawn from these results is that, in the grasslands of the Drakensberg, competition is the main constraint to higher seedling establishment. The competitive interactions of seedlings of *T. triandra* recorded in this study have important implications in the rehabilitation of disturbed sites. The positive response of seedlings of *T. triandra* to reduced competition indicates that seedling establishment may be successful in degraded areas where neighbours are few. However, since plant size and reproductive output were strongly and negatively correlated with density, a knowledge of optimal sowing densities will be necessary for effective rehabilitation. Since disturbance by fire is important in determining the competitive interactions of species, burning can be used as a management tool to manipulate the performance of selected species.

Chapter 9
General discussion and conclusions

The grasslands of the Drakensberg are the major vegetation of the conserved mountain catchment areas and of the lower lying areas occupied by subsistence and large-scale commercial farmers. With increased population pressure on a limited resource base, the natural vegetation in the rural areas has been severely grazed resulting in sheet erosion and destruction of valuable pastures. In these areas soil erosion has reached crisis levels and there is a marked decrease in the area of natural grassland for grazing. There is also growing concern among land owners and conservation authorities about the continued deterioration of this environment (Cooper 1991). While reclamation of degraded catchments at Cathedral Peak has had some success in the past with exotic grass species, recent attention has focused on the use of native species as an option for rehabilitation. This study examines the potential of seedlings of *T. triandra* for use in rehabilitation programmes in montane grasslands.

Several hypotheses on grass seedling dynamics were posed in the introduction to this study. This section summarizes the findings of the research programme that was carried out to test these hypotheses. A seed budget for *T. triandra* identifies the phases in the life cycle that are critical for seedling establishment. The results are integrated in the form of a population model which outlines how the structure of the grassland community can be regulated through different burning regimes.

Varying degrees of disturbance occur in montane grasslands through such factors as fire and grazing pressure. In cases where the vegetation is completely destroyed, recovery must start from bare ground. Bradshaw (1987) outlines three options for developing degraded ecosystems, namely natural recovery, rehabilitation and restoration. Natural recovery may be an option in some mesic environments where disturbances are rapidly filled by surrounding plants (Gross 1987). However, this is not a feasible option in the Drakensberg where re-establishment of small disturbed sites (one m^2) was extremely slow with only 5% recovery after three years. Restoration of the climax community is an unrealistic option in this environment since little is known about the specific requirements of individual species. Rehabilitation, in which some of the component species are restored, is the most practical solution in areas where the primary objectives are increased productivity and soil protection.

For any rehabilitation programme to succeed, one of the key factors is availability of seed. Since *T. triandra* has decreased in abundance in rural areas, seed cannot be obtained naturally in the areas where it is most needed. However, a large seed source is available in the adjacent conserved area, the Natal Drakensberg Park. This study shows that high seed production by *T. triandra* can only be achieved with specific burning treatments. An annual burn treatment is detrimental for seed yield since seed production in this treatment was <38 seeds m^{-2} $annum^{-1}$. Seed production was higher in the longer burning rotations of two to five years (250-400 seeds m^{-2}). Since the biennial spring burn is the current burning prescription for conserved areas, a local seed source is presently available for rehabilitation purposes.

The probability of colonizing eroded sites by seedling establishment will depend on the size of the disturbance and distance over which the seeds are dispersed. Findings in this study are that most seeds of *T. triandra* fall in the immediate vicinity of the parent plant. This suggests that large-scale disturbances, more than 2-3 meters from a seed source, are unlikely to be colonized effectively by *T. triandra* seedlings. This is supported by observations of re-establishment by *T. triandra* in a disturbed catchment at Cathedral

Peak. This catchment has a history of disturbance since it was planted to pine trees in 1953. A wild fire in 1981 destroyed the plantation, and subsequent storms resulted in severe soil erosion and loss of top soil. The catchment was then reclaimed with *Eragrostis curvula*, which has been the only grass present for at least five years. Within the last few years, seedlings of *T. triandra* have established in the catchment, showing that natural re-establishment in this environment is a very slow process. Since establishment of the seedlings was confined to the perimeter of the catchment (Plate 9), it is likely that seeds were dispersed from plants in the adjacent grassland and did not come from the seed bank. Once established in the disturbed catchment, *T. triandra* grew vigorously, and tufts are approximately twice the size of those in the adjacent grassland. Similar increases in tuft size were recorded in the present study following the removal of nearest neighbours. It is likely that absence of competition from other species resulted in this vigorous growth. Although *T. triandra* can re-establish naturally after removal from an area, it is evident that reseeding will be necessary to accelerate this process. This will require a knowledge of the specific germination requirements of *T. triandra*.

