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Pasture cultivars in ecological perspective

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ABSTRACT An overview of the variety in New Zealand bred pasture cultivars is obtained by comparing the group against the variety that has developed in the whole spectrum of herbaceous plants during evolution. This was done by classifying each cultivar into one of seven different ecological groupings termed strategies. Each strategy grouping represents a different mature functional type; the seven groupings collectively cover the full range of mature plant types. This preliminary classification confirmed that there are different ecological strategies in our cultivar range but, as might be expected, they represent only a small part of the full range of ecological options. All cultivars are best suited to moderate grazing and high to medium fertility. The information obtained by viewing pasture cultivars in this wider context is used to predict that further breeding is needed to develop pasture cultivars for extreme situations and for use in mixtures. Stress tolerance associated with a rapid, contracted life-span appears to be the best option for cultivars for dry or low-fertility pastures. It is also predicted that complex pasture mixtures are likely to be easier to maintain and of more value in lower fertility or moderately droughted pastures than in highly fertile pastures. Opportunities exist to develop additional cultivars suited to the different niches in these pastures. Amalgamation of knowledge from agricultural and non-agricultural research can clearly help solve agricultural problems and is an efficient use of science. Means should be sought to use information from both fields to look at finer-scale questions about cultivars.

Keywords plant breeding, strategy theory, low fertility, drought, pasture mixtures, plant competition, niche differentiation, species diversity, science

INTRODUCTION

It is clear from past Proceedings that our pasture cultivars differ in their productivity and that different cultivars are suited to different places. What is not so clear is how much the variety of different pasture cultivar types covers the variety that we need for our New Zealand pastures.

One way to examine the extent of variation in our cultivar types is to expand our frame of reference momentarily and look at the range of variation that has arisen in the whole spectrum of herbaceous plants during evolution. This expanded background includes many extreme habitats and plant types that are unsuited to agriculture. But by attempting to visualise our cultivars in this wider context we agriculturalists can access information from non-agricultural research and so draw on a wider fund of information. Trends in past cultivar breeding can be looked for that may not be evident when cultivars are viewed in their usual, narrow context. In addition, the degree to which cultivars are specialised or suited to extreme habitats can be examined.

So, how does the range of New Zealand bred pasture cultivars compare against the diversity of herbaceous plant types that have arisen in different habitats during evolution?

THE CONCEPT OF STRATEGIES

This question can be addressed by classifying plants into different groupings based on the way they function, using the idea of *strategies.* A strategy is a high-level form of specialisation that is proposed to exist in a plant involving co-ordination of most of the important plant characteristics to suit the plant to a particular environment. Different strategies have arisen during evolution in response to particular selection pressures and these result in plants being suited to different habitats. This idea of a higher level of organisation and of repeated, predictable specialisation involving coordinated characteristics is still emerging in ecology and is continuing to be debated and updated.

The particular classification system that I will use here for our objective is known as the C-S-R model of plant strategies (Grime 1988). This model classifies plants according to the intensities of *competition, stress* (e.g. soil fertility) and *disturbance* (e.g. grazing) with which mature plants are able to cope. The relationship between competition, stress and disturbance in vegetation is an equilibrium and can be described by a triangle (Figure la). Seven broadly different strategies may be recognised, each corresponding to particular equilibria between competition, stress and disturbance (Figure la).These cover the full range of plant types. The circle at the centre of the triangle encloses the different strategies displayed by herbaceous plants.

At the apices of the triangle in Figure la are the extreme types of strategy C, S, and R. C-strategists (competitors) are best suited to the predominant selection force *competition* in fertile, undisturbed habitats. These plants possess a suite of attributes that rapidly shunt resources into new photosynthesising and nutrient-absorbing plant parts to maximise resource capture in the patchy, resource-rich environment. S-strategists (stress tolerators), in contrast, are best suited to the predominant selection force *stress* in infertile, undisturbed habitats. These plants possess attributes, including low growth and tissue turnover rates, mechanisms to store carbon and mineral nutrients and strong defences against grazing, which confer a capacity to maintain viable tissues over long periods where no growth is possible. R-strategists (ruderals) are best suited to the predominant selection force *disturbance* in 'fertile, severely disturbed habitats and possess characters that enable rapid growth and early seeding or other form of reproduction to increase the probability that sufficient offspring will survive to re-establish the population. The intermediate strategists (e.g. C-R) are adapted to intermediate combinations of competition, stress and disturbance and possess intermediate combinations of the above attributes. Full details of the attributes of the seven different strategists and a comprehensive description of the C-S-R model are given in Grime (1988).

