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THE GENETICS OF NATURALIZATION: A COMPARISON OF MORPHOLOGICAL VARIATION WITHIN AND BETWEEN POPULATIONS OF *AGROSTIS CAPILLARIS* L. AS AN EXOTIC IN NEW ZEALAND AND AS A NATIVE IN BRITAIN[1]

Summary: Previous work in New Zealand has shewn that genetic variation within populations of *Agrostis capillaris* can be comparable to that between populations, even between populations over a very wide environmental range. To determine whether this reflects the recent advent of *A. capillaris* in New Zealand, with a small founding gene pool and a short time for ecotypic differentiation, populations from a comparable range of environments were sampled randomly in the same way in Britain. Populations were grown in comparable conditions in the two countries, but to ensure comparability only proportional variation was examined. Characters used in the assessment of within- and between-population variation were stem+sheath length, lamina length, lamina width and relative growth rate.

Within populations, there were highly significant genotypic differences, especially in the British populations. Differences between populations were rather greater than those within-populations, and for lamina length this was significant in both countries.

For both Britain and New Zealand, there were cases where the two genotypes sampled from a population were similar in a particular character. In some cases, populations from comparable habitats in the two countries were similar to each other.

For the three morphological characters, total genotypic variation over all populations sampled was greater in Britain than in New Zealand. For some characters this was due to between-site variation, and for some to within-site variation.

It is concluded that some of the evidence for non-adaptation in *A. capillaris* in New Zealand is caused by a more limited gene pool, and insufficient time for sorting of genotypes into habitats.

Keywords: Adaptation; selection; exotic species; genetic variation.

Introduction

How fast and how efficiently does micro-evolution occur, adapting species ecotypically to local conditions? (Al-Hiyaly, McNeilly and Bradshaw, 1990; Macnair, 1989). Opportunities to answer this question are rare.

One view of micro-evolution is that ecotype formation is efficient and ubiquitous. For example, "the pattern of [genetic] differentiation follows the pattern of the environment meticulously" (Bradshaw, 1972); or "species with wide geographic ranges almost always develop locally adapted populations called ecotypes that have optima and limits of tolerances adjusted to local conditions" (Odum, 1971). If the selective pressure is strong enough, ecotypic tolerance can evolve quickly: within four years of exposure to copper (Wu, Bradshaw and Thurman, 1975), within six years of lime application (Snaydon and Davis, 1972) or within seven years of herbicide application (Gressel, 1984). However, most of these situations seem to be one-character or even one-gene adaptations to extreme selection pressure (Verkleij *et al.,* 1991).

The opposite point of view is that adaptation is not so tightly coupled to environmental conditions. Fowler (1990) expressed the concept of disorderliness in plant communities, and suggested that the concept could apply also to selection within populations. There is evidence for such genetic disorderliness in *Agrostis capillaris* L. in New Zealand - there is often as much variation within populations as between (Rapson and Wilson, *in prep.*), and when population differences can be seen they are very difficult to relate to environmental trends (Rapson and Wilson, 1992a). Reciprocal transplantation (Rapson and Wilson, 1988) shewed

[1] GLR thanks Dr W.G. Lee, of Landcare, Dunedin, for assuming the role of Editor with respect to this submission.

that this failure to form ecotypes was seen in the adaptation of the whole genotype to its environment: in spite of considerable within-population variation in performance, and in spite of strong environmental differences between sites, there was very little evidence of adaptation to a genotype's home site. There are two likely reasons for this:

a. non-adaptation is common; or
b. population genetic structure is different in *A. capillaris* in New Zealand because it was introduced relatively recently (*c.* 1853 - Rapson and Wilson, 1992b); there is therefore a limited species pool (the founder effect), and there has been insufficient time for selection to sort genotypes into habitats.

We aimed to distinguish between these possibilities by repeating the New Zealand work within part of the geographic range within which *A. capillaris* is native, in Britain. Though we cannot know just where the original genotypes introduced into New Zealand came from, doubtless some came from Britain, and the climates are comparable between the two areas. However, in some respects climate matching was impossible, e.g.:

- no area in Britain has rainfall as low as that at the Alexandra, New Zealand site;
- because of the climate, *A. capillaris* does not reach the same altitudes in Britain that it does in New Zealand. (In both cases the high altitude site was within a few metres of its upper altitudinal limit.)

