Ecology of subtropical grasses in temperate pastures: an overview

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Abstract

Subtropical grasses can be a significant component of northern North Island pastures. Several annual and perennial types with different functional characteristics are widely established, allowing a range of different climatic, soil and moisture situations to be colonised. Many of the species have persistent seed banks or vegetative propagation facilitating long-term persistence. Biochemical types associated with moist conditions arc most common but types associated with arid conditions are also represented. Abundant rainfall at temperatures above 25°C, and factors which reduce temperate grass productivity (lowered soil fertility and winter/spring grazing damage) appear to favour higher proportions of both annual and perennial subtropical grasses such as summer grass and paspalum. Grazing pressure and timing, and level of fertiliser inputs appear important for species such as ratstail and carpet grass in less productive sites; The nature of competitive interactions between subtropical (C_4) species and temperate (C_3) species is poorly understood and invertebrate herbivory can be important in altering the balance between these species. An analysis of present subtropical grass species distributions in northern districts of New Zealand indicates that knowledge of the underlying species biological characteristics is useful in predicting subtropical grass abundance. To predict likely problem years and to develop management strategies to minimise problems, a better understanding is needed of the effects of climate on subtropical grass abundance in temperate pastures and competitive interactions. There may be scope for developing improved varieties for dry areas.

Keywords: C,, C,, climate, competition, ecology, grazing, pasture, subtropical grasses, temperate

Introduction

Subtropical grasses can constitute a significant component of summer pastures in northern areas of New Zealand. If managed correctly, some of these grasses such as paspalum (*Paspalum dilatatum)* and kikuyu (*Pennisetum clandestinum)* have the potential to make a useful contribution to forage supply. However, in certain years, particular combinations of climatic conditions, grazing management and fertiliser use can dramatically increase the proportions of these grasses. Such increases are of concern to farmers and dairy companies because of the poorer feed quality of these grasses and the risk of suppression and loss of desirable ryegrass and white clover (Simmonds 1990). Several species of subtropical grasses, differing in ecology, life-span, and agronomic value, are now present in New Zealand pastures.

Some common species were introduced to New Zealand last century (e.g., paspalum was recorded in the Auckland region in 1896 (Cheeseman 1906)) while others arrived quite recently and have spread rapidly (e.g., smooth witchgrass appears to have arrived accidentally on American aircraft during World War II (Healy 1946; Edgar & Shand 1987; Miles *et al.* 1991)). Many are now considered to be volunteer weed species which are regenerated from persistent annual seeding populations, seedbanks or vegetative material.

A sound knowledge of species ecology is needed to identify management solutions for maximising the potential benefit of subtropical grasses and minimising the problems they cause in pastures. In this paper we provide a brief overview of the characteristics and ecology of different subtropical grass species in temperate pastures, and test this understanding using recent survey data. The information is used to assess current understanding of subtropical grass biology.

Subtropical grass characteristics

Background

Subtropical grasses evolved in habitats different from those of the temperate species used in our pastures and therefore have several different characteristics. Most have a special photosynthetic pathway (termed the C_4 pathway) which is distinctly different from the C_3 photosynthetic pathway common in the temperate grasses and clovers.

The C_4 photosynthetic pathway is a concentrating mechanism to pump CO_2 from outer to inner regions of a leaf so as to maintain higher internal CO_2 pressures for incorporating carbon into growing tissues (Pearcy & Ehleringer 1984). This allows potentially higher photosynthetic efficiency than C_3 species at higher temperatures and also potentially higher water use efficiency (the ratio of photosynthesis to transpiration) and nitrogen use efficiency, because of the smaller amount of protein needed to fix CO_2. The C_4 species can also grow very rapidly in high light environments. Most grass genera are consistently either C_3 or C_4 but in four genera (including *Panicum*) both C_3 and C_4 species, as well as C_3-C_4 intermediates, are known to exist (Hattersley & Watson 1992). Different biochemical types (NADP-ME, NAD-ME and PCK types) and leaf structural variants also exist within the C_4-type species, giving a total of 10–13 different C_4 types (Hattersley 1992).