Plate 9. Establishment of *T. triandra* in a catchment rehabilitated with *E. curvula*.

The germination and seed bank experiments indicate that *T. triandra* has an after-ripening period which lasts *ca.* 9-10 months. This indicates that ten month-old seed should be used for rehabilitation projects. However, viability of seeds is reduced by up to 40% during this dormancy period. This poses a problem for managers since non-dormant seed has poor viability. This unusual strategy may be a relic of colder climatic conditions in which viability was maintained through the dormancy period.

In montane grasslands, seeds that persist through the dormancy period are susceptible to predation. This study demonstrates that seed predation reduces the seedling population of *T. triandra.* in these grasslands. Although seeds of *T. triandra* are not specifically adapted for ant dispersal, predation experiments indicated that granivory by ants is an important process in the depletion of the soil-stored seed bank. While the clumping of seeds in the predation experiment may over-estimate predation, the poor dispersal of seeds of *T. triandra* in the grassland will result in seeds falling in close proximity to each other. In this study predators removed 70-98% of the seeds. Since *T. triandra* releases its seeds in a short period of time predators may become satiated and some seeds escape predation. These seeds enter the seed bank where they remain until conditions are favourable for establishment. Because such conditions depend on the burning regime imposed, it was hypothesized that density of seeds in the soil seed bank increases with time after fire.

This study showed no consistent relationship between fire interval and size of the seed bank. The highest density of *T. triandra* was recorded in the fire-exclusion treatment (14 seeds m^{-2}). However, the density of seeds in the soil was higher in the annual burn (7.1 seeds m^{-2}) when compared with the biennial burn treatment in which no seeds germinated. Although *T. triandra* was poorly represented in the seed bank, the actual number of seedlings in the field indicates that they must have been present. One of the reasons for this discrepancy may be that the emergence technique is inappropriate to break the dormancy of *T. triandra* seeds. This is likely since germination of *T. triandra* was low (<37%) under controlled laboratory conditions. The density of seeds of all species in the seed bank was low (<1 732 seeds m^{-2}) when compared to the seed bank of 12 227 m^{-2} in other grasslands (Major & Pyott 1966), supporting the hypothesis that these grasslands do not have a persistent seed bank. Thus, in montane grasslands the seed bank will contribute little to revegetation following disturbance. This highlights the importance of maintaining existing grasslands as a resource for seeds in restoration programmes.

An interesting feature of these seed banks was the prevalence of seeds of *Eragrostis curvula*. The seed source of this species is likely to be plants sown from commercially purchased seed used for reclamation purposes in the study area. Since *E. curvula* behaves like an early successional species and is capable of surviving on exposed soil, it may be a useful pioneer until conditions change enough to allow the entry of later successional species such as *T. triandra*.

An important finding of this study was that seedling establishment of *T. triandra* was high in the biennial spring burn (184 m^{-2}). However, high mortalities led to acceptance of the hypothesis that in the climax grasslands of this study, seedlings contributed little to the structure of the community. While microclimatic factors such as light intensity play an important role in seedling establishment, the major factor affecting seedling survival is competition. Increased growth, vegetative reproduction and survival of seedlings in sites with few competitors indicates that seedlings of *T. triandra*, under conditions of optimal spacing, have potential for restoration of degraded grassland.

9.1 Annual seed budget of *T. triandra*

The processes affecting the life cycle of *T. triandra* are summarized in an annual seed budget determined for a square meter of grassland with a biennial spring burn treatment (Fig. 9.1). The budget commences with mature plants, of which there are approximately ten individuals per m^2 in a biennial spring burn. Each of these produces approximately 25 seeds, resulting in an annual seed production of 250 m^{-2}. Taking the lower value of predation recorded, approximately 70% of these are removed by predators, resulting in 75 seeds in the seed pool. Sixty percent of these seeds retain their viability after 10 months, resulting in 45 viable seeds entering the seed bank. The number of seeds remaining from previous years is likely to be negligible because of decay and further loss of viability. An estimated five seeds from this source contributes to a total seed bank size of 50 seeds m^{-2}. Although germination in the laboratory was low, actual germination in the field reached a maximum of 90% (Chapter 6). Germination from the seed bank contributes 45 seedlings m^{-2} to the population. However, high mortality of seedlings in winter (80%) results in the establishment of only 9 seedlings m^{-2} out of the initial 250 seeds produced.

