The impact of extreme climatic events on the ecology of grasslands

A thesis presented in partial fulfilment of the requirements for the degree of

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Todd Andrew White

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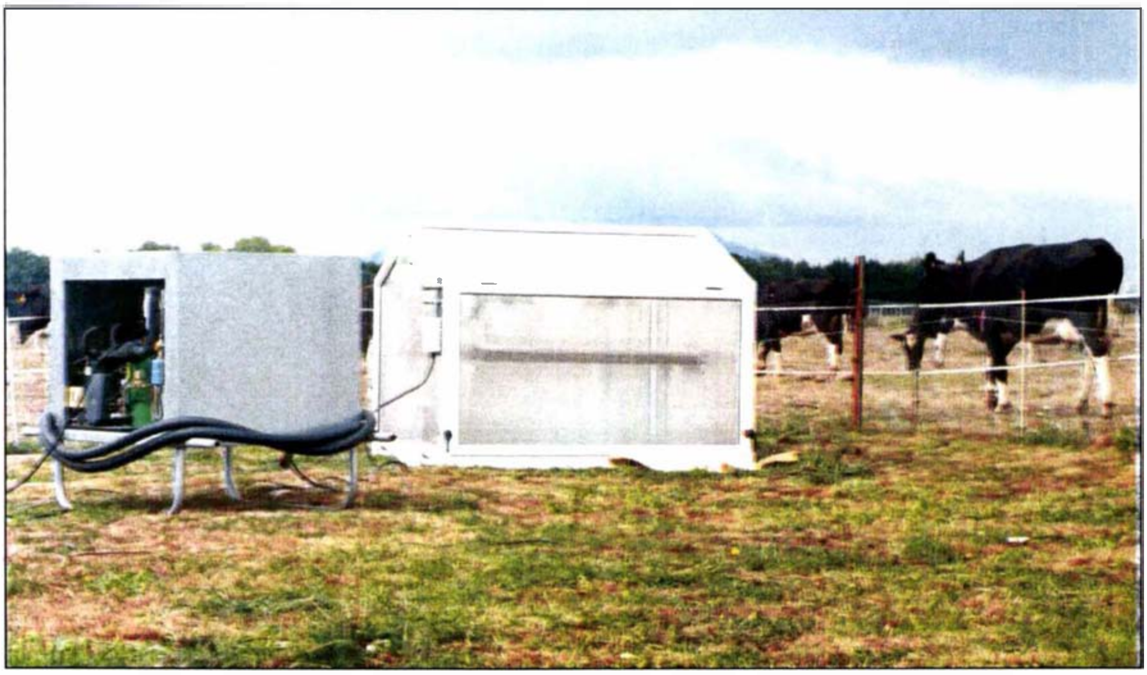

To Mac and Mary

Abstract

The impact of extrinsic factors, such as climate, fertility and disturbance, on plant communities has traditionally been determined at constant levels, spatially and temporally. However, projected future increases in climate variability dictate that a greater emphasis is needed on understanding plant species and community responses to fluctuations in climate. In particular, stochastic, transient but highly disruptive extreme climatic events are predicted to become more prevalent. Their impact on the dynamics and structure of productive grassland communities in New Zealand are the focus of this thesis.

Particular emphasis was placed on quantifying plant functional traits of common grassland species. This was achieved by laboratory screening methods that targeted both regenerative and established life-cycle stages. Field screening methods were also used to quantify functional traits and group species into functional types. Photosynthetic pathway, relative growth rate and life-history were identified as key functional traits differentiating grassland species.

Regenerative phase functional traits were determined on a total of 26 grassland species. Differences in the dependency on warm temperatures for germination and seedling desiccation tolerance were used to generate predictions of species invasiveness. C_3 species were predicted to have a greater ability to invade than C_4 species. Seed size and life-history were also found to be related to invasiveness.

The competitive abilities of five C_4 grassland species were determined relative to a common C_3 grass, *Lolium perenne*, in a glasshouse pot experiment. The most competitive C_4 species were the annuals, *Digitaria sanguinalis* and *Panicum dichotomiflorum*. The impact of extreme climatic events on competition and competitive ability was examined by exposing plants to extreme temperature (frost and heat) and extreme water (drought and flood) events. Species responses from these simple mixtures were extrapolated to predict the impacts of extreme climatic events on grassland communities.

Field and laboratory screening predictions were tested in a large-scale field experiment, which employed novel techniques to simulate extreme heating and rainfall events over grassland. Species with C_4 photosynthesis, fast-growth and short life-histories (collectively named FT1 species) were confirmed as being the species to be most advantaged by an extreme heating event.

Functional traits possessed by species (species identity) were found to be more important in determining community sensitivity to extreme climatic events than the number of species (species richness). Competition was identified as highly important in limiting the invasion of C_4 species into solely C_3 grasslands. Extreme heating events are expected to suppress competition and promote the invasion of C_4 species, in particular, the FT1 species.

By examining responses to short-term fluctuations in climate, this set of investigations has shown that fluctuating temperature and water levels can have important consequences for plant species and the ecology of their communities. Key evolutionary specialisations were recognised as important in determining climate response, and with further development, they could lead to a new functional type classification for use in vegetation-climate analysis. In future, there should be greater emphasis in ecology on the role of short-term but extreme fluctuations in climate in determining plant community dynamics and structure. This will increase the predictive power of ecology in relation to vegetation responses to current and future climates.

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Structure of Thesis

This thesis is based on a series of papers. Chapter Four has been accepted for publication in Global Change Biology. Chapters Two, Three and Five have been prepared for submission to Functional Ecology, New Zealand Journal of Agricultural Research and Global Change Biology, respectively. The only difference between the chapters and paper manuscripts is the formatting of the headings and the insertion of figures and tables into the body of the text. The references relevant to individual chapters are at the end of each chapter.

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1 Introduction

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1.1 Functional plant ecology and climate

Scale and time constraints are increasingly channelling plant ecological research on climate-vegetation relationships away from a species-specific approach toward a function-specific approach (Woodward & Cramer 1996). The identification of plant functional types (PFTs) is a powerful tool for understanding and predicting vegetation response to both current climate and future global change (Smith *et al.* 1996).

Species vary in a wide range of physiological, morphological and/or life history characteristics (collectively known as plant functional traits), but particular combinations of traits have been observed to occur more commonly than others (Grime 1974; Grime 1977). Consequently, there is the potential to describe the almost infinite variety of species in terms of a relatively small set of similarly functioning groups of species, or plant functional types (Westoby & Leishman 1996). The premise is that species with similar plant functional traits will respond similarly to changes to their environment and have similar effects on dominant ecosystem processes (Walker 1992).

There are two basic methods for identifying PFTs, inductive and deductive (Woodward & Cramer 1996). The inductive approach derives PFTs from sets of observations or experimental results (e.g. Leishman & Westoby 1992; Chapin *et al.* 1996; Thompson *et al.* 1996; Diaz & Cabido 1997; Grime *et al.* 1997), whereas the deductive approach derives functional types from a theoretical understanding of processes that control the function of vegetation (e.g. Box 1996; Noble & Gitay 1996).

Both approaches have their limitations. For example, what limits a species to a particular inductive functional type? Under a changing environment, Woodward & Cramer (1996) suggest that the mechanistic basis (or plant functional attribute) may change for some species but not for others who are currently assigned to the same PFT. This highlights the importance of testing the robustness of PFT classifications through experimentation and monitoring of PFT response (MacGillivray *et al.* 1995; Chapin *et al.* 1996). Grouping species on an ecological as opposed to taxonomic basis is by no means a recent development in ecology (Raunkiær 1934; Ramenskii 1938; MacArthur & Wilson 1967; Grime 1974; Noble & Slatyer 1980), nor is it without its limitations, but it has been accepted as a feasible tool for the forecasting of community responses to climate change (Diaz 1995; Box 1996).

1.2 Plant functional types for climate-vegetation predictions

In order to "bridge the gap" between climate change and vegetation response by the use of PFTs, we must first predict future changes in climate and identify the changes that are most likely to impact on ecosystem properties and processes. For example, climate change is likely to result in shifts in resources (CO_2, water), disturbance (floods, frosts, fire), dispersal (wind), decomposition and nutrient cycling (temperature). We must also identify which plant functional traits or sets of traits will confer an advantage or disadvantage to those changes.

1.2.1 An example

In a recent experiment with the flora of central-western Argentina, Diaz & Cabido (1997) used an inductive approach to develop PFTs and to predict the impact of global climate change on vegetation structure and ecosystem function. A total of 24 vegetative and regenerative traits were measured either in the field or laboratory on the 100 most common species along a steep climatic gradient from sub-humid mountainous plateau's to semi-arid low-land plains. Diaz & Cabido (1997) analysed the large trait by species matrix using two multivariate techniques and identified eight PFTs. The main trend of variation in the data closely agreed with the recurrent patterns of specialisation in plants observed in other floras (Grime *et al.* 1997). That is, there was maximum separation of fast-growing palatable short-lived species from the slow-growing well-defended persistent species.

Species that occupied intermediate positions between these two extremes were predicted to attain maximum growth stimulation from global climate change on the basis of their functional traits - high sink strength for carbon, C_3 photosynthesis, moderate nutritional demands and resistance to drought and frost. The approach was then extended to predict changes in ecosystem function, based on the assumption that the functional attributes of the dominant species determine ecosystem function (Schulze & Mooney 1993). For example, an increase in temperature is likely to cause an upward expansion (to higher altitudes) of PFTs typical of lowland vegetation. Diaz & Cabido (1997) predict that invasion by low-land PFTs would increase productivity, water uptake and persistence but decrease biomass turnover, nutrient cycling and carrying capacity of large herbivores.

Diaz & Cabido (1997) and others (Leishman & Westoby 1992; McIntyre *et al.* 1995; Chapin *et al.* 1996; Grime *et al.* 1997) recognised that there lacked a strong association between regenerative and vegetative traits. No one regenerative trait was exclusively assigned to one PFT. This complicates predictions on how different PFTs will differ in their ability to colonise new areas or re-establish current habitats following disturbance. However, it also suggests that no PFT will be eliminated by climate change simply because of a dispersal limitation.

1.3 Current and future climates

1.3.1 Variability

Variation in climate is partially determined by naturally occurring oscillations between persistent climatic patterns (Houghton 1997). The major climatic pattern to influence the climates of the Pacific region and beyond is ENSO, the El Niño Southern Oscillation (Allan *et al.* 1996). ENSO originates in the ocean and atmosphere of the tropical Pacific and is comprised of two opposing phases (Allan *et al.* 1996).

The negative phase, commonly known as El Niño, corresponds with higher than normal sea surface temperatures (SST) in tropical eastern Pacific and cooler than normal in tropical western Pacific. This strengthens upward air motion in the east and weakens it in the west. The rising warm air cools by expansion causing water vapour to condense into cloud and rain. Under the positive phase, or La Niña, the opposite occurs. The direction and strength of the oscillation has been found to be strongly correlated to the air pressure difference between tropical western Pacific (Darwin) and tropical eastern Pacific (Tahiti) and forms the basis of the Southern Oscillation Index (SOI).

While ENSO is a naturally occurring inter-annual climatic pattern, recent climate modelling predicts possible impacts of global warming on ENSO (Timmermann *et al.* 1999). Global warming is associated with an enhancement of the natural greenhouse effect. Thermal radiation absorbing gases, such as water vapour, CO_2, CH_4 and N_2O, within the Earth's atmosphere elevate mean global temperature by approximately 20°C, making the existence of life on earth possible (Houghton 1997).

Since the beginning of industrial times (mid 18th century) the concentrations of CO_2, CH_4 and N_2O have increased by 30, 145 and 15% respectively, largely due to anthropogenic activities such as the burning of fossil fuels and deforestation. As a result, it is estimated that global surface temperatures have, to date, increased by about 0.3 to 0.6°C since the late 19th century (Houghton *et al.* 1995). Continuing increases in the concentration of these and other greenhouse gases are expected to dramatically alter Earth's climate in the 21^{st} century.

Timmermann *et al.* (1999) constructed a model that simulated an irregular ENSO cycle with similar amplitude and dynamics of observed ENSO cycles. Two 300-year integrations were performed, one with fixed present-day and one with increased greenhouse gas concentrations. Strong changes in the ENSO system were found to occur under increased gas concentrations. Specifically, the mean of the oscillations was found to shift toward the El Niño state. In agreement, there has been a shift to strongly negative SOIs over the last 20 years (Allan *et al.* 1996). In addition to changes in the mean state, inter-annual variability was predicted to become stronger, leading to more extreme year to year variations, with variations being skewed toward the positive La Niña phase.

An illustration of how inter-annual climate variability phenomenon can impact on community composition is shown in Fig. 1-1. Within the productive grasslands of north-eastern New Zealand, the greatest abundance of subtropical grasses appears to coincide with the years when the climatic patterns associated with the La Niña phase of the El Niño/Southern Oscillation prevail.

1.3.2 Extremes

Expectations of changes in the frequency of extreme climatic events are determined by predicting changes in probability distributions (Wigley 1985). As mean global temperatures increase, we can expect an increase in the number of days that an upper temperature threshold is exceeded and a decrease in extreme cold days. This is illustrated in Fig. 1-2 by the shift from μ (mean of the solid curve) to μ^* (long dashed curved) where x is the extreme threshold. It also illustrates that an increase in probability of an extreme event is not proportional to a shift in the mean. In agreement, Mearns, Katz & Schneider (1984) found that a relatively small increase in mean temperature (1.7°C), resulted in a three fold increase in probability of five consecutive days with maximum daily temperatures in excess of 35°C.

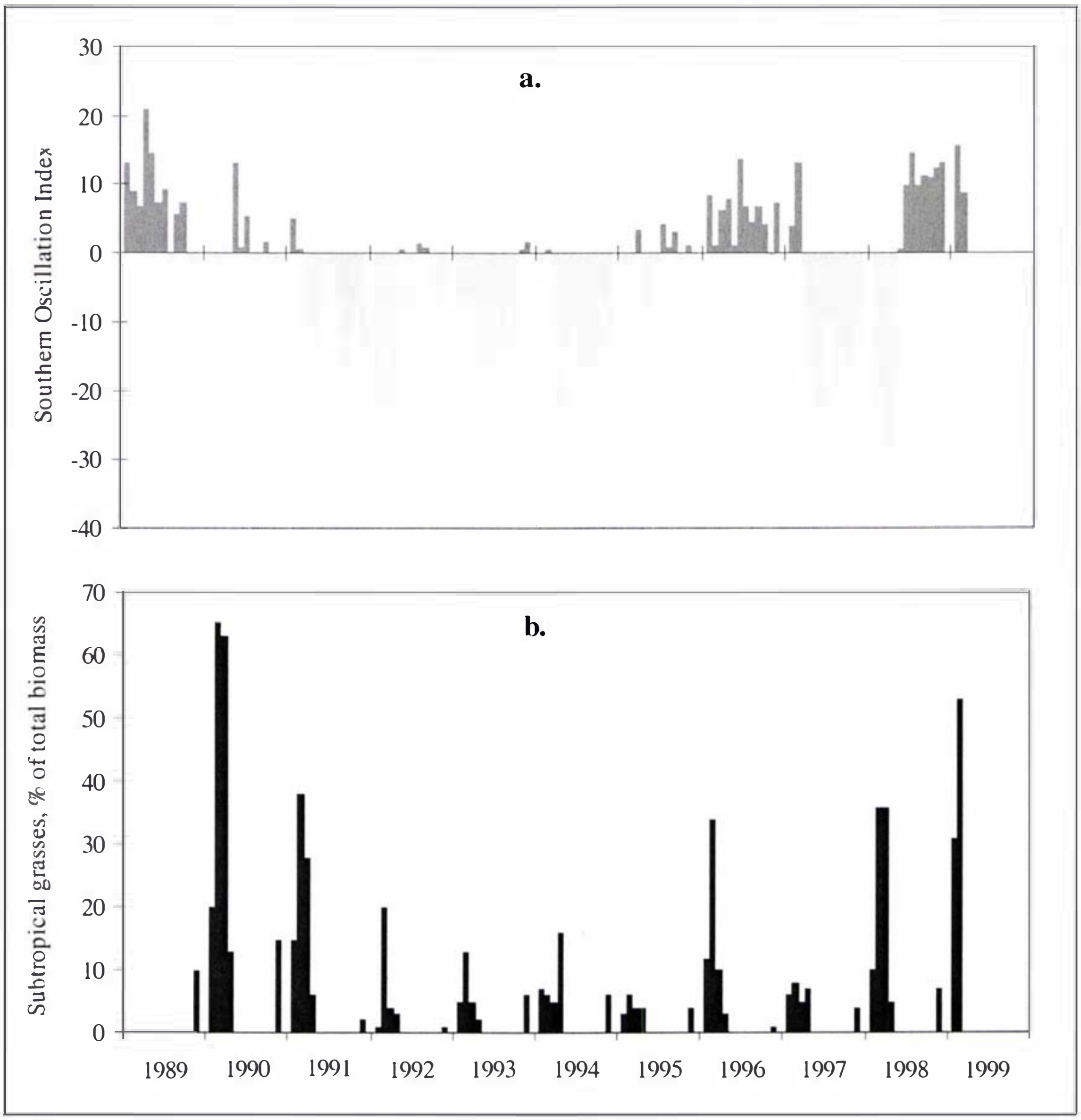

Fig. 1-1 (a.) Southern Oscillation Index for the last ten years. Positive values are associated with La Niña climatic patterns, negative values are associated with El Niño. (b) Percent contribution of subtropical grasses to total biomass of the grasslands of north-eastern New Zealand (the Bay of Plenty region) for the last ten years (B.D. Campbell, T.A. White and B. Keene, unpublished data).

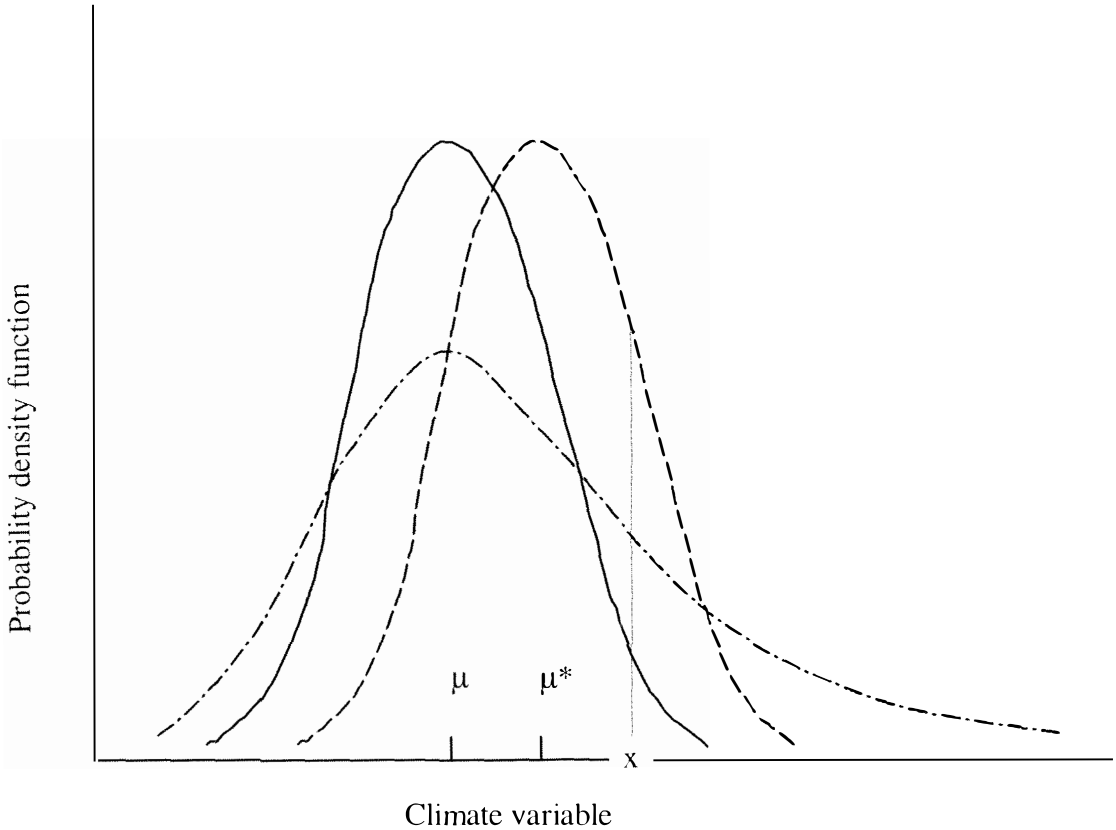

Fig. 1-2 Changes in the probability distribution of a climate variable (solid curve). Firstly, constant variance but increased mean (long dashed curve), and secondly, constant mean but increased variance (short-long dashed curve). Extreme threshold shown as level 'x' of the climatic variable. Adapted from Katz & Brown (1992) and Houghton (1997).

The effect of increased mean global temperatures on the probability of precipitation extremes is less certain. As the globe warms the hydrological cycle is expected to become more intense, leading to more heavy rainfall events (Kattenberg *et al.* 1995). In agreement with this Gordon *et al.* (1992) found that the return period for heavy rainfall events decreased under a warming scenario of twice current CO_2 concentrations.

While shifts in climatic means are important, it has been found that increases in climate variability have a greater impact on the frequency of extreme climatic events. Katz & Brown (1992) demonstrated that the frequency of extreme events is relatively more dependent on changes in the *scale* parameter (variance) than the *location* parameter (mean) of the probability distribution. When the location parameter is held constant and the scale parameter is increased the shape of probability distribution changes, particularly in the tail region, which determines the probability of extreme events (Fig. 1-2; compare solid curve with short-long dashed curve).

This relationship between climate variability and the frequency of extreme climatic events has important implications for vegetation in regions that are influenced by the ENSO climatic pattern. The increased variability of ENSO predicted by Timmermann *et al.* (1999) is, therefore, likely to result in an increased frequency of extreme climatic events. For eastern New Zealand this could mean more severe droughts during El Niño or greater number of heavy rainfall events and hot days during La Niña. For western New Zealand, El Niño related floods or La Niña droughts might become more prevalent (Brenstrum 1998).

1.4 Climate extremes and plant function

1.4.1 Background

Most research agendas that have attempted to predict the impact of global climate change on terrestrial ecosystems have focused on the projected gradual shifts in climatic means (Watson *et al.* 1995). However, as examined in sections 1.3.1 (page 4) and 1.3.2 (page 5), global climate change is also expected to be punctuated by an increase in the temporal variability of climate and extreme climatic events.

The potential of extreme climatic events to impact on plant communities has been emphasised by Woodward (1987):

> "....infrequent natural catastrophes, which were times when the environmental range exceeded plant tolerance, could have dramatic effects on plant distribution, in a background

of tolerable climatic conditions which probably selected the local range of plant species." (Woodward 1987, p 27)

Extreme climatic events have the potential to cause more rapid changes than those associated with gradual shifts of climatic means, given their abrupt and damaging nature (Walker 1991). Westoby *et al.* (1989) also suggest that natural catastrophes such as extreme events have the impetus to cause permanent changes to plant community structure. Unfortunately, most predictions are theoretical, based on current knowledge of ecosystem processes and feedbacks, highlighting the need for studies that examine natural events or those that experimentally simulate extreme events.

Pioneering but controversial studies of the impact of a natural extreme event on plant communities and ecosystem processes were those of Tilman & El Haddi (1992), Tilman & Downing (1994) and Tilman (1996). Tilman & El Haddi (1992) aimed to determine the impact of severe drought on species richness (number of species) and local invasion and extinction within prairie grasslands of Minnesota. It was found that an extreme drought can limit the number and type of species within a community by causing the local extinction of rare species. Tilman & Downing (1994) and Tilman (1996) concluded that greater plant species richness leads to greater stability of plant community biomass after perturbation but not stability of community composition (the abundance of individual species). Tilman (1996) explained this difference between productivity and compositional stability by suggesting species with functional traits for resistance to an extreme event will be released from the competitive suppression of pre-event dominants that were less tolerant.

The controversies surrounding the conclusions of Tilman and those based on a large-scale laboratory experiment (Naeem *et al.* 1994; Naeem *et al.* 1995) relate to recent research, which fails to support that species richness per se begets ecosystem stability (Hooper & Vitousek 1997; Wardle *et al.* 1997). Further doubt has been cast by Huston (1997), who identified that Tilman & Downing's (1994) stability-diversity relationship can be explained in terms of 'hidden treatments' that affected plant productivity independent of species richness. An alternative hypothesis is that functional diversity and composition are more important in determining ecosystem stability (Grime 1997).

One major limitation in using natural catastrophes to examine their impact on plant communities is that they are unpredictable random events. The conclusions of Tilman on the impacts of drought were based on the results of data from a long-term preexisting experiment that was originally aimed at determining the effects of nitrogen supply on the composition, dynamics, and diversity of successional grasslands (Tilman 1987). A less opportunistic and more controlled approach is to experimentally simulate extreme perturbations over artificial or natural plant communities, such as the innovative experiments of Sankaran & McNaughton (1999) and MacGillivray *et al.* (1995).

Sankaran & McNaughton (1999) performed a large-scale field experiment in the savannah grasslands of India. These authors measured ecosystem response to perturbation across an existing gradient of diversity generated by extrinsic factors such as climate, soil fertility and the frequency of disturbance. The results of their study highlight the need for a greater understanding of the impact of extreme events on plant communities. Contrary to previous studies of diversity their results show that variation in diversity owing to extrinsic determinants (e.g. disturbance caused by extreme events) may dominate the relationship between biodiversity and ecosystem properties, whereas variation in diversity within communities may play a substantially smaller or different role.

MacGillivray *et al.* (1995) identified differences in nutrient stress tolerance of 21 herbaceous species, based on 26 plant functional traits measured (screened) under standardised laboratory conditions (Hendry & Grime 1993). The main aim was to test Leps *et al.*'s (1982) predictions of resistance and resilience on five contrasting plant communities exposed to three types of simulated extreme event – drought, frost and fire. Leps *et al.* (1982) argued that traits which promote nutrient stress tolerance leads to greater *resistance* to other forms of damage but at the expense of an ability to rapidly recover after damage (*resilience*).

Their results agreed with Leps *et al.*'s (1982) contentions. There was a positive correlation between nutrient stress tolerance and resistance to damage from an extreme event and a negative correlation with resilience (after one year). Equally important were the outcomes that "resistance of a species to drought and frost damage was largely a function of the traits possessed by that species rather than a function of the community context in which it occurred" and "frost and drought resistance... at the community level can be explained by, and are consistent with, trends observed at the species level" (MacGillivray *et al.* 1995, pp 646 and 647). This illustrated that the functional traits of component species can determine community and ecosystem function, a view strongly endorsed by Grime (1997). Furthermore, the quantification of plant functional traits and identification of recurrent patterns (plant functional types) provides a basis for predicting the impact of extreme climatic events on plant communities.

1.4.2 Scale and community context

Diaz & Cabido (1997) examined the plant functional attributes of a diverse array of plant types originating from an equally broad spectrum of environmental conditions leading to predictions of coarse-scale shifts in vegetation across regions. The characteristics of the species and communities of MacGillivray *et al.* (1995) also differed greatly. The strength of their convictions can largely be attributed to the considerable differences between the traits of their functional types. Under the classification scheme of Diaz & Cabido (1997), New Zealand grassland species would be classified into one or possibly two functional types. What will be the impact of global climate change on these communities, which dominate vast landscapes? At this coarse-scale, the functional diversity of these communities is minimal. Will this make them more vulnerable or sensitive to extreme climatic events? That is, if the functional traits for tolerance are not present to tolerate a particular extreme event, will these communities be more prone to invasion from functional types which are tolerant? Clearly there is a need for finer-scale more-specific studies that recognise functional differences within comparatively homogeneous communities and landscapes.

This study focused on managed grassland communities within the North Island of New Zealand. The soils on which these communities are based are typically of high fertility due to their moderately-nutrient rich alluvial or volcanic parent materials and substantial additions of exogenous nutrients through fertiliser applications. The combination of high fertility and temperate/mesic climates (see section 1.5.1, page 12) results in highly productive communities (Daly 1990). Both annual and perennial grasses and forbs co-exist within a dense community of rapidly-growing shoots and roots.

The main factor moderating the density of vegetation is frequent removal of above-ground biomass by large ungulate herbivores, specifically dairy cattle. Typically, depending on plant growth rates and animal demands, cattle graze these communities for short (one day) but intense periods every 2-4 weeks. The intensity of disturbance as a result of grazing depends not only on animal density and duration of grazing, but also on soil physical properties, such as moisture content. High moisture content soils are weaker (McLaren & Cameron 1990), and consequently, offer less resistance to the action of hooves in disturbing the soil surface. Accordingly, the intensity of disturbance from grazing is typically the greatest in winter and spring, and the least in summer and autumn.

This thesis aims to predict the impact of increased temporal variability of climate and extreme climatic events on these productive grassland communities by identifying differences in the functional attributes of their constituent species. The following section describes the typical climate and vegetation of New Zealand grassland communities. It also reviews the important functional differences already recognised between species.

1.5 New Zealand grassland communities

1.5.1 Climate

New Zealand is located in the south-west Pacific, with the two main islands covering a latitude range of 34° south to 47° south. Its climate is strongly influenced by the prevailing westerly wind-flow, a large expanse of surrounding ocean and by its mountainous topography.

Both the western and eastern regions of the north and south islands of New Zealand are separated by mountain ranges. Westerly-moving air is forced to rise over the mountains thereby cooling and condensing, leading to the formation of clouds and rain on the windward side. Once past the mountains the air is able to fall back toward sea level, and as it does so it warms by compression and most of the water vapour evaporates (Sturman & Tapper 1996; Brenstrum 1998). Consequently, the predominant westerly climatic pattern leads to below average temperatures but above average rainfall in southern and western areas whereas eastern areas experience below average rainfall. Typical climatic ranges for the North Island are: rainfall, 800-1300 mm per annum; maximum temperature (mid-summer daily average), 20-25°C; minimum temperature (mid-winter daily average), 0-9°C (Zwartz 1998). There is a strong seasonal rainfall pattern, with the majority of rain falling in the winter and spring periods. The number of days (24 hour period) where temperatures reaches, or is less than 0°C, also varies depending on altitude, latitude and distance from the ocean. Coastal and far northern localities can remain frost free, whereas 30 to 35 frosts are recorded annually in central North Island (Sturman & Tapper 1996).

1.5.2 Past

Lowland productive grasslands were originally established in New Zealand after deforestation in the mid 19th century. Species sown then were all of temperate origin. Some common examples include *Lolium perenne* L., *Dactylis glomerata* L., *Agrostis capillaris* L., *Trifolium pratense* L. and *Trifolium repens* L. (Daly 1990).

Grasses of subtropical origin first appeared in New Zealand in the latter half of the 19th and early 20th centuries (Cheeseman 1906; Edgar & Shand 1987). Their introduction was probably accidental, as a contaminant of imported seed. Common species include annuals, *Digitaria sanguinalis* (L.) Scop., *Eleusine indica* (L.) Gaertn. and *Panicum dichotomiflorum* Michx., and perennials, *Axonopus affinis* Chase, *Cynodon dactylon* (L.) Pers., *Paspalum dilatatum* Poir., *Paspalum distichum* L., *Pennisetum clandestinum* Chiov., *Setaria geniculata* auct. and *Sporobolus africanus* (Poir.) Robyns & Tourn (Edgar & Shand 1987). They are noted as invasive weeds of crops (Matthews 1971), and importance in grassland communities has become increasingly apparent (Field & Forde 1990).

1.5.3 Present

New Zealand grasslands are situated in a temperate-subtropical vegetation transition zone. Temperate species, such as *L. perenne* and *T. repens*, are ubiquitous but, at present, subtropical species are mostly restricted to grasslands of the North Island, with their abundance decreasing from warmer northern to cooler southern regions. In the far north, perennial subtropical species (e.g. *Pennisetum clandestinum* and *Paspalum dilatatum*), are dominant grassland components (Lambert 1967). Further south, in the Waikato and Bay of Plenty regions, subtropical annual species are particularly prevalent (e.g. *Digitaria sanguinalis* and *Panicum dichotomiflorum*), their abundance increasing and decreasing dramatically during spring/summer and autumn/winter periods, respectively (Baars *et al.* 1991). In the most southern regions of the North Island, for example the Manawatu, subtropical species are common inhabitants of disturbed ground (e.g. cultivated soil or road-side verges), but are scarce within grassland communities.

1.5.4 Functional differences between species

Species within a plant community vary considerably with respect to their functional traits. Diaz & Cabido (1997), for example, measured a total of 24 traits on the flora of central-western Argentina and Grime *et al.* (1997) measured 67 traits on species commonly found in central England. Examples of the traits measured included canopy height, life-history, the area, tensile strength, stomatal density and palatability of leaves, genome size, and seed size.

Species in New Zealand grassland communities equally differ in such functional traits. With respect to response to climate, one of the key functional trait differences recognised between plant species, is photosynthetic pathway. There are two main photosynthetic pathways represented, termed C_3 and C_4, which differ, biochemically, in two main ways. Firstly, C_4 plants produce four carbon acids (malate and aspartate) and C_3 plants produce three carbon acids (3-phosphoglycerate) as the initial product of primary CO_2 fixation. Secondly, the reactions of the Calvin cycle are restricted to the bundle-sheath cells of C_4 plants. C_4 plants fix CO_2 in the mesophyll cells then transfer (effectively pump) four carbon acids into the bundle-sheath cells where CO_2 is released and carboxylation proceeds (Salisbury & Ross 1992).