The C_4 photosynthetic pathway does not in itself explain the complete ecology of these species. Numerous other biochemical, physiological and morphological adaptations accompany the C_4 pathway, so that the subtropical (C_4) species tend to have a higher temperature optimum for growth, greater tolerance of high temperatures, higher water use efficiency, higher nitrogen use efficiency, and a greater sensitivity to chilling temperatures and frost, relative to temperate (C_3) species. Individual species can differ in these attributes.

Characteristics of some common types in New Zealand pastures

Several of the common perennial subtropical grasses in New Zealand (e.g., paspalum, kikuyu) can regenerate both from vegetative expansion and/or from persistent seed banks in soil and have moderate tolerance of chilling, frost and drought (Table 1). Common annual species generally also regenerate from persistent seeds in soil (as opposed to a strictly seasonal seed bank) and this may explain their widespread success. Seven of the ten species listed in Table 1 are NADP-ME or PCK types, which are commonly associated with less arid conditions (Hattersley 1992). Indian doab, crowfoot grass and smooth witchgrass are examples of the NAD-ME biochemical types commonly associated with drier conditions. A variety of morphological and regenerative types are evident in Table 1. The importance of these adaptations in determining growth, survival and pasture community structure is considered further in the following sections.

Factors controlling species abundances

Climate

Temperature correlates very highly with the percentage of C_4 grasses in different areas of the world. Higher water use efficiency means they are more likely than C_3 grasses to survive in hot, arid and semi-arid environments. Different physiological characteristics and temperature optima for growth in C_4 and C_3 species mean that seasonally-varying combinations of temperature, rainfall and irradiance have a strong influence over C_3/C_4 competitive interactions and species distributions (Hattersley 1983). The C_3 grasses appear to be favoured by cool, wet spring or very dry, summer conditions. If the temperature is less than 25°C when rain falls then C_3 grasses are likely to dominate (Hattersley 1992). In contrast, the C_4 species are favoured by hot, wet summers. Early dominance established by growth of cool-season C_3 species in spring can provide a distinct competitive advantage over the later developing C_4 species.

Results of a study of the distribution of native C_4 grasses in Australia (Hattersley 1992), indicated that the proportion of NADP-ME and PCK biochemical types was highly positively correlated with annual rainfall, whereas the proportion of NAD-ME types was highly negatively correlated with annual rainfall. This suggests that NAD-ME type species could be considered for C_4 species selection and management in drier regions. Past atmospheric CO_2 and/or temperatures appear to have been the main selection pressures responsible for the evolution of the C_4 pathway, whereas rainfall in tropical and subtropical climates may have been the main factor responsible for divergence within the C_4 type (Hattersley 1992).

Subtropical C_4 grasses are often sensitive to chilling but this is not attributable to the photosynthetic pathway *per se.* The percentage of C_4 species in grassland vegetation is often highly correlated with minimum night temperature (Hattersley 1992). As a consequence, relatively frost-tolerant species (e.g., paspalum) tend to be quite widely dispersed through New Zealand but other more frost susceptible species (e.g., kikuyu) have a distribution that is more restricted to northern areas of New Zealand (Field & Forde 1990).

Soil fertility and structure

Addition of nitrogen fertilisers in spring and late autumn is believed to increase the growth of ryegrass relative to subtropical grasses and therefore increases its competitive dominance. Conversely, nitrogen fertiliser applications in summer and early autumn increase the proportion of kikuyu and suppress cool-season production from ryegrass. Phosphate applications must be maintained to support clover growth in competition with vigorous subtropical grasses in summer.

In general, heavier, higher fertility soils are more likely to be dominated by paspalum, whereas light soils are more likely to be dominated by the annuals such as summer grass, smooth witchgrass and crowfoot grass. Lower fertility hill country pastures tend to have a greater proportion of ratstail on the northerly aspects and carpet grass on the moister, southerly aspects.

Grazing and pasture management

Grazing management influences subtropical species dominance through a combination of effects, including: removal of leaf mass of the species, removal of cover of companion temperate species allowing switches in composition, and damage to pasture cover at critical periods (e.g., during moisture stress) allowing subsequent ingress from seed banks or regeneration from stolons. Timing of management decisions in relation to temperate or subtropical grass growth phases will affect competitive interactions.