Thus, the aim was to cover a comparable range of habitats, not to duplicate habitats exactly (Table 1).

Work comparing genotypes from different continents is rare, presumably because of the difficulties associated with statuary quarantine restrictions. We therefore grew the plants under similar experimental conditions in the two countries, and used log transformation of variates to examine only proportionate variance. In determining characters such as relative growth rate there is inevitably a large estimation error. Our response to this was to sacrifice the number of genotypes collected from the field, in order to be able to use sufficient experimental replicates of each genotype to obtain reliable means. We ensured these were genuine replicates by growing each replicate separately in the multiplication and preconditioning phase as well as in the experiment itself.

Methods

Population sampling

Britain

Five populations were sampled, four in west Wales and one in eastern England to include a lower-rainfall site (Table 1). A 10 m x 10 m plot was laid down at each site. Within the plot, a 0.1 m x 0.1 m quadrat was randomly placed. If *A. capillaris* was present, the tiller nearest to the centre of the quadrat was taken. Further quadrats were randomly placed within the plot until two tillers had been obtained. (Four random selections were made from the Dorglwyd population, but to avoid bias only the first two are included in statistical analyses.) The tillers

Table 1: *The locations of the British and New Zealand sites sampled.*

Habitat type	Britain	New Zealand
Dry, open (under the driest climate in the country)	Lakenheath Warren, rainfall = 590 mm per year, moderate rabbit grazing	Alexandra, rainfall = 339 mm per year, moderate rabbit grazing
Shaded (under the shade of conifer trees)	Dorglwyd, under *Pseudotsuga menziesii,* light = 13% of that in the open, not disturbed	Ross Creek, under *Pinus radiata,* light = 30 % of that in the open, not disturbed
Coastal (at the lower altitudinal limit of *A. capillaris*)	Tan-y-Bwlch, 12 m a.s.l., grazed by stock	Waianakarua, 6 m a.s.l., grazed by stock
High elevation (at the upper altitudinal limit of *A. capillaris*)	Pumlumon Fawr, 645 m a.s.l., lightly grazed	Rock and Pillar Range, 1060 m a.s.l., lightly grazed
Soil stress	Goginan mine, in heavy-metaliferous soil, recently disturbed	Sutton Lake, in saline soil, grazed by stock

were grown in randomised layout in a greenhouse, in high-fertility John Innes Potting (J.I.P.) Compost No. 2 (Whitehead, 1957), with supplementary heat and light. Ten sub-clones were taken from each genotype and grown in separate pots, again in a randomised block design. These 10 subclones were used as replicates, ensuring that variation in pre-experiment propagation conditions was included in the statistical error, not as genotype differences. Repotting in J.I.P. occurred twice more before the experiment.

New Zealand
The populations sampled were all in southern New Zealand, maximising the climatic similarity with the British populations sampled. Tillers were sampled and propagated in exactly the same way, except that there were 12 replicates.

Character evaluation

Britain
For evaluation of characters, the genotypes were grown in a ventilated greenhouse in mid summer (June-July), as in the experiment of Wilson (1988), in J.I.P. No. 2. There were three harvests. During propagation over winter the plants had been kept under long day conditions (16 hours) to prevent floral induction, and no flowering occurred.

Morphological and growth characters can change with plant growth; to ensure the values recorded were not critically dependent on the time of measurement, two subsequent harvests were taken, at 17 and 28 days after the first. Morphological characters were measured on the plants taken at both these latter harvests. The characters measured were:

- stem+sheath length (from the ground along the stem/sheath to the ligule),
- lamina length,
- lamina width,
- shoot RGR (relative growth rate).

To standardise, but allow for tillers at different stages in the plastochron (leaf production cycle), the morphological characters were measured on the second or third emerged leaf back from the apex, whichever had the longer lamina. The population x harvest and genotype x harvest interactions were non-significant for all three morphological characters ($P > 0.2$ in every case), and the mean of two harvests is used, giving an increase in effective replication.

Growth rate was measured as shoot RGR to avoid errors due to variable efficiency of root recovery; Shipley (1989) shewed that in herbs it can be very highly correlated with total RGR. RGR was slightly lower over the longer (28 day) period. Whilst this may have been due to ontogeny, since there was no interaction with population or with genotype, weather fluctuation seems as likely a cause. The absence of interactions made it appropriate to use the mean of the two values.