A fundamental physiological difference between C_3 and C_4 species is their growth in response to temperature. C_4 species generally have a higher optimal temperature for growth than C_3 species, which largely explains present regional and global distributions of C_3 and C_4 species (Teeri 1988; Epstein *et al.* 1997; Campbell *et al.* 1999). Different temperature optima for growth arise through differences in carboxylation efficiency of photosynthesis. As temperature increases so does the competitiveness of O_2 for active sites on the carboxylating enzyme ribulose-bis-phosphate carboxylase/oxygenase (Rubisco), leading to increased photorespiration (Pearcy & Ehleringer 1984). C_4 plants overcome this problem by concentrating CO_2 within the bundle sheath cells, which reduces the affinity of O_2 for Rubisco and increases photosynthetic efficiency.

C_4 plants also assimilate more CO_2 relative to water lost through transpiration than C_3 plants making C_4 photosynthesis more water-use efficient and, therefore, potentially more suited to existing in drier environments (Pearcy & Ehleringer 1984). However, differences in water-use efficiency are generally not as robust predictors of C_3 and C_4 species distribution as temperature optima differences (Kemp & Williams 1980; Teeri 1988).

C_4 species are also generally more tolerant of extreme high temperatures and are more sensitive to chilling and frosting temperatures than C_3 species (Atwell, Kriedemann & Turnbull 1999). In spite of this commonly recognised difference in heat tolerance between C_3 and C_4 species, it has been found that disruption of thylakoid membrane structures and processes involved in primary energy conversion (e.g.

photophosphorylation), rather than the enzymes of the carboxylation reactions, are the primary cause of irreversible heat stress damage (Weis & Berry 1988). Therefore, differences in thermal tolerances of C_3 and C_4 species are more likely to be a reflection of adaptation to the habitat of origin than a result of different photosynthetic pathways (Smillie & Nott 1979; Osmond *et al.* 1987).

C_4 species also have higher fibre, lower protein (nitrogen), lower soluble carbohydrate contents and lower organic matter digestibility than C_3 species of comparable age (Forde *et al.* 1976; Taylor *et al.* 1976; Minson 1981; Jackson *et al.* 1996). The lower nitrogen content of C_4 tissues results from greater nitrogen-use efficiency of C_4 photosynthesis. In other words, C_4 species assimilate more carbon per unit leaf nitrogen than C_3 species (Pearcy & Ehleringer 1984).

While of considerable importance to mixed C_3/C_4 communities, photosynthetic pathway is only one of many functional traits that determines a plants response to its abiotic and biotic environment. For example, a plant's competitive ability has been found to depend on a suite of morphological and physiological attributes (Gaudet & Keddy 1988; Campbell *et al.* 1991; Grime *et al.* 1991; van der Werf *et al.* 1993; Goldberg 1997; but c.f. Crawley 1997a, page 618). A primary aim of this study is to contribute a better understanding of key traits in plant and ecosystem function in grazed grassland communities in relation to climate.

1.6 Research approach based on plant function

In selecting traits to measure, emphasis needs to be placed on characteristics with maximum predictive power in determining response at the whole plant and community level (Diaz & Cabido 1997; Grime *et al.* 1997). Diaz & Cabido (1997) also recognised the potential of surrogate traits, which are easily measured but quantify other more labour-intense or technically-demanding traits. For example, specific leaf area (SLA) has been found to be positively correlated with relative growth rate (Lambers & Poorter 1992).

As mentioned previously, no consistent association has been found between regenerative phase and vegetative phase traits (Shipley *et al.* 1989; Grime *et al.* 1997; but c.f. Rees 1997), but both types play critical roles in determining the structure and dynamics of plant communities (Grubb 1977; Harper 1977; Grime 1979; Crawley 1997b). Regenerative traits, such as seed size and number and length of juvenile phase, are important in determining dispersal, recruitment and invasion (Noble 1989; Burke &

Grime 1996; Rejmánek & Richardson 1996), whereas vegetative traits, such as SLA, leaf nutrient concentration, leaf life span, palatability and investment in support and defence structures are important in determining competitive ability versus stress tolerance (Grime *et al.* 1997).

In recognition of the lack of a consistent association between regenerative and established phases, experimentation targeted key life-cycle and seasonal stages where vegetation processes such as recruitment and competition were considered to be most important in determining community structure. This is shown schematically in Fig. 1-3. Life cycle stages were related to season and the environmental conditions most likely to be experienced at those stages. On this basis, plant functional traits critical to success at those stages were identified and quantified in experiments, described in Chapters Two, Three and Five. Predictions of the impact of extreme climatic events based on established phase functional differences between species were tested by actual community responses, described in Chapters Four and Five.

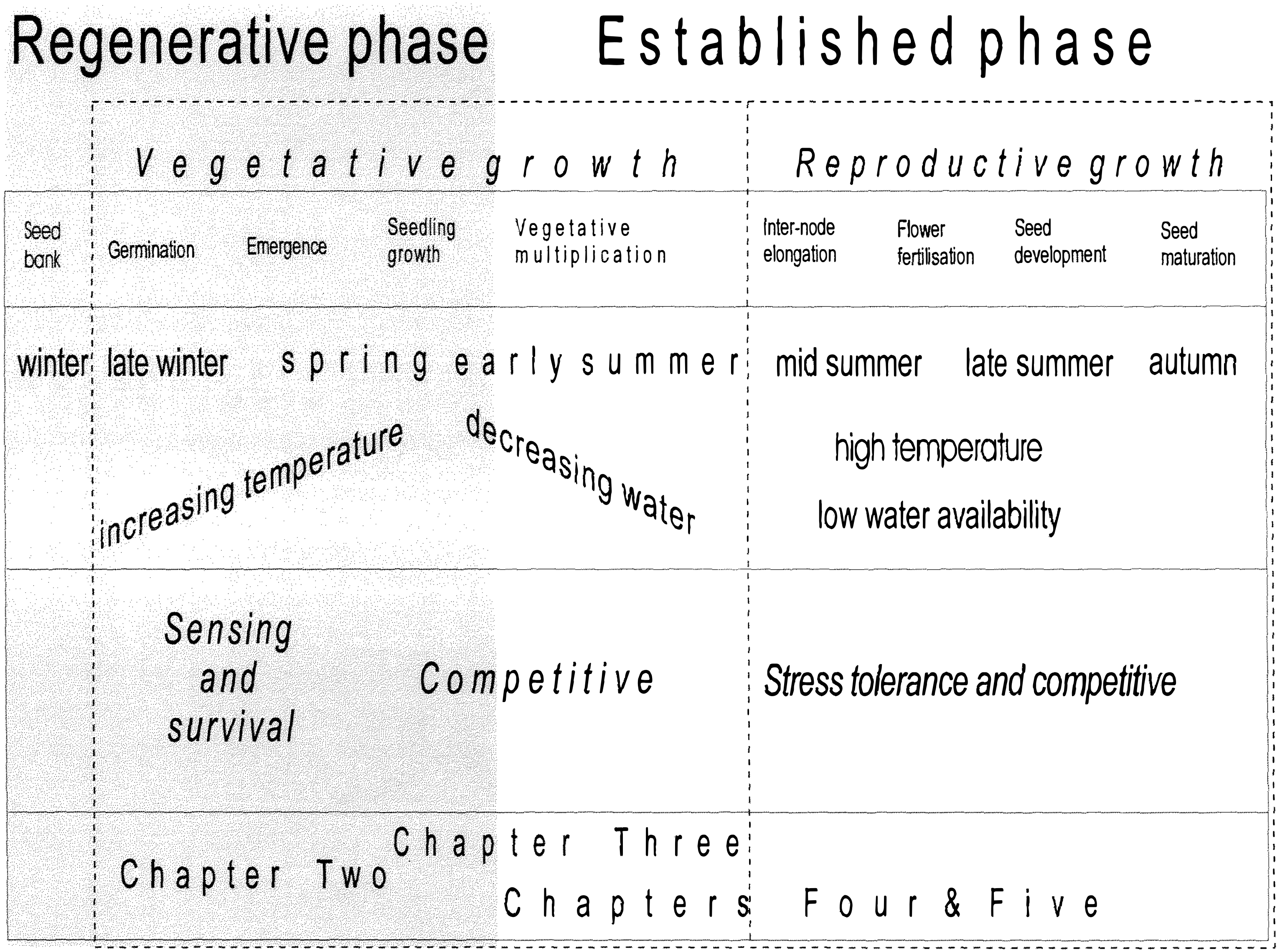

Fig. 1-3 Research programme based on laboratory screening and field testing at key life cycle stages. I life cycle stages; II stage of season and environmental conditions; III key plant functional attributes; IV chapters of thesis.

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2 Laboratory screening of juvenile response of grassland species to warm temperature pulses and water deficits to predict invasiveness

CONTENTS

2.1 Abstract

Two laboratory screening experiments tested the juvenile phase responses of fourteen C_3 and twelve C_4 grassland species to pulses of warm temperature and water deficits. The first experiment determined germination response in relation to duration of warm temperature (30/20°C day/night) exposure. The second experiment determined the desiccation tolerance of seedlings immediately following germination.

The C_4 species were more dependent on warm temperatures for germination than the C_3 species, however there was considerable variation within C_3 and C_4 types. In particular, *Panicum dichotomiflorum* was identified as the C_4 species least dependent on warm temperatures, exhibiting greater than 50% of maximum germination in continuous cold (7°C).

In general, the C_3 species were more desiccation tolerant than the C_4 species but there were several exceptions. *Trifolium repens* (C_3) was ranked as the least desiccation tolerant whereas *Setaria geniculata* (C_4) was the eighth most tolerant species. Large-seeded species were more desiccation tolerant than small-seeded species.

It is suggested that poor desiccation tolerance contributes to C_4 invasion currently being restricted to wetter regions. On the basis of juvenile phase attributes the C_3 species were ranked as more invasive than the C_4 species and annuals as more invasive than perennials. Having invasive juvenile phase attributes is an advantageous adaptation for species that solely rely on regeneration from seed.

2.2 Introduction

Seed germination and seedling establishment are critical to the recruitment of new individuals into plant communities (Grubb 1977; Harper 1977; Fenner 1992; Rees 1997). Seedlings, however, are highly disadvantaged relative to mature plants in their ability to secure resources essential for growth (Fenner 1987). Therefore, seeds have evolved to sense and respond to their external environment, such that germination is triggered by light and nitrate levels, temperature and/or water conditions that will maximise the probability of successful seedling establishment (Koller 1972; Bewley & Black 1982; Roberts 1988; Fenner 1992; Bewley & Black 1994; Rees 1997).

The seasonal temperature cycle is the primary factor regulating the timing of germination in temperate grassland communities (Probert 1992; Benech-Arnold & Sánchez 1995). Germination is prevented until the required thermal conditions are met. For example, seeds of warm season species are prevented from germinating until minimum temperature thresholds are achieved in the spring (Baskin & Baskin 1980; Bouwmeester & Karssen 1992). Specific minimum temperatures required to initiate germination vary with species (Bewley & Black 1982; Bewley & Black 1994), but within the context of increasing climatic variability and 'out of season' warm temperature episodes, warm period duration will be more important in determining rate and extent of germination. Seeds that require only a short warm period to initiate germination may confer an emergence and establishment advantage over those with longer warm period requirements.

Numerous studies of temperature and/or light effects on germination of C_3 and C_4 grassland species provide physiological explanations for the field observations of emergence. C_4 species have a higher temperature optimum for germination than the C_3 species (Eggens & Ormrod 1982; Charlton *et al.* 1986; Maun & Barrett 1986; Ahmed & Wardle 1991; Qi & Redmann 1993). Diurnally fluctuating temperatures promote germination in numerous grassland species (Young *et al.* 1975; Thompson *et al.* 1977; Naylor & Abdalla 1982; Thompson & Grime 1983; Williams 1983; Probert *et al.* 1986) but many C_4 species specifically require fluctuating diurnal temperatures for any germination to proceed (Fausey & Renner 1997; Henskens 1997; Martinez Ghersa *et al.* 1997; Nishimoto & McCarty 1997). An obligatory requirement for light for germination is more pronounced in C_4 species than C_3 species (Taylorson 1980; Henskens 1997; Nishimoto & McCarty 1997).

Germination responses to changes in light quantity (increased photon flux density) and quality (reduced red to far-red ratio) and/or increased diurnal temperature fluctuations have long been recognised as 'gap-detection' mechanisms in seeds (Thompson *et al.* 1977; Collins & Pickett 1987; Vazquez Yanes & Orozco Segovia 1990; Vázquez-Yanes & Orozco-Segovia 1994). Given the different responses of C_3 and C_4 grassland species to alternating temperature and light described above, the ability to detect gaps was more apparent in the C_4 species, particularly in the invasive annuals that form persistent seed banks, than the C_3 species. However, regardless of locality in relation to vegetation gaps, exceeding minimum temperature requirements will be the primary factor controlling the onset of germination of C_4 seeds in spring.

A consequence of increased diurnal temperature fluctuations and increased photon flux density within vegetation gaps is decreased relative humidity and soil moisture at the soil surface (Collins & Pickett 1987; Vázquez-Yanes & Orozco-Segovia 1994). In addition to surface drying due to vegetative cover removal, soil moisture contents are naturally decreasing in New Zealand with decreasing rainfall during the transition from winter to summer (Daly 1990). While these marginal changes in resource availability at the soil surface are of minimal consequence to established plants, seedlings are more sensitive to surface drying given the limited soil volume explored by their roots (Buldgen *et al.* 1995; Awan *et al.* 1996; Dear & Cocks 1997; Defosse *et al.* 1997). Therefore, it is conceivable that seedlings may experience water stress during the first stages of growth immediately after germination (Olsson *et al.* 1996). Under such conditions, an establishment advantage is most likely to be conferred to those species that can tolerate desiccation.

In this study two comparative screening experiments were performed to test the juvenile phase responses of 26 common New Zealand grassland C_3 and C_4 species (Table 2-1) to simulated warm temperature pulses and water deficits of increasing duration. Both experiments were performed within controlled environment rooms using standardised experimental conditions in order to identify variation in responses between species. This provided evidence on which to base predictions of recruitment and regeneration in the field. The specific objectives of the two experiments were to:

1) test the dependency on a warm temperature period to initiate germination,
2) test the desiccation tolerance of seedlings immediately following germination,
3) predict potentially invasive species on the basis of these two juvenile phase functional attributes.

Table 2-1 Characteristics of the 26 grassland species tested in the two experiments. All species belong to the Gramineae family except for the three *Trifolium* species which belong to the Leguminosae family. Life history: A = annual; SLP = short-lived perennial; P = perennial. * only tested in experiment 2. Nomenclature from Hafliger & Scholz (1980); Webb *et al.* (1988); Lambrechtsen (1992).

Species	Photosynthesis	Life history	Seed mass (mg)
Agrostis capillaris L.	C_3	P	0.069
Axonopus affinis Chase	C_4	P	0.149
Bromus stamineus Desv.	C_3	P	10.538
Cynodon dactylon (L.) Pers.	C_4	P	0.216
Dactylis glomerata L.	C_3	P	0.786
Digitaria sanguinalis (L.) Scop.	C_4	A	0.211
Echinochloa crus-galli (L.) Beauv.	C_4	A	1.716
Eleusine indica (L.) Gaertn.	C_4	A	0.620
Festuca arundinacea Schreb.	C_3	P	1.837
Holcus lanatus L.	C_3	P	0.271
Hordeum murinum L.	C_3	A	5.098*
Lolium multiflorum Lam.	C_3	A	3.828
Lolium perenne L.	C_3	P	1.478
Panicum dichotomiflorum Michx.	C_4	A	0.340
Paspalum dilatatum Poir.	C_4	P	1.318
Paspalum distichum L.	C_4	P	0.584*
Pennisetum clandestinum Chiov.	C_4	P	2.315
Phalaris aquatica L.	C_3	P	1.364
Poa annua L.	C_3	A	0.236
Rytidosperma clavatum (Zotov) Connor et Edgar	C_3	SLP	0.683
Setaria geniculata auct.	C_4	P	0.503
Setaria viridis (L.) Beauv.	C_4	A	0.446
Sporobolus africanus (Poir.) Robyns & Tourn.	C_4	P	0.181
Trifolium pratense L.	C_3	SLP	1.745
Trifolium repens L.	C_3	P	0.496
Trifolium subterraneum L.	C_3	A	6.715

2.3 Methods

A total of 26 grassland species were tested, these can be classified according to taxonomic, photosynthetic and life history characteristics (Table 2-1). The same species were used for both experiments except *Hordeum murinum* and *Paspalum distichum* were not used in the germination experiment due to insufficient seed. The seeds of the C_3 species were sourced from commercial seed-lots, whereas the C_4 species' seeds were collected from wild plants, from throughout the North Island of New Zealand in 1994.

2.3.1 Experiment 1

2.3.1.1 Cold imbibition

Seeds were placed on two layers of moistened (10 ml distilled water) germination card contained within petri-dishes (90 mm diameter). During this pre-treatment phase it was desired to imbibe the seeds but not stimulate germination. Accordingly, the seeds were placed in a controlled environment room set at a constant temperature of 7°C (Plate 2-1). Seeds were not imbibed at lower than 7°C due to seeds of tropical origin being irreversibly damaged at 4-5°C (Pollock & Roos 1972). For each species and treatment there were 4 replicates of 100 seeds per replicate (100 seeds per petri-dish). The four dishes were stacked one on top of the other, and placed in a plastic bag. Dish-stacks were contained within plastic trays with a white sheet of paper placed over top (Plate 2-1). A "dummy" petri-dish containing only moistened germination card was placed on the top of the stack. The purpose of the paper and the dummy dish was to reduce light level differences between the top and lower dishes and to prevent the top dish from drying out. The seeds remained within the cold pre-treatment for 7 days.

2.3.1.2 Warm temperature

Seeds were removed from the cold room and placed in the warm room for six different pre-determined periods: 0, 12, 24, 48, 96, and 192 hours at 30°C day and 20°C night. The 12 hour treatment was constant 30°C. Both the cold and warm rooms were synchronised for a 12 hour light and 12 hour dark period.

Plate 2-1 Controlled environment room with seeds contained in petri-dishes. Petri-dishes were stacked into sets of four replicates, placed in plastic bags and then into trays and covered with a sheet of paper.

Plate 2-2 Plating-out *P. dichotomiflorum* seedlings for a desiccation treatment.

2.3.1.3 Cold post-treatment

On completion of each warm temperature treatment period the seeds were transferred back to the 7°C cold room. All petri-dishes were checked daily, with germinated seeds being removed and discarded. The criteria for successful normal germination were the presence of healthy radicle and shoot. For the grass species there had to be a healthy leaf emerging from the coleoptile. The experiment was terminated after 27 days.

2.3.1.4 Data analysis

Germination percent was calculated as the mean (of the four replicates, with associated stand error) number seeds germinated per dish by the end of the experiment.

The cumulative germination data were modelled on the total number of seeds per species (i.e. 400 seeds), using the CUMDISTRIBUTION procedure of the statistical package Genstat (Genstat 5 Release 4.1). Close agreement was achieved between predicted and actual cumulative germination (Fig. 2-1). A germination rate was estimated for each curve using Equation 2-1. Germination rate represents the time (in days) to achieve 50% of the *maximum* number of seeds germinated for each species. Fifty percent of maximum germination was used to calculate germination rate because the inherent germinability differed considerably between species. A standard error for each germination rate was estimated using an RFUNCTION directive within the CUMDISTRIBUTION procedure.

$$t = \exp\left(m + \frac{\ln\left(\frac{p}{1-p}\right)}{b} \right) + lag, \quad where \quad p = \frac{N}{2n}$$

Equation 2-1 Cumulative logistic equation for calculating time for 50% of maximum germination. Model parameter descriptions: t = time in days; m = mid point of curve; b = slope at mid point; lag = time to start of germination; N = maximum number of seeds germinated over all treatments; n = maximum number of seeds germinated for a particular treatment.

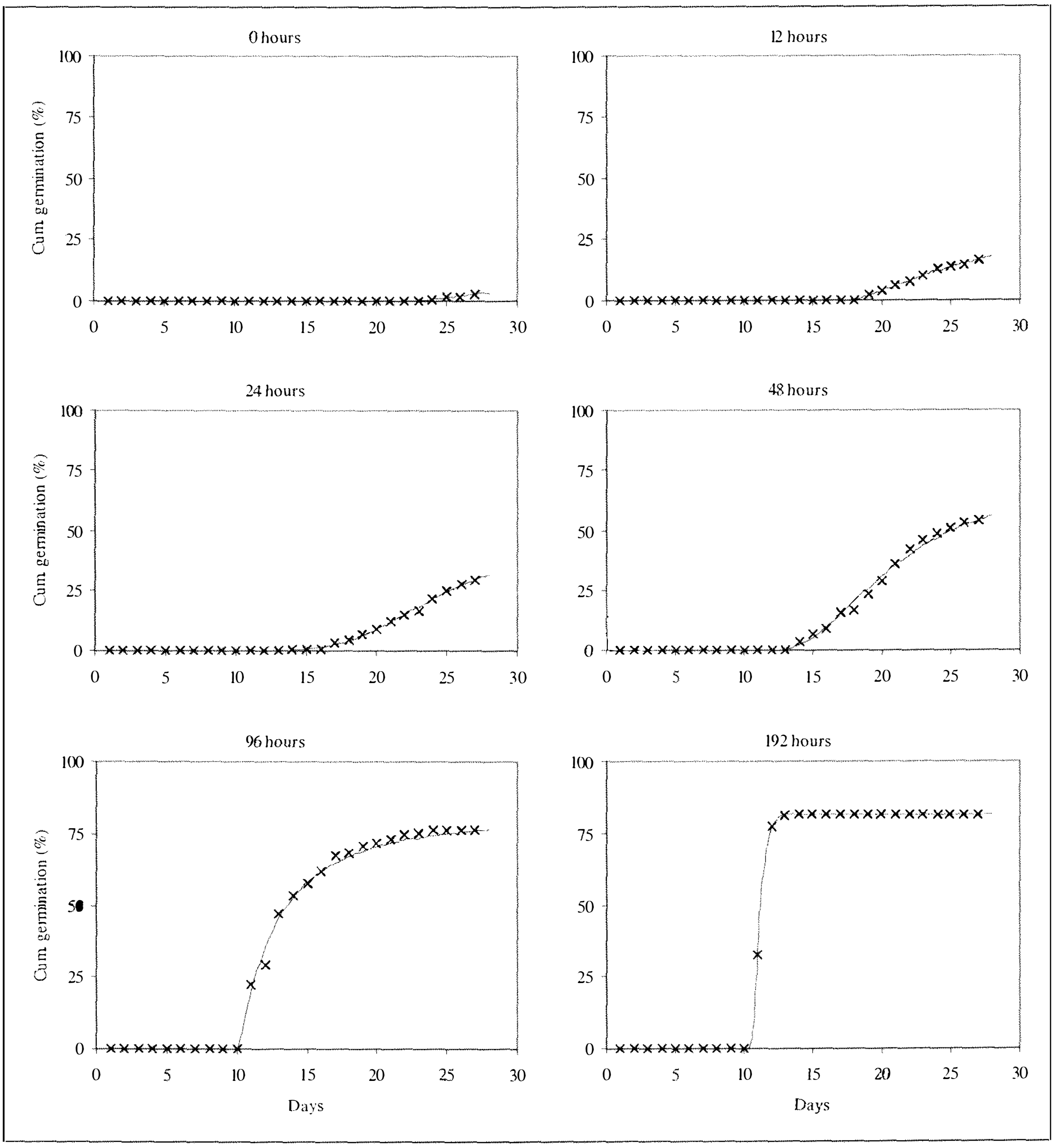

Fig. 2-1 Modelled (—) and actual (×) cumulative germination for *P. clandestinum* exposed to increasing warm temperature periods (hours at 30/20°C).

To determine relative dependency on a warm temperature pulse for germination an index was derived for each species from its germination rate data. The temperature dependency index was calculated as the germination rate at maximum exposure time (192 hours) less the mean of the germination rates at all shorter exposure times. For those species by treatment combinations that did not achieve 50% of maximum germination and those with no germination, rates of 30 and 35 days respectively, were used for the calculation.

2.3.2 Experiment 2

2.3.2.1 Germination

Seeds were germinated on two layers of moistened (10 ml distilled water) germination card. Germination was performed in a germination cabinet set for 12 hours light at 30°C and 12 hours dark at 20°C. Sufficient seeds were germinated to generate greater than 100 seedlings per species. Germination was timed according to germination rate so that species germinated together. Seedlings were desiccated 1 to 2 days after germination.

2.3.2.2 Desiccation

The desiccation treatments followed the principle outlined by Raynal *et al.* (1985), whereby seedlings were removed from moist substrate and transferred to dry substrate for various predetermined periods. Desiccation treatments were performed in a controlled environment room set for 12 hours light (700 μmol m^{-2} s^{-1}) at 25°C and 12 hours dark at 20°C. There were nine base water stress treatment levels applied to all species (0, 2, 4, 8, 12, 24, 48, 96 and 192 hours without water) and two additional treatment levels (20 and 40 days without water) for four resilient species (*H. murinum*, *Lolium multiflorum*, *Bromus stamineus* and *Trifolium subterraneum*).

For each species and treatment level 100 seedlings in total were desiccated. The 100 seedlings were divided into four replicates of 25 seedlings and placed on dry germination card contained within petri-dishes. The dishes were stacked one on top of the other and placed in plastic bags. Preliminary trials of the technique identified that seedlings on higher dishes desiccated more rapidly than lower stacked seedlings. To minimise this effect a 'blank' dish containing dry germination card was placed on the top of the stack. The stacking order was maintained throughout the experiment.

2.3.2.3 Re-hydration and counting

After the desiccation time had elapsed the dry substrate was re-hydrated with 10 ml of distilled water. Dead and alive counts were performed 96 hours after re-hydration. Classification was primarily based on shoot appearance – shoots had to be turgid and have a healthy green colour. Dark translucent green was indicative of irreversible tissue damage and seedlings were classified as dead. A brown dead primary root did not necessarily indicate seedling death as some species grew adventitious roots from, or near, the junction of the root and shoot.

2.3.2.4 Data analysis

The relationship between seedling mortality and desiccation time followed a "S" shaped curve, with slow mortality initially then rapid seedling death, before slowing down prior to complete mortality (Fig. 2-2). Accordingly, a logistic function was fitted to the data. Better agreement between predicted and actual values was achieved by using $\log_e$(time) for the logistic regression. A desiccation tolerance index was derived for each species as the number of hours without water to death of 50% of seedlings. It was estimated by linear interpolation of the logit of the predicted proportion dead with $\log_e$(time). Each index value has 95% upper and lower confidence limits.

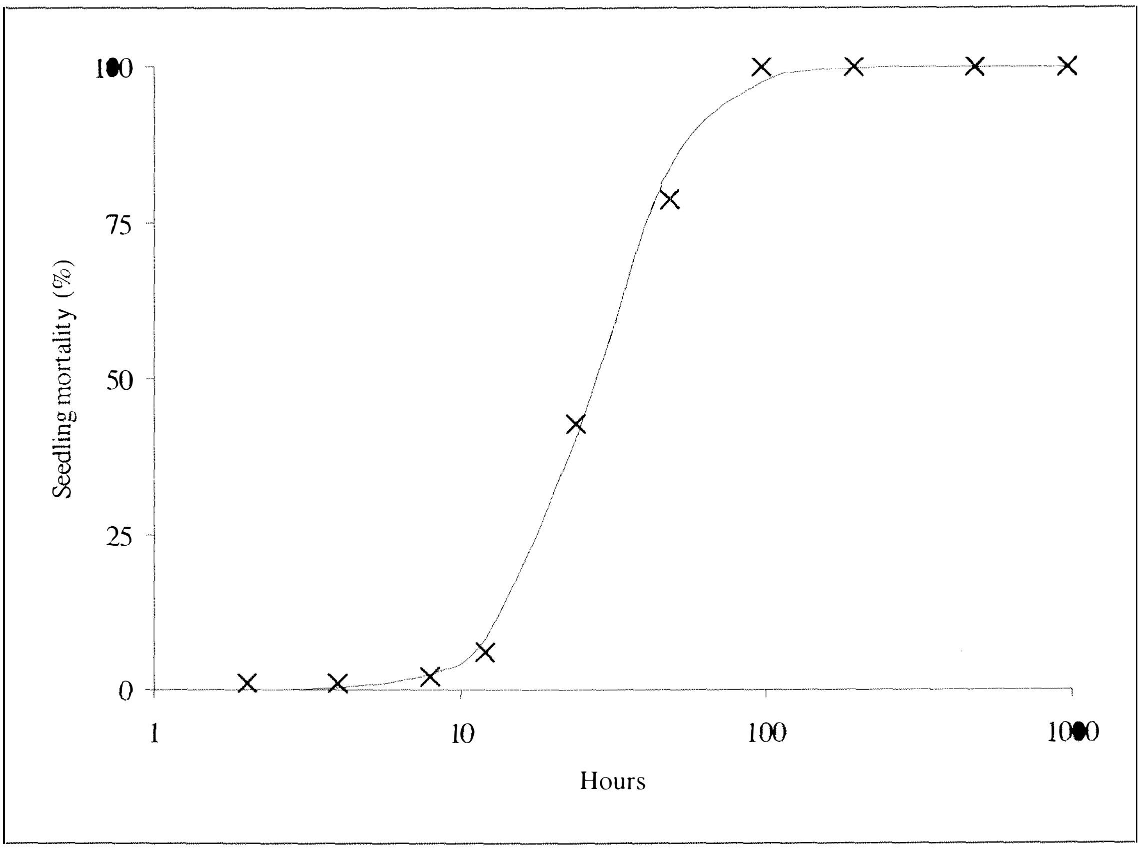

Fig. 2-2 Modelled (—) and actual (×) seedling mortality in relation to time (hours, expressed on logarithmic scale) without water for *P. clandestinum*.

2.4 Results

2.4.1 Experiment 1

2.4.1.1 Onset of germination

Most species achieved some germination at 7°C without exposure to elevated temperatures (Table 2-2). However, an obligatory requirement for a warm temperature period to initiate germination was apparent for 7 out of the 23 species tested. *Axonopus affinis* and *Cynodon dactylon* required greater than 24 and 48 hours warm exposure, respectively, to stimulate any germination. *Paspalum dilatatum*, *S. geniculata*, *Digitaria sanguinalis*, *Sporobolus africanus*, and *Echinochloa crus-galli* did not germinate in continuous 7°C conditions, but all showed some germination after 12 hours of 30/20°C.

2.4.1.2 Extent of germination

The extent of germination was measured as the cumulative germination percentage 27 days after imbibition. This varied considerably between treatments and species (Table 2-2). The absolute maximum germination percentage achieved ranged from 40-50% for *D. sanguinalis* and *A. affinis*, to 90-100% for *E. crus-galli*, *Poa annua*, *T. repens* and *T. subterraneum*.

Cynodon dactylon and *D. sanguinalis* both had less than maximum germination at exposure times of 96 hours or less. Warm periods of 48 hours or less reduced percentage germination for *A. affinis*, *S. geniculata*, *Pennisetum clandestinum* and *Setaria viridis*. *Axonopus affinis* only achieved 3% germination after 48 hours warm exposure. Final percentage germination of *P. dilatatum*, *S. africanus*, *P. dichotomiflorum*, *Phalaris aquatica* and *E. crus-galli* was lower than the maximum only if the warm exposure period was 24 hours or less. *Agrostis capillaris* only achieved 48% germination in continuous cold compared to a maximum of 80-90% when exposed to warm temperatures. The remaining species, all C_3, showed no differences in the extent of germination between treatments.

2.4.1.3 Rate of germination

Germination rate was observed to decrease with decreasing duration of exposure to warm temperatures (Table 2-3).

Table 2-2 Germination percent 27 days after imbibition. Presented as the mean (± standard error) of 4 replicates.

	Hours at 30/20°C											
Species	0		12		24		48		96		192	
	mean	se	mean	se	mean	se	mean	se	mean	se	mean	se
Agrostis capillaris	48	9	81	1	85	3	85	2	89	2	85	1
Axonopus affinis	0	0	0	0	0	0	3	2	40	10	37	9
Bromus stamineus	74	0.3	81	3	81	2	77	3	78	2	82	3
Cynodon dactylon	0	0	0	0	0	0	0	0	39	4	71	3
Dactylis glomerata	73	4	77	3	78	2	73	2	76	2	66	4
Digitaria sanguinalis	0	0	3	1	23	3	33	4	42	3	52	2
Echinochloa crus-galli	0	0	50	8	57	4	90	3	99	0.4	100	0.3
Eleusine indica	1	1	15	4	46	9	58	14	58	14	55	18
Festuca arundinacea	86	4	84	2	85	3	86	2	91	1	89	3
Holcus lanatus	86	1	82	2	80	1	82	3	81	2	83	1
Lolium multiflorum	76	0.4	75	2	74	4	77	3	83	5	68	4
Lolium perenne	82	3	82	3	85	2	80	3	83	0.3	80	2
Panicum dichotomiflorum	38	11	54	5	55	1	73	3	74	2	79	3
Paspalum dilatatum	0	0	6	4	14	7	53	5	62	4	58	2
Pennisetum clandestinum	3	1	17	5	30	5	54	5	76	1	82	2
Phalaris aquatica	41	6	51	8	64	6	78	4	73	3	78	4
Poa annua	89	2	91	1	95	1	94	1	92	2	90	2
Rytidosperma clavatum	76	8	80	6	82	7	82	5	77	6	81	5
Setaria geniculata	0	0	2	2	5	2	32	2	58	2	49	4
Setaria viridis	13	5	40	9	52	4	54	1	65	4	74	4
Sporobolus africanus	0	0	21	10	62	14	89	6	96	1	93	3
Trifolium pratense	77	3	77	3	79	1	74	2	82	1	67	2
Trifolium repens	91	1	89	2	91	2	93	1	91	2	87	2
Trifolium subterraneum	91	1	92	2	91	1	96	2	94	2	92	3

Table 2-3 Germination rate of 24 grassland species in relation to warm temperature pulse duration. Germination rate (± standard error) was calculated from Equation 1 and represents predicted time (in days) to achieve 50% of the maximum germination particular to each species. * indicates final germination percentage less than 50% of maximum. ** indicates no germination.