The few studies conducted in New Zealand on management of mixed temperate/paspalum pastures (Baars *et* al. 1979; Percival & McClintock 1982) indicate that lax grazing in spring decreases paspalum and increases ryegrass, whereas hard grazing in spring has the opposite effect. Very lax grazing in summer maximises the content of ryegrass. Hard grazing in summer with cattle may increase the proportion of paspalum as a result of ryegrass death through pulling (Baars *et* al. 1979). In extreme cases, severe pugging damage to pastures in winter, when soil moisture conditions are high, has the potential to severely damage temperate grass tiller populations and to create gaps for colonisation by annual subtropical grasses from the buried seed bank in spring. By contrast, paspalum may be quite tolerant of treading damage in winter due to the presence of tough rhizomes (Hunt 1979). This emphasises that consideration of the effect of grazing on competitive balances of species is especially important.

In Northland, removal of kikuyu leaf and stolon mass during autumn is critical for growth of ryegrass during winter. Intensive grazing of kikuyu during April–May is necessary to switch composition to temperate dominance in June.

Competition processes and vegetation dynamics

The role of competition in affecting the success of subtropical grasses in temperate pastures is, for most species, poorly understood. In warmer conditions it is usually unclear whether the success of subtropical species results from actively displacing temperate species, or simply from colonising pasture openings created by failure of temperate species to persist. However, vegetation gaps created by opening up of pasture can act as foci for invasion by annual weedy species (Panetta & Wardle 1992). including subtropical grasses. Oscillations between cool-season annuals (annual poa) and warm-season annuals (summer grass) occupying gaps in pasture may prevent perennial forage species from establishing (Wardle *et al.* 1994, 1995).

Once established, subtropical grasses have the potential to persist through suppressing establishment of temperate species. In New Zealand, in-depth studies have been conducted only for paspalum. Thorn *et al.* (I 986a,b) transplanted perennial ryegrass seedlings into swards with high and low paspalum density, and with and without the paspalum being trimmed. Generally, ryegrass survivorship and tiller production were greater under low levels of paspalum. Ryegrass tiller production was several times greater when paspalum was clipped. Addition of nitrogen resulted in large growth responses by ryegrass, but these were not sufficient to enhance survivorship. The frequency of ryegrass and white clover already in the pasture was considerably less in the presence of paspalum, especially during summer. The physiological basis of the apparently superior competitive ability of paspalum over ryegrass needs further investigation. For example, paspalum stores considerably more reserves (e.g., nitrogen, non-structural carbohydrates) in subterranean tissues between autumn and early spring, than does ryegrass (Thom *et al.* 1989). This suggests that some perennial subtropical species may be more effective than temperate species at competing under low nitrogen conditions, a conclusion also supported by overseas studies (e.g., Wedin & Tilman 1993).

Characteristics of perennial temperate grass species also determine competitive effects on subtropical grasses. Forage species which exhibit strong summer activity and have greater root mass, such as tall fescue or cocksfoot, can be more competitive than ryegrass in some situations (Moloney 1990).

Invertebrate pests

Pasture damage by invertebrates can also reduce the general fitness of temperate species, allowing subtropical grass invasion. For example, lucerne flea and slugs will selectively feed on clover foliage, root knot and cyst nematodes on clover roots, and black beetle on ryegrass roots and crowns (King *et al.* **1981;** Barker 1989). Invertebrates selectively feeding on temperate species can also create gaps through enhancing the phenomenon of “ryegrass pulling”, whereby cattle pull out weakened plants (e.g., Blank & Olsen 1988); the resultant gaps provide suitable microsites for annual subtropical grass (and annual poa) establishment. Gaps created by black field crickets feeding along summer cracks in pasture can result in ingress by weedy grasses, notably poa species, which can in turn be colonised by subtropical grasses the following summer (G.M. Barker, pers. obs.). Selective

Table 1 Characteristics of some common subtropical (C_4) grasses in New Zealand pastures.

