ABSTRACT

New Zealand populations of Italian and perennial ryegrass were first studied intensively in the 1920s, some 70 years after the initial extensive sowings of the two species in this country. There is a current renewed interest in the potential contribution of old pasture populations to ryegrass breeding programmes.

Past work is reviewed and compared with new data. It is shown that there is considerable genetic variation within the better populations, that some reportedly perennial populations are not perennial, and that there has been interesting development in hybrid types. However, there is no evidence of populations with mean performance superior to those of current cultivars.

KEYWORDS

Italian ryegrass, perennial ryegrass, hybrid ryegrass, ecotypes, field populations, ecotypic differentiation, grazing management.

INTRODUCTION

Perennial, Italian and hybrid ryegrass (Lolium perenne, L. multiflorum and L. x hybridum) may remain in New Zealand pastures for 20 years or more. Seed lines and plants taken from old pastures have been studied and used as sources for breeding programmes. This paper compares previous work with recent experience and new data.

The ryegrasses were sown extensively in New Zealand from the 1850s and by 1900 most seed used was locally grown (Cockayne 1912). Their importance has increased with the use of fertiliser and they now dominate well managed swards in all intensive pastoral areas. They are also present in swards dominated by other grass species, for example, in predominantly Agrostis tenuis swards in moist infertile hill soils and in Pennisetum swards in the warm north. Perennial ryegrass pastures are maintained under drier conditions than are usual for the species in Europe.

Levy and Davies (1929, 1930a, b) studied seed lines available in New Zealand in the 1920s, and their best perennial populations became the basis of the first certified perennial ryegrass strain in 1930. Certified perennial ryegrass was continuously improved until 1960, when it was named Grasslands Ruanui. More recently, interest in old field populations has been renewed. The perennial cultivars Grasslands Nui and Yates Ellett were derived in the 1960s from an old (60 year) population at Mangere (Fig. 1), and the success of these cultivars has spurred the collection and testing of other populations.

Figure 1. Location of old pasture populations.
EARLY NEW ZEALAND RESEARCH ON RYEGRASS STRAINS

Starting in the late 1920s, ryegrass seed lines from a wide variety of sources within New Zealand and overseas were compared, both in small broadcast plots and as single plants, at a single site (Levy and Davies 1929, 1930a, b; Levy 1932; Levy and Saxby 1933). Just as Turesson (1922, 1925), using similar methods, had recognised ecotypes within several wide-ranging heterogeneous species, Levy and coworkers distinguished different population “types” within the ryegrasses. Five population types of perennial ryegrass were described, ranging from the elite (fine leaved, densely tillered, reliably persistent) Hawkes Bay and Poverty Bay type, to a poor (open, free-seeding), false perennial type characteristic of South Island sources (Levy and Davies 1930a, b). The reputed superiority of North Island populations had been alluded to by Cockayne (1912).

The best New Zealand perennial seed lots were superior to any imported lines studied. Levy (1932) concluded that in the 60-80 years in which the species had been used in New Zealand, different types had evolved as a consequence of differences in farming practices, and to a lesser extent climate and soil factors. The elite Hawkes Bay and Poverty Bay type was ascribed to the influence of a system of long term, closely grazed pastures imposing natural selection for a dense persistent type; the short-lived false perennial was ascribed to the influence of arable ley-farming favouring an opportunist free-seeding type.

The use of well-defined types by Levy and Davies to describe the variation found within the ryegrasses implied homogeneity within and discontinuity between populations. This was, however, tempered by their single spaced plant trials which clearly showed variation between individuals within populations, thus allowing selection and culling of individual plants, in the development of improved pastoral cultivars.

Wide variation within lines was particularly apparent within the Italian ryegrasses, in which Levy and Saxby (1933) found no evidence for the development of distinct types and no lines superior to imported (British) cultivars. Subsequent breeding involved largely imported material.

The lack of ecotypic differentiation within the Italian ryegrasses in New Zealand by the early 1930s was attributed to the wide distribution and mixing of often unreliably labelled seed lines so that selection was acting on a continually changing genetic base. Yet Levy (1932) referred to high production land of dominantly Italian ryegrass that had not been ploughed or sown for over 30 years. There is now good evidence that within much shorter time spans, natural selection has led to changes in population structure within short-term ryegrasses in New Zealand (see below, Brougham et al., 1960).

RECENT WORK WITH PERENNIAL RYEGRASS

Comparison of lines

Results from a small plot grazing trial comparing 7 old field populations with cultivars Nui and Ruanui illustrate variation in yield (Table 1). Persistence and other quantitative traits also vary in this and other experiments, but no populations out-perform the best cultivars. Two other features are regularly observed.