	Hours at 30/20°C											
Species	0		12		24		48		96		192	
	rate	se	rate	se	rate	se	rate	se	rate	se	rate	se
Agrostis capillaris	17.6	0.65	13.6	0.30	12.3	0.31	9.9	0.45	8.9	0.06	9.3	0.09
Axonopus affinis	**		**		**		*		10.1	0.26	10.6	0.09
Bromus stamineus	14.4	0.12	13.6	0.12	12.8	0.16	12.3	0.22	9.7	0.11	10.1	0.08
Cynodon dactylon	**		**		**		**		20.7	18.3	11.3	0.10
Dactylis glomerata	16.7	0.21	16.5	0.25	15.3	0.25	15.8	0.56	14.2	0.40	12.2	0.26
Digitaria sanguinalis	**		*		*		13.7	0.97	9.5	0.13	9.4	0.16
Echinochloa crus-galli	**		27.1	4.32	23.9	0.50	10.1	0.50	9.0	0.50	8.8	0.02
Eleusine indica	*		*		15.6	1.44	9.0	0.13	8.3	0.06	8.4	0.06
Festuca arundinacea	13.8	0.13	15.5	0.54	13.1	0.22	12.7	0.18	11.0	0.45	10.7	0.14
Holcus lanatus	10.8	0.50	10.3	0.07	9.0	0.09	8.0	0.02	8.1	0.05	8.3	0.03
Lolium multiflorum	11.1	0.18	10.7	0.30	10.6	0.27	8.7	0.21	8.4	0.13	9.1	0.12
Lolium perenne	10.7	0.16	10.6	0.21	9.6	0.16	9.1	0.20	8.2	0.43	8.5	0.09
Panicum dichotomiflorum	27.6	0.40	18.9	0.69	17.5	0.75	9.2	0.12	8.4	0.07	8.3	0.06
Paspalum dilatatum	**		*		*		18.7	0.36	9.2	0.11	9.6	0.06
Pennisetum clandestinum	*		*		*		22.3	2.02	12.5	0.44	11.1	0.01
Phalaris aquatica	21.0	1.03	15.7	0.53	14.8	0.34	11.9	0.32	10.4	0.12	10.5	0.06
Poa annua	11.4	0.1[illegible]	11.9	0.09	10.6	0.13	9.9	0.08	9.4	0.51	9.3	0.05
Rytidosperma clavatum	15.1	0.19	14.8	0.16	11.5	0.11	10.3	0.13	8.8	0.09	9.1	0.04
Setaria geniculata	**		**		*		21.8	4.51	9.6	0.06	9.9	0.05
Setaria viridis	*		25.8	0.37	20.0	0.66	10.0	0.27	8.8	0.03	8.7	0.04
Sporobolus africanus	**		*		23.3	1.19	13.4	0.23	8.9	0.06	9.0	0.01
Trifolium pratense	8.7	0.51	6.9	0.16	7.2	0.19	7.0	0.18	6.8	0.18	7.5	0.61
Trifolium repens	3.9	0.51	4.5	0.11	4.1	0.13	4.1	0.04	4.0	0.51	4.6	0.12
Trifolium subterraneum	4.3	0.12	4.7	0.20	5.1	0.20	4.6	0.16	4.3	0.08	4.8	0.15

Species varied not only in their sensitivity to warm temperature exposure period, but also in their inherent germination rate. Seeds from the Leguminosae family had inherently faster germination rates than seeds from the Gramineae family.

As the duration of the warm period decreased from 192 to 96 hours, *C. dactylon* showed a decrease in germination rate (11.3 to 20.7 days). A further decrease from 96 to 48 hours resulted in an approximate halving of germination rate for *S. geniculata*, *P. dilatatum* and *P. clandestinum*. Reducing exposure time to 24 hours decreased germination rate for all remaining C_4 species. Particularly sensitive were *D. sanguinalis*, *P. dilatatum*, *P. clandestinum* and *S. geniculata*, which failed to attain the 50% of maximum requirement under the 24 hour treatment. *Sporobolus africanus* and *Eleusine indica* failed to achieve 50% of maximum germination as the warm period was further reduced from 24 to 12 hours whereas the germination rates of *E. crus-galli* and *S. viridis* were decreased to 27.1 and 25.8 days respectively. *Panicum dichotomiflorum* was unique in that it was the only C_4 species to achieve 50% of maximum germination, albeit at a slow rate (27.6 days), without any exposure to warm temperatures.

All the C_3 species achieved 50% of maximum germination under constant 7°C by the end of the experiment. *Agrostis capillaris* and *P. aquatica*, showed the greatest decrease in germination rate with decreasing exposure time. *Poa annua*, *Lolium perenne*, *Holcus lanatus* and *L. multiflorum* were the C_3 grass species to show the least variation in germination rates between exposure times. Germination rate of the legumes, *Trifolium pratense*, *T. subterraneum* and *T. repens*, was independent of temperature treatment.

2.4.2 Experiment 2

There was considerable variation between species in their ability to survive without water as seedlings immediately after germination. For example, *T. repens* suffered 50% mortality after only 3.7 hours without water whereas the *L. multiflorum* required 699 hours for 50% death (Table 2-4). Ranking the 26 species on desiccation tolerance index showed that the majority of C_4 species were ranked lower than C_3 species. Nine of the 13 least desiccation tolerant species were C_4 species. In particular, the C_4 annuals *D. sanguinalis* and *P. dichotomiflorum* suffered 50% mortality after only 7.1 and 8.8 hours without water, respectively. *Pennisetum clandestinum*, *S. africanus* and *S. geniculata* were the exceptions to the rule, with indices of 27.5, 28.5 and 38.4 hours, respectively.

Similarly, not all C_3 species were desiccation tolerant, for example, *T. repens* and *H. lanatus* (7.9 hours).

A distinct high-tolerance group was evident from the desiccation tolerance indices (Table 2-4). In order of increasing tolerance, *Lolium perenne*, *F. arundinacea*, *T. subterraneum*, *H. murinum*, *B. stamineus* and *L. multiflorum* all achieved desiccation tolerance indices of greater than 100 hours. In addition to C_3 photosynthesis, these species all had high seed mass (Table 2-1). Regression of the logarithm values of desiccation tolerance index and seed mass identified a significant positive linear relationship (R^2 = 0.57, P<0.0001). However, the assumptions of normality and homogeneity were not satisfied. These assumptions were satisfied and a greater proportion of the variation was explained when a simple exponential model was fitted to the data (Fig. 2-3; R^2 = 0.67, P<0.0001).

Table 2-4 Desiccation tolerance of 26 grassland species. Index represents predicted hours (with 95% confidence limits) to death of 50% of seedlings. Rank intepretation: 1 to 26; most to least tolerant.

Species	Desiccation tolerance index			Rank
Agrostis capillaris	14.5	**16.0**	17.8	18
Axonopus affinis	9.0	**9.7**	10.5	21
Bromus stamineus	380.5	**429.4**	474.2	2
Cynodon dactylon	8.8	**9.5**	10.2	22
Dactylis glomerata	31.3	**34.7**	38.4	9
Digitaria sanguinalis	6.4	**7.1**	7.7	25
Echinochloa crus-galli	16.2	**17.9**	19.7	16
Eleusine indica	13.8	**15.2**	17.0	19
Festuca arundinacea	134.7	**149.8**	164.6	5
Holcus lanatus	7.3	**7.9**	8.4	24
Hordeum murinum	363.1	**413.2**	450.8	3
Lolium multiflorum	621.4	**699.3**	787.5	1
Lolium perenne	94.3	**103.2**	114.3	6
Panicum dichotomiflorum	8.1	**8.8**	9.5	23
Paspalum dilatatum	16.6	**18.3**	20.1	15
Paspalum distichum	14.8	**16.3**	18.1	17
Pennisetum clandestinum	24.9	**27.5**	30.7	12
Phalaris aquatica	82.2	**90.0**	95.8	7
Poa annua	25.1	**27.4**	30.2	13
Rytidosperma clavatum	28.0	**31.1**	34.7	10
Setaria geniculata	34.4	**38.4**	42.6	8
Setaria viridis	11.7	**12.7**	14.0	20
Sporobolus africanus	26.1	**28.5**	31.5	11
Trifolium pratense	24.3	**26.7**	29.5	14
Trifolium repens	3.4	**3.7**	4.0	26
Trifolium subterraneum	289.2	**329.5**	372.1	4

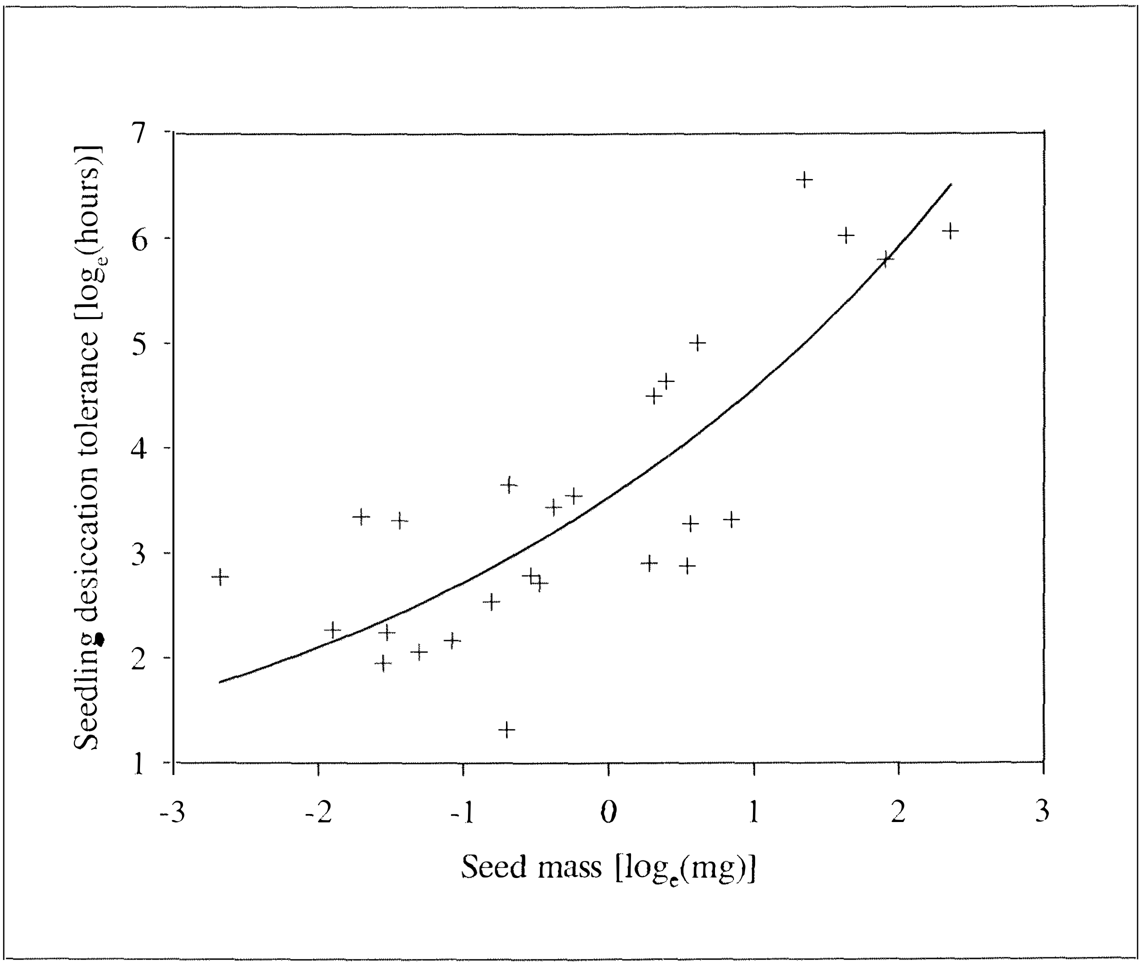

Fig. 2-3 Relationship between seedling desiccation tolerance and seed mass for 26 grassland species. Individual seed mass (expressed as the natural logarithm) was calculated as the total mass of 100 oven dry seeds divided by 100.

2.5 Discussion

2.5.1 Germination response to warm temperature pulses

This experiment made no attempt to accurately emulate the natural environment, therefore it would be wrong to categorically state minimum warm period requirements of the 24 species tested. The relative difference in responses between species are of greater predictive value. It was assumed that species with short or no warm period requirement to stimulate germination have a greater probability of germinating, emerging and establishing before those with longer warm period requirements.

As expected the C_4 species were more dependent on a warm temperature period to initiate germination than the C_3 species (Charlton *et al.* 1986; Ahmed & Wardle 1991; Qi & Redmann 1993). The most warm temperature dependent C_4 species were *C. dactylon* and *A. affinis*. The next most dependent species were *S. geniculata*, *D. sanguinalis*, *P. dilatatum*, *S. africanus* and *E. crus-galli*, all requiring at least some exposure to warm temperatures to stimulate germination. However, differences were apparent within this group. *Setaria geniculata* showed the greatest reduction in germination percent and rate with decreasing exposure time whereas *E. crus-galli* showed the least (Table 2-2 and Table 2-3). *Setaria viridis*, *P. clandestinum*, *E. indica* and *P. dichotomiflorum* all germinated in continuous cold but on the basis of germination percent and rate *P. dichotomiflorum* was identified as the C_4 species least dependent on warm temperatures. All the C_3 species germinated in continuous cold but varied with respect to germination rate. The C_3 species most dependent on warm temperatures were *P. aquatica* and *A. capillaris* whereas the legume species, *Trifolium pratense*, *T. subterraneum* and *T. repens*, were the least dependent.

2.5.2 Seedling desiccation tolerance

Greater than a 200-fold variation was identified in the desiccation tolerance of immediate post-germination seedlings of C_3 and C_4 grassland species. In agreement with Qi & Redmann (1993), the C_4 species were less desiccation tolerant than the C_3 species but there were several exceptions to the rule. *Trifolium repens* and *H. lanatus* (C_3) were particularly intolerant whereas *P. clandestinum*, *S. africanus* and *S. geniculata* (C_4) were quite tolerant of desiccation.

Qi & Redmann (1993) argued that seedling morphology was important in determining drought survival. Species with a thread-like subcoleoptile internode tended to be less water stress tolerant because of reduced water conductivity from roots to leaves (Redmann & Qi 1992). Under the conditions of no water availability in this experiment, differences in ability to transport water from roots to shoots are unlikely to relate to the observed differences in desiccation tolerance. However, it is interesting to note that the two most desiccation sensitive C_4 species, *P. dichotomiflorum* and *D. sanguinalis*, had this morphology whereas the most tolerant C_4 species did not.

Seed size has been related to numerous key plant functional attributes during seedling establishment, including survival in dry environments (Westoby *et al.* 1992; Leishman 1999). Similarly, the positive relationship between seed size and desiccation tolerance in this experiment (Fig. 2-3), agreed with the laboratory experiments of Qi & Redmann (1993) and Leishman & Westoby (1994b). While the relationship between environmental water availability and seed size has been largely accepted (Baker 1972; Salisbury 1974; Buckely 1982, but see Mazer 1989; Westoby *et al.* 1992), the mechanism remains unresolved.

Leishman & Westoby (1994b) suggested that regardless of relative allocation, larger seeded species avoid drought by producing larger seedlings with larger absolute roots that are able to reach deeper wetter soil and so get disproportionally more water than small seeded seedlings. The results suggest that greater absolute allocation to roots is probably not responsible for greater drought survival of large seeded species, as a seed size - seedling survival relationship was identified on media where the variation in rooting depth between large and small seedlings was eliminated. The significant exponential relationship between desiccation tolerance and seed mass suggested that as seed mass increased so did its importance in conferring protection against low water availability. This may reflect the suggestion of Leishman & Westoby (1994b) that large seeded species have greater reserves available for production of non-essential compounds such as osmoticants or dehydrins proteins (Close 1996; Close 1997). Alternatively, it may simply be the result of smaller seedlings having greater surface area relative to volume from which to lose water.

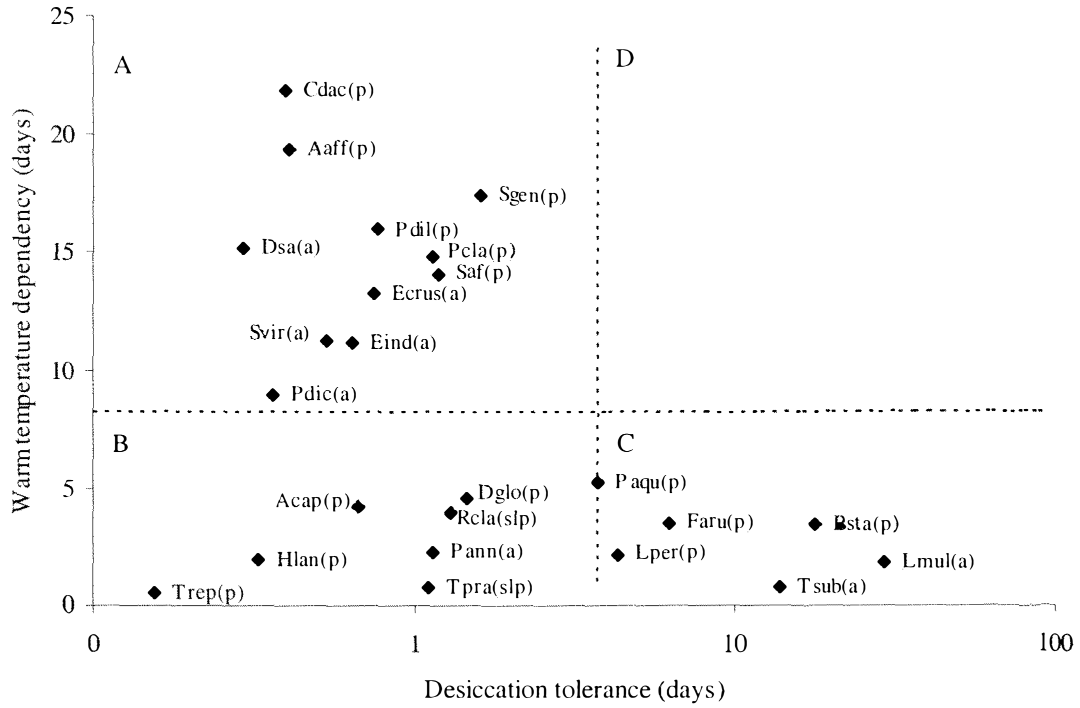

Fig. 2-4 Juvenile phase attributes of 24 grassland species. Temperature dependency index: germination rate at maximum exposure time (192 hours) less mean of the germination rates at all shorter exposure times. Desiccation tolerance index (logarithm scale): time to achieve of 50% seedling mortality. Dashed lines represent means of germination and desiccation indices. Species abbreviations (a = annual; slp = short-lived perennial; p = perennial): Acap, *A. capillaris*; Aaff, *A. affinis*; Bsta, *B. stamineus*; Cdac, *C. dactylon*; Dglo, *D. glomerata*; Dsa, *D. sanguinalis*; Ecrus, *E. crus-galli*; Eind, *E. indica*; Faru, *F. arundinacea*; Hlan, *H. lanatus*; Lmul, *L. multiflorum*; Lper, *L. perenne*; Pdic, *P. dichotomiflorum*; Pdil, *P. dilatatum*; Pcla, *P. clandestinum*; Paqu, *P. aquatica*; Pann, *P. annua*; Rcla, *R. clavatum*; Sgen, *S. geniculata*; Svir, *S. viridis*; Saf, *S. africanus*; Tpra, *T. pratense*; Trep, *T. repens*; Tsub, *T. subterraneum*.

2.5.3 Climatic specificity

Indices for the two juvenile phase attributes are plotted in Fig. 2-4. The means of the two indices are shown as horizontal and vertical dashed lines in order to categorise the species into above or below average specificity in climate conditions for emergence and establishment. On this basis category A species are predicted to be restricted to warm season germination and establishment in high water availability sites. Category B species are predicted to be able to germinate in cool and warm seasons but be restricted to moist sites. Category C species are predicted to be the least climate specific, having an ability to germinate and establish over the widest range of temperature and moisture combinations. Category D species are predicted to be warm season specific but be able to establish in drier environments. Three separate groups of species are apparent in Fig. 2-4 and are contained within the bounds of three of the four categories.

The most climate specific category (A) is comprised solely of C_4 species. The juvenile phase attributes of this group agree closely with actual spatial and temporal distributions in the field. Firstly, the germination and emergence of these species is largely restricted to the onset of the warm season (Baars *et al.* 1991; Wardle *et al.* 1994) and secondly, C_4 abundance has been found to be positively related to rainfall within New Zealand grasslands (Campbell *et al.* 1999) and rangelands of the U.S. Great Plains (Paruelo & Lauenroth 1996; Epstein *et al.* 1997). A poor ability to tolerate desiccation as seedlings must be a contributing factor in restricting C_4 invasion into drier environments.

Predicted climatic specificity of species in categories B and C also agree with actual grassland distributions. All are C_3 species which germinate readily with the onset of the cool season (Hume & Barker 1991; Porter *et al.* 1993; Dodd *et al.* 1995). There is also close agreement with differences in desiccation tolerance between categories B and C. Category C species are common in grasslands of dry environments (Chapman *et al.* 1986; Stewart 1992; Milne *et al.* 1993) whereas category B species prefer moist habitats (Langer 1973; Chapman *et al.* 1986). *Dactylis glomerata* was a notable exception. It had relatively poor seedling desiccation tolerance but is recognised for its ability to persist within dry environments (Hunter *et al.* 1994).

2.5.4 Invasive species

According to Crawley (1997), it makes no sense to refer to species as invasive or non-invasive because all species pass the invasion criterion. That is, all non-extinct species must exhibit the ability to increase when rare. Furthermore, Crawley (1997) states that "if all species are invasive then it must follow that it is pointless to search for traits that will separate invasive from non-invasive species". However, it cannot be denied that some species have a greater ability to establish and exist in alien environmental conditions (i.e. beyond those found in their native habitat) than other species and that ability has been associated with particular traits (Rejmánek & Richardson 1996; Crawley *et al.* 1997).

Based on the juvenile phase responses to two specific tests of temperature and water effects, this study predicts the relative probability of establishment (termed here as *invasiveness*) of different species within the productive grazed C_3/C_4 composite grasslands of New Zealand. Species with the least specific climatic requirements for germination and seedling survival are assumed to have a greater probability of invading than more specific species. In accordance with this, the three groups of species were ranked C > B > A for invasiveness and, therefore, it was concluded that overall the C_3 species are potentially more invasive than the C_4 species.

Differences in predicted invasiveness of the C_3 species are predominantly associated with variation in desiccation tolerance, an important attribute for regeneration from seed at the end of the warm season when there may be limited soil moisture. For example, all the *Trifolium* species had low dependency on warm temperatures for germination, however, *T. subterraneum* is predicted to be more invasive than *T. pratense* and *T. repens* under conditions of limited water availability. The probability of *T. pratense* and *T. repens* establishment will increase only as soil moisture content increases.

The C_4 species varied more in their dependency on warm temperatures for germination compared to their ability to tolerate desiccation. Low overall desiccation tolerance will restrict C_4 species invasion to more mesic environments and, in contrast to the C_3 species, the most invasive species will be the least warm temperature dependent. Accordingly, the four annual species, *P. dichotomiflorum*, *S. viridis*, *E. indica* and *E. crus-galli* are predicted to be the most invasive. *P. dichotomiflorum* is predicted to be particularly invasive as it readily germinated without any warm temperature exposure whereas *Cynodon dactylon* and *Axonopus affinis* are predicted to be the least invasive.

The succession of invading C_4 species during the warm season can be predicted from their temperature dependency and desiccation tolerance pattern shown in Fig. 2-4. Initially, the annual species, *P. dichotomiflorum*, *E. indica*, *S. viridis* and *E. crus-galli*, are predicted to be most invasive but as temperatures increase so will the probability of emergence and establishment of the perennial C_4 species, *S. africanus*, *P. clandestinum*, *P. dilatatum* and *S. geniculata*. These perennial species are predicted to invade later than the annual species not only because of the greater dependency on warm temperatures for germination but also their greater desiccation tolerance will confer an advantage at a time when soil moisture content is typically decreasing.

A trend apparent within the more temperature dependent C_4 species but also consistent with the C_3 species, was that the least warm temperature dependent species had short life histories. This is an advantageous adaptation for species that solely rely on regeneration from seed. A shorter warm period requirement will lead to earlier germination and emergence and, therefore, gain maximum benefit from favourable conditions when they arise.

2.6 References

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3 The impact of simulated extreme temperature and water events on competition between C_4 grasses and *Lolium perenne* L.

CONTENTS

3.1 Abstract

The impact of the extreme water and temperature events on C_3 and C_4 competition was determined in a glasshouse pot experiment. Five C_4 grasses of contrasting ecology were grown from seedlings as pure stands and as additive mixtures with a common C_3 perennial grass, *Lolium perenne.* The artificial plant communities were subjected to the nine treatment combinations of three water levels; drought (1.5% soil water), mesic (13.8%) and flood (23.4%) and three treatment levels; frost (short [six-hour] pulses of −5°C), ambient (continuous 25/15°C diurnal cycle) and heat (short [six-hour] pulses of +50°C). Under mesic/ambient conditions *Digitaria sanguinalis* and *Panicum dichotomiflorum* were identified as the most competitive C_4 species. *Pennisetum clandestinum* had intermediate competitiveness and *Paspalum dilatatum* and *Sporobolus africanus* were the least competitive. In droughted, flooded and, in particular, heated conditions, the competitiveness of *L. perenne* was reduced. Frost conditions severely reduced the competitiveness of the C_4 species.

The results allow predictions on shifts in competition and the balance of mixed C_4 /*L. perenne* grasslands. Under equally favourable conditions, *L. perenne* was either as, or more competitive than the C_4 species, therefore, increases in C_4 abundance are unlikely to be the result of active displacement of *L. perenne* from grasslands. We predict that *D. sanguinalis* and *P. dichotomiflorum* will be particularly advantaged by a drought, and *P. dilatatum* and *P. clandestinum*, by a flood. The C_4 species, in particular *D. sanguinalis* and *P. dichotomiflorum*, are predicted to be advantaged by the large suppression of competition from *L. perenne* after an extreme heating event. Only an extreme low temperature event is predicted to suppress all C_4 species and advantage *L. perenne* abundance.

3.2 Introduction

Experiments on both grassland (Harris *et al.* 1981b; Christie & Detling 1982), and crop species (Pearcy *et al.* 1981; Flint & Patterson 1983; Alberto *et al.* 1996), have consistently suggested that C_4 species gain a competitive advantage over C_3 species as temperature increases. The primary reason for this is that C_3 plants have lower carboxylation efficiency of photosynthesis at higher temperatures (>25-30°C) compared to C_4 plants (Pearcy & Ehleringer 1984; Collatz *et al.* 1998). Accordingly, C_4 plants are dominant in warmer tropical and subtropical regions, whereas C_3 plants are more abundant in cooler temperate regions (Teeri 1988; Hattersley & Watson 1992).

In addition, C_4 plants assimilate more CO_2, relative to water lost through transpiration, than C_3 plants and, therefore, are more water-use efficient (Pearcy & Ehleringer 1984). Therefore, changes in water availability might also be expected to alter competitive interactions between C_3 and C_4 species. However, differences in water-use efficiency are generally not as robust predictors of C_3 and C_4 species distribution as temperature optima differences (Kemp & Williams 1980; Teeri 1988).

Despite this general assumption that C_3 and C_4 competition will be altered by changing temperature and water conditions, there have been relatively few experiments specifically testing this in controlled environment conditions. Harris *et al.* (1981a) found that *L. perenne* (C_3) achieved greater biomass at low temperatures (14°C day/8°C night) than at high temperatures (24/18°C), whereas *P. dilatatum* (C_4) showed the opposite response. When grown in simple replacement series mixtures, *L. perenne* was dominant under both low and high temperature regimes because it established more rapidly than *P. dilatatum.* Only when the initial dominance of *L. perenne* was suppressed by defoliation did the *P. dilatatum* plants become dominant at the higher temperatures (Harris *et al.* 1981b).

It has generally been found that the cross-over temperature for C_3 or C_4 dominance in grasslands coincides with a maximum mean-monthly temperature of 22°C (Rundel 1980; Tieszen *et al.* 1997; Collatz *et al.* 1998), and at temperatures above 22-25°C, C_4 species gain a competitive advantage over C_3 species (Pearcy 1985; Wilen & Holt 1996). For example, Christie & Detling (1982), found that the C_4 grass *Bouteloua curtipendula* dominated the C_3 grass *Agropyron smithii* under conditions of 30/15°C, whereas at 20/12°C the situation was reversed.

There have been no studies of the effects of climatic extremes on C_3 and C_4 competition. Extreme climatic events such as frosts, hot days, droughts and floods, have the potential to greatly influence C_3 and C_4 competition because, in addition to different optimal growth requirements, C_3 and C_4 plants also differ greatly in their tolerance of environmental extremes (McWilliam 1978; Long 1983; Osmond *et al.* 1987; Atwell *et al.* 1999).

A glasshouse pot experiment was designed to test the impact of extreme climatic events on competition between *Lolium perenne* L. cv. Grasslands Pacific (a C_3 grass) and five C_4 grasses commonly found in New Zealand grasslands: *Digitaria sanguinalis* (L.) Scop., *Panicum dichotomiflorum* Michx., *Paspalum dilatatum* Poir. cv. Grasslands Raki, *Pennisetum clandestinum* Chiov. cv. Whittet Kikuyu and *Sporobolus africanus* (Poir.) Robyns and Tourn. (Table 3-1). The specific objectives of the experiment were to measure in controlled conditions:

1) the effect of extreme water and temperature events on C_3 and C_4 growth,
2) the relative competitive ability of the five C_4 grasses under mesic water and ambient temperature conditions, and
3) the impact of the extreme water and temperature events on C_3 and C_4 competition.

The results are used to predict likely changes in competition and structure of grassland communities due to extreme climatic events.

Table 3-1 Characteristics and common habitats of the species examined in this experiment. Descriptions adapted from Campbell *et al.* (1996), White *et al.* (1997), Campbell *et al.* (1999) and White *et al.* (2000a, Chapter Five).

Species	Description and common habitat
D. sanguinalis	C_4 annual grass, spreading tussock, 50-150 cm culm length, rooting at nodes, pubescent. Disturbed fertile habitats (intensely managed dairy cattle grasslands, cultivated fields, roadside drainage ditches). Warmer regions.
L. perenne	C_3 perennial grass, up-right tussock grass, <50 cm culm length, glabrous. Very widely distributed, both cooler and warmer regions. Fertile, grassy habitats, most common as species of productive managed grassland or as an amenity species.
P. dichotomiflorum	C_4 annual grass, spreading tussock, 50-150 cm culm length, glabrous. Disturbed fertile habitats (intensively managed dairy cattle grasslands, cultivated fields, roadside drainage ditches). Warmer regions.
P. dilatatum	C_4 perennial grass, rhizomatous spreading tussock, 50-150 cm culm length, partly pubescent. Widely adapted (including cooler and drier regions). Common habitats are productive grasslands and/or amenity areas.
P. clandestinum	Large C_4 spreading perennial grass, mat-forming, highly pubescent. Mostly restricted to warm, moist fertile sites. Common to productive grasslands.
S. africanus	C_4 perennial grass, < 50 cm culm length, partly pubescent. Adapted to drier regions. Commonly found within low fertility, warm aspect steep hill grasslands or dry warm road shoulders. Uncommon to moist productive grasslands.

3.3 Methods

3.3.1 Plant arrangement

This competition experiment is an additive design where the density of each component in pure and mixed stands are identical. An additive design has the advantage of allowing the direct effects of experimental treatments on plant performance to be distinguished from competitive effects (Snaydon 1991). The design is also based on the phytometer approach of Gaudet & Keddy (1988), where the competitive ability of several test species are determined relative to one phytometer species. In this experiment five test (C_4 grasses) and one phytometer species (C_3 grass) were grown as pure stands. In addition, each test species was grown in an additive mixture with the phytometer species. As a consequence the experiment contained a total of 11 plant community types.