Species Name	Common Name	Life history[1]	C_4 structural type[2]	C_4 biochemical type[2]	Growth form[1]	Regenerative type[3]	Chilling and frost sensitivity	Common habitats	Agronomic value	Additional References
Axonopus affinis Chase	carpet grass	Perennial	'classical NADP-ME	NADP-ME	spreading, stoloniferous, culm 250–700 mm, erect-bent, branching, rooted at nodes	V, Bs	low	warm, moist sites, low fertility, summer-dry soils	low, commercial cultivars exist	Arnold (1953)
Cynodon dactylon L.	Indian doab, Bermuda grass	Perennial	'classical NAD-ME	NADME	spreading, mat-forming, stoloniferous and rhizomatous, culm 50–1000 mm, erect to bent, branching and rooting at nodes	V, Bs	low to moderate	moderate to high fertility, tolerates summer-dry soils. dry to *very* dry sites	moderate, commercial cultivars exist	Arnold (1953)
Digitaria sanguinalis (L.) Scop.	summer grass	Annual	'classical NADP-ME	NADP-ME	tufted, culm 100–300 mm, bent, branching rooting at nodes	S, Bs	low	disturbed sites, light soils	moderate, commercial cultivars exist	Matthews (1971)
Eleusine indica Gaertn.	crowfoot *grass*	Annual	'classical NAD-ME	NAD-ME	tufted, spreading, culm 350–900 mm, erect to bent, branching at nodes	S, Bs	moderate	heavily disturbed areas. warm, moist soils, drought tolerant	low	Matthews (1971)
Panicum dichotomiflorum Michx.	*smooth* witchgrass	Annual	'classical PCK	NAD-ME	tufted, culm 500–2000 mm, erect-bent, branching	S, Bs	low–moderate	adventive in pastures and disturbed sites, survives in drier situations	low	Matthews (1971)
Paspalum dilatatum Poir.	paspalum	Perennial	'classical NADP-ME'	NADP-ME	tufted-rhizomatous, culm 500–1500 mm, erect, branching from lower nodes	V, Bs	moderate-high	widespread, wan, moist sites, moderate drought tolerance	moderate-high commercial cultivars exist	Cockayne (1918), Levy (1926), Arnold (1953), Percival (1977), Percival & Couchman (1979). Percival *et al.* (1979), Langer (1990)
Paspalum distichum L.	Mercer grass	Perennial	'classical NADP-ME	NADP-ME	spreading, stoloniferous, rhizomatous forming loose mat. culm ZOO-400 mm, bent, branching	V, Bs	low	wet sites, heavily trodden areas	low, commercial cultivars exist	Arnold (1953)
Pennisetum clandestinum Chiov.	kikuyu	Perennial	'classical NADP-ME	NADP-ME	spreading, stoloniferous, rhizomatous, culm 50–300 mm, branching, rooting at nodes	V, Bs	low–moderate	warm. moist, fertile sites but can withstand some drought	moderate, commercial cultivars exist	Syme (1940), Bell (1940), Arnold (1953), Langer (1990), Piggot & Morgan (1983), Little (1983)
Setaria geniculata (Poir.) P. Beauv.	knot-root bristle grass	Perennial	'classical NADP-ME'	NADP-ME	spreading, rhizomatous. culm 400–1200 mm, bent, branching, rooting at nodes	(V), Bs	moderate-high	moderate-high fertility	low	
Sporobolus africanus (Poir.) Robyns & Tourn.	ratstail	Perennial	'classical PCK	PCK	tufted, culm 50-500 mm, erect-bent, branching	(V), Bs	moderate-high	sunny, dry north facing slopes and dry, light soils, coastal pastures	low	Levy (1928)

1. Hafliger & Scholz (1980, 1981), Lambrechtsen (1992)
2. Hattersley (1992, 1987)
3. Regenerative types as classified by Grime, Hodgson & Hunt (1988):(V) Vegetative expansion: new shoots vegetative in origin and remaining attached to parent plant until well established, (S) Seasonal regeneration: Independent offspring (seeds or vegetative propagates) produced in a single cohort: (Bs) Persistent seed bank: viable but dormant seeds or spores present throughout year, some persisting for more than 12 months; (W) Widely dispersed seeds or spores: offspring *numerous* and exceedingly buoyant in air.

defoliation by some invertebrates also reduces fitness of subtropical species, for example black beetle feeding can significantly reduce paspalum populations (Watson & Wrenn 1980). The composition of establishing plant communities may also be altered by selective consumption of seeds and seedlings. For example, black field crickets feed on ryegrass (and to a lesser extent clover) seeds in preference to those of paspalum and broadleaf weed species (Blank *et al.* 1980).