- New Zealand populations of perennial ryegrass are early flowering and there is no great variation between them in flowering date.
- Populations from old swards harbour a high frequency of the lolium endophyte, Acremonium lolii (Latch and Christensen 1982), and yield and persistence are poor if it is lost. Latch (pers. comm.) and Easton found the endophyte to be present in British and French populations but not as generally as in New Zealand.

Variation within populations

Genetic control of variation within populations was studied by growing diallel families of Ruanui and old field collections from Sandon (Manawatu) and North Canterbury. For each population, 16 plants were interpollinated in four 4-parent diallels. Data were taken from small (0.5 m²) plots sown with bulked reciprocal full-sib families (Table 2). The North Canterbury families all harboured the lolium endophyte; the Ruanui and Sandon families were almost free of it.

There were significant mean differences between populations for most characters, the Sandon population being open in habit, slow growing and slow in autumn recovery. This population has performed poorly in several of our trials. Levy and Davies (1930a,b) listed Sandon ryegrass as a major group of seed lines, many very good but including some which were poor. The endophyte status of different lines may account for some variation in persistence and vigour, but not in habit. The North Canterbury population was a little more dense and prostrate than Ruanui and grew less quickly. It conforms to Levy and Davies’ description of a superior (elite) type.

For 7 of the 12 data sets there was significant variation

Table 1. Annual yield of perennial ryegrass in small plots (kg/ha) at Palmerston North 1983/84'.

<table>
<thead>
<tr>
<th>Nui</th>
<th>Ruanui</th>
<th>Field populations</th>
<th>Springburn</th>
<th>Sandon</th>
<th>lsd</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mean of 14 lines)</td>
<td>(mean of 13 lines)</td>
<td>(mean of 7 lines)²</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>11386</td>
<td>10330</td>
<td>10391</td>
<td>11381</td>
<td>9348</td>
<td>605</td>
</tr>
</tbody>
</table>

¹ Data courtesy J. Lancashire
² From Sandon (2), Springburn (2), Waipara, Rangiora, Poverty Bay
Table 2. Significance of variance in analysis of diallel populations.

<table>
<thead>
<tr>
<th></th>
<th>Between populations</th>
<th>Between families</th>
<th>Ruanui</th>
<th>Nth Canterbury</th>
<th>Sandon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Measured height</td>
<td>Oct 81 ***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Density note</td>
<td>Mar 82 ***</td>
<td>May 83 ***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth note</td>
<td>Jan 82 ***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn recovery note</td>
<td>Mar 83 ***</td>
<td>May 83 ***</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rust note</td>
<td>Jan 82</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habit note</td>
<td>Oct 81 ***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf shape note</td>
<td>Oct 81 ***</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* significant at 5% probability level
*** significant at 0.1% probability level

gca — general combining ability
sca — specific combining ability

between families within populations, no less in Ruanui, a 7-parent synthetic cultivar, than in the field populations. General combining ability (GCA) variance was significant in 15 of 36 situations (in some cases when overall family mean square was not); specific combining ability (SCA) in only 5. In several cases, one or two GCA means for individual parents were very distinct. The priority of GCA variance accords with the literature for perennial ryegrass (Breese and Hayward 1972).

The lack of any variation for the rust score is not typical of work with field populations. The trait means for the North Canterbury population always fell within the range of family means for Ruanui. For the Sandon population they fell outside in 3 cases, reflecting its tall coarse growth and its dying off in late summer. However the field populations, particularly North Canterbury, included families and diallel array means (half-sib families) of very good performance.

Hill country populations

Forde and Suckling (1980) studied perennial ryegrass collected in moist hill country. The 60 site populations varied in morphology and heading date (one population was 9-14 days later than Ruanui), but 81-94% of phenotypic variance was within the populations. No characteristic “hill country type” could be discerned and some persistent plants did not conform to Levy and Davies’ description of a “true perennial” ryegrass.

Seed from this hill country collection was harvested after open pollination of the 60 populations in one block and a structured sample of half-sib families was grown as spaced plants. Between family variance was generally significant whereas the variance of population means was not (Table 3). This accords with Forde and Suckling’s analysis of phenotype variance and has direct bearing on breeding methods. Individual plants cannot be identified and assessed in a hill country sward. The unit of assessment must be the plot. For the first attempt to exploit this material each plot was planted with a site population. The within-population variation was hidden within plots and little was achieved. Current experiments comparing rows sown to half-sib families appear more encouraging.

RECENT WORK WITH ITALIAN AND HYBRID RYEGRASSES

Many old ryegrass pastures have proved to be essentially Italian or hybrid ryegrass. The dominance of short term ryegrasses in such pastures is maintained by natural reseeding. These pastures have been noted to show rapid autumn recovery from summer drought and good growth in winter, spring and early summer.