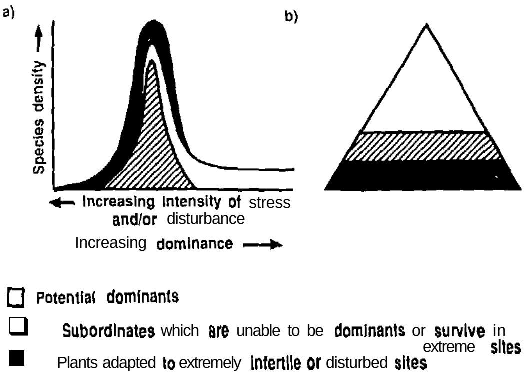

Figure 2 Distribution of three plant types in (a) the hump-backed model of diversity and (b) the C-S-R model of strategies from Figure 1 (redrawn from Grime 1988).

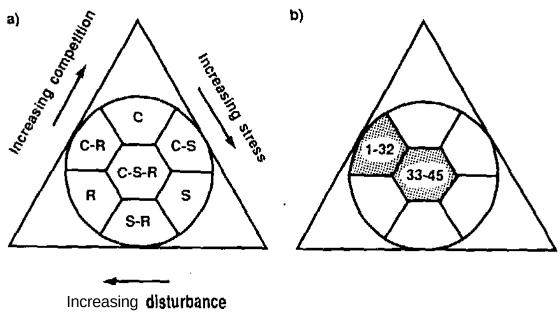

Figure 1 The C-S-R model of plant strategies. (a) Triangular inter-relationship between competition, stress and disturbance and location of seven strategies. C, competitor; S, stress tolerator, R, ruderal; C-R, S-R, C-S, C-S-R, intermediate strategists (e.g. C-R, competitive-ruderal). The circle encloses the strategies of herbaceous plants. (b) Provisional classification of New Zealand pasture cultivars according to strategy. Perennial ryegrass *(Lolium perenne)* 1, Droughtmaster; 2, Ellett; 3, Marathon; 4, Nui; 5, Ruanui; 6, Supernui; 7, Takapau Persistor; 8, Yatsyn. Hybrid ryegrass *(L. x boucheanum)* 9, Ariki; 10, Greenstone; 11. Manawa; 12, Marsden. Italian ryegrass *(L. multiflorum)* 13, Concord; 14, Corvette; 15, Moata; 16, Progrow; 17, Tama. Smooth brome grass *(Bromus inermis)* 18, Tiki. Upland brome *(B. sitchensis)* 19, Hakari. Prairie grass *(B. willdenowii)* 20, Matua. Paspalum *(Paspalum dilatatum)* 21, Raki. Cocksfoot *(Dactylis glomerata)* 22, Kara; 23, Wana. Tall fescue *(Festuca arundinacea)* 24, Roa. Timothy *(Phleum pratense)* 25, Kahu. White clover *(Trifolium repens)* 26, Huia; 27, Kopu; 28, Pitau; 29, Tahora. Pink serradella *(Ornithopus sativus)* 30, Koha. Sulla *(Hedysarum coronarium)* 31, Aokau; 32, Necton. Browntop *(Agrostis capillaris)* 33, Muster. Phalaris *(Phalaris aquatica)* 34, Maru. Yorkshire fog *(Holcus lanatus)* 35, Massey Basyn. Chicory *(Cichorium intybus)* 36, Puna. Red clover *(T. pratense)* 37, Colenso; 38, Hamua; 39, Pawera; 40, Turoa. Lotus *(Lotus uliginosus)* 41, Maku. Lucerne *(Medicago sativa)* 42, Oranga; 43, Otaio; 44, Rere; 45, Wairau.

CLASSIFICATION OF CULTIVARS

By making use of this C-S-R model and what we know of the life-cycle, morphology, flowering and seasonal growth characteristics of our New Zealand pasture cultivars, each cultivar can be provisionally classified into one of the seven different strategy groupings. This has been achieved in Figure lb by classifying each cultivar using the standard dichotomous key reported on p. 28 in Grime *et al.* (1988) for analysing all herbaceous plant types. The classification procedures used were identical to those followed by Grime *et al.* (1988) so that cross-comparisons can be made between the results in the two studies. The classifications assigned to our cultivars using this procedure (Figure 1b) are generally consistent with those species for which data are available in Grime et al. (1988).