New Zealand
For character evaluation, the genotypes were grown in a growth room at an irradiance of 791 $\mu E\ m^{-2}\ s^{-1}$ for a 14 hour photoperiod. The rooting medium was sand, with Hoagland's nutrient solution supplied three times per day. There were two harvests, the first five days after planting, and the second when the plants had reached the ontogenetic age of 15 tillers (20-34 days later). No flowering occurred. Character evaluation was identical to that in the British experiment.

Statistics

Because growth conditions in the two countries were unavoidably different, raw values are difficult to compare. However, *proportional* differences should be comparable. We therefore used $\log_e$ transformation for all variates. The differences between sites were tested against differences between genotypes within sites, giving a variance ratio (V.R.), effectively a Random Effects model. From the variances (mean squares), i.e.:

- differences between sites (V_s),
- differences between genotypes within sites (V_g),
- environmental differences [between replicates within genotypes] (V_e),

components of variance were calculated:

- Variance between sites: (V_s - V_g) / (number of genotypes per site x number of replicates),
- Variance between genotypes: (V_g - V_e) / (number of replicates).

Results

In Britain the two highest ratios of between-site to within-site variation (V.R.) were for Lamina length and for RGR (Table 2), with the difference being significant for Lamina length but not for RGR (P = 0.068). In New Zealand, the same two characters again shewed the highest V.R. values, and again that for Lamina length was significant but that for shoot RGR was not (P = 0.098). (There was a significant difference between the New Zealand sites in total [shoot + root] RGR, but shoot RGR is used here for comparability with the British experiment.) Differences between genotypes within populations were, in both countries, most highly significant for Stem+sheath length and for Lamina width. They were significantly different for the other two characters within the British populations.

Table 2: *Analyses of variance for four characters of* Agrostis capillaris *in Britain and New Zealand, testing variation between sites against that within.*

	Britain			New Zealand		
	Genotypes within sites	Between sites		Genotypes within sites	Between sites	
Character	*P*	V.R.	*P*	*P*	V.R.	*P*
Stem+sheath length	<0.000001	3.484	n.s.	0.00072	1.168	n.s.
Lamina length	0.000050	6.000	0.038	n.s.	7.520	0.024
Lamina width	<0.000001	1.630	n.s.	0.000001	2.170	n.s.
Relative growth rate	0.048	4.387	n.s.	n.s.	3.563	n.s.

Table 3: *Components of variance (expressed as s.d., from log transformed data) for four characters of* Agrostis capillaris *across 5 sites in each of Britain and New Zealand, and for the pooled variation for two genotypes within each.*

	Total		Site		Genotype	
Character	Britain	N.Z.	Britain	N.Z.	Britain	N.Z.
Stem+sheath length	0.749	0.422	0.397	0.088	0.344	0.268
Lamina length	0.315	0.190	0.190	0.122	0.110	0.042
Lamina width	0.366	0.173	0.127	0.076	0.223	0.093
Relative growth rate	0.144	0.135	0.084	0.097	0.049	-0.072

In Britain, for each of the four characters (Fig. 1) there was notable similarity between the two genotypes from one particular population, as implied by trend in V.R. above. However, within-population similarity was shewn in different populations for different characters. For Stem+sheath length the two Soil-stress (heavy metal) genotypes were similar; for Lamina lengths the two Dry site genotypes stood out; in Lamina width the two Coastal genotypes were very similar. The two Soil-stress (heavy-metal) genotypes had the lowest RGR values, though significantly different from each other.

Amongst the New Zealand populations, in Stem+sheath length the two High-altitude sites were similar. In Lamina length those two were similar again, and also the two Soil-stress (salt) and Coastal genotypes. In Lamina width, only for the Shaded site were the two genotypes not significantly different from each other. In RGR, the two High-altitude genotypes were similar, and also the two Coastal site genotypes.

Although we intended only to cover a similar environmental range in the two countries, not to replicate habitat conditions exactly between matching British and New Zealand sites, and bearing in mind that for means (as opposed to proportional variance) the non-identical evaluation conditions are a limitation, some indication of patterns can be seen. In both Britain and New Zealand the Dry site population had short stem/sheaths bearing narrow laminae. The Shaded site populations had an RGR higher than most other genotypes in both countries, but the notably long Stem+sheath found in two British genotypes was not observed in our small sample of the New Zealand shaded population. At least some of the Coastal population in both countries shew long laminae of medium width, and RGRs in the upper half of the range recorded.