Each experimental pot consisted of a polythene planting bag (180 mm diameter x 200 mm height) filled with river sand (< 3 mm particle coarseness). A 20-30 mm drainage layer of fine road gravel was placed at the base of each planting bag. The planting arrangement for pure stands consisted of five plants, four forming the corners of a 90 mm sided square and one in the middle (Fig. 3-1a). The mixed stand planting pattern can be considered as two pure stand patterns, oriented 45° out of phase with each other (Fig. 3-1b). The two central plants were evenly spaced in the centre of the pot.

3.3.2 Glasshouse conditions

The plants used in the experiment were established from seed. Germination conditions were 30°C day and 20°C night, with 12 hour day/night lighting. Timing of imbibition was manipulated according to germination rate so that all species germinated at the same time. The pots were planted on 14 October 1996. One seedling was placed in each planting hole, then fine sand was used to cover the seedling's roots to prevent drying out. All pots were placed in a glasshouse where plants were watered daily by a hand-held fine misting nozzle. Temperature within the glasshouse diurnally cycled from a minimum of 15°C at 0600 hours to a maximum of 25°C at 1400 hours.

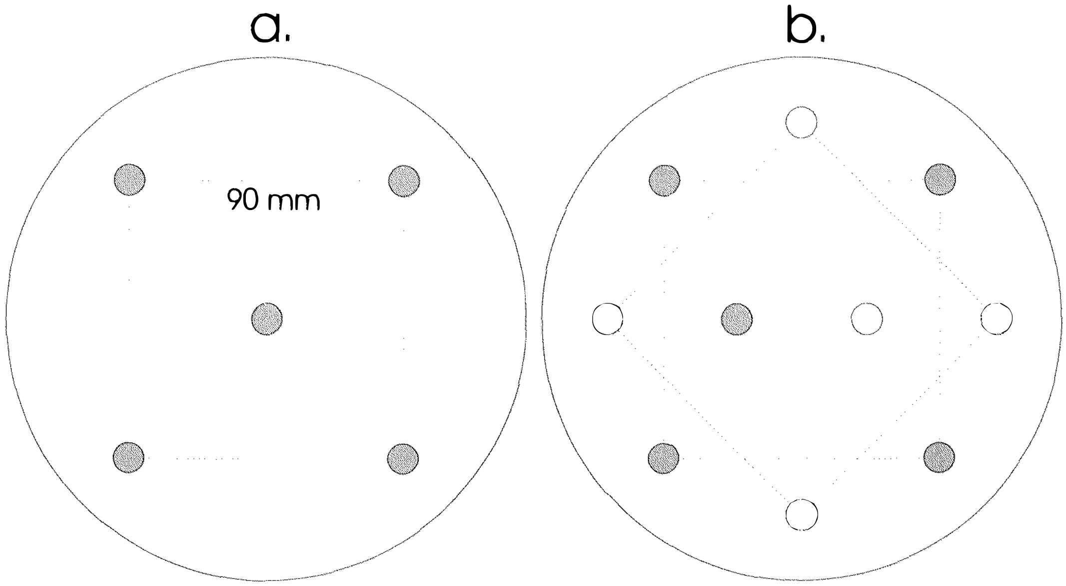

Fig. 3-1 Planting positions and dimensions of a) pure and b) mixed stands. Closed circles, C_4 pure and mixed stand positions. Open circles, *L. perenne* positions in mixed stand.

Plate 3-1 Glasshouse pot experiment, October 1996.

3.3.3 Water extremes

The treatment period commenced 6 November 1996 when the seedlings were three weeks old and lasted for 4 weeks. Three levels of water availability were established – drought, mesic and flood.

Drought conditions were established by discontinuing watering. After one week without water some of the plants were becoming severely wilted. Small quantities of water were added to all droughted pots so that the plants survived to the end of the treatment period. Initially, 50 ml was applied to each pot once every two days. After two weeks this amount was increased to 100 ml. The total amount of water applied to the droughted pots over the treatment period was 650 ml.

The mesic treatment involved continuing the once per day watering.

Flood conditions were established by sealing off the drainage holes at the base of planting bags and watering to maintain a layer of water above the sand surface. The drainage holes were sealed by placing each planting bag inside a plastic bag, and then placing those two bags inside another planting bag. This resulted in a three layered arrangement with the middle layer acting as a water proof barrier.

3.3.4 Temperature extremes

Three temperature conditions were applied – frost, ambient and heat. The ambient treatment involved allowing plants to continue to grow within the glasshouse conditions. The frosting and heating conditions were created within controlled environment rooms (National Climate Laboratory, Horticultural & Food Research Institute, Palmerston North, New Zealand), and were applied as single events, once per week, for four weeks. Pots only remained within the controlled environment rooms while being treated.

The frosting treatment involved a single six-hour period at 0°C in week 1 and -5°C in weeks 2, 3 and 4. To avoid frost damage to roots, pots were placed in insulated heated trolleys and gaps between pots were filled with a peat-soil mix. Frosting room temperature ramped down from 18°C over three hours and ramped back to 18°C over one hour. Lighting was set to 14 hours day (700 μmol m^{-2} s^{-1} photosynthetically active radiation created by four 1000W Sylvania 'metal-arc' high pressure discharge lamps, together with four 1000W Phillips tungsten iodide lamps) and 10 hours night. Relative humidity was maintained at 75% and CO_2 at 360-390 ppm.

Plate 3-2 Frost treatment within controlled environment room. To avoid frost damage to roots, pots were contained within insulated, heated trolley's.

The heating treatment was a single six-hour period at 45°C in week 1 and 50°C in weeks 2, 3 and 4. Heating room temperature ramped up to and down from 18°C over four-hour periods. Relative humidity, lighting and CO_2 were as for the frosting rooms. Heating treatments were applied during the day and frosting treatments were applied at night.

For the purpose of treatment description, the nine treatment combinations of temperature and water availability were coded DF, DA, DH, MF, MA, MH, FF, FA and FH. The first letter represents the water levels (Drought, Mesic and Flood), and the second letter represents the temperature levels (Frost, Ambient and Heat).

3.3.5 Sand moisture content

To determine the final water content of the sand growing media, pots were weighed immediately after removal of plant material, dried (for 24 hours at 80°C) and re-weighed. By the end of the experiment there were large differences in the sand moisture content between the water levels. The average water content of the droughted, mesic and flooded pots was 1.5, 13.8 and 23.4% respectively (Table 3-2; $P<0.001$ for water main effect). There was some evidence (Table 3-2; $P=0.05$ for heat main effect) to suggest that the heat treated pots were drier than the frost treated pots but the difference was only slight (10.3% c.f. 11.1%). There were significant differences between species in sand moisture content of droughted pots. For example, *D. sanguinalis* pure stand DA pots were drier (0.7%) than *S. africanus* pure stand DA pots (1.4%) (Table 3-2; $P < 0.001$ for W by T by Sp interaction effect).

3.3.6 Plant measurements

The experiment was concluded on 4 December 1996. Only plant material above the junction of the shoot and root was removed. Plant material was first separated into species, then into live and dead tissue. All material was dried (at 80°C for 24 hours) and then weighed.

3.3.7 Data analysis

Biomass and sand moisture data were analysed by analysis of variance. The experiment was a randomised-block two-factor factorial of split-plot design. Community types (split plots) were randomised within nine water by temperature combinations (whole plots). The four blocks were arranged perpendicular to the long axis of the glasshouse.

Table 3-2 Sand moisture content (%, on dry weight basis) for all water, temperature and community type combinations. Treatment abbreviations - water extremes (first letter): D, drought; M, mesic; F, flood and temperature extremes (second letter): F, frost; A, ambient; H, heat. Presented as back-transformed means (bold font) from analysis of square root transformed data. Square-root transformed means (small font) are presented for means discrimination by least significant differences (LSD = 0.13). PS = pure stand, MS = mixed stand.

		DF	DA	DH	MF	MA	MH	FF	FA	FH
L. perenne	PS	**1.5**	**1.0**	**3.9**	**13.7**	**14.1**	**13.8**	**24.0**	**23.2**	**22.4**
		1.23	0.98	1.97	3.70	3.76	3.71	4.90	4.81	4.73
D. sanguinalis	PS	**3.5**	**0.7**	**1.4**	**13.0**	**13.8**	**13.9**	**25.6**	**26.0**	**22.5**
		1.86	0.86	1.17	3.61	3.72	3.73	5.06	5.10	4.74
	MS	**1.4**	**1.2**	**0.8**	**13.6**	**12.4**	**12.0**	**25.2**	**24.0**	**21.5**
		1.17	1.09	0.88	3.68	3.52	3.47	5.02	4.90	4.64
P. dichotomiflorum	PS	**2.6**	**1.0**	**1.2**	**13.5**	**15.3**	**13.5**	**23.8**	**25.0**	**23.8**
		1.60	1.01	1.12	3.67	3.92	3.67	4.88	5.00	4.88
	MS	**1.6**	**0.9**	**1.1**	**13.8**	**14.0**	**14.4**	**24.2**	**25.7**	**21.8**
		1.26	0.94	1.06	3.72	3.75	3.79	4.92	5.07	4.67
P. dilatatum	PS	**3.3**	**1.1**	**1.2**	**13.5**	**14.7**	**14.1**	**26.0**	**26.1**	**19.0**
		1.82	1.04	1.10	3.67	3.83	3.75	5.10	5.11	4.36
	MS	**1.6**	**1.1**	**1.1**	**13.0**	**14.2**	**14.1**	**23.6**	**26.2**	**20.4**
		1.25	1.05	1.07	3.60	3.76	3.76	4.86	5.12	4.52
P. clandestinum	PS	**1.9**	**1.0**	**1.4**	**14.0**	**15.2**	**13.1**	**24.2**	**24.6**	**24.8**
		1.37	0.99	1.19	3.74	3.90	3.63	4.92	4.96	4.98
	MS	**1.0**	**1.1**	**1.3**	**13.7**	**14.3**	**14.1**	**24.4**	**20.8**	**20.8**
		1.01	1.01	1.13	3.70	3.78	3.76	4.94	4.56	4.56
S. africanus	PS	**4.3**	**1.4**	**2.0**	**13.0**	**14.1**	**13.8**	**21.3**	**24.8**	**23.7**
		2.07	1.20	1.41	3.60	3.75	3.72	4.62	4.98	4.87
	MS	**1.5**	**0.9**	**2.2**	**13.0**	**14.8**	**13.8**	**21.6**	**22.4**	**21.8**
		1.23	0.95	1.48	3.61	3.84	3.72	4.65	4.74	4.67

Separate analyses were performed for the combined pure and mixed stand biomass data of each species (see Table 3-3a; five for C_4 species and five for *L. perenne* in combination with each C_4 species). In addition, two separate analyses were performed to determine differences between species in pure and mixed stands (see Table 3-3b). No transformation of the biomass data was required to satisfy the assumptions of analysis of variance. The original randomisation of treatment combinations was maintained when pots were returned to the glasshouse from the controlled environment rooms after each temperature treatment session.

Significant differences in sand moisture content between treatments and community types were determined by analysis of variance of square-root transformed sand moisture data.

Table 3-3 Statistical significance of effects for a) pure vs. mixed stand and b) species comparisons for biomass data in Table 3-4. Effect abbreviations: W, water; T, temperature; C. competition; Sp, species. Level of significance: NS, $P>0.05$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

a) Pure stand vs. mixed stand comparisons

	Whole-plot effects			Split-plot effects			
	W	T	WxT	C	WxC	TxC	WxTxC
D. sanguinalis	***	***	***	**	NS	***	NS
P. dichotomiflorum	***	***	***	***	*	***	NS
P. dilatatum	***	***	***	***	NS	***	*
P. clandestinum	***	***	***	***	NS	NS	NS
S. africanus	***	***	*	***	NS	***	NS
L. perenne (D. sanguinalis)	***	***	**	**	NS	***	*
L. perenne (P. dichotomiflorum)	***	***	***	**	NS	***	**
L. perenne (P. dilatatum)	***	***	***	*	NS	***	*
L. perenne (P. clandestinum)	***	***	***	*	NS	***	**
L. perenne (S. africanus)	***	***	***	*	NS	*	*

b) Species comparisons

	Whole-plot effects			Split-plot effects			
	W	T	WxT	Sp	WxSp	TxSp	WxTxSp
Pure	***	***	***	***	***	***	***
Mixed	***	***	***	***	***	***	***

3.4 Results

3.4.1 Above ground biomass in pure stands

The biomass of *D. sanguinalis* (24.2 g pot^{-1}) and *P. dichotomiflorum* (23.4 g) was greater than that of all other species (Table 3-4a and c; *P*<0.001 for pure stand biomass W by T by Sp interaction effect). *Pennisetum clandestinum* and *P. dilatatum* achieved 13.4 and 12.1 g, respectively. The biomass of *L. perenne*, at 9.9 g, was significantly less than that of *P. clandestinum*, but not *P. dilatatum*. *Sporobolus africanus* was the least productive species, at 2.8 g.

The water and temperature treatments both had significant effects on growth (Table 3-3b; *P*<0.001 for pure stand W and T main effects). The drought treatment lowered biomass for all species except *S. africanus* (Table 3-4; *P*<0.001, pure stand W by Sp interaction effect). Expressing biomass relative to MA pot biomass indicated that *S. africanus* had higher relative production in DA (83%) and DH (59%) pots than all other species (Table 3-5). Its higher drought tolerance was not an artefact of higher moisture content of *S. africanus* pots, as *S. africanus* droughted pots were only slightly moister than the other species (less than 1%) and sand moisture content was not found to be a significant covariate for *S. africanus* biomass or any other species.

Pure stand biomass was not significantly different between mesic and flooded treatments when averaged across all species. However, *P. clandestinum* growth appeared to be promoted by flooding, it had considerably higher relative biomass in FA (135%) than MA pots (Table 3-5). *Digitaria sanguinalis* was the only species to be adversely affected by flooding. It had significantly lower biomass in flooded pots (Table 3-4; *P*<0.001 for W by Sp interaction).

Overall, frost severely restricted growth for all species (Table 3-4). The species to attain the greatest biomass in the frosted pots were *L. perenne* and *P. dilatatum*. Biomass relative to MA conditions also indicated that *L. perenne* and *P. dilatatum* were the least affected by the frost treatment (Table 3-5). *Panicum dichotomiflorum* and *D. sanguinalis* were the most affected, having virtually no live biomass in all frosted pots.

The heat treatment also resulted in lower biomass than ambient conditions but responses varied between species (Table 3-4; *P*<0.001 pure stand T by Sp interaction effect).

Table 3-4 Aboveground biomass (g pot^{-1}) of five C_4 grass species grown in a) pure and b) mixed stands with *L. perenne* and aboveground biomass of *L. perenne* grown in c) pure and d) mixed stands under nine combinations of temperature and water availability. Values are means of four replicates. Treatment abbreviations - water extremes: D, drought; M, mesic; F, flood and temperature extremes: F, frost; A, ambient; H, heat. Least significant differences (LSD) values (P<0.05) for comparison within species between pure and mixed stands: *D. sanguinalis* 3.3, *P. dichotomiflorum* 4.1; *P. dilatatum* 2.6; *P. clandestinum* 3.7; *S. africanus* 0.4; *L. perenne* with *D. sanguinalis* 2.1; *L. perenne* with *P. dichotomiflorum* 1.9; *L. perenne* with *P. dilatatum* 2.1; *L. perenne* with *P. clandestinum* 1.8; *L. perenne* with *S. africanus* 1.9. LSD values (P<0.05) for comparison between species: pure stand 3.2, mixed stand 2.3.

Extreme temperature events	Extreme water events											
	a) Pure stand			b) Mixed stand			c) Pure stand			d) Mixed stand		
	D	M	F	D	M	F	D	M	F	D	M	F
	Digitaria sanguinalis						*Lolium perenne*					
F	0.0	0.0	0.1	0.0	0.0	0.0	1.3	0.9	1.1	1.0	1.2	2.2
A	4.0	24.2	18.7	3.0	15.0	7.8	3.6	9.9	12.3	1.2	5.1	5.3
H	2.3	22.6	13.6	2.7	21.2	13.3	0.0	0.0	0.1	0.0	0.4	0.5
	Panicum dichotomiflorum						*L. perenne*					
F	0.0	0.0	0.0	0.0	0.0	0.1	1.3	0.9	1.1	0.8	1.0	3.0
A	5.2	23.4	25.3	3.3	11.9	14.8	3.6	9.9	12.3	1.4	5.4	5.3
H	2.5	20.2	24.3	2.6	19.7	22.6	0.0	0.0	0.1	0.0	0.2	0.3
	Paspalum dilatatum						*L. perenne*					
F	0.8	0.4	1.3	0.1	0.6	0.5	1.3	0.9	1.1	0.8	1.3	2.5
A	3.0	12.1	14.1	1.1	4.4	11.1	3.6	9.9	12.3	2.4	8.9	7.6
H	2.6	9.5	9.2	1.6	9.5	9.6	0.0	0.0	0.1	0.0	0.1	0.4
	Pennisetum clandestinum						*L. perenne*					
F	0.5	0.7	0.8	0.0	0.5	0.7	1.3	0.9	1.1	1.5	0.9	2.2
A	3.2	13.4	16.4	1.5	7.2	14.0	3.6	9.9	12.3	1.8	7.2	6.2
H	1.7	13.0	10.4	1.4	8.3	7.6	0.0	0.0	0.1	0.0	0.1	0.4
	Sporobolus africanus						*L. perenne*					
F	0.1	0.1	0.2	0.1	0.1	0.1	1.3	0.9	1.1	1.1	0.7	2.2
A	2.4	2.8	2.8	0.5	1.1	1.2	3.6	9.9	12.3	2.5	9.1	8.8
H	1.7	2.6	2.1	0.9	2.3	2.1	0.0	0.0	0.1	0.0	0.0	0.1

Table 3-5 Pure stand live biomass as a percentage of pure stand mesic/ambient biomass. Values are means (± standard error in parentheses) of four replicates. Treatment abbreviations - water extremes: D, drought; M, mesic; F, flood and temperature extremes: F, frost; A, ambient; H, heat.

	Extreme water events					
Extreme temperature events	D	M	F	D	M	F
	Digitaria sanguinalis			*Lolium perenne*		
F	**0** (0)	**0** (0)	**0.2** (0.2)	**14** (3)	**9** (5)	**12** (3)
A	**17** (1)	**100**	**79** (13)	**35** (3)	**100**	**127** (21)
H	**10** (1)	**94** (7)	**60** (4)	**0** (0)	**0.4** (0)	**2** (1)
	Panicum dichotomiflorum			*Paspalum dilatatum*		
F	**0** (0)	**0** (0)	**0** (0)	**7** (2)	**4** (1)	**11** (4)
A	**22** (1)	**100**	**111** (16)	**25** (2)	**100**	**119** (18)
H	**11** (1)	**90** (17)	**106** (14)	**22** (2)	**77** (13)	**77** (6)
	Pennisetum clandestinum			*Sporobolus africanus*		
F	**4** (2)	**6** (3)	**5** (1)	**2** (1)	**5** (2)	**5** (3)
A	**26** (4)	**100**	**135** (32)	**83** (6)	**100**	**102** (16)
H	**13** (1)	**93** (10)	**80** (6)	**59** (3)	**95** (11)	**74** (4)

Specifically, the C_4 species showed only small reductions (or no significant reduction in the case of *S. africanus*) in growth compared to ambient, whereas *L. perenne* was severely affected by heating.

Digitaria sanguinalis was sensitive to the combination of heat and flooding. It had lower absolute (24.2 c.f. 13.6 g) and relative biomass (57%) in FH pots compared to MA pots (Table 3-4; $P<0.001$ for W by T by Sp interaction and Table 3-5). This appears to be largely a flooding effect as the percentage reduction in biomass in MH pots (94%) was only slight compared to FH pots (57%).

3.4.2 Above ground biomass in mixed stands

The effect of competition was examined by calculating (from the means in Table 3-4), both the absolute reduction (Equation 3-1) and relative reduction (Equation 3-2) in growth between pure and mixed stands for each C_4 species and for *L. perenne* grown with each C_4 species.

$$C_A = a_i - b_i$$

Equation 3-1 Absolute competitive effect. Symbol abbreviations: a_i, pure stand biomass of the ith species; b_i, mixed stand biomass of the ith species.

$$C_R = \frac{(a_i - b_i)}{a_i} x\,100$$

Equation 3-2 Relative competitive effect. See Equation 3-1 for symbol abbreviations.

The growth of all C4 species was significantly reduced by competition from *L. perenne* and *L. perenne* growth was reduced by competition from all C_4 species (Table 3-4; $P<0.05$ for C main effect). Competition in favourable conditions was examined by the responses in the MA treatment (Fig. 3-2 and Fig. 3-3b). The relative competitive effects (C_R values, from highest to lowest) of the C_4 species in the MA pots were: *P. dilatatum* 64%; *S. africanus* 63%; *P. dichotomiflorum* 49%; *P. clandestinum* 46%; *D. sanguinalis* 38%. There were also large differences between the C_4 grasses in the extent that they reduced *L. perenne* mixed stand biomass. The C_R value for *L. perenne* grown with *D. sanguinalis* was 48%, 46% with *P. dichotomiflorum*, 27% with *P. clandestinum*, 10% with *P. dilatatum* and 8% with *S. africanus*.

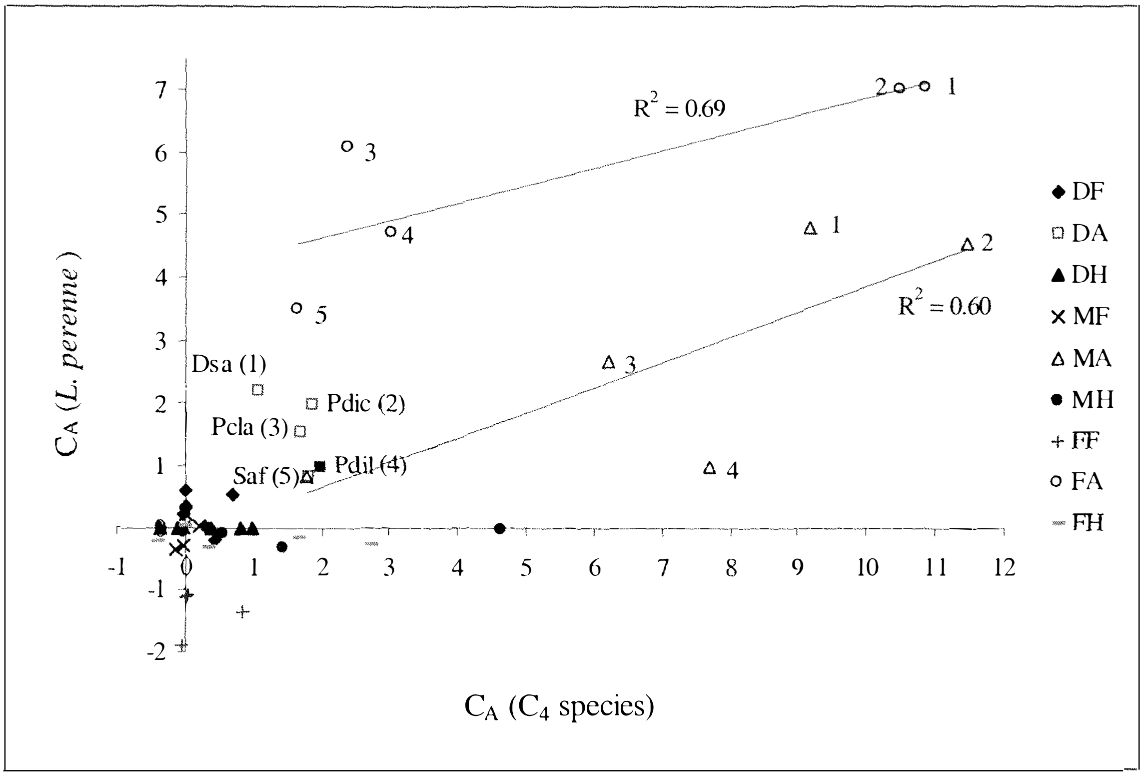

Fig. 3-2 Absolute competitive effect (C_A) for all water and temperature treatment combinations for each C_4 species and versus the corresponding C_A values for *L. perenne*. C_A is the difference between pure and mixed stand biomass (g pot^{-1}, see Equation 3-1). Legend shows treatment abbreviations. First letter corresponds to the water levels: Drought, Mesic and Flood. Second letter corresponds to the temperature levels: Frost, Ambient and Heat. Species abbreviations: Dsa, *D. sanguinalis*; Pdic, *P. dichotomiflorum*; Pdil, *P. dilatatum*; Pcla, *P. clandestinum*; Saf, *S. africanus*. Note that species labels are replaced by numbers for treatments other than DA.

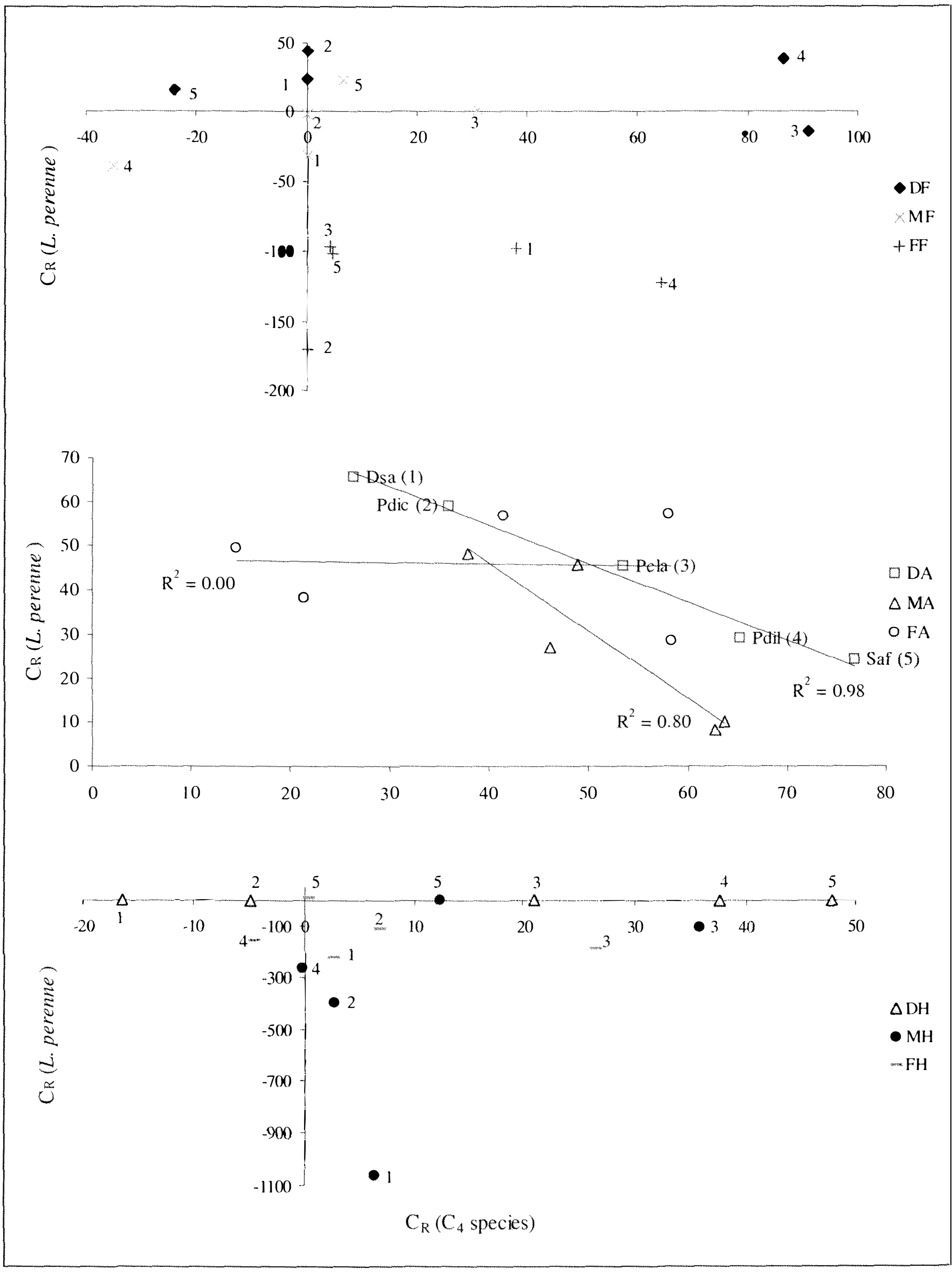

Fig. 3-3 Relative competitive effect (C_R) for the a.) frost, b.) ambient and c.) heat by water treatment combinations for each C_4 species versus the corresponding C_R values for *L. perenne*. C_R is the difference between biomass achieved in pure and mixed stands divided by pure stand biomass (%, see Equation 3-2). See For legend and species abbreviations see Fig. 3-2. Note that species labels are replaced by numbers for treatments other than DA.

Those C_4 species that were the least reduced by competition, in turn reduced the *L. perenne* MA performance the most (Fig. 3-3b). This negative relationship between the C_4 species and *L. perenne* for C_R was, however, not apparent when expressed as C_A (Fig. 3-2).

Rather, larger absolute differences between MA pure and mixed stand *L. perenne* biomass coincided with larger absolute differences in C_4 biomass. This positive relationship arose due to the combination of two factors. Firstly, because *L. perenne* pure stand biomass was a constant in the calculation of C_A (*L. perenne*) values, C_A (*L. perenne*) actually reflects C_4 competitive ability. Secondly, in this experiment, the most competitive C_4 species also achieved the greatest biomass in pure stand, where the maximum possible difference between pure and mixed stands will always be greater than with a small pure stand biomass.

The absolute differences between pure and mixed stand performance indicated that the water treatment had little effect on competition (Table 3-3a). Only *P. dichotomiflorum* showed a significant difference between water levels in terms of the difference in biomass between pure and mixed stands (Table 3-4a & b; P<0.05 for W by C interaction effect). For this species, there was a greater absolute competitive effect in mesic and flooded pots compared to droughted pots.

An effect of water availability on competition was apparent, however, in the C_R values of the C_4 species and *L. perenne* (Fig. 3-3b). The percentage reduction in biomass due to competition was consistently greater for *L. perenne* in DA and FA conditions compared to MA conditions. *Sporobolus africanus* was also more sensitive to competition, whereas *D. sanguinalis* and *P. dichotomiflorum* showed a reduced effect of competition in DA compared to MA pots. Under FA compared to MA conditions, *D. sanguinalis* showed much greater sensitivity to competition whereas *P. clandestinum* and *P. dilatatum* were less sensitive to competition (Fig. 3-3b).

The extreme temperature treatments had an over-riding effect on competition. The significant temperature by competition effects in Table 3-3a resulted from competition being severely restricted for all species by both -5°C and +50°C temperatures, but not by ambient temperatures (Table 3-4 and Fig. 3-2). Minimal live biomass achieved in pure stands under heat and frost conditions resulted in extreme C_R indices that trended to negative infinity (Fig. 3-3a & c). The low biomass of *L. perenne* due to its poor heat stress tolerance led to virtually no competitive suppression of the C_4 species in heated pots. Similarly, severe tissue damage and death of C_4 species in frosted pots resulted in minimal competitive suppression of *L. perenne.*

The significant water by temperature by competition interaction effect (Table 3-3a; $P<0.05$) for *P. dilatatum* resulted from the absolute competitive effect in ambient pots being disproportionally more in mesic than drought and flood conditions compared to frosted and heated pots (Fig. 3-2). In contrast, the significant water by temperature by competition interaction effect for *L. perenne* resulted from the absolute competitive effect in ambient pots being disproportionally more in flood than drought or mesic conditions compared to frosted and heated pots. In frosted pots C_A values were consistently negative for *L. perenne* in flood conditions (Fig. 3-2).

3.5 Discussion

3.5.1 Species differences in water and temperature tolerances

The response of the C_3 and C_4 species to the temperature extremes agreed with previously recognised differences in thermal tolerances of C_3 and C_4 plants (McWilliam 1978; Osmond *et al.* 1987; Atwell *et al.* 1999). That is, the C_4 species were more heat stress tolerant than *L. perenne*, whereas the overall frost tolerance of the C_4 species was lower than *L. perenne*. Differences in frost tolerance between the C_4 species were apparent. *Paspalum dilatatum* was clearly the most frost tolerant C_4 species. The higher relative frost tolerance of *P. dilatatum* has also been observed in other field and laboratory experiments. Rowley (1976), Forde & Davies (1979) and Davies & Forde (1991) all identified *P. dilatatum* as the most frost tolerant C_4 species.

Frost tolerance is related to a plant's ability to tolerate extra-cellular ice formation and therefore cell dehydration (Krause *et al.* 1988). A consequence of this physiological response is that frost and drought tolerance have been found to be closely associated (Cloutier & Siminovitch 1982). However, this association was not apparent in results of this experiment. The most frost tolerant C_4 species, *P. dilatatum*, was no more drought tolerant than the other C_4 species (Table 3-5). Similarly, the most drought tolerant species, *S. africanus*, was not particularly frost tolerant. In general, this relationship may not exist for C_4 species as many plants of tropical and subtropical origin are killed by chilling temperatures, well before ice crystals start to form (Levitt 1980).