Two things are immediately apparent from Figure lb. The analysis confirms that there are different ecological strategies in our cultivar range. But it is also clear on this expanded scale that our New Zealand pasture cultivars still encompass a rather narrow range of ecological options. As might be expected, all cultivars were found to be associated with plant characteristics best suited to situations with high to medium fertility and moderate intensities of grazing. Other strategies likely to be important in extreme grassland situations are poorly represented, for example those associated with success in chronically infertile or heavily disturbed habitats.

IMPLICATIONS

This result is not surprising. In this wider context most of our soils sustaining agriculture would be classified as high to medium fertility, and we know that tolerance of grazing is an important attribute for a pasture plant. The variety in our cultivars covers that which might be expected to be needed for most of our productive New Zealand pastures. But additional points can be extracted from this analysis to assist two particular areas of debate in relation to pastures: (1) breeding of cultivars for extreme environments; and (2) the use of pasture mixtures.

Breeding for extremes

Reductions in fertiliser inputs to pastures, increased emphasis on low-input farming and the predicted effects of climate change on pastures mean that emphasis on extremes of fertility, moisture and grazing carnage in farming is likely to increase. There will be more pastures with combinations of stress, disturbance and competition which encroach towards the base of the triangle in Figure la. The above analysis suggests that strategies likely to be important in these extreme pasture situations are currently poorly represented in our cultivar selection. It can be concluded that a sustained breeding effort is needed to provide improved plants suitable for the widening range of pasture situations likely in New Zealand in the future. Current or recently completed breeding programmes in New Zealand on browntop, dryland browntop *(Agrostis castellana)*, sweet vernal *(Anthoxanthum odoratum)*, crested dogstail *(Cynosurus cristatus)*, red fescue *(Festuca rubra)*, Yorkshire fog, birdsfoot trefoil *(Lotus comiculatus)*, plantain *(Plantago lanceolata)* and sheep's bumet *(Sanguisorba minor)* are welcome developments in this regard. But what are the attributes to be exploited to further increase tolerance of low fertility for example, and what problems are likely to be encountered incorporating them into cultivars?

The emerging understanding of plant ecology recognised in the idea of strategies and supported by evidence from habitats as diverse as arctic tundra and tropical forest, is that many plant characters abt in partnership to confer success in a particular habitat. Therefore, tolerance of nutrient stress is generally associated with a combination of slow growth and slow tissue turnover (Chapin 1980), uncoupling of resource capture from growth, storage of carbon and mineral nutrients, infrequent flowering, small or needle-like leaves, and tissues strongly defended against grazing by chemical or physical deterrents (Bryant & Kuropat 1980; Coley 1987; Coley *et al.* 1985).

Clearly, many of these attributes are undesirable for pasture cultivars. An inevitable trade-off of desirable agronomic characteristics against stress-tolerant characteristics is likely. This means that attempts to select for higher growth rates or increased palatability in a stress-tolerant species will reduce stress-tolerance. A more effective means of breeding for stressed pastures may be to develop plants adapted to moderate intensities of stress and disturbance (S-R strategists) rather than plants tolerant of severe stress. These plants exploit the growth window in a temporarily dry and/or nutrient-poor habitat, with a rapid, contracted growth phase and regeneration from a seed-bank or buds in soil during favourable conditions. This suggests that more attention should be given to developing New Zealand cultivars of annual species like annual medicks *(Medicago lupulina, M. polymorpha, M. arabica)*, suckling clover *(Trifolium dubium)* and subterranean clover *(Trifolium subterraneum)*.

Pasture mixtures

From studies of the composition of different natural vegetations, the number of species that can co-exist in a mixture apparently varies predictably with intensities of stress and disturbance. This relationship is formalised in Figure 2a in a close relative of the C-S-R model called the hump-backed model (Grime 1973). This model predicts a corridor of diversity where moderate intensities of stress and disturbance coincide. For temperate, herbaceous vegetation, it appears that more than 20 species can coexist where the peak standing biomass is held between 350 and 750 g/m^2. This biomass coincides approximately with that seen in infertile pastures. The model is consistent with the experiences of Sir Bruce Levy (I 970) who observed:

> .. the higher we build the soil fertility and the more uniform the grazing management the fewer are the species . . . as soon as a state of retrogression sets in, the way is open to invasion by added species in the sward. Retrogression will continue until a static state is reached, and once more relatively few species, attuned to those poorer conditions will dominate the sward.