Subtropical grasses also have the potential to alter subsequent plant community structure by hosting invertebrates which may then switch to temperate species. Black beetle populations can build up under paspalum, and then become a ryegrass pest once the paspalum supply is exhausted (Watson & Wrenn 1980). Kikuyu facilitates population increases of invertebrates of potential pest status against temperate species by promoting a dense ground cover and favourable microclimates, e.g., soldier fly (Robertson & Blank 1982), black beetle (Watson & Wrenn 1980) and slugs (Barker 1989). Such hosting of invertebrate pests by subtropical species can lead to subsequent damage to ryegrass and white clover when subtropical pastures are renovated and sown to temperate species (Blank & Olsen 1988; Barker *et* al. 1990).

Weed ingress as a result of invertebrate pests, or management factors can also lead to invasion by other pest species. As indicated above, annual subtropical grasses may contribute to invasion by annual poa during the winter. Barker (1993) has shown that annual poa can lead to rapid population build-up of Argentine stem weevil in pastures which can then switch to and damage perennial ryegrass.

Species distributions in pastures

Ordination analysis

The assortment of different subtropical (C_4) grasses and temperate (C_3) species in response to different climatic, soil, management and other factors in New Zealand pastures can be examined in part by using ordination techniques and pasture survey data. This form of analysis identifies similarities and differences in species ecology and distributions.

This analytical process sorts samples from vegetation to give ordered changes in species importance that reflect underlying environmental gradients. In the following analysis, species profiles collected from pastures in Northland, Auckland and the Waikato region in a pasture survey conducted in 1987438 (Field & Forde 1990) have been sorted along two ordination axes. Each profile represented the abundance of the various species growing on a specific land use capability (LUC) class, as estimated from 25 to 30 sampling points along a 1 km farm walk. The 120 sampled farms were randomly selected to represent the appropriate proportions of the various land classes within counties from Mangonui in the north to Waitomo and Ohinemuri in the south.

Ordination scores for samples and species, obtained from a correspondence analysis using the package BIOMECO (Roux 1985), identified similarities and differences among species in their ecology and distributions along two ordination axes. The axes reflect the importance of the underlying gradients in species ecologies (Figure 1). The distribution of samples from different farming enterprises, geographical locations and LUC classes indicated that Axis 1 represents a productivity and disturbance gradient. Species found predominantly in rotationally-grazed pastures on better land classes have high Axis 1 scores, with those restricted lo set-stocked, hill country pastures having large negative scores. Axis 2 represents a climatic gradient with the few species having high scores restricted to either warm, dry locations or pastures north of Auckland.

Ryegrass and white clover were found across a wide range of environments and therefore are centrally located on the axes. Paspalum appears to have a wide adaptation in the north, falling close to ryegrass and white clover. Indian doab, summer grass, crowfoot grass and Mercer grass are grouped with prairie grass in being restricted to flatter land under rotational grazing. The positioning of the annuals indicates that the opportunity to establish occurs only where the severe disturbance of rotational grazing opens niches during early summer. Ratstail is adapted to the same steeper land that is the centre of distribution of browntop, sweet vernal, crested dogstail and Yorkshire fog. The increasing displacement above Axis 1 of ratstail, carpet grass and kikuyu is evidence of their better competitiveness on warmer, drier north-facing slopes and warmer, northerly locations. Carpet grass shares a range of adaptation with vulpia hair grass and subterranean and suckling clovers, while kikuyu appears to be out on its own. South of Auckland, there was, at least in 1988, little evidence of penetration of subtropical grasses into the moister, cooler hill country.

