Genetic diversity within white clover (*Trifolium repens* L.)

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Abstract

White clover is a widely adapted species found in many environments, but not endemic to New Zealand. We are therefore reliant upon the introduction of populations from overseas. The range of genetic variation in physiological and morphological characters found within white clover is described and the significance this has for New Zealand pastoral agriculture is discussed. Genetic variation has been documented for shoot and root morphology, nutrient uptake and utilisation, tolerances of a range of climatic stresses, pathogens and pests, and seed production. The relationship of this variation to origin may identify important regions that need to be further sampled, to provide further variation to continue improvements of white clover performance in our grazed pastures.

Additional keywords: *morphology, physiology, adaptation, cultivars, populations, variation, stress tolerance*

Introduction

The wide habitat tolerance of white clover has ensured its success in temperate (Brougham *et al.*, 1978), Mediterranean (Davies and Young, 1967) and some subtropical regions (O'Brien, 1970). Its wide geographical and ecological distribution is matched by an equally wide range of genetic variation in morphology and physiology. Populations vary morphologically from prostrate, small-leaved, densely-stoloniferous types, apparently adapted to close grazing, through to upright, large-leaved, sparsely-stoloniferous types, apparently adapted to lax grazing or cutting. Much of this variation is genetic (Williams, 1987), but a considerable amount of morphological variation is attributable to phenotypic plasticity (Wilman and Asiegbu, 1982), i.e., plants of a given genotype may have different morphological attributes depending upon the environment in which they are grown. Genetic variation in extent of phenotypic plasticity has also been recorded (Caradus *et al.*, 1993). In this paper I aim to profile the range of genetic diversity within white clover by (a) describing broad ecotype groups, (b) describing cultivar classification, (c) cataloguing the morphological and physiological variation observed, and (d) relating this to germplasm adaptation to specific biotic and abiotic stresses.

Origin and Distribution

The centre of origin and diversity of white clover is considered to be the Mediterranean region (Vavilov, 1951). However, white clover is indigenous to Europe and Asia, southwards from 70°N, and throughout south-western Asia, Siberia, China and northern Africa. It has been introduced into most temperate areas of the world, notably New Zealand, Australia, Japan, USA, Canada, South Africa and parts of South America. It also grows well at high altitude in the tropics, in Indonesia, Papua New Guinea and Colombia. In North America white clover extends from 67°30'N in Alaska to Florida in the south. It has been recorded from up to 6000m altitude in the Himalaya Range.

Classification of 'wild types'

The term 'wild type' is used to refer to collected populations that have not undergone any deliberate selection by man. These include ecotypes that can be defined as a population adapted to a particular habitat. The following description relates to their behaviour in New Zealand.

Ladino ecotype

The ladino ecotype, originated in the Lodi-Cremona district near Milan in the Po River Valley, Italy. This ecotype, typified by large organ size (leaves, stolons, roots and flowers), most likly developed by natural selection in irrigated fertile soils from smaller-leaved types from surrounding areas in northern Italy. It is also characterised by being acyanogenic, a property linked to survival of the cold winters experienced in the Po Valley. It tends to have a peak flowering period in late summer.

Large-leaved Mediterranean ecotypes

Characteristically, white clover originating in regions of the Mediterranean where moisture is not limiting for long periods, is large-leaved and highly cyanogenic. Flower initiation is from autumn through winter and ceases in spring, whereas northern European types begin initiating flowers in spring and continue through into summer. In New Zealand these types are often winter-active but in response to high temperatures and drought may be summer dormant. They can have a very distinctive white chevron leaf mark.

Large-leaved types from arable, non-grazed fields

White clover ecotypes originating in situations where defoliation is infrequent, but where shading can occur, tend to be large-leaved and upright. One early cultivar, Kersey, developed in 1924 from a plant selected from a lucerne field in Suffolk, England, typifies this type.

Maritime ecotypes

These are typically medium to small-leaved, moderately cyanogenic types found in climates with mild winters and summers which rarely exceed 30°C.

Free-seeding, heat tolerant ecotypes

In hot and often drought-prone regions, white clover ecotypes tend to be profusely flowering and commonly rejuvenate from seed, so that they behave much like annuals. In southern USA the Louisiana ecotype typifies this white clover type. It is an upright, open, large-leaved form that is cyanogenic.