3.5.2 Competition and competitive effects

There were considerable differences in C_4 competitive ability under those conditions without the influence of extreme climatic events, that is, within the MA treatment. Here, there was considerable variation in the competitive ability of the C_4 species. The most competitive C_4 species were the annual species, *D. sanguinalis* and *P. dichotomiflorum*, which were larger than *L. perenne* and suppressed the performance of *L. perenne* in mixed stand the most (Table 3-4d and Fig. 3-3b). The least competitive C_4 species were the perennial species, *P. dilatatum* and *S. africanus*. These species, under the MA conditions of this experiment (15-25°C), remained smaller than *L. perenne* and had the least effect on its performance. *Pennisetum clandestinum* was of intermediate competitiveness, it reduced *L. perenne* biomass but not to the same extent as *D. sanguinalis* or *P. dichotomiflorum*.

These differences in competitiveness agree with Campbell *et al.* (1996) who recognised differences in the ecology of several C_4 grassland species based on their abundance relative to habitat characteristics. Campbell *et al.* (1996) found that productive (high fertility, moist) and disturbed (frequently grazed with high animal densities) habitats had greater abundance of the more competitive species such as *D. sanguinalis* and low abundance of less competitive species such as *S. africanus*. In contrast, the less productive (low fertility, drier) and less disturbed habitats had a greater abundance of *S. africanus* than *D. sanguinalis*.

Campbell *et al.* (1996) also identified that there was a poor understanding of the role of competition in determining the success of invading C_4 species into C_3 grasslands. A particular area of uncertainty surrounds C_4 competitive ability. Specifically, to what extent are C_4 species able to actively displace C_3 species and to what extent are they merely occupying vegetation gaps created in the previous cool season. Wardle *et al.* (1994) suggest that *D. sanguinalis* (a summer-annual) and *Poa annua* (a winter-annual) occupy the same niche in grasslands but at different times of the year. That is, vegetation gaps created by the natural demise of *P. annua* in spring are colonised in the summer by emerging *D. sanguinalis* seedlings.

Overall, the relative reduction in biomass due to competition was either approximately equal for both the C_4 species and *L. perenne* (Fig. 3-3b; *D. sanguinalis* and *P. dichotomiflorum*), or greater for the C_4 species than *L. perenne* (Fig. 3-3b; *P. clandestinum*, *P. dilatatum* and *S. africanus*). This implies that within the reasonably static and equally favourable MA conditions, the competitive ability of *L. perenne* was at least the equal or greater than that of the C_4 species. This is consistent with cyclic oscillations between C_3 winter-annual and C_4 summer-annual grasses (Wardle *et al.* 1994), acting as a mechanism for the seasonal shifts in C_3 and C_4 abundance. Active competitive displacement is only likely to occur when seasonal changes in temperature and water availability favour C_4 growth relative to C_3 growth (Kemp & Williams 1980; Christie & Detling 1982). Extreme climatic events may further impact on these competitive interactions to the advantage of either C_3 and C_4 species.

3.5.3 The impact of extreme events on competition

3.5.3.1 Extreme water events

The impact of the extreme water events on competition were more apparent in terms of the relative, compared to the absolute, differences between pure and mixed stands. Here, the competitiveness of *L. perenne* was found to decrease under conditions of extremely low and high water availability (Fig. 3-3b). We therefore predict that a greater prevalence of both types of hydrological extremes will disadvantage *L. perenne.* However, not all C_4 species were equally advantaged by the reduced competitiveness of *L. perenne.*

As water availability was reduced, so did the competitive suppression of the most competitive C_4 species under MA conditions (*D. sanguinalis* and *P. dichotomiflorum*), whereas the less competitive species (*P. clandestinum*, *P. dilatatum* and *S. africanus*), were more suppressed (Fig. 3-3b). Accordingly, we predict that an extreme summer drought will shift the community structure toward competitive C_4 species, such as *D. sanguinalis*, that are normally most prevalent at that time.

It is interesting to note how competition modified the response of *S. africanus* to low water availability. This species was identified as desiccation tolerant, which agrees with observations of its abundance in relation to environmental productivity (Campbell *et al.* 1996; Campbell *et al.* 1999). However, its greater drought tolerance did not confer a competitive advantage over the time span of this experiment. Over a longer period of dry conditions the initial advantage of *L. perenne* may eventually be overcome by *S. africanus.*

Under flood conditions, *P. clandestinum* and *P. dilatatum* showed the largest decrease in competitive suppression, whereas *D. sanguinalis* was affected more by competition under flood conditions (Fig. 3-3b). Therefore, we predict a flood will decrease the dominance of *D. sanguinalis* in favour of an increase in the abundance of *P. dilatatum* and *P. clandestinum.*

The advantage to *P. dilatatum* under flooding conditions agreed with the findings of Rubio *et al.* (1995), who found that *P. dilatatum* showed a high ability to tolerate waterlogging. The high water logging tolerance of *P. dilatatum* was related to root morphological adaptations. Specifically, the synthesis of root aerenchymatic tissues, aerotropic and adventitious roots, which all aid the supply of oxygen to roots under waterlogged conditions. In addition, in spite of reduced root biomass relative to shoot biomass, *P. dilatatum* maintains high growth rates under waterlogged conditions through increasing nutrient uptake per unit of root (Rubio *et al.* 1997; Rubio & Lavado 1999).

3.5.3.2 Extreme temperature events

Extreme heating advantaged the C_4 species by preferentially damaging C_3 species, causing the *competitive release* of C_4 species. However, not all C_4 species were equally advantaged by the extreme +50°C heating events (Fig. 3-3c). In Fig. 3-3c the most competitive species under ambient conditions, *D. sanguinalis* and *P. dichotomiflorum*, are mainly located near to, or on the left of the y-axis (small or negative C_R values), whereas the less competitive species, *P. clandestinum*, *P. dilatatum* and *S. africanus*, are mainly located on the right of the y-axis (larger, more positive C_R values). This suggests that the former species were advantaged more by the extreme heating event than the latter species. This differentiation between species was particularly pronounced under combined heat and drought (Fig. 3-3c). Accordingly, we predict that an extreme heating event will drive community composition further towards the already dominant C_4 species, particularly if water availability is low. In agreement, *Digitaria sanguinalis* was the C_4 species most advantaged by an extreme heating event in mixed *L. perenne*/C_4 grasslands (White *et al.* 2000b, Chapter Four).

The responses of the C_4 species and *L. perenne* to our -5°C event implied that a frost will have the opposite effect to an extreme heating event. That is, frosts will reduce C_4 competitive ability and result in the competitive release of *L. perenne*. However, in contrast to an extreme heating event, frosts are most likely to occur during the cool season - a time of year when C_4 abundance is naturally low. Anomalous frosts that occur early (late summer/autumn) or late (mid to late spring) will, therefore, have a greater impact on the structure of C_3/C_4 grassland communities.

3.6 References

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4 Sensitivity of three grassland communities to simulated extreme temperature and rainfall events

CONTENTS

4.1 Abstract

Three grassland communities in New Zealand with differing climates and proportions of C_3 and C_4 species were subjected to extreme heating and rainfall events. A novel experimental technique using portable computer-controlled chambers simulated the extreme heating events. The productive, moist C_3/C_4 community was the most sensitive to the extreme events in terms of short-term community composition compared with a dry C_3/C_4 community or an exclusively C_3 community. An extreme heating event caused the greatest change to plant community species abundance by favouring the expansion of C_4 species relative to C_3 species, shifting C_4 species abundance from 43% up to 84% at the productive, moist site. This was observed both in the presence and absence of added water. In the absence of C_4 species, heating reduced community productivity by over 60%. The short term shifts in the abundance of C_3 and C_4 species in response to the single extreme climatic events did not have persistent effects on community structure nor soil nitrogen one year later. There was no consistent relationship between diversity and stability of biomass production of these plant communities, and species functional identity was the most effective explanation for the observed shifts in biomass production. The presence of C_4 species resulted in an increased stability of productivity after extreme climatic events, but resulted in greater overall shifts in community composition. The presence of C_4 species may buffer plant community productivity of grasslands against an increased frequency of extreme heating events associated with future global climate change.

4.2 Introduction

Although long-term (year to decade-long) relations between climate and vegetation composition are well documented (Teeri & Stowe 1976; Rundel 1980; Teeri 1988; Paruelo & Lauenroth 1996; Cabido *et al.* 1997; Cerling *et al.* 1997; Ehleringer *et al.* 1997; Epstein *et al.* 1997; Collatz *et al.* 1998) the effects of short term (day-long) extreme events on vegetation structure and community dynamics are less well understood. These extreme climatic events, while often transient, can cause shifts in community structure (MacGillivray *et al.* 1995). Certain extreme climatic events are predicted to increase in frequency in the future due to global climate change (Mearns *et al.* 1984; Wigley 1985), especially with an increased frequency of inter-annual climate fluctuation phenomenon such as the El Niño/Southern Oscillation (Timmermann *et al.* 1999).

Particular uncertainty surrounds the factors determining the sensitivity of a particular grassland community to an extreme event, as prior exposure of communities to certain climatic regimes can condition tolerance to subsequent extremes. For example, a plant community within an environment with mean climatic conditions closer to the extreme would be expected to have greater tolerance because exposure to sub-lethal intensities can reduce sensitivity to a stress event (Levitt 1980b; Pollock 1990).

Species richness (Baskin 1994; Johnson *et al.* 1996; Chapin *et al.* 1998) has also been suggested as a key community attribute determining the stability of ecosystem productivity. The "diversity-production stability" relationship introduced by MacArthur (1955) and supported by Tilman & El Haddi (1992), Tilman & Downing (1994) and Tilman (1996) contends that species-rich ecosystems will have a greater probability of containing species that are tolerant of a particular disturbance.

An alternative hypothesis is that functional diversity and composition have critical importance in determining community stability (Tilman *et al.* 1997; Symstad *et al.* 1998). This concept originated from Walker (1992), who proposed that species within groups of species with similar functional attributes (morphological, physiological, reproductive and life history characteristics that determine response to a plant's abiotic and biotic environment) will compensate for those species removed by the perturbation. Walker suggested that ecosystem function will be *independent* of diversity as long as all members of a functional group are not deleted. In agreement with this, Tilman *et al.* (1997) found in a large-scale grassland removal experiment, that functional diversity (defined as the number of functional groups added) was a greater determinant of ecosystem productivity than species diversity. In addition, functional composition (defined as which groups were added) was a greater determinant of ecosystem productivity than functional diversity.

The results of Tilman *et al.* (1997) emphasise the importance of composition on ecosystem processes. In the context of impacts of increasing frequency of extreme climatic events on grassland ecosystems, those plant communities containing species with functional attributes responsible for tolerance to stress associated with an extreme event would be expected to be more resistant to damage. In support of this, MacGillivray *et al.* (1995) found that resistance to damage at the community level was largely related to functional attributes of species, especially nutrient stress tolerance.

New Zealand exotic grassland communities vary both in community diversity (Heads 1997) and also in the identity and functional properties of the component species. Typically, highly productive lowland grassland communities are comprised of 5 to 10 plant species (Langer 1990; Wardle *et al.* 1999) and many northern grassland regions of New Zealand experience a warm season increase in the abundance of C_4 species (Baars *et al.* 1991). One of the most striking differences in the functional properties of species in these northern grasslands is the differences between C_3 and C_4 species. C_4 plants have a higher optimum temperature for growth (Mitchell 1956; Kemp & Williams 1980; Collatz *et al.* 1998) and an inherently greater ability to tolerate heat stress than C_3 species (Pearcy & Ehleringer 1984).

Elevated temperature (Wilen & Holt 1996) and water availability (King & Oliver 1994; White *et al.* 1997) are important determinants of C_4 grass growth and abundance in grasslands. Accordingly, shifts in extreme events (Houghton *et al.* 1995), are highly likely to have direct implications for the balance of C_3 and C_4 species in grassland communities.

This study was focused on three dairy cattle grassland regions which differ in climate and seasonal vegetation composition: Manawatu - cool temperate climate, only C_3, *Lolium perenne* (perennial), *Poa annua* (annual) and *Trifolium repens* (perennial) dominant; Bay of Plenty - warm temperate climate, summer dry, C_3/C_4 composite, *L. perenne*, *P. annua* and *T. repens* cool season dominant, *Digitaria sanguinalis* and *Panicum dichotomiflorum* (annual C_4 species) warm season abundant; Waikato - warm temperate climate, summer wet, C_3/C_4 composite (dominant species same as Bay of Plenty). In these grasslands extreme hot days can result in temperature exceeding 35 -

50°C in meristematic tissue adjacent to the exposed soil surface (Mitchell 1957; Mitchell & Bieleski 1964; Brock & Kim 1994). Subtropical cyclone weather systems can occasionally result in excess of 100 mm of rain in a single day event (Hickman 1984; Thompson 1987). How such temperature and rainfall events alter short-term and longer-term grassland vegetation structure and C_4 grass abundance is not well understood.

In this experiment, extreme rainfall and heating events were field simulated over three different grassland environments. A novel technique, involving the use of portable climate controlled chambers, was employed to artificially create, and accurately control, the extreme heating events. By superimposing exactly the same intensity of extreme event, it was possible to identify which environment was most susceptible to change. Sensitivity to extreme climatic events was measured as the deviation from untreated areas in two important plant community characteristics - 1) aboveground community biomass and 2) species abundance. The objectives of this experiment were to identify:

1) which plant community was most sensitive after an extreme climatic event to a short-term shift in total productivity,
2) the consequences of particular events for individual species, and
3) the persistence of short-term shifts in community structure over the longer term.

4.3 Methods

4.3.1 Experimental Sites

Three experimental sites were established on dairy grasslands: Manawatu, 40°24'S, 175°37'E; Bay of Plenty, 37°59'S, 176°49'E and Waikato, 37°49'S, 175°46'E. Height above level for each site: Manawatu, 90 m; Bay of Plenty, 5 m; Waikato 70 m. Time since cultivation and sowing was at least 15 years for all of the grasslands. Experimental sites measured 40 x 20 m and each was selected for a flat topography. In mid-November 1997, twenty 2 x 2 m plots were located within each site. Care was taken to ensure uniform distribution of grassland species within and between plots.

4.3.2 Soil seed load and soil nutrient content measurements

Twenty-five cores (five per replicate block) of 25 mm diameter and 75 mm depth were taken per site in mid-October 1997. Samples were submitted to the Seed Testing Station, Ministry of Agriculture and Forestry, Palmerston North, New Zealand for full seed content analysis. Twenty 75 mm deep soil cores per site were combined, dried, crushed and thoroughly homogenised for nutrient analysis at the Soil Fertility Service, AgResearch Ruakura, New Zealand.

4.3.3 Grazing

It was desired to keep the experimental sites within the rotational grazing regime operating at each site, therefore each site was grazed by dairy cattle three to four weeks prior to treatment application (Plate 4-1). Cattle grazed the vegetation to a height of 70 to 100 mm above ground level and then were removed. Afterwards, the site was mowed to 70 mm above ground level.

4.3.4 Climate data

Daily rainfall and 100 mm depth soil temperature data (Fig. 4-1) were obtained from the land owners records for the Bay of Plenty and Waikato sites. A meteorological station, situated 2 kilometres north of the site, provided the Manawatu records.

Plate 4-1 Dairy cattle grazing the Waikato site.

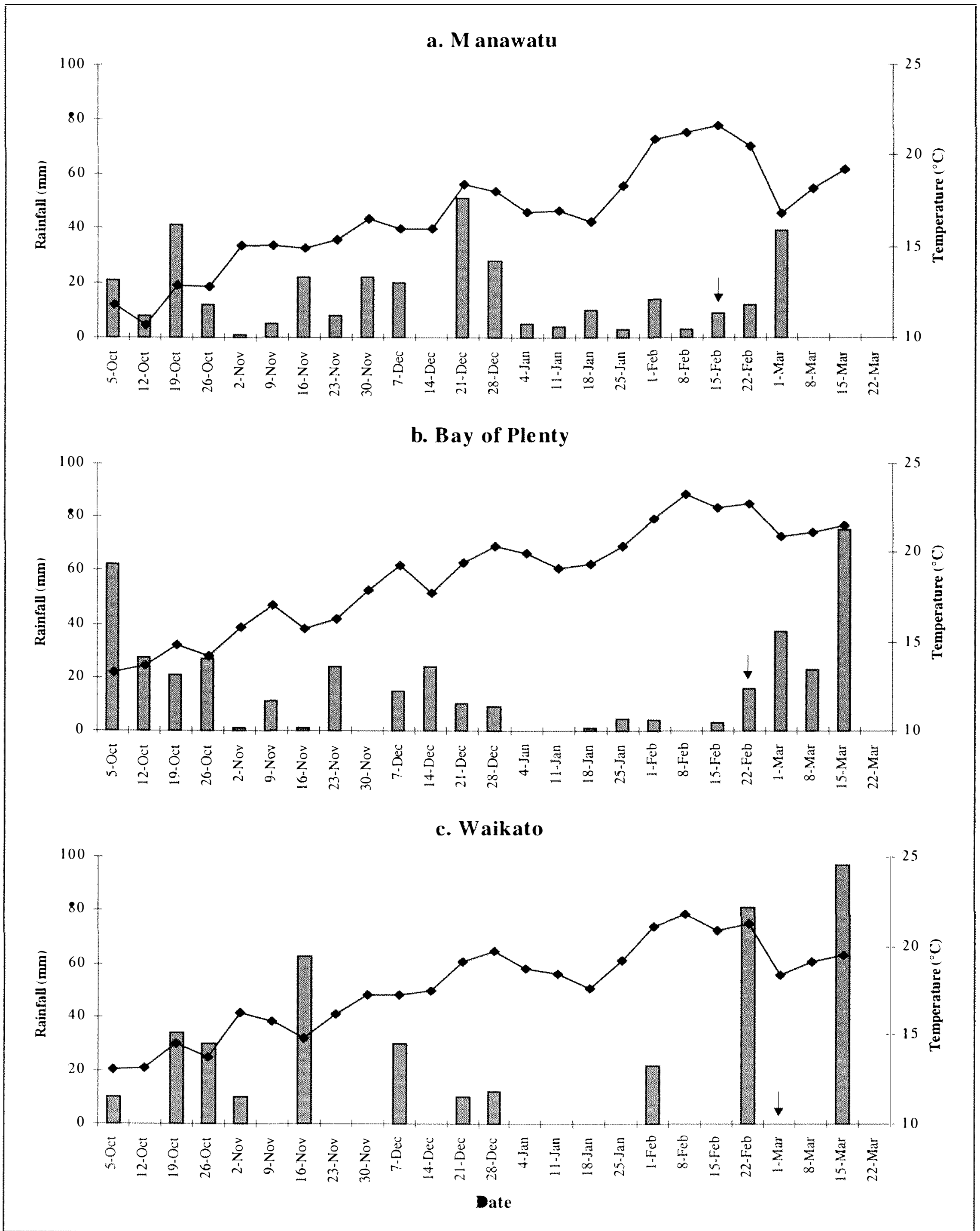

Fig. 4-1 Rainfall and soil temperature for the 1997/98 spring and summer period. Rainfall data presented as end of week total (columns). Temperature data (at 10 cm soil depth) presented as a weekly average (line). Arrow indicates the week in which treatments were applied.

4.3.5 Treatment application

Treatment applications began 9 February 1998 at the Manawatu site. Two controlled environment polycarbonate chambers were available for the experiment, therefore treatments were applied to one replicate per day. As a consequence, five days were spent at each site applying the treatments. Subsequently, the Bay of Plenty (commencing 16 February 1998) and Waikato sites (commencing 23 February 1998) were treated. Plots were mowed to 70 mm height two days before treatment application at each site.

4.3.6 Extreme heating event

Extreme heating was applied to grassland by the use of two identical computer-regulated chambers (Plate 4-2). Each chamber had base dimensions of 1.6 x 1.6 m and a roof apex height of 1.3 m. The walls and roof were constructed out of Polygal Polycarbonate Structured Sheet™. Polygal transmits at least 80% of 400 – 1600 nm wavelength light. Inside the chamber were three 2 kW heating elements suspended 0.6 m above ground level. Electricity to power the heating elements was provided by a 15 kVA portable diesel generator.

The extreme heating treatment (+H) involved maintaining the air temperature at 52.5°C at canopy height continuously for 8 hours. Temperature within the chamber was computer controlled via two sensors located 50 mm above ground level. The temperature linearly elevated from ambient to treatment set point over one hour and lowered back to ambient set point for one hour at the end of the treatment period (Fig. 4-2). The chambers were removed from the plots when not applying treatments.

4.3.7 Extreme heavy rainfall event

The extreme heavy rainfall event (+W) was simulated by applying 100 mm of water using a watering can. The watering of each plot took approximately 40 minutes, during which time 400 litres was applied over the entire 2 x 2 m plot area. Care was taken to minimise run-off. Watering was performed in the late afternoon the day before the heat treatment was due to be applied to each replicate.

Plate 4-2 Computer-regulated transparent-polycarbonate chambers, with generator and refrigeration units. Applying heat treatment at the Bay of Plenty site, February 1998.

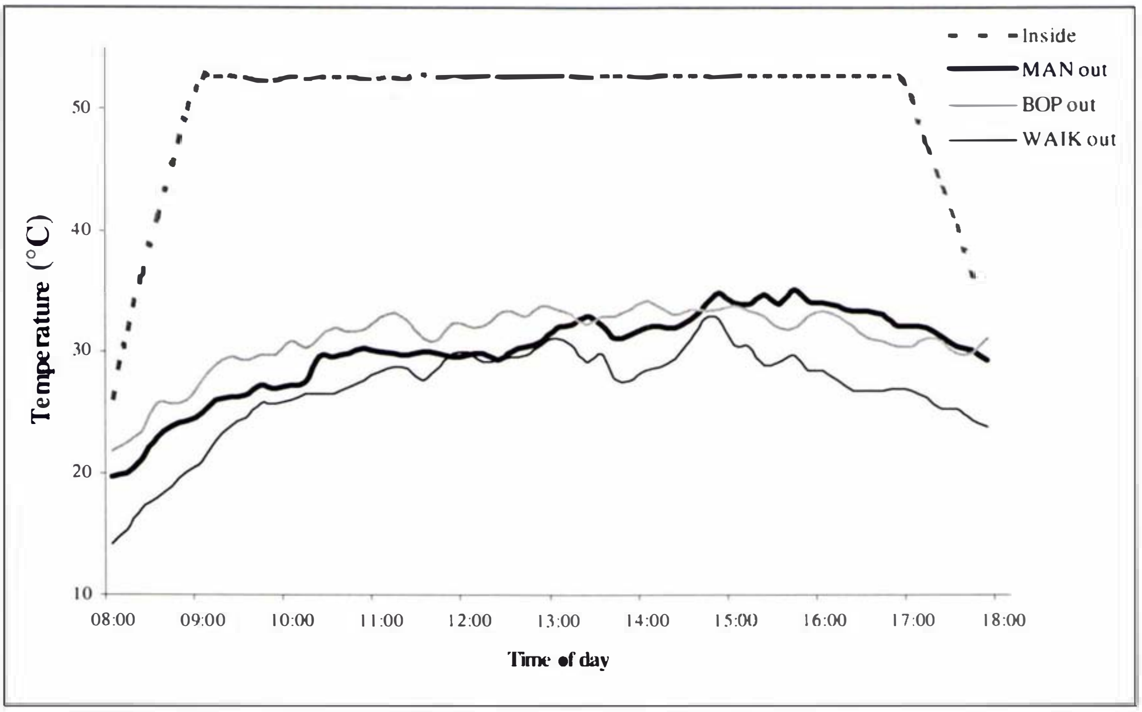

Fig. 4-2 Canopy height air temperature at each site, inside and outside polycarbonate chamber at the time of imposing the +H simulated extreme event (average values per site). Site abbreviations: B O P, Bay of Plenty; M A N, Manawatu; W A I K, Waikato.

4.3.8 Data acquisition

4.3.8.1 Immediately after treatment

Soil volumetric water content to 150 mm depth was measured by time domain reflectometry (TDR) (Topp & Davis 1985), immediately after the heating treatments were applied (using a Trase 1 device, Soil Moisture Equipment Corp. CA, USA).

4.3.8.2 Three weeks after treatment

After treatment, the plots were allowed to recover for three weeks before the herbage material was harvested. A 0.1 m^2 area of grassland was cut to ground level with motorised hand shears in the centre of each plot. The herbage material was dissected into individual grass species, legumes (only *T. repens* was found to be present), forbs and dead material, dried at 80°C for 24 hours and then weighed.

4.3.8.3 One year after treatment

One year after treatment, plots were mowed to 70 mm above ground level, allowed to recover for three weeks, then a 0.1 m^2 area of grassland was cut to ground level with motorised hand shears in the centre of each plot. Herbage samples were dissected into the same categories as above, dried at 80°C for 24 hours and weighed.

Soil mineralisable nitrogen was determined by pre-incubation of re-wetted soil, based on the technique of Franzluebbers *et al.* (1996). Soil cores (75 mm depth) were taken from each clipped area. The cores (five from each plot) were crushed, thoroughly mixed and left to air dry. Once dry, a 10 g subsample of soil was taken from each plot sample. Distilled water was added to each 10 g subsample, which were then incubated for two weeks at 25°C. The quantity of distilled water added was equivalent to 60% of the water holding capacity for each of the three soil types. The soil subsamples were then shaken for one hour with 100 ml 2N KCl. Nitrogen determinations were performed by the Soil Fertility Service, AgResearch Ruakura, New Zealand. Nitrate-N was determined on a flow injection analyser using a cadmium reduction column. Ammonium-N was determined colorimetrically using a modified Gehrke-Wall procedure on a technicon auto-analyser (Gehrke *et al.* 1972).

4.3.9 Data analysis

The experiment was a factorial design with two treatment types (heat and water) at two levels (added or not added), applied at three sites. The four treatment combinations were randomly allocated to each of five blocks of four 2 x 2 m plots. Data were analysed by analysis of variance. Replicates were treated as being nested within sites. The absolute production (g m^{-2} aboveground biomass), relative production (% of total live aboveground biomass) and available soil nitrogen (μg g^{-1}) of each grassland component were tested against their respective residual errors. Only the data from the Bay of Plenty and Waikato sites were included in the analysis of the C_4 grassland components. *Trifolium repens* data from the Waikato site were excluded from the analysis due to high incidence of zero values. Least significant differences were derived from the ANOVA residual error.

The aboveground live biomass data was used to derive two measures of diversity - the Shannon index of diversity and species richness (Magurran 1988). For Shannon indices the proportional abundance of the i^{th} species was calculated by dividing the i^{th} species productivity (g m^{-2} live biomass) by the total plot productivity (g m^{-2} live biomass). If the Shannon index is calculated for a number of samples the resulting distribution of indices will be normal (Taylor 1978). Therefore, analysis of variance can be used for generating appropriate error terms and discriminating between means. Species richness for each plot was calculated as the total number of plant species per clipped area (0.1 m^2) (Tilman 1996).

4.4 Results

4.4.1 Site attributes prior to treatment

The Manawatu and Waikato sites had similar total summer (December to February) rainfall prior to treatment application (138 mm and 155 mm respectively, Fig. 4-1). However, there was a more uniform distribution of rain at the Manawatu site. Two rainfall events occurred at the Waikato site after December, 22 mm at the start of February and 81 mm immediately prior to treatment application. Long-term (>50 years) averages for the same period (i.e. summer period) for the Manawatu and Waikato regions are 207 and 252 mm, respectively (Hickman 1984). The Bay of Plenty was the driest site, receiving 71 mm of rain over the December to February period, with 58 mm occurring in December. Virtually no rain fell at the Bay of Plenty site during January and February. This is considerably drier than the 254 mm long-term average for the Bay of Plenty (Hickman 1984). For the period December 1997 to February 1998 soil temperature at the Bay of Plenty and Waikato sites were higher than the Manawatu site (Fig. 4-1). Long–term daily mean 100 mm soil temperature for the three sites are: Manawatu 17.3, 18.5, and 18.1°C; Bay of Plenty 18.3, 20.1 and 20.3°C; Waikato 17.7, 18.9 and 18.9°C for the months December, January and February, respectively. Maximum soil temperature occurred in February, at the time of treatment application.

The seed bank of the Bay of Plenty and Waikato grassland communities were characterised by high densities of seeds of subtropical species in mid October 1997, particularly, the annual grasses *D. sanguinalis* and *P. dichotomiflorum* (Table 4-1). Another subtropical species, *Eleusine indica*, made a considerable contribution to the soil seed bank at the Waikato site. These C_4 species were absent from the seed bank at the Manawatu site. Seeds of the dominant C_3 grass, *L. perenne*, were not found at any of the sites at the time of sampling.

All sites were of high fertility, with no deficiencies of the major nutrients (

Table 4-2). Soil pH was similar for all sites and was within acceptable limits for grassland species growth. The Waikato site was characterised by high phosphate levels. However, the volcanic parent material from which the Waikato site was derived results in large amounts of phosphate not being readily available for plant uptake, as illustrated by the high value for anion storage capacity.

Table 4-1 Buried seeds (number m^{-2}) to 75 mm depth at the three experimental sites in October 1997.

Species	**Manawatu**	**Bay of Plenty**	**Waikato**
Achillea millefolium	-	-	94
Agrostis sp	75	-	94
Amaranthus sp	-	527	188
Anagallis arvensis	-	-	94
Capsella bursa-pastoris	-	75	1036
Chenopodium album	377	226	94
Coronopus didymus	301	-	-
Digitaria sanguinalis (C_4)	-	5726	3014
Eleusine indica (C_4)	-	527	3296
Juncus bufonius	75	-	-
Malva sp	-	-	471
Oxalis sp	-	226	471
Panicum dichotomiflorum (C_4)	-	9794	9982
Plantago major	1055	377	753
Poa sp	3089	2185	2260
Polygonum aviculare	-	301	-
Polygonum periscaria	75	-	-
Rumex sp	75	151	-
Sisymbrium officinale	-	-	188
Solanum nigrum	527	-	94
Stellaria media	-	75	188
Taxacum officinale	151	75	-
Trifolium dubium	151	-	-
Trifolium pratense	-	-	94
Trifolium repens	2336	2185	1507
Veronica sp	527	452	377

Table 4-2 Soil nutrient content in October 1997 at the three experimental sites based on cores 75 mm deep. * centi-moles of charge per kilogram of soil

Nutrient	**Units**	**Manawatu**	**Bay of Plenty**	**Waikato**
Calcium	$cM^{(+)}$ kg^{-1} *	6.25	5.00	5.63
Potassium	$cM^{(+)}$ kg^{-1}	0.51	0.31	0.36
Magnesium	$cM^{(+)}$ kg^{-1}	1.00	0.92	1.26
Sodium	$cM^{(+)}$ kg^{-1}	0.15	0.13	0.11
Phosphorus	$\mu g\ g^{-1}$	44	62	97
Sulphur	$\mu g\ g^{-1}$	22	20	32
Organic Sulphur	$\mu g\ g^{-1}$	10	10	8
Anion Storage Capacity	%	25	52	80
pH		5.9	5.7	5.8

4.4.2 Environmental conditions at treatment

Air temperature at canopy height over the period that treatments were applied reached a maximum of about 30°C outside the controlled environment chamber compared with 52.5°C attained inside (Fig. 4-2). Volumetric soil water content taken immediately after treatment showed that overall the Bay of Plenty environment was the driest (Table 4-3). The heavy rainfall event substantially increased water content at all sites. The response from the Waikato site indicates that the extreme heating event reduced soil water content. This did not occur at the Manawatu and Bay of Plenty sites.

4.4.3 Grassland biomass productivity three weeks after treatment

There was no significant difference between sites in live biomass three weeks after treatment (Table 4-4; $P>0.05$ for site main effect). The heating treatment (+H and +H+W plots) decreased live biomass whereas the watering (+H+W and +W plots) treatment increased live biomass ($P<0.01$ and $P<0.05$ for heat and water main effects, respectively). The heating treatment caused a proportionally greater reduction of live and total biomass at the Manawatu site ($P<0.05$ for site by heat interaction effect), particularly in those plots that received the +H treatment only (Table 4-4).

4.4.4 Grassland composition three weeks after treatment

4.4.4.1 Manawatu site

Lolium perenne comprised 44% of the total live biomass of the untreated vegetation (Fig. 4-3a). *Trifolium repens* was the second most abundant species at 26%. Other minor components of the vegetation were *Agrostis capillaris* (9%) and *P. annua* (6%). The heating treatment promoted *L. perenne* abundance to approximately 64% and total C_3 grass abundance to 72% (Fig. 4-3b and c; $P<0.001$ for site by heat interaction effect). Even though *L. perenne* abundance was promoted relative to other grassland components, the absolute production of *L. perenne* was reduced (96 to 70 g m^{-2}) by the heating event (Table 4-4). The addition of water had little effect on grassland composition.

Table 4-3 Volumetric soil water content (%) after simulated extreme climatic events (±standard error of mean in parentheses). Treatment abbreviations: +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered.

Treatment	Manawatu	Bay of Plenty	Waikato
Immediately after simulated heating event			
Control	20.0 (±2.3)	10.1 (±0.9)	25.8 (±2.7)
+H	18.9 (±2.4)	10.1 (±0.9)	18.9 (±1.1)
+H+W	33.8 (±1.8)	18.6 (±1.1)	23.9 (±2.7)
+W	34.1 (±2.2)	18.8 (±1.2)	29.4 (±2.6)
One year after simulated extreme events			
Control	14.7(±0.5)	14.4(±1.2)	13.1(±1.4)
+H	14.5(±0.3)	17.7(±0.5)	13.4(±0.9)
+H+W	14.7(±0.6)	15.3(±1.3)	13.0(±0.6)
+W	15.4(±0.9)	16.6(±1.6)	12.8(±0.8)

Table 4-4 Herbage biomass (g m^{-2}), life history (A = annual; P = perennial) and photosynthetic pathway (C_3 or C_4) of grassland constituents three weeks after simulated extreme climatic events. Least significance difference (LSD) values (P=0.05) are for comparisons between sites, heating and watering treatments. Treatment abbreviations: con, control; +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered.