This test of the above predictions confirms that the relative distributions of species are predictable, in part, from an understanding of the plant characteristics of the different species. In particular, the annual species (summer grass and crowfoot grass) and Mercer grass tend to be associated with higher fertility disturbed sites with similarity to weedy species such as dock and plantain. Paspalum tends to have a general coverage across sites reflecting tolerance of a wide range of climatic, soil and management conditions. Carpet grass and ratstail tend to occupy lower fertility sites with similarity to dogstail, vulpia hair grass and other lower fertility grasses. Kikuyu shows a tendency for lower fertility, warmer sites. This possibly reflects poorer frost tolerance and a higher temperature requirement for growth. However, as kikuyu can occupy a wide range of sites, the result may reflect the high effectiveness of pasture renewal programmes which artificially displace kikuyu out of dairy farming systems.

Distribution between pastoral land uses in Northland

It is valuable to examine how these differences in species ecology translate into the distribution of these different subtropical species in different pastoral land uses in the Northland region (Table 2). The distribution and relative abundance of subtropical grass species at 53 locations throughout Northland from Cape Reinga to Kaiwaka was surveyed in 1990 (Woods & Andrewes 1990). Sites were stratified into different land use types and several locations within major land use classes were sampled. Within each selected habitat, species presence was recorded in a 200 cm^2 quadrat placed at 10 m intervals along three 100 m long transects.

Kikuyu and paspalum were the most prevalent species, both in abundance and distribution among habitats (Table 2). Carpet grass, ratstail and Mercer grass were the other common perennial species. Species abundance differed depending on land use. Ratstail and carpet grass tended to be more abundant in sheep and beef cattle pasture than in dairying. Mercer grass tended to be more abundant in dairying and cattle enterprises. Crowfoot, summer grass and smooth witchgrass were the most prevalent annual species. These annuals tended to be more prevalent in cattle enterprises, consistent with greater disturbance of vegetative cover by cattle grazing.

Figure 1 Ordination analysis of distributions of subtropical and temperate grasses in northern New Zealand pastures. Axis 1 is associated with increasing fertility and disturbance, and Axis 2 is associated with increasing temperature. Central locations on the axes represent widespread distributions and increasing extremes represent more restricted distributions. Species with similar locations on the axes indicate similar distributions (see text). Subtropical (C_4) grasses (closed circles) Aaf, *Axonopus affinis*; Pcl, *Pennisetum clandestinum;* Pdil, *Paspalum dilatatum;* Dsa, *Digitaria sanguinalis;* Ein, *Eleusine indica*; Pdis, *Paspalum distichum;* Cda, *Cynodon dactylon*; Saf, *Sporobolus africanus*. Temperate (C_3) grasses (open circles): Lol, *Lolium* spp (ryegrass); Aca, *Agrostis capillaris* (browntop); Aod, *Anthoxanthum odoratum* (sweet vernal); Hla, *Holcus lanatus* (Yorkshire fog): Ptr, *Poa trivialis* (poa trivialis); Bwi, *Bromus willdenowii* (prairie grass): Dgl, *Dactylis glomerata* (cocksfoot); Fru, *Festuca rubra* (Chewings or red fescue): Vbr, *Vulpia bromoides* (vulpia hair grass); Rra, *Rytidosperma racemosa* (danthonia); Bho, *Bromus hordeaceus (goose* grass); Ccr, *Cynosurus cristatus* (crested dogstail). Temperate (C_3) legumes (open triangles) Tre, *Trifolium repens* (white clover): Lan, *Lotus angustissimus* (slender birdsfoot trefoil): Lpe, *Lotuspedunculatus* (lotus); Tdu, *Trifolium dubium* (suckling clover); Tpr, *Trifolium pratense* (red clover); Tsu, *Trifolium subterraneum* (subterranean clover); Tfr, *Trifolium fragiferum* (strawberry clover). Temperate (C_3) forbs (open squares) Hra, *Hypochaeris radicata* (catsear); Rac, *Rumex acetosa* (sorrel); Rob, *Rumex obtusifolius* (dock); Tof, *Taraxacum officinale* (dandelion); Rsa, *Ranunculus sardous* (buttercup); Pla, *Plantago lanceolata* (plantain); Ami, *Achillea millefolium* (yarrow); Pma, *Plantago major* (greater plantain).