Spring and winter growth of several old field populations of Italian and hybrid ryegrasses, scored on spaced plants at Palmerston North, are shown in Table 4. Productivity is compared with Grasslands Manawa (Lolium

Table 3. Mean squares in analysis of hill country structured sample.

<table>
<thead>
<tr>
<th></th>
<th>Population</th>
<th>Family within population</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Degrees of freedom</td>
<td>24</td>
<td>75</td>
<td>99</td>
</tr>
<tr>
<td>Growth in autumn</td>
<td>4.05</td>
<td>3.54*</td>
<td>2.47</td>
</tr>
<tr>
<td>Rust in autumn</td>
<td>1.52</td>
<td>2.00*</td>
<td>1.12</td>
</tr>
<tr>
<td>Winter growth</td>
<td>5.57</td>
<td>3.75*</td>
<td>2.55</td>
</tr>
<tr>
<td>Spring growth</td>
<td>6.68</td>
<td>6.49*</td>
<td>4.22</td>
</tr>
</tbody>
</table>

* Significantly greater than the error mean square, P < .05
Table 4. Growth scores of Italian and hybrid ryegrass field populations compared with Grasslands Manawa and Grasslands Paroa at Palmerston North, planted autumn 1980.

<table>
<thead>
<tr>
<th></th>
<th>Manawa</th>
<th>Paroa</th>
<th>Field populations (mean of 5 lines)</th>
<th>Taupaki</th>
<th>Whangarei</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring 1980</td>
<td>100</td>
<td>113</td>
<td>103</td>
<td>106</td>
<td>102</td>
</tr>
<tr>
<td>Winter 1981</td>
<td>100</td>
<td>31</td>
<td>105</td>
<td>150</td>
<td>49</td>
</tr>
<tr>
<td>Winter 1982</td>
<td>100</td>
<td>38</td>
<td>92</td>
<td>107</td>
<td>37</td>
</tr>
</tbody>
</table>

1 From Inglewood, Ngarua, Te Puna, Urenui and Thames

Table 5. Growth scores (± SEM) of progenies of selections from short term ryegrass field populations (Table 4), compared with Grasslands Manawa planted in autumn 1983 in rows at Palmerston North.

<table>
<thead>
<tr>
<th></th>
<th>Manawa</th>
<th>Te Puna</th>
<th>Inglewood</th>
<th>Taupaki</th>
<th>Thames</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st winter</td>
<td>100±13</td>
<td>122±13</td>
<td>122±9</td>
<td>128±7</td>
<td>121±4</td>
</tr>
<tr>
<td>2nd winter</td>
<td>100±9</td>
<td>136±9</td>
<td>132±6.5</td>
<td>128±5</td>
<td>131±3</td>
</tr>
</tbody>
</table>

x hybridum), and in some cases is consistently better. Within population variability was an important component. In the poorer populations all plants were depauperate in the second winter, whereas in the better populations vigorous plants persisted alongside failing neighbours.

High yielding, persistent and rust free plants from this trial were included in an isolation of short rotation ryegrass, and their progeny compared in closely planted rows (Table 5). The high progeny mean performance confirms the heritable nature of the variation in the populations and the presence of valuable material in them all.

The pastures from which the samples were taken were all sown down 20 or more years ago and have been managed to allow considerable growth between grazings and some seed set and shedding in the summer. A collection from one such pasture in the Orini district of the Waikato has formed the basis of Concord Italian ryegrass, first released in 1985. Concord, not used in these trials, is the first release of an Italian ryegrass cultivar based on an old field collection.

**DISCUSSION**

The wide geographic and ecological distribution of ryegrasses in New Zealand has been associated with some ecotypic differentiation. This has taken place over a relatively short time span (30-100 years) and in response to farming practices. It remains possible, however, that observed differences between field populations in yield, heading date, habit and rust susceptibility derive, in part, from diverse original seed sources.

Recent results diverge from those of Levy and coworkers, first, in providing evidence of differentiated high performing Italian and hybrid ryegrass populations of New Zealand origin, and second, in questioning their contention that only very dense, fine leaved perennial ryegrass of the Hawkes Bay type is reliably persistent (Forde and Suckling 1980). This view is belied in practice by the success of cultivars Nui and Ellett, derived from the more open, large-tillered Mangere population.