Species		Manawatu				Bay of Plenty				Waikato				
		Con	+H	+H+W	+W	Con	+H	+H+W	+W	Con	+H	+H+W	+W	LSD
Agrostis capillaris	P-C3	16	1	8	1	0	0	0	0	0	0	0	0	-
Bromus willdenowii	P-C3	0	0	0	0	0	0	6	0	0	0	0	0	-
Cynosurus cristatus	P-C3	0	0	0	0.1	0	0	0	0	0	0	0	0	-
Dactylis glomerata	P-C3	0	0	0	0	0	0	0	0	1	0	0	0	-
Digitaria sanguinalis	A-C4	0	0	0	0	53	39	57	81	51	141	141	115	84
Eleusine indica	A-C4	0	0	0	0	0	0	0	6	0	1	19	5	-
Elytrigia repens	P-C3	0	0	8	0	0	0	0	0	0	0	0	0	-
Holcus lanatus	P-C3	0	0	0	0.1	0	0	0	0	1	0	0	0	-
Lolium perenne	P-C3	84	45	94	109	51	46	49	46	53	10	11	47	37
Panicum dichotomiflorum	A-C4	0	0	0	0	13	33	15	17	18	24	23	12	27
Paspalum dilatatum	P-C4	0	0	0	0	13	0	18	1	0	0	0	0.2	-
Poa annua	A-C3	11	1	5	15	0	0.1	1	1	1	0.3	0.3	1	-
Trifolium repens	P-C3	46	18	24	47	21	8	11	7	4	3	1	3	19
Forbs	AP-C3	27	5	9	31	40	21	36	52	26	5	10	16	34
C3 grass		111	47	115	125	51	46	56	47	55	11	11	48	36
C4 grass		0	0	0	0	78	73	90	104	69	166	182	132	91
Live material		184	70	148	203	190	148	193	210	154	185	204	199	66
Dead material		69	62	76	71	72	59	66	52	60	62	62	58	27
Total		253	132	224	274	262	207	259	262	214	247	266	257	70

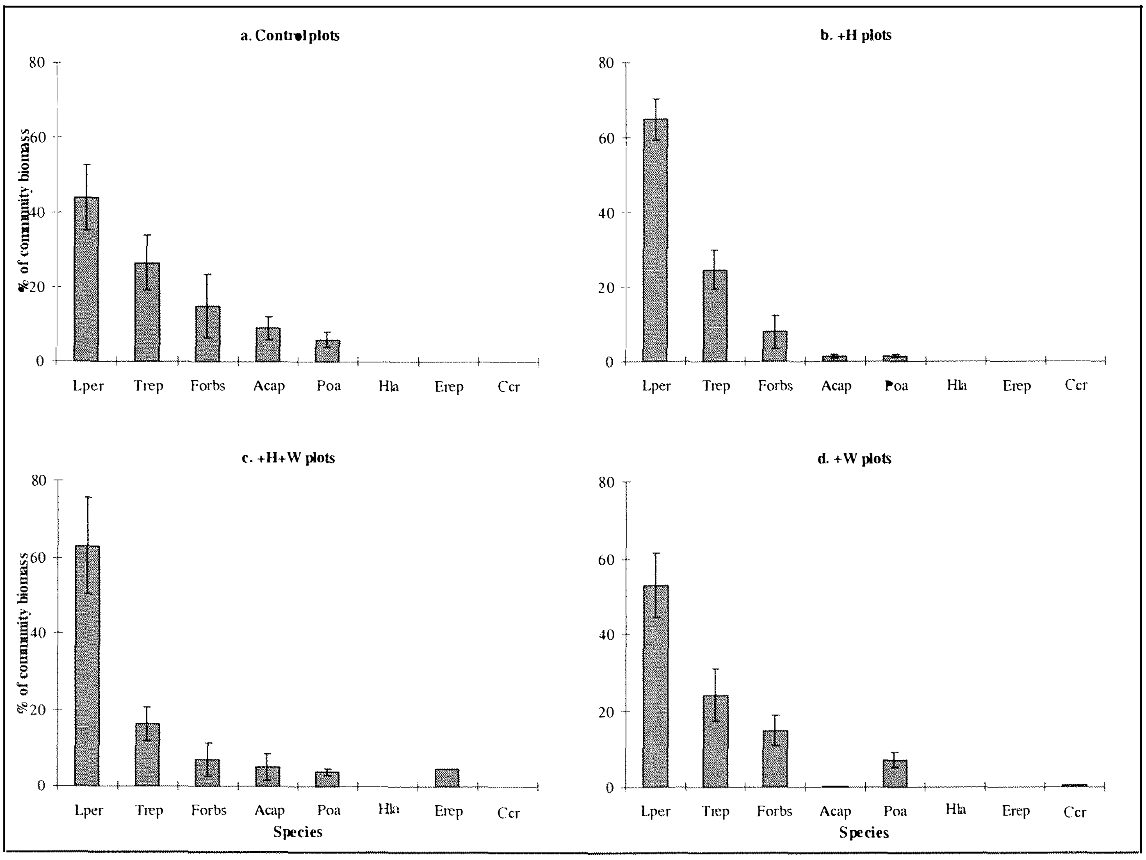

Fig. 4-3 Grassland composition three weeks after simulated extreme climatic events: Manawatu site. Live biomass based percentage contribution from each species. Error bars represent the standard error of each mean. Least significant differences (P=0.05) for within species comparison between treatments and sites are given in parentheses. Species abbreviations: Acap, *Agrostis capillaris*; Bwil, *Bromus willdenowii*; Ccr, *Cynosurus cristatus*; Dglo, *Dactylis glomerata*; Dsa, *Digitaria sanguinalis* (28%); Ein, *Eleusine indica*; Erep, *Elytrigia repens*; Hla, *Holcus lanatus*; Lper, *Lolium perenne* (20%); Pdic, *Panicum dichotomiflorum* (14%); Pdil, *Paspalum dilatatum*; Poa, *Poa annua*; Trep, *Trifolium repens* (12%); Forbs (21%). Treatment abbreviations: +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered.

4.4.4.2 Bay of Plenty site

The untreated Bay of Plenty grassland was characterised by a greater proportion of C_4 grasses than C_3 grasses (Fig. 4-4a; 40% c.f. 27%). The major grass species were *D. sanguinalis* (27%) and *L. perenne* (27%) with minor contributions from *P. dichotomiflorum* (7%) and *Paspalum dilatatum* (6%). *Trifolium repens* contributed less to the Bay of Plenty than the Manawatu untreated vegetation (12% c.f. 26%).

The heating treatment did not significantly alter absolute or relative productivity of the C_4 grass component within the Bay of Plenty grassland (Fig. 4-4 and Table 4-4). However, the abundance of *P. dichotomiflorum* appeared to be promoted within the +H treated plots (Fig. 4-4b). The contribution from *P. dichotomiflorum* was approximately equal to that of *D. sanguinalis* (20% and 24%, respectively). Neither the absolute or the relative production of *L. perenne* and *T. repens* were changed by the heating treatment at the Bay of Plenty site.

The watering treatment did not significantly alter the absolute or relative production of the grassland components at the Bay of Plenty site (Table 4-4; $P>0.05$ for water by site interaction effect for all components). The addition of water prior to the extreme heating event (+H+W) resulted in a grassland composition similar to that of the control plots (Fig. 4-4c). *Lolium perenne* and *D. sanguinalis* were still the dominant C_3 and C_4 species at 27% and 28% of total live biomass. Other minor C_3 species were *Bromus willdenowii* (3%) and *P. annua* (<1%). Within the plots that only received the extreme rainfall simulation (+W), the abundance of *D. sanguinalis* appeared to be promoted above that of *L. perenne* (Fig. 4-4d).

4.4.4.3 Waikato site

The control plots were dominated by C_4 grasses (43%, Fig. 4-5a). *Lolium perenne* and *D. sanguinalis* were the most abundant individual species at 36 and 30% of total live biomass, respectively. Forbs contributed similar proportion (16%) to that at the Manawatu and Bay of Plenty sites. The contribution of *T. repens* was very low at 3% of live biomass.

The heating treatment had a large effect on grassland composition (Fig. 4-5). The C_4 grass component increased in abundance to 84% of live biomass ($P<0.05$ for site by heat interaction effect). *Digitaria sanguinalis* became highly dominant at 74% and 59% of total live biomass in +H and +H+W plots, respectively.

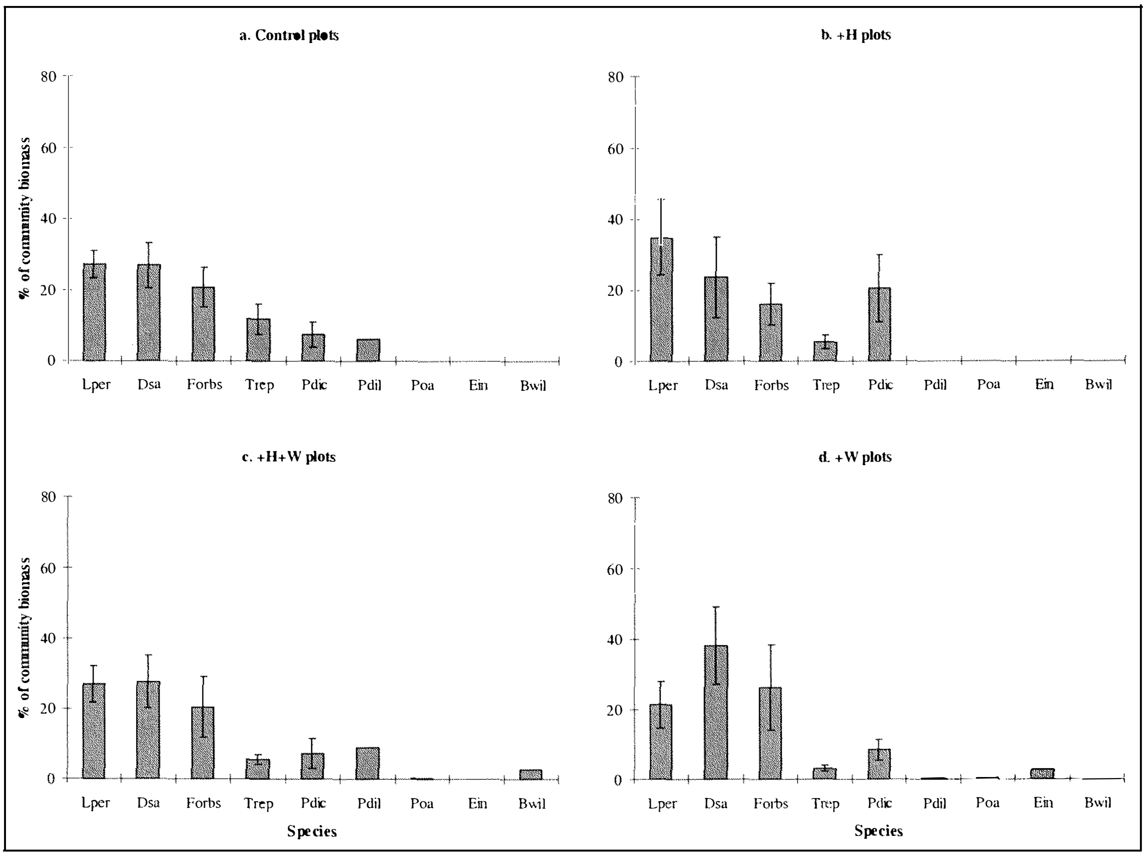

Fig. 4-4 Grassland composition three weeks after simulated extreme climatic events: Bay of Plenty site. Live biomass based percentage contribution from each species. Error bars represent the standard error of each mean. LSD's, species and treatment abbreviations are shown in Fig. 4-3 legend.

Panicum dichotomiflorum was the other major contributing C_4 grass at 15% and 12%. The increased C_4 contribution was mainly attributable to a large increase in *D. sanguinalis* biomass (83 to 141 g m^{-2}, Table 4-4). The C_3 grasses declined in live biomass (52 to 11 g m^{-2}) and as a proportion declined from 33 to 8% (P<0.05 for site by heat interaction effect for both absolute and relative production).

As occurred at the Bay of Plenty and Manawatu sites water had little effect on the abundance of grassland components at the Waikato site. The addition of water prior to the heating event (+H+W) did not alter the biomass of the C_3 grass component (11 g m^{-2}, Table 4-4). The C_4 grass *E. indica*, appeared to increase in abundance (9%) under the +H+W treatment. In those plots that received water only (+W), the C_3 grass component - predominantly *L. perenne* - increased in absolute (11 c.f. 48 g m^{-2}, Table 4-4) and relative (6 c.f. 28%, Fig. 4-5d) production when compared to the heat treated plots.

4.4.5 Plant community diversity three weeks after treatment

The Bay of Plenty grassland was more diverse than the Manawatu and Waikato grasslands (Fig. 4-6; P<0.001 for site main effect for both Shannon and species richness indices). Diversity, when based on the Shannon index, was significantly decreased by the heating treatment, particularly at the Manawatu and Waikato sites (P<0.05 for heat main effect). The watering treatment significantly reduced the effect of heating on diversity (P<0.05 for water and heat interaction effect).

4.4.6 Soil and plant response one year after treatment

The volumetric soil water content one year after treatment was not different between treatments (Table 4-3). However, in contrast to the previous year, the Bay of Plenty site was significantly wetter than the Waikato site in 1999 (P<0.001 for site main effect). Both the Waikato and Manawatu sites had lower soil moisture content in 1999 than in 1998.

The short term shift in C_3 and C_4 species abundance as a result of the extreme heating event did not affect mineralisable soil nitrogen one year after treatment (Table 4-5; P=0.84 for heat main effect). Similarly, there was no difference between the watered and non-watered plots. However, the Bay of Plenty site had a lower nitrogen content than the Manawatu and Waikato sites (P<0.001 for site main effect).

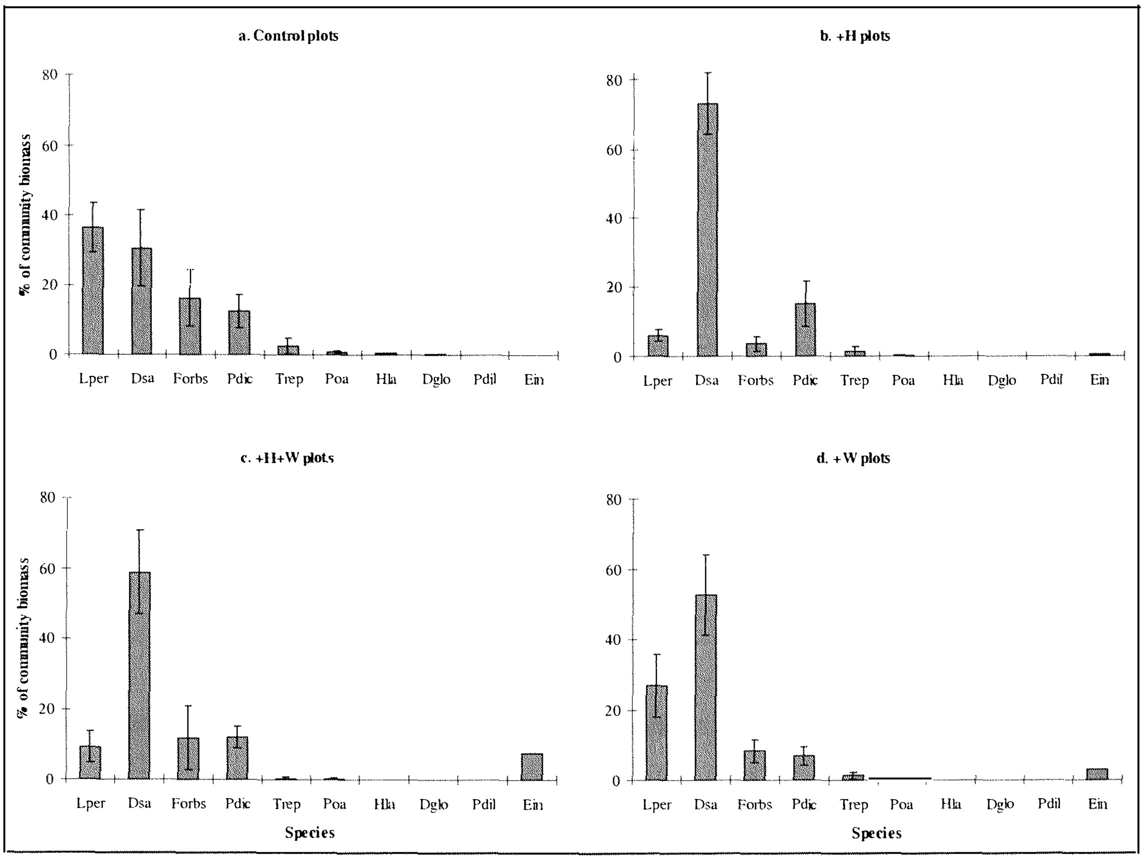

Fig. 4-5 Grassland composition three weeks after simulated extreme climatic events: Waikato site. Live biomass based percentage contribution from each species. Error bars represent the standard error of each mean. LSD's, species and treatment abbreviations are shown in Fig. 4-3 legend.

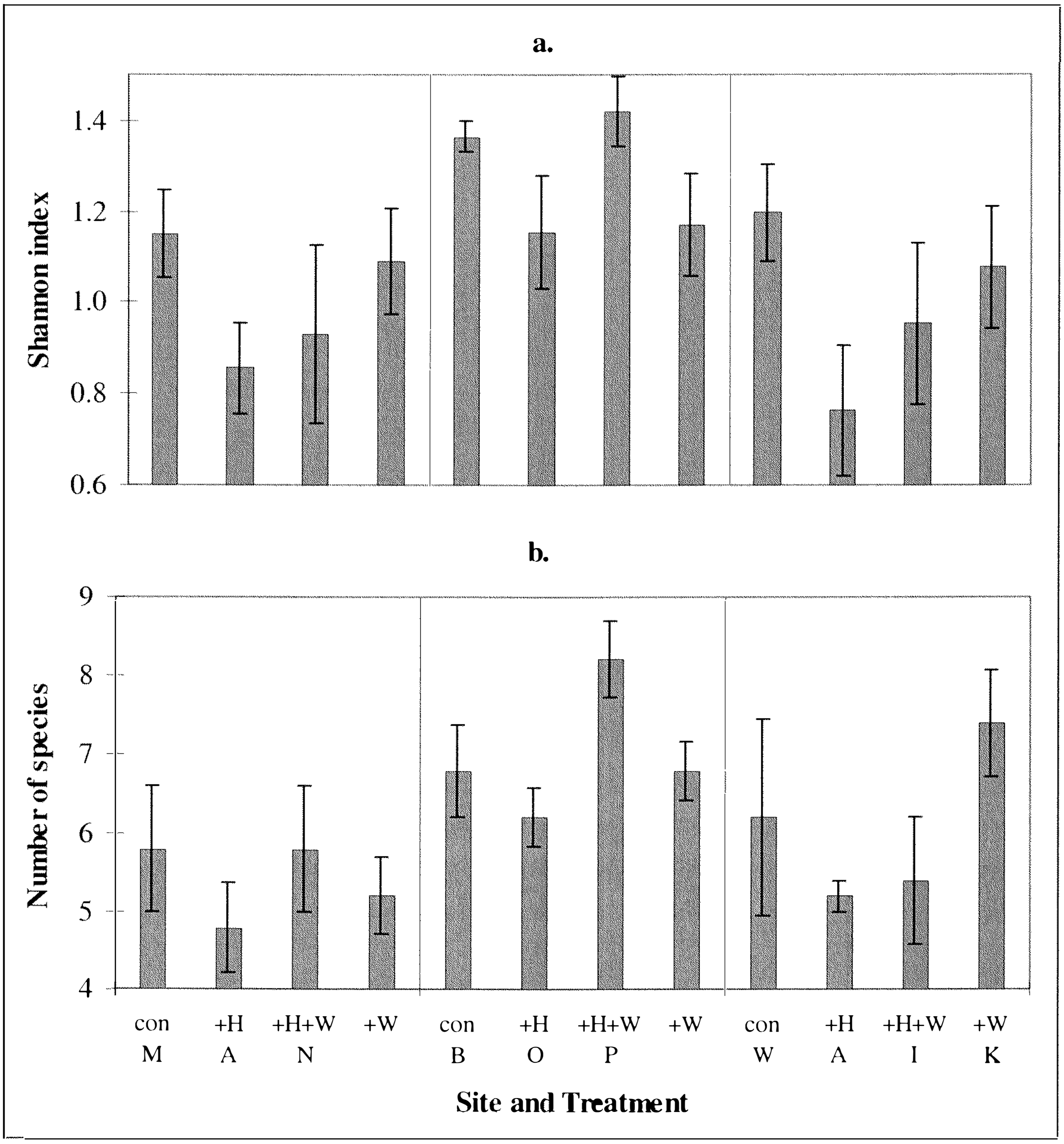

Fig. 4-6 Diversity measures of the three grassland communities three weeks after simulated extreme climatic events: a) Shannon index and b) species richness. Site abbreviations: B O P, Bay of Plenty; M A N, Manawatu; W A I K, Waikato.

Table 4-5 Mineralisable soil nitrogen ($\mu g\ g^{-1}$) one year after simulated extreme climatic events (±standard error in parentheses). Treatment abbreviations: +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered.

Treatment	**Manawatu**	**Bay of Plenty**	**Waikato**
Control	734 (±65)	500 (±47)	636 (±82)
+H	834 (±143)	504 (±62)	870 (±139)
+H+W	758 (±115)	318 (±55)	728 (±165)
+W	774 (±88)	475 (±43)	776 (±90)

Table 4-6 Herbage biomass (g m^{-2}) of grassland constituents one year after simulated extreme climatic events. Least significance difference (LSD) values (P=0.05) are for comparisons between sites, heating and watering treatments. Treatment abbreviations: con, control; +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered.

Species		**Manawatu**				**Bay of Plenty**				**Waikato**				
		Con	+H	+H+W	+W	Con	+H	+H+W	+W	Con	+H	+H+W	+W	LSD
Agrostis capillaris	P-C3	2	6	3	2	0	0	0	0	0	0	0	0	-
Anthoxanthum odoratum	P-C3	0	0.06	0	0	0	0	0	0	0	0	0	0	-
Digitaria sanguinalis	A-C4	0	0	0	0	37	82	55	83	39	40	64	58	49
Eleusine indica	A-C4	0	0	0	0	0	0	0	0	0	0.5	0	0.09	-
Lolium perenne	P-C3	24	27	22	38	69	52	67	29	12	16	18	16	16
Panicum dichotomiflorum	A-C4	0	0	0	0	1	12	10	30	13	7	1	7	19
Paspalum dilatatum	P-C4	0	0	0	0	5	9	1	14	0	3	0.4	0.1	-
Poa annua	A-C3	2	0.07	1	1	0.5	0.05	2	1	0	0.4	0.05	0	-
Setaria geniculata	P-C4	0	0	0	0	0	0	0	0	0	0	0	0.3	-
Trifolium repens	P-C3	26	26	12	26	24	9	14	20	11	10	8	15	15
Forbs	AP-C3	5	2	3	5	31	29	28	33	23	14	15	4	29
C3 grass		27	33	26	41	70	52	69	31	12	16	18	16	18
C4 grass		0	0	0	0	42	103	66	126	52	51	65	65	63
Live material		58	60	40	72	167	192	177	209	97	91	107	100	33
Dead material		61	66	61	91	101	109	122	78	76	82	88	79	44
Total		119	126	101	162	268	301	298	287	173	173	195	179	53

In general, the large short-term shifts in grassland composition observed three weeks after the extreme climatic events did not persist for one year (Table 4-6). The heat and water main effects for biomass or grassland composition were not significant. The one notable exception to this was the significantly lower biomass in the heated compared to the non-heated plots for *T. repens* at all sites ($P<0.05$).

Differences were apparent between sites in productivity and grassland composition, a reflection of soil moisture content. Total live biomass at the Bay of Plenty site was significantly greater than that achieved at the Waikato site, which was greater than the Manawatu site. The C_4 species *D. sanguinalis* and *P. dichotomiflorum* were a major component of the Bay of Plenty and Waikato grasslands, and there was a significantly lower percentage contribution of *L. perenne* at those sites ($P<0.001$ for site main effect).

4.5 Discussion

4.5.1 Stability of community productivity

The most pronounced effect of the C_4 functional types was to buffer their plant communities against short-term reductions in total biomass productivity due to extreme high temperature events. Overall, there was high consistency of total productivity between the three grassland communities, apart from the significant reduction in biomass in response to the extreme heating event at the Manawatu grassland. Primary differences in composition between the three communities provide a likely explanation for the greater sensitivity to the extreme heating event at the Manawatu site (Osmond *et al.* 1987). All four broad groupings of species (viz. C_3 grasses, C_4 grasses, legumes and forbs) were present within the Waikato and Bay of Plenty plant communities whereas C_4 grasses were absent from the Manawatu vegetation. Where heat stress tolerant C_4 species (e.g. *D. sanguinalis* and *P. dichotomiflorum*) were present stability of community productivity was maintained, whereas the absence of C_4 species (the Manawatu site) resulted in a significant reduction in productivity after the extreme heating event.

The lower stability of productivity and species diversity exhibited by the Manawatu grassland is in agreement with the "stability-diversity" hypothesis (MacArthur 1955; Tilman & Downing 1994). However, the Waikato site was no more species diverse than the Manawatu grassland, yet displayed high stability of productivity. This highlights the importance of functional attributes of the species lost or absent from an ecosystem - i.e. its functional composition (Walker 1992; Tilman *et al.* 1997; Symstad *et al.* 1998) - as opposed to a reduction in species richness *per se* (Tilman & Downing 1994). In an experiment performed on a very similar Waikato grassland community, Wardle *et al.* (1999) also showed the importance of functional identity. It was found that removal of all C_4 grass species reduced total community biomass in the summer. The remaining C_3 species were unable to compensate for the loss of the "warm season productive" functional group.

The response of the ecosystem was specific to the type of extreme event. The absence of C_4 species at the Manawatu site was not as deleterious to community productivity when the extreme heating event occurred in combination with an extreme, heavy rainfall event. As air temperature increases there is a pronounced increase in transpiration due to increasing diffusion of water and steepening of the water pressure gradient (Levitt 1980b), assuming stomatal conductance remains constant. Under these conditions secondary heat-induced drought injury can occur if water supply is not adequate. Therefore, copious water applied prior to the +H treatment reduced the extent of this type of drought injury. In addition, the +H+W treated plants were able to sustain transpirational cooling of leaves for longer than the +H treated plants (Kolb & Robberecht 1996). It is concluded that an extreme heating event will have greatest impact on biomass production of "C_3 only" grasslands (Manawatu), especially if soil conditions are dry (Brock & Kim 1994).

4.5.2 Stability of community composition

Our results indicated that actively growing grassland communities that are comprised of both C_3 and C_4 species will be the most sensitive, in terms of a short-term change in community structure, to an extreme heating event. The greatest deviation from the abundance values in the control treatment occurred at the Waikato site (Fig. 4-5). The C_4 grass, *D. sanguinalis*, was advantaged by all climatic manipulations, in particular, the +H and +H+W treatments caused large short-term shifts in grassland composition.

The observation that the treatment combination of +H and +W did not result in greater *D. sanguinalis* abundance than the +H treatment alone suggests that extreme heat was the primary driver altering community structure (Weis & Berry 1988). Overall, C_4 species (particularly *D. sanguinalis*) will be highly advantaged by extreme heating events, at the expense of the C_3 species, because of their ability to tolerate heat stress.

The observed stability of biomass production, but instability of species abundance after perturbation means that (1) constituent species differed in their susceptibility to disturbance, and (2) the inherently tolerant species compensated for the susceptible species via *competitive release* (Tilman 1996). In the case of Tilman (1996), more drought resistant species compensated for the more drought sensitive species. In the grasslands of this experiment, competitive release operated through heat stress tolerance differences between the two major community components, that is, the C_3 and C_4 species. An extreme heating event damages tissue, mainly mediating its effect through irreversible disruption of the photosynthetic apparatus, particularly chloroplast membranes (Quinn 1988; Weis & Berry 1988). The C_4 species were damaged less (suffering proportionally less tissue necrosis) than C_3 species during the +H treatment, which resulted in the post-treatment canopy of photosynthetically active tissue being predominantly of the C_4 type. The C_4 species would have, therefore, monopolised light resources during recovery and gained a competitive advantage over the C_3 species.

The presence of species differing in their susceptibility to heat damage was fundamental to the large compositional change at the Waikato site. Similarly, the less dramatic changes in community structure at the Manawatu site were the result of the absence of heat tolerant species. The response from the Bay of Plenty site appears to contradict this explanation given the presence of both C_3 and C_4 species but reasonably high stability of community structure after the +H and +H+W treatments.

The explanation for this difference between the Waikato and Bay of Plenty vegetation response may lie in the physiological state of the vegetation at the time of treatment. The Bay of Plenty vegetation was in a quiescent physiologically-stressed state with considerable tissue death due to the severe dry hot conditions experienced for two months prior to treatment. These conditions are likely to have lead to greater heat stress resistance of the surviving C_3 species through acquired thermotolerance (Levitt 1980a; Pollock 1990; Howarth 1991; Howarth & Ougham 1993). Water stressed plants have also been found to display increased hardiness against high temperature damage (Kappen & Lange 1968; Valladares & Pearcy 1997). Arora *et al.* (1998), in agreement with Sabehat *et al.* (1998), found that the relationship between heat stress and desiccation tolerance was associated with the accumulation of several heat-stable dehydrin proteins. The substantial rain in the 4 weeks prior to treatment at the Waikato site resulted in non-stressed and actively growing plants at the time of treatment. Consequently, the C_3 plants within the Waikato environment exhibited greater sensitivity to the extreme heat.

The short-term impacts of increased climatic variability associated with future global climate change on grassland communities have been found to depend on community composition and physiological state. While local species abundances in moist C_3/C_4 grassland communities would be highly sensitive to an extreme heating event, the presence of C_4 species would buffer against a reduction in plant community productivity.

4.5.3 Persistence of effects

Our experiment has demonstrated that a single heating (52.5°C) or rainfall event can substantially modify community composition in the short-term. Although other extreme events such as fire, frost and drought have been found to have persistent effects on community structure (Neilson 1986; Westoby *et al.* 1989; MacGillivray *et al.* 1995), the effects observed immediately after treatment were transient, and were not observable one year later. Furthermore, there was no evidence to indicate that the large immediate above-ground changes in community composition were retained in the ecosystem, as persistent effects on below-ground microbial processes and properties (Table 4-5). The lower nitrogen content and higher fibre content (Minson 1981; Jackson *et al.* 1996) of litter entering the soil organic matter in the plots with abundant C_4 grasses might have been expected to negatively impact on the quantity of nitrogen mineralised from the soil (Wardle & Lavelle 1997). However, due to the stability and size of organic matter pools in grassland soils the effect of inputs of lower quality litter is likely to be manifested only after much longer time scales than one year (Wardle *et al.* 1999).

The lack of a persistent shift in community structure was probably associated with the life history characteristics of the species promoted by the extreme event. Plants of the summer annual species *D. sanguinalis* and *P. dichotomiflorum* do not persist throughout the year but instead over-winter as dormant seeds in soil until environmental conditions are conducive for germination. While an increase in the abundance of annual species would increase soil seed-bank loading, it is unlikely to be coupled to an increase in C_4 seedling emergence in the following year given the saturating seed numbers already present in these temperate zone C_3/C_4 grasslands (Table 4-1). However, in grasslands with low levels of C_4 species, these extreme heating events could act to subsequently favour vegetative and reproductive growth, and an increase in seed numbers which are incorporated in the seed-bank at the end of summer. These would provide a source of individuals for future invasions and lead to an increase in C_4 abundance.

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5 Impacts of extreme climatic events on competition during grassland invasions

CONTENTS

5.1 Abstract

Phytometers of five C_3 and five C_4 species were transplanted into three different grasslands to study the effects of extreme climatic events on community invasibility and competition. Single extreme heating and rainfall events in factorial combinations were superimposed on the grassland communities. A novel technique involving portable computer controlled chambers was used to create the heating events. To generate predictions of response to the extreme climatic events, the 10 phytometer species were categorised on the basis of 12 key plant functional traits. Using principal components analysis, two functional types (FTs) were identified as most likely to be advantaged (FT1 - fast-growing C_4 annuals) and disadvantaged (FT2 – slower-growing C_3 perennials) by an extreme climatic event. Competition between the resident vegetation and FT1 plus other C_4 phytometers was consistently more intense within the exclusively C_3 community compared to the dry C_3/C_4 community or moist C_3/C_4 community. The single extreme heating event had the greatest impact on competition, lowering the intensity of competition between the phytometers and resident vegetation. The results indicate that competition is highly important in limiting the invasion of C_3 grasslands by C_4 species. Predictions based on plant functional traits were confirmed by the FT1 and FT2 responses, whether growing as phytometers or as part of the resident vegetation. Future increases in climatic variability and the incidence of extreme climatic events are expected to suppress C_3 competitive dominance and promote invasion of C_4 species, in particular, the FT1 species.