If this budget is applied to rehabilitation programmes, it is apparent that several "windows" are open for managers to experimentally increase seedling survival. The first process that markedly decreases seed numbers is predation. While this cannot be readily controlled in the field, losses to predation can be overcome by using seedlings instead of seeds for rehabilitation. No damage to seedlings by insects or rodents was observed during the study.

The next "window" that can be manipulated is that of viability. If seed longevity can be maintained by storage of seeds in a viable dormant state, the cost of collecting seeds annually could be reduced considerably.

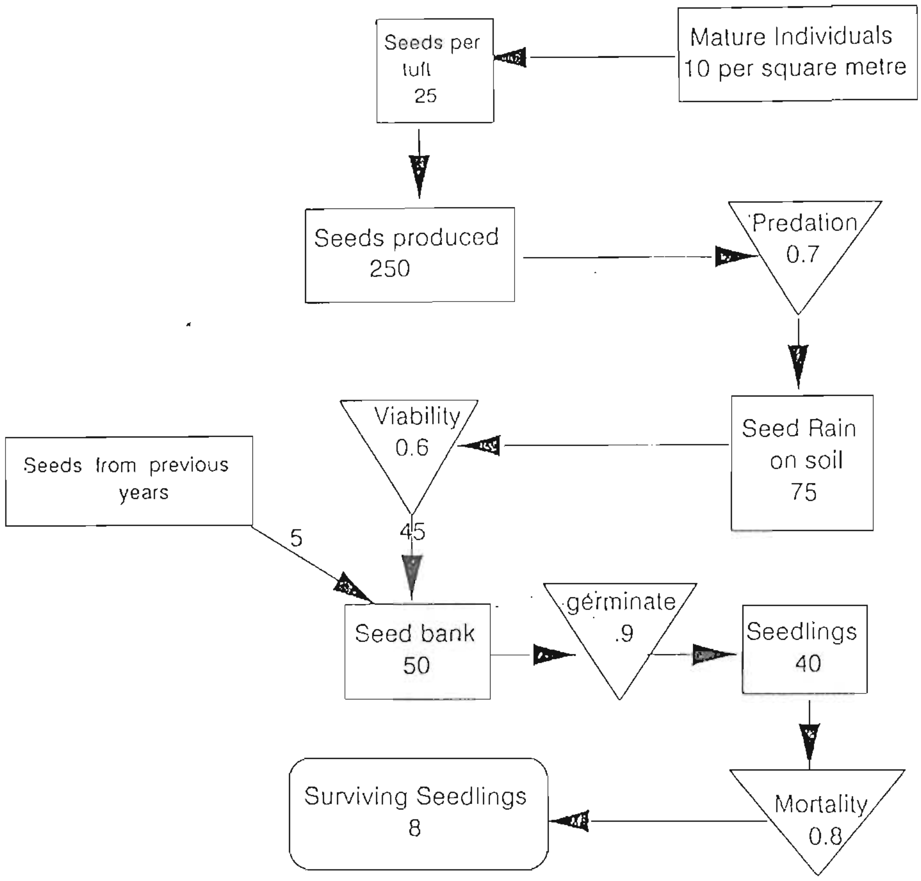


Figure 9.1 Annual seed budget of *T. triandra*. The numbers of individuals are shown in boxes, while the values in the triangles indicate the probability of going from one stage to the next.

The "window" that will have the greatest impact on increasing survival is that of mortality of seedlings. This study indicates that microclimate (e.g. mulching) and competition (e.g. spacing of seedlings) can be manipulated to reduce mortality.