Northern European - Scandinavian ecotypes

Ecotypes from these regions are typically small-leaved and acyanogenic. The ability of plants to survive winters in these northern regions is related to winter dormancy, their prostrate and small-leaved habit, and low productivity. Acyanogenic plants are less injured by frost than cyanogenic plants (Daday, 1965). They are late flowering and are usually long-day responsive. Northern European ecotypes have little or no white chevron marking. Ecotypes from these northern regions were often used in early breeding programmes. The most frequently used of these ecotypes were Morsø and Strynø, both from Denmark.

High altitude ecotypes

As a type these are very similar to ecotypes from northern Europe, being small-leaved, prostrate and acyanogenic. In response to the effects of early spring cold, they tend to flower in late summer..

Small-leaved heavily grazed ecotypes

Persistent types of white clover found under frequent, intense grazing, they are typically prostrate, small-leaved and densely stoloniferous and are often low yielding. These types, often referred to as 'wild white' clover, were used in the development of cultivars in the early part of this century. One of these still in production in England is Kent Wild White.

Dutch white clover

Although its origin is uncertain, this type was the first used in commerce in Europe and closely followed European colonisation of the New World. It is typified by a very lax open habit, medium leaf size, profuse flowering and low cyanogenesis. As a result of its habit and flowering behaviour it has poor vegetative persistence.

Classification of cultivars

The term 'cultivar' is used to refer to a variety produced by selective breeding. The most recent study comparing a wide range of white clover cultivars (Caradus *et al.*, 1989b) proposed four broad groups with some possible sub-groups. Their description relates to their behaviour in New Zealand.

Small-leaved cultivars

Previously classified as *sylvestre* type (Erith, 1924), these are characterised by small leaf size, prostrate habit, high stolon growing point density and a moderately low (approx. 30-40%) percentage of genotypes that are cyanogenic (having dominance at both substrate and enzyme loci). This group is typified by the cultivar S.184.

Intermediate or medium-leaved cultivars

A large group, containing about 50% of compared cultivars, previously classified as *hollandicum* (Erith, 1924), characterised by medium leaf size and moderately low (approx. 15-40%) percentage of cyanogenic genotypes. Further subgroups could be identified by (a) a high proportion of no white chevron leaf mark (typified by cv Undrom), (b) late flowering (typified by cv Milka) and (c) early and profuse flowering (typified by cv Irrigation). Subgroup (a) tended to come from northern continental Europe and Scandinavia. Cultivars in subgroups (b) and (c) had very diverse origins.

Large-leaved cultivars

Typically large-leaved and highly cyanogenic, this group was previously classified as *giganteum* (Zohary and Heller, 1984). There have been two subgroups identified, (a) profusely flowering (typified by cv Tamar) and (b) sparsely flowering (typified by cv Crau). Few cultivars in either of these sub-groups have their origin in the colder northern European or Scandinavian region.

Ladino cultivars

Characterised by large leaves, but in contrast to other large-leaved cultivars they are acyanogenic. This group was previously classified as *giganteum* (Erith, 1924). Two subgroups have been identified as having (a) a high proportion without a white chevron leaf mark (typified by cv Dusi) and (b) a high proportion with a white chevron leaf mark (typified by cv Ladino Giganteum Lodigiano). All ladino cultivars bred in USA, except cv Tillman, are in subgroup (a). Ladino cultivars are later flowering than the other three groups of cultivars.

Variations within populations

As an outbreeding species all genotypes of white clover are unique, and hence even within populations or cultivars considerable morphological and physiological variation can be observed. In a study (Caradus *et al.*, 1993) of 11 cultivars there were significant ($P<0.05$) differences among genotypes within cultivars for 14 plant characters for 151 of the possible 154 cultivar/plant character combinations. Significant variation was also found for 22 characters among 50 genotypes collected from a 60 year old pasture in North Wales (Burdon, 1980).

There are significant genetic associations for several plant characters within white clover. The most common negative associations are between leaf size and stolon growing point density (Caradus *et al.*, 1989), and between proportion of nodes branching and proportion of nodes flowering (Caradus and Mackay, 1988). Leaf size is positively associated with taproot diameter (Caradus and Woodfield, 1986), internode length, stolon diameter (Caradus *et al.*, 1990a) and canopy height (Caradus *et al.*, 1989).

Genetic variation in seed production ranges from nil, due to either lack of flowering or the production of sterile inflorescences, to an estimated 6000 kg/ha (PTP Clifford, pers. comm.); most New Zealand commercial seed crops produce around 600 kg/ha. Although flowers are predominantly white, flower colour can vary from pink to red and purple (Pederson *et al.*, 1994).