5.2 Introduction

On global (Cabido *et al.* 1997; Epstein *et al.* 1997; Collatz *et al.* 1998), and regional scales (Rundel 1980; Campbell *et al.* 1999), the relative contribution of C_3 and C_4 species to plant communities is closely associated with temperature. Plants with C_4 photosynthesis are favoured in warmer regions whereas C_3 plants are favoured in cooler regions. In a transition zone from C_4 to C_3 dominated communities, such as that found in New Zealand, differences are apparent in the spatial distribution of C_3 and C_4 species at the local-scale. For example, within warmer northern regions C_3 and C_4 grasses are ubiquitous, existing within 'closed' grassland habitats and 'open' habitats such as tilled soil, road verges and waste areas (Cheeseman 1906; Matthews 1971; Field & Forde 1990; Baars *et al.* 1991). However, in cooler more southern regions of New Zealand C_4 plants are virtually absent from grasslands but exist in high numbers in immediately adjacent 'open' habitats. This difference between potential and realised amplitude of the C_4 species raises the question, is competition limiting the invasion of C_4 species into more southern grasslands?

As occurs with many aspects of ecology opinions are divided on the primary determinants of local species abundances, community composition and diversity (Huston 1999). At one extreme it is contended that local inter-specific biotic interactions, such as competition and herbivory, are critical in determining composition and diversity (Tilman 1982; Pimm 1991). Contrary to this, is the regional perspective which emphasises the importance of colonisation limitations (dispersal and recruitment limitations) (Ricklefs 1987; Cornell & Lawton 1992).

Recent evidence supports an intermediate perspective, which emphasised the importance of colonisation limitations but recognised the contribution of local biotic interactions in determining diversity (Tilman 1997). This perspective has a sound theoretical basis. If inter-specific biotic interactions were the sole determinant of community composition then the best competitor would eventually dominate. In reality this does not occur, communities are spatial arrangements of many different species. Inferior competitors are hypothesised to exist in plant communities after disturbance by being first to colonise sites left vacant by the dispersal limitations of superior competitors (Tilman 1994). In addition, even if more-competitive late-successional species are present, early-successional species are often temporally dominant because their rapid growth in resource-rich disturbed sites (Pacala & Rees 1998).

Successful invasion of plant communities depends on several key plant functional attributes. Critical reproductive and regenerative phase attributes include wide seed dispersal and low specificity for germination requirements (Noble 1989), large seed size (Burke & Grime 1996; but c.f. Rejmánek & Richardson 1996), short juvenile period and short interval between large seed crops (Rejmánek & Richardson 1996). After germination, complete invasion success becomes dependent on an ability to compete with other invaders and resident vegetation (Newsome & Noble 1986).

Studies on the effect of temperature on C_3 and C_4 competition have shown that as temperature increases above optimal for C_3 types, the superior growth of the C_4 types enables them to gain a competitive advantage (Harris *et al.* 1981; Pearcy *et al.* 1981; Pearcy 1985). Accordingly, predicted future increases in mean global temperature (Houghton *et al.* 1995), are likely to shift the balance of existing C_3/C_4 grasslands and promote C_4 invasion but these effects will occur over an extended period. More instantaneous effects of changes in global climate means are likely to be associated with increased climate variability (Mearns *et al.* 1984; Timmermann *et al.* 1999). In agreement with this, the abundance of C_3 and C_4 grassland species have been found to be highly sensitive to extreme climatic events, with a single-day heating event promoting the abundance of C_4 species relative to C_3 species (White *et al.* 2000, Chapter Four).

The invasion of C_4 species into southern North Island New Zealand grasslands is probably both colonisation and climate limited. Few C_4 propagules have been found in the soil seed bank under these grasslands (for example, F.E.T. Suckling unpublished data, and White *et al.* 2000). However, a recent experiment based on the same grassland found that overcoming colonisation limitation by adding seed of the C_4 annual species, *Digitaria sanguinalis*, did not promote invasion into intact vegetation (White *et al.* 1997). This suggests that inter-specific biotic interactions, specifically competition, are also important in restricting the invasibility of these grassland communities (Crawley 1986).

The experiment reported here directly tests the effect of increased climatic variability on competition during invasion. To examine C_3 and C_4 competition within solely C_3 and C_3/C_4 grasslands, the colonisation limitation to invasion was overcome by transplanting seedlings of different 'test' grassland species, otherwise known as 'phytometers' (Keddy 1989). The effect of competition on invasion was determined by comparing performance of phytometers inserted into vegetation cleared and vegetation intact areas (Reader *et al.* 1994; Wilson & Tilman 1995).

Following the approach of Diaz & Cabido (1997) and Grime *et al.* (1997), the phytometer species were grouped on the basis of 12 key morphological, physiological, and life history characteristics (i.e. plant functional traits) using principal components analysis. The resulting *functional types* (FTs) were used to develop predictions on the effect of extreme climatic events on invasion and competition in three grassland communities: Manawatu; cool temperate climate, only C_3 species; Bay of Plenty; warm temperate climate, summer dry, C_3/C_4 composite; Waikato; warm temperate climate, summer wet, C_3/C_4 composite.

The specific objectives of this experiment were to determine:

1) trait sets and functional types predicted to have differing potential to invade these grasslands,
2) differences in the actual growth of the differing grass functional types with different extreme events,
3) the importance of competition in limiting grassland community invasibility, and
4) the influence of extreme events on competition between resident and invading species in exclusively C_3 versus C_3/C_4 grasslands.

5.3 Methods

5.3.1 Functional traits and types

Following the approach of Diaz & Cabido (1997), 12 morphological, physiological and life history traits were identified as important in determining competitive ability and response to environmental constraints and disturbances (see Table 5-1 for trait descriptions). A 'soft' approach (Hodgson *et al.* 1999), was taken by making measurements of the twelve traits on intact field plants. Measurements were made in late February 1999 (Table 5-2).

5.3.2 Experimental sites

Three experimental sites were established on dairy grasslands: Manawatu, 40°24'S, 175°37'E; Bay of Plenty, 37°59'S, 176°49'E and Waikato, 37°49'S, 175°46'E. Experimental sites were 40 x 20 m in size and each site contained twenty 2 x 2 m plots. A full description of site establishment and characteristics is given in White *et al.* (2000) (Chapter 4).

Within each site the field plots were arranged into five blocks of four plots. The experiment was a factorial design with two treatment types (heat and water) at two levels (added or not added). The four treatment combinations (control, +H, +H+W and +W) were randomly allocated to each block. Plots were divided into two halves - hereafter called *cleared grassland* and *intact grassland.* The halves that were designated as *cleared* were sprayed with a translocated herbicide mixture (10 ml/L Glyphosate™ and 40 g/ha Granstar™). A sharp and exact division between the two plots halves was ensured through the use of a 2 x 1 m sheet of Perspex bolted to a 2 x 2 m aluminium frame. The frame, when placed over each plot, left half of the vegetation uncovered, to which the herbicide was applied.

5.3.3 Phytometer preparation and field growth

The ten phytometers used in this experiment were selected on the basis of being common to New Zealand grasslands but having diverse functional and life history traits (Table 5-1 and Table 5-3). Germination of the set of seeds for each site was spread over three weeks to standardise plant age at treatment. Seeds were germinated on moist blotting paper in an incubator set at 30°C day and 20°C night.

Table 5-1 Functional trait description and rationale.

Trait	Description and matrix classes	Rationale and source
P/S	Photosynthetic pathway C_3 = 1; C_4 = 2	Related to seasonal growth habitat, heat stress tolerance and water-use efficiency[1]
LH	Life history (persistence of an individual in the established phase) annual = 1; perennial = 2	Related to resource allocation, reproductive vs. vegetative
Pb	Pubescence glabrous = 1; partly pubescent = 2; pubescent = 3; highly pubescent = 4	Hairs are prominent "xeromorphic" structures of leaves and stems[2]. Based on field observation and literature[3]
LfN	Leaf nitrogen content (N% in mature leaves) low < 3 N% = 1; medium 3 ≤ N% < 4 = 2; high N% ≥ 4 = 3.	Strong explanatory factor between plants with rapid growth of productive competitive environments and slow growing plants with high resource retention in chronically unproductive environments[4]. Based on published data for leaf nitrogen content[5]
LF	Life form (plant shape or growth habit) upright tussock = 1; spreading tussock = 2; mat = 3	Based on field observation and literature[3]
LFSze	Life form size (maximum culm length for a mature plant) small 0-50 cm = 1; medium 50-150 cm = 2 and large > 150 cm = 3	Based on field measurements and literature[3]
LfS	Leaf succulence (turgid leaf mass / dry leaf mass)	Higher succulence enhances survival under water stress[6]. Also a measure of tissue density, related to balance between leaf 'structure' and leaf 'function'[7]
SLA	Specific leaf area (cm^{2} g^{-1})	A prime factor in determining interspecific variation in relative growth rate[6,7&8]
SGCL	Abaxial stomatal guard cell length (μm)	Stomata size positively related to DNA content (genome size)[9]. DNA content related to the timing and rate of seedling growth at low temperatures and frost resistance[10].
AdSD	Adaxial stomatal density (stomata mm^{-2})	Related to survival and growth under water stress. Represents a balance between water stress tolerance and gas exchange[11].
AbSD	Abaxial stomatal density (stomata mm^{-2})	see above
SdM	Seed mass (mg)	Correlated with rate of development, relative growth rate, desiccation tolerance of establishing seedlings, seedling survival in shade and seed persistence in soil[12].

Pearcy & Ehleringer (1984); Collatz *et al.* (1998)
Parker (1968)
Hafliger & Scholz (1980); Hafliger & Scholz (1981); Lambrechtsen (1992)
Grime *et al.* (1997)
Wilson (1975); Forde *et al.* (1976); Taylor *et al.* (1976); Betteridge (1979); Ulyatt (1981); Nuwanyakpa *et al.* (1983); Rugambwa *et al.* (1991); Stevens *et al.* (1992); Jackson *et al.* (1996); Johnson & Thomson (1996); Woods *et al.* (1996); Harris *et al.* (1997)
Diaz & Cabido (1997)
Hodgson *et al.* (1999); Wilson *et al.* (1999)
Lambers & Poorter (1992); Poorter & Bergkotte (1992); Reich *et al.* (1992)
Hodgson *et al.* (2000)
Grime & Mowforth (1982); MacGillivray & Grime (1995)
Quarrie & Jones (1977); Ristic & Cass (1991); Buttery *et al.* (1993); Xia (1994); Clifford *et al.* (1995); Paakkonen *et al.* (1998); Sayed (1998)
Jurado *et al.* (1991); Westoby *et al.* (1992); Thompson *et al.* (1993); Leishman & Westoby (1994a); Leishman & Westoby (1994b); Saverimuttu & Westoby (1996); Zhang (1996); Reich *et al.* (1998)

Table 5-2 Methodology for measurement of soft traits.

Trait	Methodology
Leaf succulence	Three fully emerged non-senescing leaves were cut off at the ligule from ten field plants per species. Leaves for each plant were immediately placed in sealed plastic bags. In the laboratory leaf triplets were weighed fresh, then returned to the plastic bags with 20 ml distilled water. After 24 hours at 5°C, leaves were patted dry with paper towels and weighed turgid. Leaves were then dried at 75°C for 24 hours and re-weighed. The turgid weight divided by the dry weight gives the succulence ratio.
Specific leaf area	Leaf area was measured on the fresh leaves used for leaf succulence. Leaf area (cm^2) for each set of three leaves was measured with a Li-Cor leaf area meter. The three leaflets of *T. repens* leaves constituted "one leaf" and were separated at their junction with the petiole and fed through the area meter separately. Specific leaf area was calculated as the area divided by the dry mass ($cm^2\ g^{-1}$) of three leaves per plant, mean of ten plants.
Leaf epidermal anatomy	Twelve freshly cut leaves from twelve different field grown plants per species were immediately transferred to the laboratory in sealed plastic bags. Leaf surfaces were painted (in fume-hood) with a thin coat 4% formvar in chloroform. The film was removed from the leaf surface with clear adhesive tape, which was then stuck to labelled microscope slides. Leaf replicas were made of both adaxial and abaxial leaf surfaces and viewed at 200X magnification on image analysis apparatus.
Stomatal guard cell length	Stomatal guard cell length was measured on the longest axis of abaxial stomata, fifteen stomata per species. On-screen measurements were made to nearest millimetre then converted into actual length and expressed as µm.
Adaxial and abaxial stomatal density	Adaxial (upper) and abaxial (lower) stomatal numbers were counted on-screen. Area captured on-screen was equivalent to 0.1134 mm^2 on leaf surface. Three such areas were randomly chosen per leaf surface. Twelve leaves were counted per species. Decision rule: if area boundary bisected stomata, add to count if more than 50% within counting area.
Seed mass	Individual seed mass (expressed as mg) was calculated as the total mass of 100 oven dry seeds divided by 100.

Two seedlings of the same species were planted into a peat-bark-fertiliser (Osmocote^{TM}) mix contained within small planting bags. After a week the smallest seedling of the pair was removed. The seedlings remained in the glasshouse for 3 weeks then were "hardened" outside for one week prior to field planting.

Transplanting of the potted plants into the field commenced at the Manawatu site on 15 December 1997. The Bay of Plenty site was planted on 19 December 1997 and the Waikato site was planted on 21 December 1997. Field sites were grazed immediately prior to planting then fine wire mesh and electric fences were erected around each experimental site to exclude small (rabbits) and large (cattle) herbivores. Ten planting holes (80 mm diameter x 100 mm depth) per plot half were created in a 2 x 5 grid by the use of a motorised soil auger (Plate 5-1). The distance between each planting hole and its nearest neighbour was 250 mm.

One plant of each species was transplanted into one of the ten holes of each plot half (Plate 5-2). The order of species was re-randomised for each plot half. Plants were watered immediately after planting and a molluscicide (Mersurol^{TM}) was applied. Shade cloth was temporarily pinned down over the newly planted seedlings to reduce water loss (Plate 5-3).

Plant survival was monitored after planting and due to the unusually dry conditions it was necessary to apply small quantities of water to aid establishment, particularly at the Bay of Plenty site. Seedlings establishing from endogenous seeds were regularly weeded from the cleared plot halves.

The grassland was maintained within the rotational dairy cattle grazing regime operating at each site by being grazed four weeks after field planting (Plate 4-1). Cattle grazed the vegetation to a height of 70 to 100 mm, then the site was mowed to 70 mm above ground level.

5.3.4 Treatment application

Treatment applications began 9 February 1998 at the Manawatu site. Subsequently, the Bay of Plenty (commencing 16 February 1998) and Waikato sites (commencing 23 February 1998) were treated. Plots were mowed to 70 mm height two days before treatment application.

Plate 5-1 Field planting phytometer species, Manawatu site. Ten seedlings were transplanted into both vegetation intact and vegetation cleared areas.

Plate 5-2 Phytometer species transplanted into vegetation cleared area, Manawatu site.

Plate 5-3 Strips of shade-cloth laid over the phytometers immediately after transplanting, Manawatu site

Extreme heating events were superimposed over the grassland by the use of two identical computer-regulated transparent-polycarbonate chambers (Plate 4-2). Each chamber had base dimensions of 1.6 x 1.6 m and a roof apex height of 1.3 m.

Inside the chamber were three 2 kW heating elements suspended 0.6 m above ground level. Electricity to power the heating elements was provided by a 15 kVA portable diesel generator. The extreme heating treatment (+H) involved maintaining an air temperature of 52.5°C at canopy height continuously for 8 hours. Temperature within the chamber was computer controlled via two sensors located 50 mm above ground level. The temperature linearly elevated from ambient to treatment set point over one hour and lowered back to ambient set point for one hour at the end of the treatment period. The chambers were removed from the plots when not applying treatments.

The extreme heavy rainfall event (+W) was simulated by applying 100 mm of water using a watering can. The watering of each plot took approximately 40 minutes, during which time 400 litres was applied over the entire 2 x 2 m plot area. Care was taken to minimise run-off. Watering was performed in the late afternoon the day before the heat treatment was due to be applied to each replicate.

5.3.5 Collection of plant material

Above ground parts of the transplanted phytometers were removed three weeks after treatment. A scalpel was used to cut through the base of each plant approximately 1 cm above ground level. If the plant had growing points above this height then the plant was cut off approximately 1 cm above the growing points. Plant material was dissected into dead and live material, dried for 24 hours (at 80°C) and weighed.

5.3.6 Data analysis

Principal components analysis (PCA) was performed on the plant functional traits data (Table 5-3) using the SAS statistical package (release 6.11). Firstly, to fit a principal components model to the ordinal data, a monotone transformation was performed using the PRINQUAL procedure. To aid interpretation, the principal components derived from the PCA (using PROC PRINCOMP) on the continuous and transformed ordinal data matrix, were correlated with each of the 12 plant functional traits.

Field data for the phytometer plants and grassland components (White *et al.* 2000) were analysed as a randomised-block factorial design using analysis of variance. The logarithm-transformed live aboveground biomass data for each phytometer species were tested against their respective residual errors. Replicates were treated as being nested within sites. Prior to treatment application almost all *Poa annua* transplants had flowered and died. *Poa annua* was therefore excluded from measurements and analysis. *Dactylis glomerata* data from the Bay of Plenty site were excluded from the analysis due to high incidence of zero values. *Panicum dichotomiflorum* data from the Waikato site were also excluded as most plants were removed by grazing. The equivalent of least significant differences of back-transformed data (least significant ratios, LSR) were derived from the ANOVA residual error.

Competition indices were calculated as the average of the differences between the average logarithm transformed biomass of the cleared grassland phytometers and logarithm transformed biomass of the intact grassland phytometer for each replicate (Equation 5-1). The competition data were analysed separately for each species as a randomised-block factorial design. A greater competitive index indicated a greater difference between cleared and intact half performance reflecting greater competition intensity. Least significant differences were derived from the ANOVA residual error.

$$CI_{ij} = \frac{\sum_{ij}\left(\left[\frac{\sum(\ln R_{ij})}{r}\right] - \ln(I_{ij})\right)}{n}$$

Equation 5-1 Competition index. Character definitions: i = site level; j = treatment level; r = number of cleared grassland phytometers; n = number of intact grassland phytometers; R_{ij} = cleared grassland phytometer biomass; I_{ij} = intact grassland phytometer biomass.

Table 5-3 Functional traits of the phytometer species. See Table 5-1 for trait description and units of measure. Nomenclature from Hafliger & Scholz (1980); Baker & Williams (1987); Lambrechtsen (1992). *, adaxial ribs prevented taking accurate leaf replicas. FT = functional type.

		P/S	**LH**	**Pb**	**LfN**	**LF**	**LFSze**
Dactylis glomerata L.	FT2	C_3	P	G	M	URT	S
Digitaria sanguinalis (L.) Scop.	FT1	C_4	A	P	L	ST	M
Festuca arundinacea Schreb.	FT2	C_3	P	G	M	URT	S
Lolium perenne L.	FT2	C_3	P	G	M	URT	S
Panicum dichotomiflorum Michx.	FT1	C_4	A	G	L	ST	M
Paspalum dilatatum Poir.		C_4	P	PP	L	ST	M
Pennisetum clandestinum Chiov.		C_4	P	HP	L	M	L
Poa annua L.		C_3	A	G	M	URT	S
Sporobolus africanus (Poir.) Robyns & Torn.		C_4	P	PP	L	URT	S
Trifolium repens L.		C_3	P	PP	H	M	M

		LfS	**SLA**	**SGCL**	**AdSD**	**AbSD**	**SdM**
D. glomerata L.	FT2	3.38	175.3	27.1	217	57	0.786
D. sanguinalis (L.) Scop.	FT1	5.89	392.1	32.0	56	118	0.211
F. arundinacea Schreb.	FT2	3.75	122.9	44.1	*	61	1.837
L. perenne L.	FT2	4.95	201.9	34.4	*	5	1.478
P. dichotomiflorum Michx.	FT1	3.64	238.5	36.1	97	74	0.340
P. dilatatum Poir.		4.72	253.9	30.9	128	180	1.318
P. clandestinum Chiov.		4.61	207.9	36.6	121	104	2.315
P. annua L.		5.48	347.2	24.9	124	80	0.236
S. africanus (Poir.) Robyns & Torn.		3.13	94.9	24.6	0	125	0.181
T. repens L.		4.16	190.7	9.2	408	213	0.496

5.4 Results and Discussion

5.4.1 PCA and predictions

The first two axes of the PCA accounted for approximately equal proportions of the total variation (Axis 1, 31.4% and Axis 2, 26.6%). Axis 1 separated the species on the basis of life form, pubescence, size and abaxial stomatal density (Fig. 5-1). Large, pubescent, prostrate species with numerous abaxial stomata scored positively on Axis 1 whereas small glabrous upright tussock species with sparse abaxial stomata scored negatively. On Axis 2 species with low leaf N, short life spans, high SLA, C_4 photosynthesis and few adaxial stomata scored highly whereas long-lived C_3 species with high leaf N, low SLA, dense adaxial stomata scored lowly.

On the basis of the PCA, two key groupings were identified (Fig. 5-1). Functional type 1 (FT1) contains two species - *D. sanguinalis* and *P. dichotomiflorum* - characterised by C_4 photosynthesis, high relative growth rate (implied by high SLA and annual life history), large size and prostrate growth form. We, therefore, predict that the FT1 species will be advantaged by an extreme heating event, through greater heat stress tolerance and an ability to rapidly colonise areas left vacant by less heat tolerant grassland functional types.

Functional type 2 (FT2) contains three species – *Lolium perenne*, *Festuca arundinacea* and *D. glomerata* – which are less heat stress tolerant (C_3 photosynthesis), slower growing (low SLA) and smaller than FT1. Accordingly, FT2 species are predicted to be disadvantaged by an extreme heating event.

FT1 and FT2 represent the groupings predicted to have widely contrasted responses to an extreme heating event. The 5 species not assigned to functional types are predicted to have intermediate responses. While potentially heat stress tolerant, the C_4 species *Pennisetum clandestinum*, *Paspalum dilatatum* and *Sporobolus africanus* are not expected to be advantaged by an extreme heating event to the same extent as FT1, given their traits predicting slower growth. *Sporobolus africanus*, scored negatively on Axis 1 and Axis 2 (close to FT2) and is, therefore, the C_4 species expected to be least advantaged by an extreme heating event (Fig. 5-1).

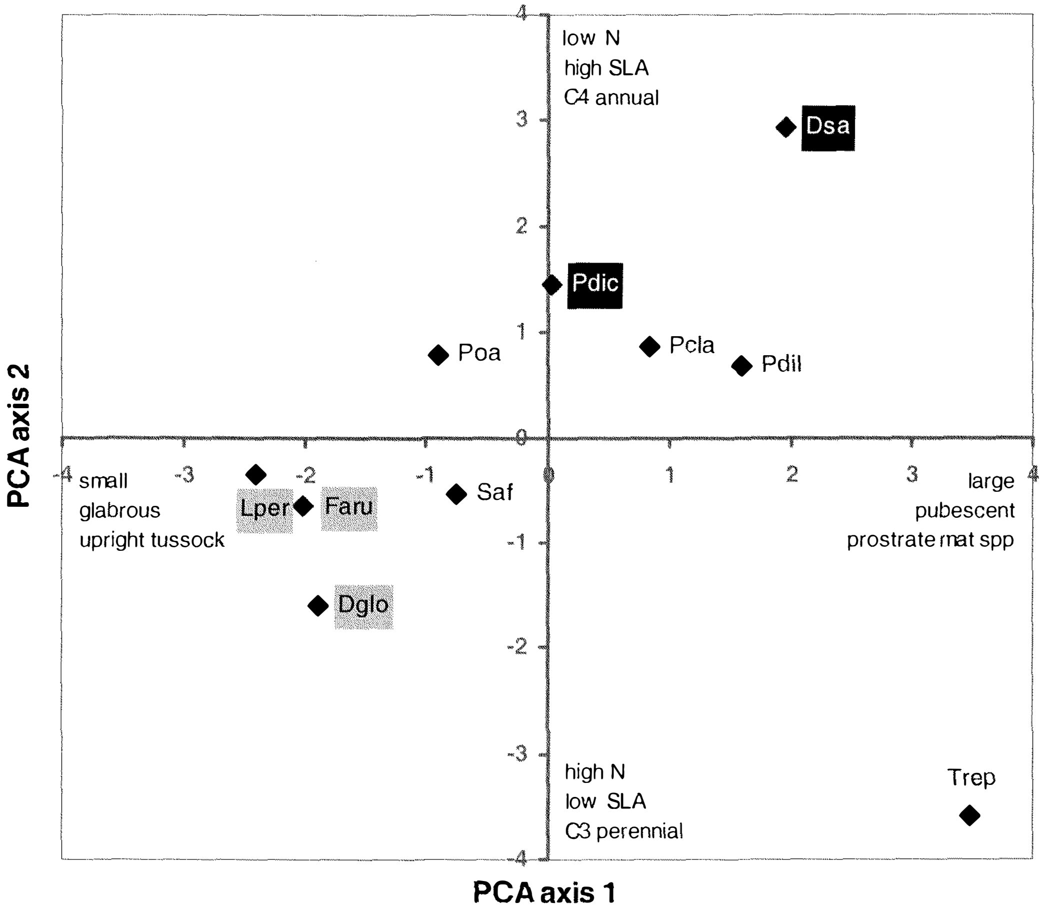

Fig. 5-1 Principal components analysis of the plant functional traits matrix. Characters highly associated with the separation between species shown on the axes. Species abbreviations: Dglo, *D. glomerata*; Dsa, *D. sanguinalis*; Faru, *F. arundinacea*; Lper, *L. perenne*; Pdic, *P. dichotomiflorum*; Pdil, *P. dilatatum*; Pcla, *P. clandestinum*; Poa, *P. annua*; Saf, *S. africanus*; Trep, *T. repens*. Functional type 1 (FT1) species shown as dark shaded labels, FT2 species shown as light shaded labels.

5.4.2 Growth of different species

5.4.2.1 Resident vegetation

The total biomass and composition response of each grassland community to the extreme climatic events are shown in Table 5-4. The impact of the extreme climatic events on the resident plants was fully examined in White *et al.* (2000). In summary, there were no significant differences between sites and treatments in total biomass except for lower total biomass in heated plots at the Manawatu site. The extreme heating event caused a large increase in the abundance of C_4 species.

5.4.2.2 Transplanted species within resident vegetation

The transplanted phytometer species in intact grassland in control plots differed in biomass in rank order (average of the three sites), *P. clandestinum* (7247 mg) > *D. sanguinalis* (5072 mg) > *P. dilatatum* (3893 mg) > *P. dichotomiflorum* (3730 mg) > *T. repens* (1038 mg) > *S. africanus* (809 mg) > *D. glomerata* (381 mg) > *F. arundinacea* (347 mg) > *L. perenne* (249 mg) (Table 5-5). The sites differed in the biomass achieved by all species except *S. africanus* ($P<0.05$ for site main effect). The biomass of *D. sanguinalis*, *P. dichotomiflorum*, *P. dilatatum* and *P. clandestinum* at the Bay of Plenty site was, on average, significantly greater than that attained at the Waikato site, which was significantly greater than that achieved at the Manawatu site. *Lolium perenne*, *F. arundinacea* and *D. glomerata* showed the opposite trend, with the greatest growth being attained at the Manawatu site compared to the Bay of Plenty and Waikato sites (Table 5-5). *Trifolium repens* biomass did not significantly differ between the Manawatu and Waikato sites but both were significantly greater than the Bay of Plenty site. These results agree with observations of current distributions of FT1 species (White *et al.* 2000). Sites where FT1 species are already abundant, promoted FT1 growth and suppressed the growth of the FT2 species. The opposite occurred where FT2 species are present but FT1 species are currently absent.

The heavy rainfall simulation had no effect on the growth of the transplanted plants, except for *T. repens*, which achieved significantly greater live biomass in the watered plots ($P<0.05$ for water main effect). All the C_3 grass species showed evidence of greater biomass in the watered plots but the differences were not significant (Table 5-5). Extreme heating had differing effects on growth of the transplanted plants.

Table 5-4 Community a) productivity (g m^{-2}) and b) composition (%) three weeks after treatment for all three sites and the major grassland constituents. Treatment abbreviations: con, control; +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered. FT = functional type.

		Manawatu				Bay of Plenty				Waikato				
a)		con	+H	+H+W	+W	con	+H	+H+W	+W	con	+H	+H+W	+W	LSD
Total live biomass		184	70	148	203	190	148	193	210	154	185	204	199	66
b)		con	+H	+H+W	+W	con	+H	+H+W	+W	con	+H	+H+W	+W	LSD
D. sanguinalis	FT1	0	0	0	0	27	24	28	38	30	73	59	53	28
L. perenne	FT2	44	65	63	53	27	35	27	21	36	6	9	27	20
P. dichotomiflorum	FT1	0	0	0	0	7	20	7	8	13	15	12	7	14
T. repens		26	25	16	24	12	5	6	3	3	1	0	1	12
Forbs		15	8	7	15	21	16	20	26	16	4	12	8	21
Other grasses		15	3	14	8	6	0	12	3	2	1	8	4	

Table 5-5 Intact grassland phytometer biomass (mg) three weeks after treatment. Treatment abbreviations: con, control; +H, heated (+52.5°C); +W, watered (100 mm); +H+W, heated and watered. FT = functional type. *, data not presented for *D. glomerata* (Bay of Plenty site) due to high number of dead or missing plants at treatment. **, data not presented for *P. dichotomiflorum* (Waikato site) due to high number of plants 'pulling' damaged or missing after grazing.

Species		Manawatu				Bay of Plenty				Waikato				
		con	+H	+H+W	+W	con	+H	+H+W	+W	con	+H	+H+W	+W	LSR
D. glomerata	FT2	339	123	440	477	*	*	*	*	438	28	15	557	8.22
D. sanguinalis	FT1	1348	3906	3807	2637	7411	8701	8174	10915	6456	5410	5883	4735	2.21
F. arundinacea	FT2	741	100	551	1022	121	56	56	188	179	3	2	348	5.63
L. perenne	FT2	403	322	384	646	152	6	86	99	193	31	30	395	7.69
P. dichotomiflorum	FT1	3016	2376	2524	2316	4444	4588	5749	4626	**	**	**	**	2.90
P. dilatatum		2006	1986	2943	1765	4463	5227	5682	6449	5210	3895	3379	3041	1.86
P. clandestinum		3684	3260	3089	4495	10637	14073	8116	13256	7420	5051	2945	12226	2.36
S. africanus		857	472	802	377	884	790	881	858	687	642	808	673	2.42
T. repens		774	583	911	1307	271	96	389	570	2071	144	537	1648	4.44

Species with C_3 photosynthesis were particularly sensitive, with all species displaying a significant reduction in growth ($P<0.01$ for heat main effect). Closer examination of the response of these species to heat revealed that the overall reductions in growth were largely due to significantly lower biomass in heated compared to non-heated plots at the Waikato site (Table 5-5; Waikato non-heated to heated means ratio > LSR for site by heat interaction for all C_3 species). This was particularly the case for *D. glomerata* and *F. arundinacea* (Table 5-5; $P<0.05$ for site by heat interaction effect).

The species with C_4 photosynthesis were more tolerant of the heating treatment. *Digitaria sanguinalis*, *P. dichotomiflorum*, *P. dilatatum*, and *S. africanus* all had non-significant main effects for heat treatments. Only *P. clandestinum* had significantly lower biomass in the heated plots ($P<0.05$ for heat main effect). *Digitaria sanguinalis* was particularly tolerant of the heating treatment at the Manawatu site, as biomass was greater in heated than non-heated plots (Table 5-5; Manawatu heated to non-heated means ratio > LSR for site by heat interaction for *D. sanguinalis*).

The growth of FT1 and FT2 after the extreme heating event agree with the predictions based on their plant functional traits. FT1 species, especially *D. sanguinalis*, were promoted by an extreme heating event within the grassland community that was most sensitive to the extreme heat in terms of biomass production (White *et al.* 2000). FT2 species were disadvantaged by the extreme heating event. Suppression of these species was greatest in the grassland that was most sensitive to shifting species abundances after an extreme heating event (White *et al.* 2000).

5.4.3 Community invasibility limited by competition

The intensity of competition between the phytometers and the established vegetation was examined by the magnitude of the difference between growth of phytometers inserted into intact and cleared grassland areas (Table 5-6). It was found that FT1 and the other C_4 phytometers had a consistently greater competitive indices within the exclusively C_3 grassland compared to the C_3/C_4 composite grasslands (Fig. 5-2 and Table 5-6; $P<0.01$ for site main effect for competition indices for all C_4 species). In the absence of competition (cleared grassland), there was no difference in growth achieved by *D. sanguinalis*, *P. dichotomiflorum*, *P. dilatatum* and *P. clandestinum* between sites. However, in the presence of competition (intact grassland) all of these species showed significantly less growth at the Manawatu site.