9.2 Matrix population model for *T. triandra*

The success or failure of seedlings can be measured by their ability to survive and ultimately reproduce. The ability of seedlings of *T. triandra* to maintain themselves in the tuft-dominated grassland communities of this study can be determined by modelling the dynamics of the system. The population structure of *T. triandra* grassland is complex since adult tillering shoot systems may live for several years and annually contribute both tillers and seeds from which new adults may arise. Such data are amenable to matrix modelling which describes the behaviour of populations with overlapping generations (Silvertown, 1987). The object of modelling population change is to be able to predict the effect of different burning regimes on the magnitude of individuals in the different stages of the population. The derivation of the transition probabilities is described in Appendix A.

The transition probabilities for the three stages of the life cycle of *T. triandra* (seeds, seedlings, flowering tufts) for each burning treatment are entered into a transition matrix, **A** (Table 9.1). A transition matrix consists of a group of proability values that represent the chance that a plant in a given stage of development will arrive at a different developmental stage during the time between population census dates. A typical matrix has the following characteristics:

	Seed	Seedling	Flowering tuft
Seed	a_{ss}	a_{rs}	a_{fs}
Seedling	a_{sr}	a_{rr}	a_{af}
Flowering tuft	a_{sf}	a_{rf}	a_{ff}

The columns from left to right represent the fate of seeds, seedlings and tufts. The element a_{ss} represents the probability that a seed this year will not germinate but will remain a viable seed next year. The probability that a seed will become a seedling next year is represented by the element a_{sr}. The element a_{sf} represents the probability that a seedling this year will be in flower next year. Since seedlings of *T. triandra* remain vegetative for one or more years after germinating, a_{sf} is replaced by zero in the matrices. Similarly the probability of a seedling producing seed in the first year (a_{rs}) is zero.

The relative proportion of individuals present in the three stages of the life cycle of *T. triandra* (seeds, seedlings, flowering tufts) can be represented by a vector $\mathbf{a}_t$ (Table 9.1). Matrix multiplication can be iterated to the point at which a stable stage distribution is reached. Matrix models are used to calculate sensitivity of λ (population growth rate) to small changes in transition probabilities between the different stages in the life cycle. Sensitivity analysis requires calculation of the reproductive value $\mathbf{V}_x$:

$$V_x = b_x + \sum_{i=1}^{i=\infty} \left(\frac{l_{x+i}}{l_x}\right) b_{x+i}$$

where $\mathbf{V}_x$ is the sum of the average number of offspring produced in the current stage ($\mathbf{b}_x$), plus the average number produced in later stage intervals ($\mathbf{b}_{x+i}$), allowing for the probability that an individual now at stage $\mathbf{x}$ will survive to each of those intervals $\mathbf{l}_{x+i}$ /$\mathbf{l}_x$ (Silvertown 1987).

Matrix models were determined for the population of *T. triandra* in an annual winter, biennial summer, biennial spring and five-year burn (Fig. 9.2). A sensitivity analysis was applied to determine the sensitivity of λ to changes in the transition probability between the three life-cycle stages in *T. triandra*. This required multiplication of the reproductive value of an individual in a stage ($\mathbf{V}_x$, Table 9.3) by the percentage of all individuals in the next stage of the stable stage structure (Table 9.2).

Table 9.1 Transition matrices (**A**) and vectors ($\mathbf{a}_t$) used to derive predicted values of population structure of *T. triandra* in different burn treatments.

Biennial spring burn

	Seed	Seedling	Flowering tuft	Present state
Seed	0.10	0	0.90	0.63
Seedling	0.10	0.20	0.09	0.17
Flowering tuft	0	0.07	0.99	0.20
		A		a_t

Annual wnter burn

	Seed	Seedling	Flowering tuft	Present state
Seed	0.03	0	0.07	0.01
Seedling	0.03	0.20	0.03	0.00
Flowering tuft	0	0.02	0.99	0.99
		A		a_t