White clover adaptation

From the perspective of cultivar development and plant breeding the importance of genetic variation for morphological and physiological characteristics is in its relationship with adaptation of germplasm to specific biotic and abiotic stresses.

Defoliation

As a forage legume found predominantly in grassland, white clover is frequently subject to defoliation either by cutting or grazing. Leaf size is associated with intensity and frequency of defoliation, with larger leaf size being expressed under lax infrequent defoliation. Much of this variation is due to phenotypic plasticity, but there is a genetic component. As an example, six populations were collected from areas that had been cut at different frequencies and intensities, or had been subjected to heavy treading (Caradus, 1984). Plants from areas that had received infrequent lax cutting were large-leaved and tall with long internodes, whereas populations collected from areas that had been cut frequently or heavily trodden had small leaves and short internodes. These differences persisted after these genotypes had been grown in uniform conditions for two years ($r = +0.90$ for leaflet width, $df = 4$) although the range of leaflet widths had reduced (Table 1).

Edaphic stresses

Genetic variation within white clover has been documented for phosphorus (P) responses in glasshouse (Snaydon and Bradshaw, 1962a; Caradus *et al.*, 1992) and field trials (Snaydon and Bradshaw, 1962b; Caradus and Snaydon, 1986a), aluminium tolerance (Caradus *et al.*, 1991), responses to calcium, magnesium and potassium (Snaydon and Bradshaw, 1969) and salinity tolerance (Rogers *et al.*, 1993).

White clover populations adapted to low-P soils tend to have more fine root (< 1mm diameter) and less very coarse root (> 2mm diameter) than populations adapted to high-P soils, when grown in a uniform environment (Table 2). In a glasshouse study populations from low-P soils had a slower rate of leaf senescence but exported less P from senescing leaves than populations from high-P soils (Caradus and Snaydon, 1986b). In another glasshouse study, populations from low-P soils accumulated more inorganic-P in their leaf tissue when grown at high-P, and were able to reduce these inorganic P levels to lower concentrations when the P supply was deficient (Caradus and Snaydon, 1987).

Climatic stress

Comparison of white clover populations from dry (< 760 mm rainfall) and wet (> 1400 mm rainfall) sites in a uniform environment, has shown that 'dryland' populations are larger-leaved, more cyanogenic, taller and have a wider taproot diameter than populations from wet environments (Table 3).

Latitudinal and altitudinal adaptive clines are well established in white clover (Daday, 1954a, b). Analysis

Table 1. Shoot morphology at time of collection and leaflet width after two years in uniform conditions, of six white clover populations collected from contrasting habitats within a 250 m radius. (Data are from Caradus, 1984)

Site description	At time of collection: Leaflet width (mm)	Petiole length (cm)	Internode length (mm)	After 2 years: Leaflet width (mm)
One cut per year to 15 cm	12.8	16.8	15.5	6.7
One cut per year to 15 cm	13.8	17.1	18.9	6.6
One cut per month to 5cm	5.4	2.3	4.5	5.2
One cut per two weeks to 5 cm	5.5	2.0	6.1	5.4
Kept short by treading	5.1	1.9	3.7	6.0
Cricket pitch	3.8	0.8	2.5	5.4
p	***	***	***	***
$LSD_{0.05}$	1.1	1.8	2.9	0.7

Table 2. Root morphology of white clover populations adapted to low-P and high-P soils when grown in pure swards in a uniform environment. Values are means of two populations (within each population group) and three harvests taken in spring and early summer of the second year's growth. (Data are derived from Caradus and Snaydon, 1986a).

Population Group	Fine root length (cm)	Very coarse root length (cm)	Fine root number
Low-P adapted	591	1.3	493
High-P adapted	369	2.5	286
p	*	**	*
$MSR^{+}_{0.05}$	x 1.51	x 1.45	x 1.51

⁺ minimum significance ratio

of a collection of white clover populations from south-west Europe, grown in a uniform environment, has shown that in this case latitude had a much more pronounced effect than altitude (Table 4). High latitude populations were less cyanogenic, smaller leaved, later flowering, and had poorer spring growth but better persistence in New Zealand than low latitude populations. Most of these differences are probably due to effects of temperature and daylength with changing latitude; high latitude populations being subjected to lower temperatures and longer days. Adaptation to frequent frosting results in natural selection of plants with small leaves, prostrate habit and low cyanogenic reaction (Caradus *et al.*, 1989a). Mediterranean populations are more winter active and summer dormant (Williams, 1987), with larger flowers having longer corolla tubes (an adaptation to different bee species acting as pollinators) and leaves with more pronounced white chevron marking (Daday, 1954a), than northern European populations.