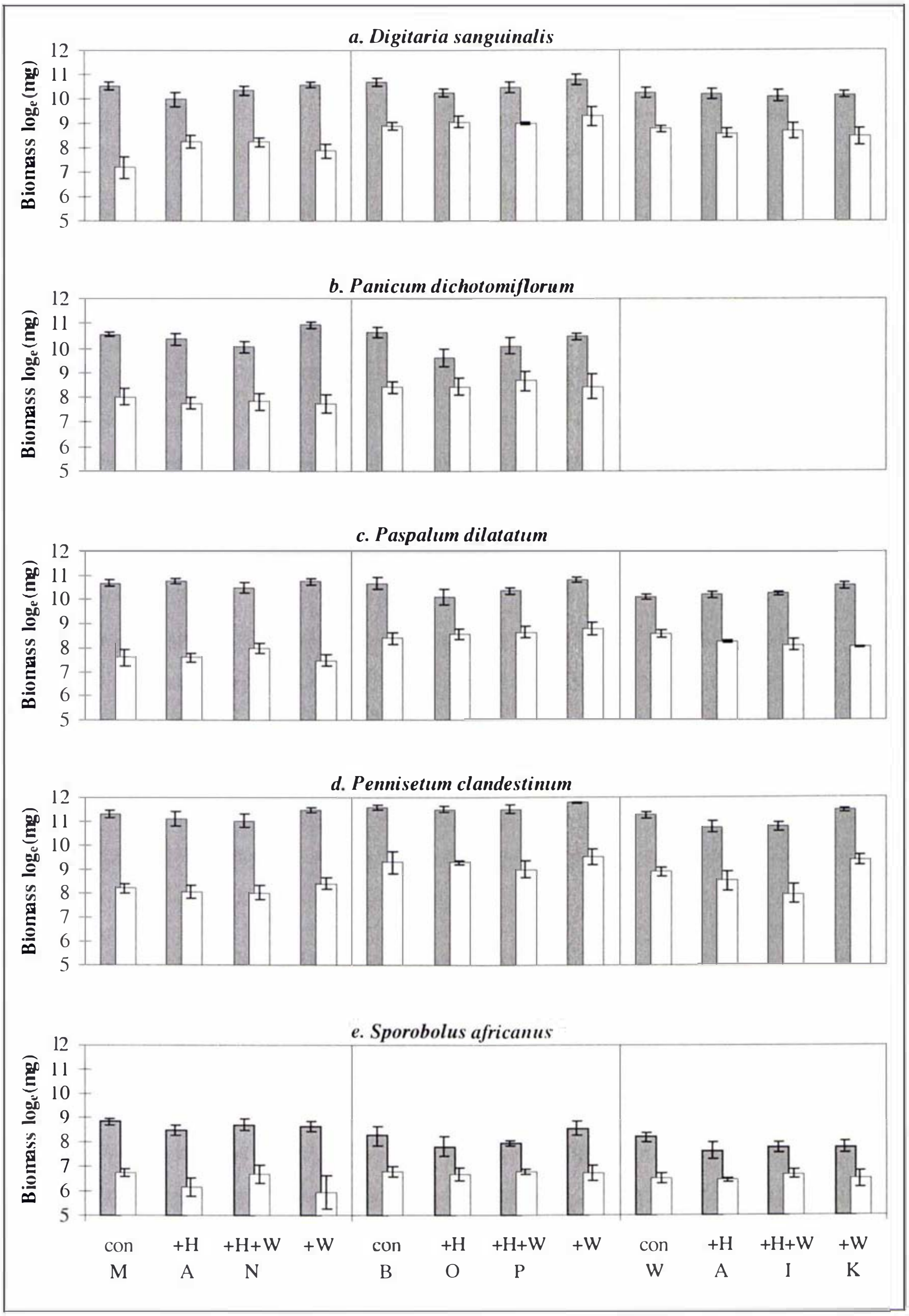

Fig. 5-2 Biomass ($\log_e$(mg) plant^{-1}) of intact (light shaded columns) and cleared (dark shaded columns) grassland phytometers three weeks after treatment: C_4 species. For treatment abbreviations see Table 5-4. Site abbreviations: B O P, Bay of Plenty; M A N, Manawatu; W A I K, Waikato. Error bars represent the standard error of each mean.

All the C_3 species showed greater cleared and intact grassland performance at the Manawatu site than the Bay of Plenty or Waikato sites (Fig. 5-3) but no consistent differences in the size of the competitive effect between sites (Table 5-6).

In native Minnesota grasslands, Tilman (1997) found that the addition of seed changed local species abundances and increased species richness, emphasising the importance of colonisation limitation rather than competition limitation to invasibility of plant communities. The absence of FT1 propagules in the Manawatu soil seed bank (White *et al.* 2000) means that invasion is colonisation limited at the local scale. However, on a regional scale there is no recruitment limitation within the Manawatu as FT1 species exist in high numbers in open habitats (e.g. road sides, tilled soil) immediately adjacent to grasslands. In addition, a recent experiment based on the same grassland found that over-coming recruitment limitation by adding the seed of the FT1 species, *D. sanguinalis*, did not promote invasion into undisturbed vegetation (White *et al.* 1997). Rather, *D. sanguinalis* seedlings were only recorded in highly disturbed areas where the competing vegetation had been severely damaged or completely removed. The consistently greater competitive suppression of the C_4 species at the Manawatu site in this experiment indicates that competition is highly important in limiting the invasibility of C_3 grasslands by C_4 grasses, in particular, by FT1 species.

5.4.4 Influence of extreme climatic events on competition and community invasibility

Extreme climatic events that remove or suppress this competitive limitation are, therefore, likely to promote invasion. For the majority of phytometer species, the extreme rainfall simulation had no effect on competition. The only species to show significant differences between grassland intact and cleared areas between watered and non-watered plots were the FT2 species, *D. glomerata*, *L. perenne* and *F. arundinacea.* All showed significantly lower competitive indices in the watered plots (Table 5-6; P<0.01 for water main effect).

The extreme heating event had a consistently greater effect on competition. The difference between intact and cleared grassland performance was significantly reduced for *D. sanguinalis*, *F. arundinacea*, *P. dilatatum* and *P. dichotomiflorum* (Table 5-6; P<0.05 for heat main effect). *Dactylis glomerata*, *S. africanus* and *T. repens* also showed strong evidence of a reduced difference (P=0.082, 0.071 and 0.084, respectively).

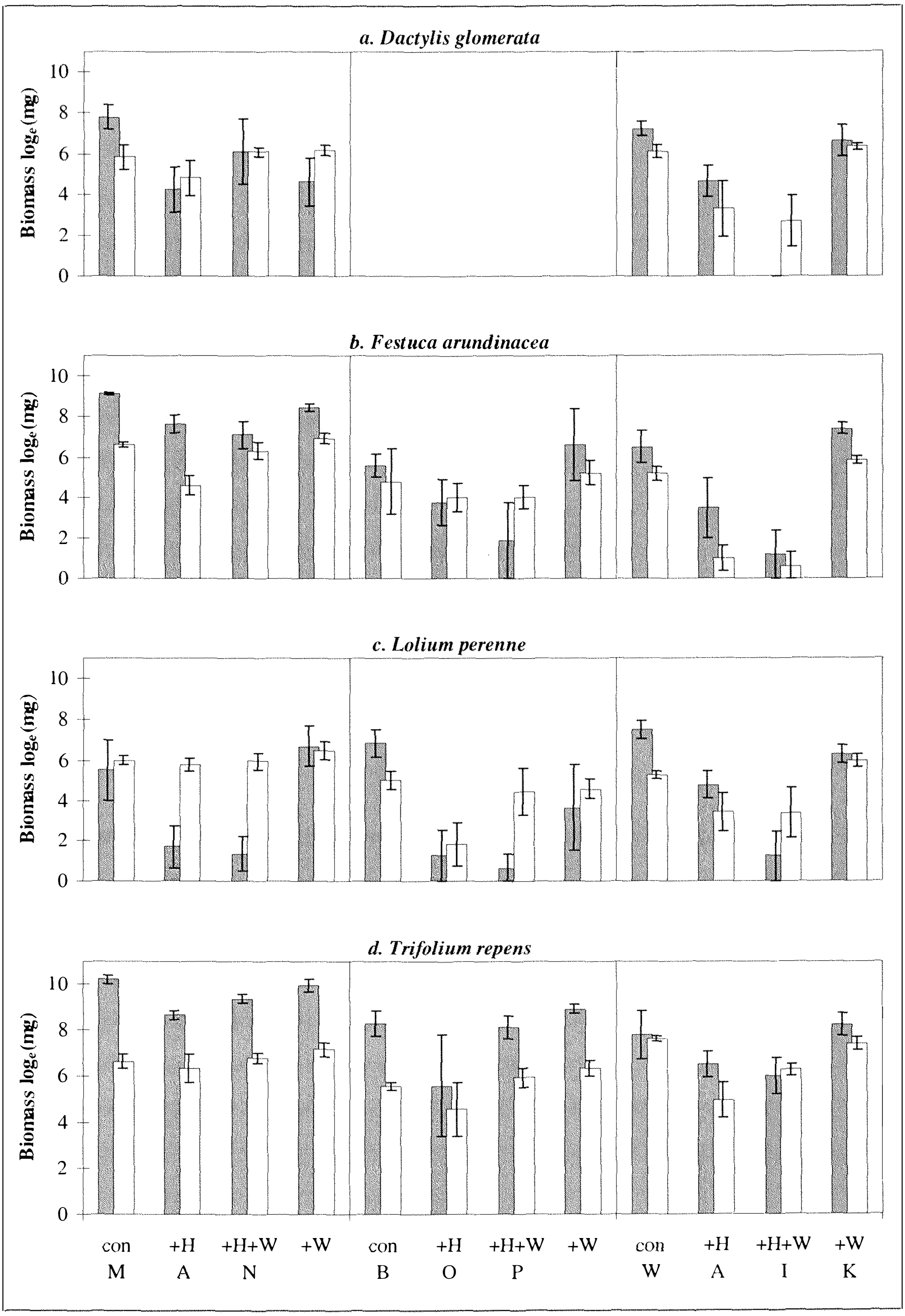

Fig. 5-3 Biomass ($\log_e$(mg) plant^{-1}) of intact (light shaded columns) and cleared (dark shaded columns) grassland phytometers three weeks after treatment: C_3 species. For treatment abbreviations see Table 5-4. Site abbreviations: B O P, Bay of Plenty; M A N, Manawatu; W A I K, Waikato. Error bars represent the standard error of each mean.

Table 5-6 Competition intensity index ($\log_e$(mg)) for transplanted phytometers. Competition indices were calculated as the average of the differences between the average logarithm transformed biomass of the cleared grassland phytometers and logarithm transformed biomass of the intact grassland phytometer for each replicate (Equation 5-1). A greater competitive index indicated a greater difference between cleared and intact half performance reflecting greater competition intensity. A negative competition index indicates that intact grassland biomass was greater than cleared grassland biomass. See Table 5-4 for descriptions and abbreviations.

Species		**Manawatu**				**Bay of Plenty**				**Waikato**				
		con	+H	+H+W	+W	con	+H	+H+W	+W	con	+H	+H+W	+W	LSD
D. glomerata	FT2	1.93	-0.55	0.02	-1.54	*	*	*	*	1.11	1.35	-2.72	0.30	2.11
D. sanguinalis	FT1	3.32	1.71	2.11	2.71	1.78	1.17	1.50	1.49	1.49	1.61	1.44	1.71	0.79
F. arundinacea	FT2	2.51	3.00	0.76	1.40	0.88	-0.25	-2.14	1.41	1.33	2.49	0.53	1.61	1.73
L. perenne	FT2	-0.42	-4.09	-4.60	0.21	1.83	-0.68	-3.80	-0.95	2.30	1.36	-2.15	0.30	2.04
P. dichotomiflorum	FT1	2.50	2.61	2.23	3.19	2.26	1.17	1.45	2.03	**	**	**	**	1.07
P. dilatatum		3.08	3.17	2.49	3.28	2.27	1.59	1.74	2.06	1.58	1.96	2.14	2.56	0.63
P. clandestinum		3.08	3.01	2.97	3.05	2.30	1.93	2.47	2.27	2.32	2.22	2.77	2.05	0.86
S. africanus		2.03	2.32	2.02	2.69	1.46	1.14	1.16	1.78	1.65	1.19	1.09	1.29	0.89
T. repens		3.56	2.29	2.55	2.77	2.63	1.03	2.15	2.57	0.16	1.55	-0.12	0.96	1.49

For *L. perenne* and *D. glomerata* the heating treatment was particularly deleterious, with intact grassland biomass being greater than cleared grassland biomass, resulting in negative competition indices. It would appear that the phytometers in the intact half were afforded protection from heat damage by neighbouring vegetation, that is, an insulating effect.

The results indicate that the extreme heating event reduced the competitive ability of the resident vegetation by physical disturbance (Keddy 1989; Campbell & Grime 1992; Wilson & Tilman 1993). Accelerated tissue senescence caused by the heat stress leads to reduced vegetation density and reduced competition for light.

The Manawatu grassland was comprised solely of plants with C_3 photosynthesis and was damaged considerably by the extreme heating event. In contrast, the presence of C_4 species within the Bay of Plenty and Waikato grasslands buffered community productivity (White *et al.* 2000). Therefore, for those phytometer species that are heat stress tolerant, the competitive effect (Table 5-6) would have been expected to be reduced by the heating treatment to a greater extent at the Manawatu compared to the Bay of Plenty and Waikato sites.

Only the FT1 species, *D. sanguinalis*, showed a proportionally greater reduction in competition index at the Manawatu site ($P<0.05$ for site by heat interaction effect). *Digitaria sanguinalis* growth at the Manawatu site was highly suppressed by competition within the control plot vegetation (Fig. 5-2). However, the disturbance caused by the heating event alleviated the competitive dominance of the resident vegetation, resulting in greater growth. This *competitive release* of stress tolerant species, such as *D. sanguinalis*, provides an explanation for low species density but high community production stability after an extreme climatic perturbation (Tilman 1996; White *et al.* 2000).

The clear separation of competitive responses within the C_4 species agrees with the predictions that the fast growing, annual species (FT1) would 1) be the most advantaged by an extreme heating event and 2) be the most likely to invade C_3 grasslands. In these C_3 grasslands, where the propagules of the invading FT1 were previously absent, short-term growth benefits are likely to give rise to a long-term source for future invasions as a result of greater soil seed loading (Noble 1989; Rejmánek 1995; Rejmánek & Richardson 1996). Loading of the soil seed bank with FT1 seeds will act as a dispersal mechanism through time until community competitive ability is again reduced by recurring extreme climatic events.

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6 Discussion

CONTENTS

6.1 Focus on invasion

As identified by Crawley (1997, p 618), "the study of invasions requires an approach involving the plant species, the abiotic and biotic environments of the target habitat, the disturbance regime, and the interactions between these and the pattern of temporal variability....". This study focused on specific vegetation processes associated with the impact of predicted future changes in climatic variability on the invasion of grazed productive grassland communities of New Zealand. The primary objective was to identify species or groups of species that would be most advantaged by an increased incidence of extreme climatic events. Experimentation focused on understanding the mechanistic basis of response to extreme climatic events by quantifying plant functional traits associated with key life-cycle stages (Fig. 1-3).

Plant functional traits were identified by two screening approaches. Functional traits were quantified by 'laboratory screening', where differences between species were identified against standardised laboratory conditions (Keddy 1992; Grime *et al.* 1997). The second method used was 'soft-trait screening' (Diaz & Cabido 1997; Hodgson *et al.* 1999), where easily-measured but informative functional traits were determined on mature plants growing in the field.

From the regenerative and established phase screening experiments it was predicted that:

- of the species regenerating within a grassland vegetation gap, species characterised by C_3 photosynthesis, large seed size and/or short life-history would be the most advantaged by short pulses of warm temperatures and have the greatest ability to tolerate desiccation as seedlings immediately after germination (Chapter Two),
- in the established phase, the competitive ability of the major temperate species, *Lolium perenne* was as great, or greater than the C_4 species, under equally favourable environmental conditions (Chapter Three). Accordingly, under such climatic conditions, C_4 species would be unlikely to actively displace *L. perenne* from these temperate grassland communities, and
- in the established phase, the species to be most advantaged by certain extreme climatic events (especially an extreme heating event), were the FT1 species, *Digitaria sanguinalis* and *Panicum dichotomiflorum* (Chapters Three and Five). FT1 species were characterised by C_4 photosynthesis, fast growth and short life-history. On the other hand, FT2 species, characterised by C_3 photosynthesis, slower

growth and longer life-history, were predicted to be disadvantaged by extreme climatic events.

6.2 Habitat and theoretical species distribution

These results can be analysed in relation to broad classifications of vegetation using plant strategy theory (Grime 1977; Grime 1979). Without the impact of disturbance, strategy theory suggests that highly competitive plant species should dominate productive habitats. Fast-growing, morphologically plastic plants that are able to grow tall, spread laterally and expand through space and time by vegetative organs should dominate. However, disturbance modifies community structure by constraining the intensity of competition (Keddy 1989). Competitive–ruderal characteristics, such as a greater emphasis on reproductive growth and seed production, are predicted to confer an advantage within productive but moderately-disturbed habitats (Grime 1979; Grime *et al.* 1988).

In agreement with strategy theory, competitive-ruderals were a dominant component of the productive but moderately-disturbed grassland communities of this study. The most common competitive-ruderal species were *L. perenne* and *Trifolium repens* (Grime *et al.* 1988). If disturbance is severe enough, strategy theory predicts that the establishment of ruderal species will also be favoured. That is, under productive but highly-disturbed conditions species with the characteristics of short life-history, high seedling growth rate, rapid curtailment of vegetative growth leading to prolific flowering and seed production, will be particularly advantaged. Ruderal species commonly found in the grasslands of this study, include *Poa annua* and *D. sanguinalis*.

The impact of disturbance on vegetation processes and plant community structure has been traditionally investigated with respect to biomass removal by grazing (Belsky 1992; Glenn & Collins 1992), or by artificial means at relatively constant spatial and temporal scales (Campbell & Grime 1992; Turkington *et al.* 1993; Wilson & Tilman 1993; White *et al.* 1997). This study concentrated on the impact of the more stochastic disturbances and stresses associated with natural catastrophes such as floods, extreme heat and drought.

One of the main mechanisms through which disturbance operates to modify community structure is by creating vegetation gaps which act as focal points for regeneration from seed (Grubb 1977). From first principles outlined by plant strategy theory, one would predict that the species which are the best adapted to respond to such temporally and spatially variable opportunities for establishment, as a result of disturbance created by extreme climatic events, are species with ruderal characteristics coupled to regeneration from a persistent seed-bank. However, once established, species that possess attributes for tolerance of the stresses associated with some extreme abiotic conditions, for example drought or heat, would be advantaged relative to less tolerant species.

6.3 Testing the predictions

One major limitation to predicting the impact of global climate change on plant communities on the basis of functional traits, is that there are limited data from actual plant community responses with which to validate predictions. Within this study and others (Nijs *et al.* 1996; Luscher *et al.* 1998; Press *et al.* 1998; Price & Waser 1998), innovative experimental techniques and apparatus have attempted to overcome this limitation by simulating climate change over plant communities growing *in situ.*

6.3.1 Regenerative phase

Traits that determine response to temperature and water conditions were considered important in determining the impact of climate change on the recruitment of new plants from seed. A total of 26 grassland species were screened for their dependency on a warm temperature pulse for germination and on their ability to tolerate desiccation immediately after germination. Large differences were observed between species and were used to generate predictions on species invasiveness (Chapter Two).

Large scale manipulations of seed numbers, soil temperature and moisture within actual grassland communities would be required to test these predictions. This was not an objective of this study but would be a productive direction for future research. However, the traits measured in Chapter Two are not only likely to confer an establishment advantage under future climates but also under current environmental conditions.

The ability to successfully compete for establishment sites has been positively associated with seed size (Rees & Westoby 1997; Turnbull *et al.* 1999). The mechanism that underpins superior establishment ability most likely results from the positive association between seed size and an ability to tolerate a variety of stresses and disturbances experienced by emerging seedlings, such as shade (Leishman & Westoby 1994a; Saverimuttu & Westoby 1996), competition (Gross & Werner 1982;

McConnaughay & Bazzaz 1987), defoliation (Armstrong & Westoby 1993), and desiccation (Leishman & Westoby 1994b).

This study also identified a positive relationship between seed size and predicted invasiveness (based on functional traits identified by laboratory screening). Species with C_3 photosynthesis tended to have larger seeds and superior predicted invasiveness, whereas the C_4 species tended to have smaller seeds and inferior predicted invasiveness (Chapter Two). Theory suggests that without a colonisation limitation, species that are better adapted to establish should restrict the establishment of others (Pacala & Rees 1998; Turnbull *et al.* 1999). In the context of C_3/C_4 composite grasslands, C_3 species should dominate establishment microsites and restrict recruitment of C_4 seedlings, through their superior invasiveness. However, in reality, C_4 species are not excluded from establishing within New Zealand grasslands.

It is contended that the most important factor enabling C_4 types to establish and co-exist with C_3 types within our productive grasslands is the temporal displacement of C_3 and C_4 regeneration. The above-ground C_3 dominants, such as *L. perenne*, *Dactylis glomerata* and *T. repens*, are perennial species, that regenerate largely by vegetative organs. Seeds shed in spring/summer exhibit minimal 'after-ripening' dormancy, readily germinate in autumn and, with the exception of *T. repens*, fail to persist in the soil (Champness & Morris 1948; Harris 1961; Thompson & Grime 1979; L'Huillier & Aislabie 1988; Hume & Barker 1991). In contrast, large warm season increases in C_4 abundance originate from spring germination of seed contained within large persistent seed banks (Egley & Chandler 1978; Burnside *et al.* 1981; Baars *et al.* 1991; Wardle *et al.* 1994; Bell 1996; White *et al.* 2000). C_4 species avoid having to compete with C_3 species for regeneration sites by germinating at a time of year when the abundance of C_3 juveniles is low. In the words of Turnbull *et al.* (1999), the C_4 species "win by forfeit".

Given that C_3 and C_4 species regenerate largely at different times, *within* C_3 and C_4 type differences in predicted invasiveness are more important than differences *between* types to the understanding of C_3/C_4 grassland community dynamics. Therefore, do the predictions of invasiveness derived from the laboratory screening experiments in Chapter Two agree with current C_4 species invasions within productive but moderately disturbed grassland habitats? The most abundant C_4 species identified within this (Chapter Four) and other studies (Baars *et al.* 1991; Bell & Keene 1996), are the annual species *Digitaria sanguinalis* and *Panicum dichotomiflorum*. The widespread distribution of *Panicum dichotomiflorum* agrees with the predictions of its potential invasiveness. Other annual species identified as potentially invasive, such as *Setaria viridis* and *Echinochloa crus-galli*, have also been noted for their contribution to productive grasslands in certain regions of New Zealand (Bell & Keene 1996).

While the results compared favourably with the distributions of some species, *Digitaria sanguinalis*, the most ubiquitous species, was not predicted to be particularly invasive. This would suggest that other traits are possibly contributing to the invasiveness of *D. sanguinalis*. A large flowering effort and rapid maturation of juveniles, attributes considered important by Noble (1989) and Grime (1979) to a species' potential for invasion, are both common to *D. sanguinalis* and *P. dichotomiflorum*. Alternatively, the higher level interactions between traits and environmental conditions (abiotic and biotic) that determine invasion success, as recognised by Crawley (1997), may be determining the success of *D. sanguinalis*. As examined in the following section, competition is one such interaction.

6.3.2 Established phase

Predictions of the impact of extreme climatic events on competition and competitive ability determined in a laboratory screening experiment (Chapter Three) were tested by simulating extreme climatic events in the field (Chapters Four and Five). Close agreement was found between the responses of species in artificial compared to actual grassland communities and with predictions based on theory.

Under temperature and water conditions that were considered equally favourable for C_3 and C_4 growth (MA pots), *Lolium perenne* was as, or more, competitive than all the C_4 species when grown as artificial two-species mixtures. It was therefore predicted that, under such conditions, C_4 species would be unlikely to actively displace *L. perenne* from grassland communities. The results from the field experiment agree with this prediction, competition from C_3 species (predominantly *L. perenne*) was a major factor limiting the invasion of C_4 species into exclusively C_3 grasslands.

Sophisticated controlled environment facilities and artificial species mixtures resulted in few restrictions to the type, intensity and combination of extreme climatic events able to be created in the glasshouse pot experiment. However, time and resources constrained the range of treatments able to be applied in the field. Only extreme heating and rainfall events were simulated over actual grassland communities, their selection based on probability of occurrence during the warm season and potential to alter community composition (Fig. 1-1 and section 1.3.1, page 4).

The laboratory competition experiment identified that extreme temperature events impact more on competition within C_3/C_4 communities than extreme water events. In agreement, a single extreme heating event consistently reduced the intensity of competition between the resident vegetation and the transplanted C_4 species whereas a single extreme rainfall event had little effect on competition.

Predictions were also made on how community structure may change by predicting which species were most likely to be advantaged by the extreme climatic events. Both the soft-trait screening and glasshouse pot experiments identified the fast-growing C_4 annual species, *D. sanguinalis* and *P. dichotomiflorum*, the most likely to be advantaged by an extreme heating event. The response of these species, especially *D. sanguinalis*, growing as phytometers within the exclusively C_3 community agreed with these predictions.

There was also consistency between the field responses and predictions based on strategy theory. The species predicted to be the most advantaged by extreme climatic events were those which (a) established from a persistent seed-bank and were able to dominate vegetation gaps through rapid seedling growth and/or (b) possessed traits for tolerance of the extreme event as adults. At the site which showed the largest shift in community composition after an extreme heating event (Waikato site), the resident species most advantaged were *P. dichotomiflorum* and, in particular, *D. sanguinalis*. While not specifically measured, it was assumed that this increase in abundance resulted from an increase in the number of plants establishing from seed, as these species have limited ability to expand vegetatively. These species were also characterised by being heat stress tolerant as a result of their C_4 photosynthesis.

This study sought to determine the impact of extreme climatic events on the ecology of productive grasslands of New Zealand at key life-cycle stages (Fig. 1-3). Large variation in species responses to extreme but transient water and temperature events highlighted the potential impact of short-term fluctuations in climate on these communities.

The functional traits identified at the species level were critical to determining community response to the extreme climatic events. In particular, species with C_4 photosynthesis, fast growth and short life-histories will be most advantaged by an extreme heating event. In the face of increasing climatic variability and incidence of such extreme events, the stability of community productivity will be greater in grasslands where these functional types are present.

The need for a greater understanding of the role of short-term but extreme fluctuations in climate will only increase in the future. Numerous aspects of the impact of extreme climatic events on the invasion of productive grassland communities remain largely unknown. For example, the impact of extreme climatic events on seed production, viability and dispersal, seed and plant predators/pathogens are aspects that require greater understanding. The functional approach of this study provides a positive framework to furthering that understanding.

6.4 Wider implications

The high sensitivity of community composition to simulated extreme climatic events at the Waikato site (section 4.4.4.3, page 103), agrees with the relationship observed between actual C_4 abundance, the prevailing climatic patterns and their associated extreme climatic events (section 1.3.2, page 5). The lack of a similar response at the Bay of Plenty site was attributed to the unusually dry conditions experienced at that time. In spite of this, the close agreement between Waikato experimental results and actual observed community responses to climate confirms:

- the close association between climate and community composition, and that indices, such as the Southern Oscillation Index, provide a useful means of forecasting shifts in composition,
- that the research approach employed in this study is positive step forward, not only in accurately predicting shifts in species distributions in relation to climate, but also understanding the mechanisms of change, and
- that understanding these mechanisms will help in determining what pre-emptive management actions may be taken to combat future invasions. For example, the species to be most advantaged by extreme heating and rainfall events established from seed. Reducing grazing intensity to maintain greater cover will restrict establishment.

Scaling-up to the ecosystem and economic repercussions of community level changes, is critical to understanding the wider implications of changes in the temporal variability of climate. Functional differences identified by screening approaches, form a basis to achieving this objective (Diaz & Cabido 1997; Wardle *et al.* 1998). It is assumed that the importance of a particular species to an ecosystem depends largely on their abundance, and that ecosystem properties are largely determined by the key functional traits of the dominant species (Schulze & Mooney 1993; Grime 1997).

A shift in the abundance of FT1 and FT2 has important ecosystem and economic implications because of basic differences in tissue quality associated with C_3 and C_4 photosynthesis. Specifically, C_4 species have higher nitrogen-use efficiency than C_3 species, and therefore, are characterised by tissues with higher carbon to nitrogen (C:N) ratios than C_3 species. C_4 tissue also has higher fibre content than C_3 tissue, lowering its palatability.

The logic of carbon and nitrogen interactions between plants and soil, as outlined in a simple ecosystem model by Tateno & Chapin (1997), can be used to address the impact of increased C_4 abundance. High N-use efficient plants (in our case, C_4 species) contribute high C:N litter to soil organic matter, which results in low N mineralisation rates. Alternatively, slower-growing, less N-use efficient plants (C_3 species) contribute higher quality litter (low C:N ratio) to soil organic matter, which results in greater N available for growth through greater mineralisation. Accordingly, without losses or additions of nitrogen to a plant-soil system, differences in plant growth from communities with species differing N-use efficiency, are predicted to diminish over time (Tateno & Chapin 1997).

Even though this model this highly simplistic, it agrees with the long-term field study of Wedin & Tilman (1996), who found that soil NO_3^- concentrations were significantly lower in fields dominated by a C_4 grass species than C_3 grass dominated fields. As the C:N ratio of community biomass increased above 30 (due to increased C_4 abundance), the immobilisation sink for mineral N provided by dead organic matter increased, soil NO_3^- decreased and a greater amount of N was sequestered in the system.

A reduction of available N is only likely to be manifested over long time-scales due to the buffering effect of low C:N organic matter already present in the system. Certainly, in this study (Chapter Four), and in that of Wardle *et al.* (1999), no effect was found of C_3 and C_4 functional type abundance on soil properties, such as NO_3^- concentration, after one and three years, respectively.

Nitrogen fixation by *Rhizobium* bacteria is an important factor adding N to plant-soil systems. *Rhizobia* form a symbiotic association with *Trifolium repens*, and contribute large amounts of N to managed plant-soil systems. Amounts of N fixed by Rhizobia range from 15 - 680 $kgNHa^{-1}yr^{-1}$, depending on grassland composition, fertility, temperature and water availability (Crush 1987). However, the contribution to soil N from nitrogen fixation is likely to decrease, as the results of this study indicate that the abundance of *T. repens* will decrease with an increased incidence of extreme climatic events.

Ultimately, an increased abundance of C_4 species has the potential to render a greater proportion of N unavailable to plants, which is likely to prompt greater extrinsic additions of nitrogen to grasslands. The costs associated with this are not only economic, but also environmental. Adding N in readily-usable forms inevitability leads to greater NO_3^- leaching, and higher NO_3^- concentrations in ground water (Ledgard *et al.* 1998; Ledgard *et al.* 1999; Silva *et al.* 1999).

An important aspect of the wider implications of grassland compositional change is the relationship between herbivores and the functional traits of the dominant species. Invertebrate and vertebrate herbivores will selectively consume plant material that is more palatable (Hodgson *et al.* 1994; Wardle *et al.* 1998). In the case of managed FT1/FT2 composite grasslands, FT1 species are less palatable than FT2 species due to their higher fibre content (Jackson *et al.* 1996). Accordingly, this will further shift the balance of species toward FT1.

Selective browsing by herbivores is also likely to cause an additional feedback on below-ground processes. Plants that herbivores avoid, also produce litter of inferior quality, because both digestion and decomposition involve microbial breakdown of tissue (Chesson 1997). This is likely to lead to further retardation of nutrient cycling between plants and soil (Pastor *et al.* 1988; Pastor *et al.* 1993), reducing community productivity.

The relationship between the functional traits of the dominant plant species and large herbivores (e.g. domestic sheep and cattle) also has important consequences. The lower palatability, lower soluble carbohydrate and protein contents of C_4 tissue decreases the nutritive value of forage (Jackson *et al.* 1996), and consequently, the production of animal products (milk, meat and fibre) from it (Betteridge 1979; Woods *et al.* 1996). For a country, such as New Zealand, where 25% of total export earning are derived from grassland-based dairy and meat production (Zwartz 1998), increases in FT1 abundance are likely to have a large impact on the wealth of individual producers, and also on entire economies.

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7 Appendix

7.1 Published Abstract

Abstract of the presentation made at the **42nd Annual Symposium of the International Association for Vegetation Science, Bilbao, July 26-30 1999.**

Sensitivity of three grassland communities to simulated extreme temperature and rainfall events.

Three grassland communities with differing climates and proportions of C_3 and C_4 species were subject to extreme heating and rainfall events. A novel experimental technique using portable computer controlled chambers simulated the extreme heating events.

The productive, moist C_3/C_4 community was the most sensitive to the extreme events in terms of community composition compared with a dry C_3/C_4 community or exclusively C_3 community. An extreme heating event caused the greatest change to plant community species abundance by favouring the expansion of C_4 species relative to C_3 species, shifting C_4 species abundance from 43% up to 84% at the productive, moist site. In the absence of C_4 species the total community productivity was reduced by heating by over 60%.

Species functional identity, as opposed to community biodiversity, was the most effective explanation for the observed shifts in biomass production. The presence of C_4 species would buffer plant community productivity against an increased frequency of extreme heating events associated with future global climate change.