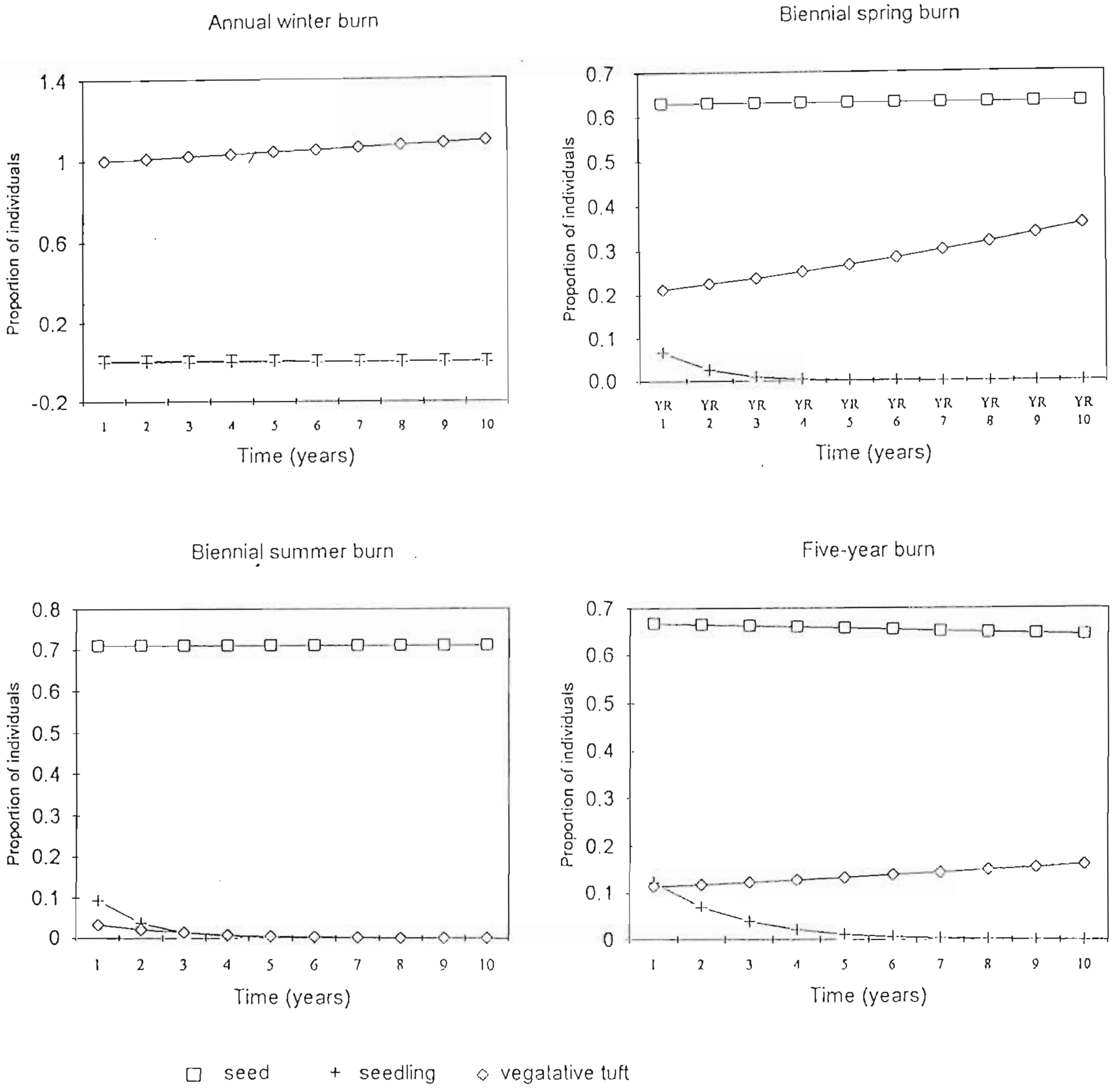
Biennial summer burn

	Seed	Seedling	Flowering tuft	Present state
Seed	0.10	0	0.90	0.71
Seedling	0.10	0.20	0.09	0.24
Flowering tuft	0	0.07	0.60	0.05
		A		a_t

Five-year burn

	Seed	Seedling	Flowering tuft	Present state
Seed	0.10	0	0.90	0.67
Seedling	0.10	0.20	0.09	0.22
Flowering tuft	0	0.07	0.99	0.11
		A		a_t

The model predicts that an annual winter burn treatment is most favourable for the vegetative growth of *T. triandra* (Fig. 9.2). The high reproductive rate of tufts ($\mathbf{V}_x$=201.0, Table 9.3) accounts for the predicted increase in this component of the population.