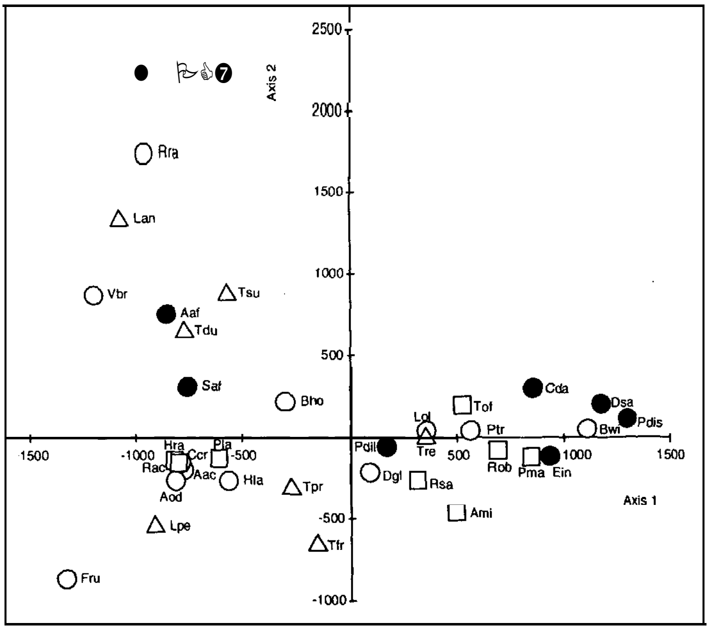

Table 2 Distribution of subtropical grasses between different land use types in Northland.

Species Name	Dairy Presence[1] (%)	Dairy Abundance[2] (%)	Sheep & Beef Presence (%)	Sheep & Beef Abundance (%)	Cattle finishing Presence (%)	Cattle finishing Abundance (%)
Axonopus affinis	48	2	43	6	60	6
Cynodon dactylon	14	.	21	2	0	0
Digitaria sanguinalis	38	2	21	1	30	2
Eleusine indica	33	13	21	8	30	11
Panicum dichotomiflorum	24	3	11	2	0	0
Paspalum dilatatum	86	15	75	7	90	19
Paspalum distichum	57	3	14	1	30	7
Pennisetum clandestinum	71	24	61	27	80	30
Setaria geniculata	0	0	7	3	0	0
Sporobolus africanus	29	1	39	4	30	2
Number of habitats	21		28		10	

1. Percentage of the number of habitats sampled where species was present.
2. Percentage of the total number of quadrats sampled where species was present.

Conclusions

Short-term and longer-term changes in climatic variability (including increases in winter and summer rainfall, decreases in frequency of frost and increases in the frequency of warm periods and short periods of water stress) may increase the abundance of both perennial and annual subtropical grasses.

The impact of climatic effects may be compounded by intensification of land use and greater grazing pressure (as with cattle grazing), leading to a greater proportion of annual grasses and additions of persistent seed bank loadings in soil.

The abundance of the annual subtropical grasses smooth witchgrass, summer grass and crowfoot grass is predicted to increase in the future. These grasses may contribute to a deterioration of pastures by developing persistent gaps and by harbouring invertebrate pasture pests.

Management strategies aimed at increasing the competitiveness of temperate species (such as use of fertiliser, summer-active temperate species and grazing strategies to reduce pasture damage in winter and overgrazing in summer) may be helpful in reducing the rate of spread of subtropical species.

Improved subtropical grass types should be investigated for New Zealand conditions. These could include the NAD-ME types characteristic of drier situations to improve drought-tolerance characteristics for summer-dry sites, and subtropical C_3 species.

An improved understanding of the role of climate in competitive interactions between subtropical and temperate species in New Zealand would be useful in developing better management of subtropical grasses in temperate pastures and in optimising forage supply and quality in livestock production systems in northern New Zealand.

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