For the three morphological characters, total proportionate genotypic variation (within- plus between-sites) was considerably greater in Britain than in New Zealand (Table 3). For RGR, there was only a small difference, though still in the same direction. The apportioning of the genetic variation was different in the three morphological characters. For Stem+sheath length the greater genetic variation in Britain was mainly between-site; for Lamina length and Lamina width the main difference was in the within-site variation. In RGR, the British and New Zealand results were comparable, with very low within-population variation (the estimate for the New Zealand data was spuriously less than zero, a result that is "not unexpected for a component of variance that is very small": Nyquist, 1991).

Discussion

Low genotypic variation in exotics

There have been previous reports of reduced within-species variation in exotic plant species, compared to native species in the same area. Taggart, McNally

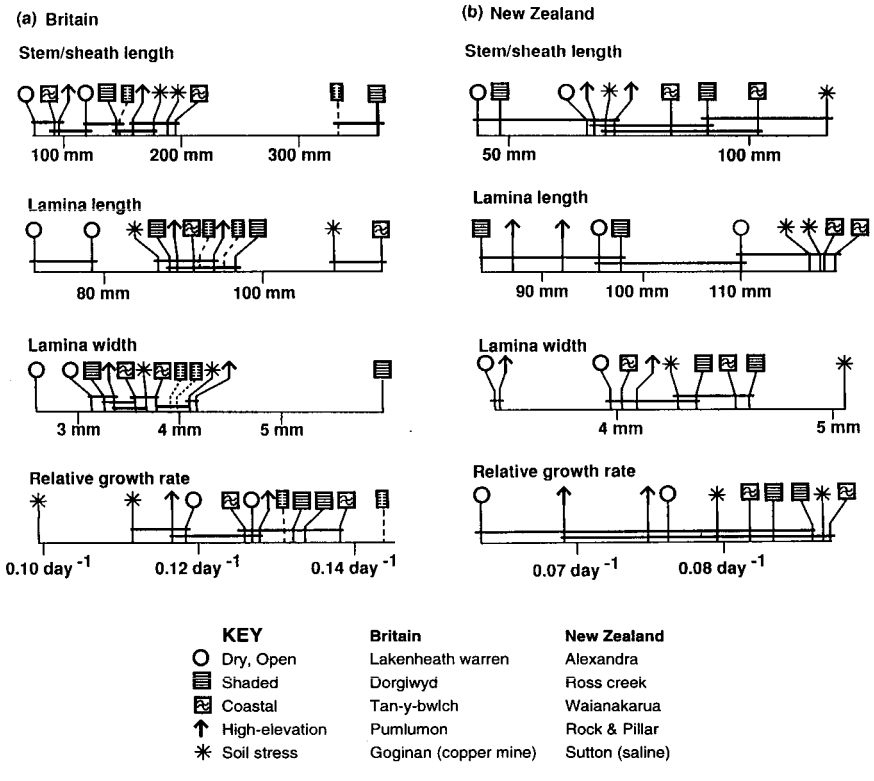

Figure 1. *Characters of genotypes from five populations of* Agrostis capillaris *in Britain, and from comparable populations in New Zealand, displayed along the x-axis. Any pair of genotypes connected by a horizontal line is not significantly different by Duncan's New Multiple Range Test. The broken symbols for the British shaded population indicate the two extra genotypes sampled at Dorglwyd.*

and Sharp (1990) found 'low' variation in Irish populations of the introduced *Sarracenia purpurea*, but this was an extreme case since the founder population was only 2-4 plants. Rejmanek, Thomsen and Peters (1991) found that out of 23 rDNA variants present in native Eurasian *Avena barbata*, nine were not found in samples from California, where it has been introduced. However, as often in studies of exotics, it is difficult to know from which part of the native range the introductions originated.

Agrostis capillaris is first recorded as being introduced into New Zealand in 1853 (Rapson and Wilson, 1992b). However, many seed mixtures were imported from Europe early in the twentieth century, and it would have been a common component of such mixtures, either deliberately or as a contaminant (Hubbard and Wilson, 1988). Therefore, a large gene pool was probably introduced. For example, the experiment of Whalley, Khan and Bradshaw (1974), sowing commercial *A. capillaris* seed on mine waste and shewing that a small proportion of the genotypes were heavy-metal resistant, was performed with seed from New Zealand. However, we found that the total estimated genotypic variation in New Zealand was still less than that in Britain.