Annual winter burn

Biennial spring burn

Biennial summer burn

Five-year burn

Figure 9.2 Predicted changes in seedling populations of *T. triandra* in different burning treatments.

Table 9.2 Sensitivity matrix of the life-cycle stages in a population of *T. triandra* in different burning treatments.

Annual winter burn	Seed	Seedling	Tuft
Seed	-		
Seedling	0.0	-	
Tuft	201.0	0.0	-
Biennial summer burn			
Seed	-		
Seedling	1.85	-	
Tuft	34.3	0.003	-
Biennial spring burn			
Seed	-		
Seedling	1.4	-	
Tuft	0.49	5.1	-
Five-year burn			
Seed	-		
Seedling	1.6	-	
Tuft	21.2	4.0	-

Table 9.3 Reproductive value (**V_x**) of the life-cycle stages in a population of *T. triandra* in different burning treatments.

Treatment	**Seed**	**Seedling**	**Tuft**
Annual winter burn	0.00	0.00	201.01
Biennial summer burn	1.42	0.002	0.06
Biennial spring burn	1.26	0.17	0.49
Five-year burn	1.33	0.23	0.26

By contrast, the model predicts that seeds and seedlings contribute little to the population structure in this treatment (Fig. 9.2). The annual rate of increase (λ) in this treatment is 1.01. Since no seeds are recruited in an annual winter burn, the relative sensitivity to transitions between stages is zero (Table 9.2).

The model indicates that in the biennial spring burn seedlings of *T. triandra* are established but do not persist for more than three generations (Fig. 9.2). The finite rate of increase in this population (λ) is equal to 1.0. This rate is most sensitive to change in two parameters of the matrix, seedlings and tufts (Table 9.2). Survival of seedlings and fecundity of tufts are therefore the crucial determinants of population growth in this treatment.

In the biennial summer burn λ=0.99 when the stable age distribution is reached. The model predicts that in this treatment recruitment of seeds is extremely sensitive to changes in transition probabilities (sensitivity = 5.4, Table 9.2). Seeds and tufts make the least contribution to the population increase and indicate the severity of this treatment.

In the five-year burn the finite rate of increase of the population is 1.01 when in a stable state. This rate is most sensitive to change in the tuft phase of the life cycle. However, tufts persist in the five-year burn with a slow rate of increase (Fig. 9.2).

Comparison of the populations in the different burning treatments indicates that management regimes play an important role in the overall fate of seed, seedling and tuft populations. Both annual winter burn and five-year burn favour growth of vegetative tufts of *T. triandra*, but are detrimental to seedling establishment. Summer burning destroys seedlings and tufts of *T. triandra* and will decrease the productivity of the grassland. The optimal treatment for both seedling and tuft establishment of *T. triandra* is a biennial spring burn. This result is supported by population studies of tillers in which a biennial burning regime maintains

T. triandra at its present level of abundance (Everson CS, Everson TM & Tainton 1985).

The matrix models in this study are a useful management tool for comparing populations of *T. triandra* in different environments to see which is the most favourable for the species. However, they give no indication of the potential of the species to rehabilitate degraded areas in which the grassland resource no longer exists. Since vegetative transplants create further disturbance and are not suitable for extensive restoration, the most practical option is establishment with grass seedlings. The present study indicates that seedlings of *T. triandra* can be used for the rehabilitation of these grasslands. However, further research on aspects of its seed biology (e.g. viability, germination) are required to provide a ready source of seedlings. With funding available for job creation programmes in rural communities, and the demand to increase sustainability of degraded land, the practical findings of this study are currently being tested in the field.

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Appendix A

Derivation of transition matrices

The matrices are derived from the numbers of individuals in each life cycle stage of the population (Table 1). The data are obtained by following the development of the different stage classes in each of the burning treatments. Column A represents the different stages of the life cycle, and columns B, C, D and E represent the numbers of individuals in a square meter of grassland in the biennial spring, annual winter, biennial summer and five-year burn respectively.

Table 1 Number of individuals in the life cycle stages of *Themeda triandra* in a square meter of grassland subjected to four burning treatments.