Table 3. Comparison of 6 populations from dry (< 760 mm rainfall) and 6 populations from wet (> 1400 mm rainfall) hill country farms in the Wairarapa, grown as spaced plants at Palmerston North. (Data are from Caradus *et al.*, 1990d).

Population Group	Leaflet width (mm)	Cyanogenesis (%)	Canopy height (cm)	Early flowering (% plants)	Taproot diameter (mm)	Root/Shoot ratio
Dry	10.6	30	3.5	48	3.3	0.33
Wet	8.8	9	2.6	38	2.9	0.32
p	**	**	**	ns	*	ns
$LSD_{0.05}$	0.6	7	0.3	-	0.3	-

Table 4. Means and standard errors of plant characters of populations collected from south-west Europe, grouped by latitude[1] and altitude. (Data from Caradus *et al.*, 1990c).

	Low latitude		Medium latitude		High latitude	
Plant Character	Low alt.	High alt.	Low alt.	High alt.	Low alt.	High alt.
Cyanogenesis (%)	99 ± 1	95 ± 5	72 ± 4	34 ± 5	9 ± 5	9 ± 5
Leaflet width (mm)	20 ± 0.9	19 ± 2.6	19 ± 0.5	16 ± 0.5	18 ± 0.8	14 ± 0.9
Early flowering (%)	55 ± 6	50 ± 11	13 ± 1	8 ± 1	6 ± 3	4 ± 2
Spring growth (0-10 scale)	4.8 ± 0.4	5.0 ± 0.6	4.4 ± 0.1	3.7 ± 0.1	3.4 ± 0.1	2.9 ± 0.1
Survival 18 mth (%)	35 ± 3	21 ± 4	67 ± 3	55 ± 3	86 ± 2	54 ± 7
No. of populations	6	5	44	49	10	9

[1] Latitude: low < 40°; medium 40°-44°; high > 44°. Altitude: low ≤ 300 m; high > 300 m.

Pathogen and pest resistance

Genetic variation in white clover has been documented for virus resistance (Gibson and Barnett, 1967; Pederson and McLaughlin, 1992), stem nematode (Williams, 1972), clover cyst and root knot nematodes (van den Bosch *et al.*, 1993; Pederson *et al.*, 1994) and some slugs and weevils (*Sitona* spp.) (Shakeel and Mowat, 1984). Damage by slugs and weevils was greatest on cultivars that had a low cyanogenic reaction. However, differences in cyanogenic reaction have not been consistently related to damage caused by invertebrate pests (Williams, 1987).

Adaptation to New Zealand Conditions

New Zealand's climate is variable but can be broadly described as maritime or temperate. White clover distribution in New Zealand is constrained principally by drought and low soil fertility; persistence and productivity can be adversely affected by the additional effects of invertebrate pests, diseases, temperature extremes, and poor grazing management. Genetic variation has been observed for tolerance or resistance to most of these stresses. However, tolerance/resistance to a single stress will not necessarily provide a successful forage cultivar. In a grazed pasture, plants must be adapted to the vicissitudes of defoliation and competition from other species.

As has occurred in other countries, initial white clover breeding programmes in New Zealand relied heavily on naturalised populations. Mediterranean germplasm was used to introduce improved winter growth; ladino germplasm has incorporated better pest resistance, principally to some of the nematodes; high altitude and northern European material has provided better frost tolerance; and southern European material has provided better summer growth. The greatest challenge is to combine what initially may seem to be conflicting characters e.g., taproot predominance for dry environments, with a medium to small-leaved type adapted to close grazing, or adaptation to winter cold but an upright habit for growth during spring.

Germplasm naturally adapted to climatic and edaphic extremes tends to exaggerate persistence strategies which are often to the detriment of production. To utilise characteristics aiding adaptation to such environments a compromise is reached balancing production against persistence. This has resulted in recent cultivars with higher stolon growing point densities than older cultivars of comparable leaf size (Caradus *et al.*, 1990b).

Conclusion

The range of genetic variation in white clover is considerable and will provide the opportunity for breeders to improve the distribution of white clover into normally marginal areas. The challenge is to combine adaptation to grazing with adaptation to climate, soil or pest related stresses, while still maintaining yield and persistence. Most cultivars produced have come from an empirical screening procedure and while this will continue to be important, because as a conservative approach it is sure to produce some result, the cultivars of the future need to combine the useful variation now observed in controlled environment studies to gain greater advances and improvements.

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