Levy and coworkers' published studies were of seed lines available in commerce. Their Canterbury and other southern perennial ryegrass lines were harvested under an arable system of short term leys. Their Hawkes Bay and other North Island lines came from permanent pastures grazed by sheep. Recently studied Canterbury lines are also from old grazed pastures and therefore have a comparable history and show similar characteristics to the classic Hawkes Bay material. Current lines from Hawkes Bay and Poverty Bay such as Takapau and Manutuke perennial ryegrasses are clearly the very material from which the first pedigree programmes began.

Levy and Davies (1930a,b) described a more open perennial type which they considered inferior but truly perennial. It was rather more prostrate and tended to a blue-green rather than deep green colour. This does not describe the Mangere population.

The Italian and hybrid-derived lines observed by Levy and Saxby, commercial lines available in the 1920s, were low yielding, stemmy, free-seeding and short-lived. The differentiated populations they do not seem to have observed — high yielding, persistent, leafy Italian and hybrid sources and more open larger tillered perennial — are from North Island dairying districts where pastures are long-standing and under a more lax grazing management allowing expression of a taller yet leafy habit. Perhaps these populations had not developed by that time. Dairy farm management changed greatly in the following decades and there are now paddocks, some based on certified seed lines of the 1930s and 1940s, which have been subject to controlled rotational grazing by dairy cows since that time.

Experimental work has shown rapid changes in genetic structure of ryegrass populations in response to different grazing managements (Brougham et al. 1960; Brougham and Harris 1967; Harris and Brougham 1970). A mixed perennial, short rotation ryegrass population (Brougham and Harris, 1967) changed, within 4 months, towards a perennial type population under frequent and intensive
grazing, and an Italian type population under less intensive and long spelled grazings. Rapid population differentiation has also been seen in other cross-pollinated grasses, including perennial species (Bradshaw 1959; Davies and Snaydon 1973; Antonovics 1971).

Within one such species in Australia, however, McWilliam et al. (1971) noted a lack of marked population differentiation. A similar evolutionary conservatism has also been noted in some New Zealand ryegasses (Levy and Saxby 1933; Forde and Suckling 1980), despite wide genetic variability and sufficient selection differentials. This may be attributed to use in the past of variable or unreliably labelled seed lines (Levy 1932), broad adaptability of individual genotypes and, especially in perennial hill country swards, contrasting microsites and reduced opportunities to regenerate from seed. Population renewal in hill country even with deliberate oversowing may be negligible (Chapman and Campbell 1986).

Populations of New Zealand origin, such as the dense Hawkes Bay type, the Mangere population and good quality Italian material have all furnished ryegrass cultivars of value to farmers. The data shown that the genetic variation within all populations is large, often obscuring differences between them. Complemented with overseas material, this variation will serve for further breeding progress.

REFERENCES


SYMPOSIUM DISCUSSION

Dr R.D. Burdon, Forest Research Institute

Did the field collections vary in the incidence of endophyte.

Burgess

It is very likely that all the old pasture populations in New Zealand have very high endophyte levels.

Burdon

Could there have been differential loss of endophyte in the storage of the seed before the experiments?

Burgess

Provided seed is stored at cold temperatures (5°C) or at low seed moisture levels (less than 10%), it is our experience that the endophyte will not be lost. It will be lost very rapidly, however, (within one year) at ambient temperatures when seed moisture levels are high.

Dr E.J. Walsh, University College, Dublin

A number of years ago there were a couple of studies in the European situation indicating that trends in yield improvement in forage grasses would indicate that there had been very little improvement in annual production over a good few years. Yesterday and this morning we have heard that it is relatively easy to improve both yield and quality. Is there something different in the southern hemisphere?
Burgess
We are looking at relatively limited increases, even in the very best populations.

Easton
We would not claim that we have had any more success than European ryegrass breeders in increasing yield per se, and I think looking at percentage increases on growth margins is rather dangerous. We show the variation increases but that does not necessarily represent the same percentage increase in dry matter. In addition, there are many experiments worldwide showing that dry matter yield has a high additive genetic variance, but there seems to be an enormous genotype and environmental interaction. The problem is that yield inheritance is very complex. The other point I wish to make in perennial ryegrass is that the main difference that was observed is that one population is poor and any breeding programme would eliminate that population very quickly.

Dr M.D. Wilcox, Forest Research Institute
Obviously some of the old pastures are resources for breeding programmes. What has been done to systematically identify the most valuable areas of variation and is anything being done to conserve these areas? I am just wondering if eventually the whole countryside will be taken over by the modern breeding resources.

Burgess
Certainly collections of old pasture populations would be valuable for breeding programmes.

There are two ways of maintaining old pasture populations as a resource — we can collect plant material and raise seed or collect seed from the pasture. This has been done, and there is a seed bank in Palmerston North. The other way is to maintain old pastures as old pastures and simply not let some areas be resown with new cultivars.