	A	B	C	D	E
Row	**Life cycle parameter**	**BSp**	**AWi**	**BSu**	**5-yr**
1	mature tufts (>100 mm^2 diameter)	21	28	5	20
2	seed production	268	2	250	411
3	probability of predation	0.7	0.9	0.7	0.7
4	seed rain	80.4	0.2	75.0	123.3
5	probability of viability	0.6	0.6	0.6	0.6
6	seeds from previous year	5	0	5	5
7	seed bank	53.2	0.1	50.0	79.0
8	probability of germination	0.5	0.5	0.5	0.5
9	number of seeds germinating	26.62	0.06	25.00	39.50
10	probability of death	0.8	0.8	0.8	0.8
11	number of seeds surviving	5.32	0.01	5.00	7.90

Rows 1-11 represent the number of individuals progressing from one stage to another. The calculations for a biennial spring burn are presented as an example.

Row 1 is the number of mature tufts greater than 100 mm^2 in diameter (21). These data are derived from the vegetation maps in each treatment (Figures 8.7-8.10, pp. 133-136).

Row 2, the number of seeds produced in the burning treatment (268), is obtained from the actual counts in the field (Table 4.1, p.38).

Row 3 is the probability of predation (0.7) and is derived from the field predation experiments (Figure 5.1, p.59).

Row 4, the seed rain, is the number of seeds that escape predation. For example, in the biennial spring burn this value is obtained from cell B2 in Table 1 (i.e column B, row 2). This indicates that 268 are seeds produced and there is a 0.7 probability of predation (B3). The seed rain is 268 - (268 x 0.7) = 80.4.

Row 5, the probability of seeds being viable (0.6), is derived from the tetrazolium laboratory tests (section 5.3.1., p.53).

Row 6 is the seed input from previous years (5). Since it was not possible to determine the number of seeds remaining in the soil from the previous year, the values in row 6 are estimates based on the number of seeds recorded in the seed bank experiment.

Row 7, the number of seeds in the seed bank, is the number of viable seeds produced in the current year plus the input of seeds from the previous year. For example, in the biennial spring burn there is a 0.6 probability of seeds in the seed rain being viable. Therefore the average number of seeds in the seed bank = (0.6 x 80.4) + 5 (from previous year) = 53.24.

Row 8, the probability of germination, is estimated as 0.5. Precise values of percentage germination were not possible because of the variability of germination in the laboratory and field.

Row 9, the number of seeds germinating, is the product of the number of seeds in the seed bank and the probability of germinating. In the biennial spring burn this is 53.24 x 0.5 = 26.62.

Row 10, the probability of death (0.8), is based on the survivorship curves (Fig. 6.3, p.83).

Row 11, the number of seedlings surviving, is the product of the number of seeds germinating and the probability of death. In the biennial spring burn this is 26.62 x 0.8 = 5.32 seedlings surviving.

The values in columns B,C,D and E are substituted in the transition matrices (Table 9.1, p.154). For example, in the transition matrix for the biennial spring burn the element a_{ss} is the probability that a seed this year will not germinate but will remain a viable seed next year. This is calculated by subtracting the number of germinating seeds, B9 (column B, row 9, Table 1), from the number of viable seeds in the seed bank (B7) and dividing by the total number of seeds.

The element a_{sr} is the probability that a seed will become a seedling next year. In the biennial spring burn this is derived from B9/B4, the number of seedlings divided by the number of seeds. The element a_{sf} represents the probability that a seedling this year will be in flower next year. Since seedlings of *T. triandra* remain vegetative for one or more years after germinating, a_{sf} is replaced by zero in the matrices of this study. Similarly the probability of a seedling producing seed in the first year (a_{rs}) is zero.

The probability of a seedling this year remaining a seedling next year (a_{rr}) is B11/B9, the number of seedlings surviving divided by the number germinating. The probability of a seedling developing into a tuft (a_{rf}) is derived from the seed rain multiplied by the probabilities of viability, germination and mortality and divided by the total number of seeds produced:
B4 x B5 x B8 x B10/B2. For the biennial spring burn this is 80.4 x 0.6 x 0.5 x 0.8 /268 = 0.07. The probability of a tuft producing seed (a_{fs}) is B2/B1, the number of seeds divided by the number of tufts. In the biennial spring burn this probability is estimated to be 0.9 since approximately 90% of the tufts produced inflorescences and seed. The probability of a tuft producing a seedling (a_{fr}) is B4 x B5 x B8/B2. In the biennial spring burn this is 80.4 x 0.6 x 0.5/268 = 0.09. The last element in the matrix is a_{ff}, the probability of a tuft this year remaining a tuft next year. In the

biennial spring burn this is estimated as 0.99 since no tuft deaths were recorded during the census period.