Ecotypic differentiation in exotics

Moore (1967) hypothesised that ecotypic differentiation had not occurred in weedy species introduced to Australia, claiming lack of genetic change in *Trifolium subterraneum* and lack of environment-related variation in *Phalaris tuberosa*. Counts and Lee (1988) found that in Ontario very little genetic change had occurred in introduced populations of wild rice after 50 years.

On the other hand, some workers have found evidence of genetic differentiation. Ganders (1990) shewed a correlation between altitude and the frequency of cyanogenic plants of *Trifolium repens* introduced into Canada, paralleling similar

correlations in its native European range. Rice *et al.* (1992) found genetic differentiation between *Bromus tectorum* populations, which could be related to habitat. Wood and Degabriele (1985) found variation between Australian populations of *Echium plantagineum*; they could relate variation in some characters to climate, suggesting ecotypic differentiation was occurring. Novak and Mack (1993) found allozymic variation between and within exotic populations of *Bromus tectorum* in North America, though between-population variation was less than in native populations. However, such allozymic variation may be selectively neutral (Skibinski, Woodward and Ward, 1993). Thus, suggestive evidence is available for ecotypic differentiation in exotics. In the present work, there was only slight evidence of such variation.

Non-adaptation

Recent evidence suggests that in plants within-population variation is often as great as between-population variation. This can be true for morphological characters (e.g., Robson, Scagel and Maze, 1988), physiological characters (e.g., Garbutt, 1986), chromosomal characters (e.g., Schaal, 1985), allozymic characters (e.g., Comps *et al.*, 1990), and in characters that directly affect fitness (e.g., Ennos, 1985). Some earlier investigations may have given spurious evidence for ecotypes because the sampling was not strictly random.

For *Agrostis capillaris* in New Zealand, Rapson and Wilson (1992b) found variation within populations comparable to that between populations for morphological characters. Rapson and Wilson (1988) shewed by reciprocal transplants the same situation for fitness in the range of environments. The high amount of variation within populations, both in Britain but especially in New Zealand, is further confirmation for non-adaptation in *A. capillaris*.

Conclusion

We conclude that some of the evidence for non-adaptation in exotics arises from a more limited gene pool and incomplete sorting of genotypes into habitats. There is some conflict with the rapid micro-evolution found by workers such as Wu *et al.* (1975), Gressel (1984) and Snaydon and Davis (1972). The difference is unlikely to be due to a difference in the section pressure, since our habitats (Table 1) covered a wide environmental range, including habitats stressful in various ways. However, the rather low heritabilities shown for similar characters by New Zealand *A. capillaris* (Rapson and Wilson, *in prep.*) will slow the rate of ecotype evolution (Bradshaw, 1984). It may be that adaptation to the habitats considered here would involve gene complexes that require much more evolutionary time than, e.g., the selection of genes for heavy-metal tolerance. It is also possible that the habitats occupied by *A. capillaris* in New Zealand are habitats that are different, physically or biotically, from those the species encounters in Britain (Wilson, Hubbard and Rapson, 1988), so that the genepool that reached New Zealand, or even the whole species, does not contain the genetic base to fully adapt; i.e. although there is genetic variation it is, as Bradshaw (1991) envisaged, 'largely irrelevant'.

We can support Bradshaw's (1984) comment: "we all tend to expect that the outcome of evolution is adaptation. But such a conclusion is simplistic and even naive".

Acknowledgements

Some of the work was done at the Department of Biological Sciences, University College of Wales, Aberystwyth, Wales, whom JBW thanks for facilities and hospitality. The New Zealand work was supported by the Miss E.L. Hellaby Indigenous Grasslands Research Trust. We thank J.J. Williams and the staff of the Botany Garden, U.C.W., for assistance, W.G. Lee for collecting the Lakenheath material, P.J. Grubb for advice, A.D. Bradshaw, W.G. Lee and A.J. Watkins for comments on a draft.

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KEY	**Britain**	**New Zealand**
Dry, Open	Lakenheath warren	Alexandra
Shaded	Dorglwyd	Ross creek
Coastal	Tan-y-bwlch	Waianakarua
High-elevation	Pumlumon	Rock & Pillar
Soil stress	Goginan (copper mine)	Sutton (saline)