The relationship suggests that there are good opportunities to raise pasture productivity and stability with mixtures of species which occupy different niches in pastures where lower fertility or moderate seasonal drought weakens potential dominants. Examples of the types of niche differentiation that might be used include differences in seasonal growth pattern (Moore 1985), timing and depth of root activity (Veresoglou & Fitter 1984; Fitter 1986) and shoot architecture. The development of a package of species for low-medium fertility hill country (Rumba11 & Claydon 1990) is a good step in this direction. Further research and breeding effort should be placed on identifying plants exploiting other niches in these environments. Natural mixtures are composed of balances of dominant and subordinate plants (Figure 2a) and presently examples of subordinate plants in our cultivar range are few (Figure 2b). The agronomic value in mixtures of very successful subordinate species like *Poa pratensis, P. trivialis,* plantain, crested dogstail, sweet vernal and mouse-ear chickweed *(Cerastium fontanum)* should be investigated.

Opportunities for niche differentiation are severely constrained in highly fertile, intensely grazed pastures due to competitive dominance. Attempts to maintain complex mixtures in balance under these conditions by strategic use of grazing to weaken potential dominants are likely to be more difficult. Results from experimental microcosms studying the role of fertility and simulated grazing in determining species richness (Campbell 1988) showed disturbance to be much less effective than nutrient stress in reducing rates of competitive exclusion and maintaining high species densities. This lends support to the suggestion of Levy (1970) that in this circumstance there should be different simple mixtures on various paddocks of the farm where dominant species may be more fully exploited than in a general mixture.

CONCLUSIONS

Our pasture cultivar range provides a choice of ecological options but the choice needs to be greater.

Problems are likely in breeding cultivars tolerant of severe nutrient stress because stress-tolerant attributes trade-off against agronomically useful attributes. Stress tolerance associated with a rapid, contracted lifespan appears to be a better option for cultivars for stressed pastures.

Maintenance of complex pasture mixtures is likely to be easier and of more value in lower-fertility or moderately droughted pastures than in highly fertile pastures. Opportunities for niche differentiation should be investigated for the former.

Information from non-agricultural research can be useful in addressing agricultural problems. At present the two fields operate largely in isolation, resulting in an inefficient use of scientific knowledge. There should be further attempts to amalgamate this knowledge. Strategy concepts have value in providing a broad overview of cultivar ecologies but cannot provide the sharp focus necessary to understand the fine-tuning of the ecology or agronomy of each cultivar. Further opportunities should be sought to link knowledge on the fine-tuning of species ecologies in agricultural and non-agricultural landscapes.

REFERENCES

Bryant, J.P.; Kuropat, P.J. 1980. Selection of winter forage by subarctic browsing vertebrates: the role of plant chemistry. *Annual Review of Ecology and Systematics 11:* 261-281.

Campbell, B.D. 1988. Experimental tests of C-S-R strategy theory. PhD Thesis, University of Sheffield.

Chapin, F.S. III. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics 11:* 233-260.

Coley, P.D. 1987. Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. New Phytologist 106 (Suppl.): 251-263.

Coley, P.D.; Bryant, J.P.; Chapin, F.S. 1985. Resource availability and plant anti-herbivore defence. *Science 230:* 895-899.

Fitter, A.H. 1986. Spatial and temporal patterns of root activity in a soecies-rich alluvial grassland. *Oecologica (Berlin) 69:* 594-599.

Grime. J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature 242:* 344-347.

Grime, J.P. 1988. The C-S-R model of primary plant strategies origins, implications and tests. *In: Plant Evolutionary Biology.* (Eds. L.D. Gottlieb & S.K. Jain). London: Chapman Hall.

Grime, J.P.; Hodgson, J.G.; Hunt, R. 1988. *Comparative Plant Ecology: a Functional Approach to common British Species.* London: Unwin Hyman.

Levy, E.B. *1970. Grasslands of New Zealand.* Wellington: Government Printer.

Moore, P.D. 1985. Nuclear DNA content as a guide to plant growth rate. *Nature 318:* 412-413.

Veresoglou, D.S.; Fitter, A.H. 1984. Spatial and temporal patterns of growth and nutrient uptake of five co-existing grasses. *Journal of Ecology 72: 259-272.*