The column vector $\mathbf{a}_t$ (Table 9.1) represents the proportion of individuals present in each stage class in the population. This requires a count of the total number of individuals of each stage. For example, in the biennial spring burn this is the sum of the number of seeds that escape predation (B4), the number of seedlings that germinate (B9) and the number of tufts (B1): 80.4+26.62+21 = 128.02. The relative proportion of each stage is entered in the column vector.

Multiplication of the transition matrix with the column vector yielded the following predicted values for the different stage classes:

Table 2 Predicted values of the stage classes of *Themeda triandra* for 10 generations

Biennial spring	YR 1	YR 2	YR 3	YR 4	YR 5	YR 6	YR 7	YR 8	YR 9	YR 10
seed	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63	0.63
seedling	0.07	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
tuft	0.21	0.22	0.24	0.25	0.27	0.28	0.30	0.32	0.34	0.36
Annual winter	YR 1	YR 2	YR 3	YR 4	YR 5	YR 6	YR 7	YR 8	YR 9	YR 10
seed	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
seedling	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
tuft	1.00	1.01	1.02	1.03	1.04	1.05	1.06	1.07	1.08	1.09
Biennial summer	YR 1	YR 2	YR 3	YR 4	YR 5	YR 6	YR 7	YR 8	YR 9	YR 10
seed	0.71	0.71	0.71	0.71	0.71	0.71	0.71	0.71	0.71	0.71
seedling	0.09	0.04	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
tuft	0.03	0.02	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00
Five-year burn	YR 1	YR 2	YR 3	YR 4	YR 5	YR 6	YR 7	YR 8	YR 9	YR 10
seed	0.67	0.66	0.66	0.66	0.66	0.65	0.65	0.65	0.65	0.64
seedling	0.09	0.03	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00
tuft	0.12	0.12	0.13	0.14	0.15	0.16	0.17	0.18	0.19	0.20

These projections are used to calculate the sensitivity of the population growth rate to small changes in the transition probabilities

Calculation of reproductive value

Sensitivity analysis requires calculation of the reproductive value $\mathbf{V}_x$:

$$V_x = b_x + \sum_{i=1}^{i=\infty} \left(\frac{l_{x+i}}{l_x}\right) b_{x+i}$$

where $\mathbf{V}_x$ is the sum of the average number of offspring produced in the current stage ($\mathbf{b}_x$), plus the average number produced in later stage intervals (b_{x+i}), allowing for the probability that an individual now at stage **x** will survive to each of those intervals $\mathbf{l}_{x+i} / \mathbf{l}_x$ (Silvertown 1987).

Values for the calculation of $\mathbf{V}_x$ are obtained from the stable age structure generated from the transition matrix. Since the stationary distribution was not reached in the biennial spring burn, the fifth generation of the transition matrix (Table 2) was arbitrarily selected for the calculation of $\mathbf{V}_x$. For example, the reproductive value of the tuft phase requires the following values:
$(\mathbf{b}_x) = 0.2$; $\mathbf{b}_{x+i} = 0.27$; $\mathbf{l}_{x+i} / \mathbf{l}_x = 0.27/0.25 = 1.08$.
Therefore, $\mathbf{V}_x = 0.2 + (1.08) \times 0.27 = 0.49$. A summary of the reproductive values for all the life stages is shown in Table 9.3.

Sensitivity analysis

A sensitivity analysis determines the sensitivity of λ to changes in the transition probability between the three life-cycle stages in *T. triandra.* The yearly rate of increase (λ) is the ratio of the age class in the fourth generation to the age class in the fifth generation:

$$\lambda = 0.63+0.0 + 0.27 / 0.63 + 0.0 + 0.25 = 1.02.$$

Sensitivity analysis requires multiplication of the reproductive value of an individual in a stage by the percentage of all individuals in the next stage of the stable stage structure. Since tufts in the fifth generation constituted 70 % of the total number of individuals, the sensitivity of the tuft stage is the product of 70 and the reproductive value of tufts (0.49) = 34.3.