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SIMPLISTIC RULES FOR SOURCING 'LOCAL' PROVENANCE SEED IN REVEGETATION IGNORE COMPLEX PROCESSES OF ADAPTATION

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ABSTRACT

The role of intra-specific diversity in maintaining species diversity and plant communities is not well understood however has significant implications for rangeland restoration because intraspecific genetic variation may reflect different scales of adaptation. Variation in quantitative traits among 28 wild populations of *Austrodanthonia bipartita*, *A. caespitosa*, *A. eriantha*, *A. fulva* and *A. setacea* collected within central western New South Wales was examined using common-garden studies. Population effects were highly significant ($P < 0.001$) for all characteristics (total biomass and flowering characteristics) suggesting local adaptation. A strong relationship between quantitative traits of *A. caespitosa* and both large-scale (spring rainfall and sunshine hours) and small-scale (shading) environmental variables strengthens this observation. Flow cytometry analysis confirmed the existence of polyploidy in most populations of all five *Austrodanthonia* species, however, no common ecological factors (small- or large-scale) clearly distinguished different chromosome forms suggesting intra- or inter-specific hybridization. This is supported by evidence of intermediate chromosome forms and overlapping flowering times may provide a possible mechanism to facilitate out-crossing. Molecular based markers (AFLP) were used to define the structure and quantify the amount of genomic variation in *A. caespitosa* and revealed low ($F_{st} = 0.16$) levels of differentiation between populations suggesting some geneflow between populations. It appears that *Austrodanthonia caespitosa* co-exists with a number of closely related species which may interact to provide historic and/or contemporary broad-scale gene flow. This then provides a breadth of genetic variation that is subsequently selected for by the wide range of environments occupied by this species. Possible pathways in the evolutionary development of *A. caespitosa* are discussed. It is concluded that for this widespread native grass it may be over-simplistic to suggest local seed sources are always ideal for revegetation.

INTRODUCTION

The adequate supply of seed is an issue of strategic importance if revegetation activities are to expand towards large-scale plantings required to meet both the revegetation and enhancement activities of Catchment Management Authorities or the utilisation of native grasses as sown pastures. The use of local provenance seed sources, both in Australia and elsewhere in the world is recommended because of an assumed home-site advantage and for the maintenance of the genetic integrity of resident populations (SER 2002; Vergeer *et al.* 2003).

Wallaby grasses (*Austrodanthonia* spp.) are widespread, C3 grasses that are assumed to largely be self-pollinating polyploids and subsequently have a high degree of population differentiation. They are an important component of native pastures in both temperate and low rainfall areas of Australia, but of particular importance in south-eastern Australia. Here, they are recognised as being persistent and productive (Groves and Whalley 2002; Garden *et al.* 2005; Waters *et al.* 2005). These qualities coupled with favourable seed dormancy and germination characteristics, have provided a focus for domestication (Lodge 1993) and selection programs (Mitchell *et al.* 2001; Waters 2008). However, when domesticated varieties of *Austrodanthonia* were compared against their wild congeners they often outperformed (in terms of biomass) local populations, in addition, locally harvested ecotypes often had inferior survival and recruitment characteristics compared with material collected from distant locations (Garden *et al.* 2005; Waters *et al.* 2005). This suggests there are differences in scales at which adaptation occurs so that rather than disruption of surrounding ecosystems, the use of inappropriate native seed sources may simply result failure to establish adaptive, self regenerative native populations. In this study, cytological, morphological and molecular variation in 28 populations

of the widespread native grass *Austrodanthonia caespitosa* and four related species (*A. bipartita*, *A. eriantha*, *A. fulva* and *A. setacea*) was examined and related to environment. The study was undertaken in central western New South Wales an area characterised by anthropogenic disturbance and asks the question what is the extent of genetic variation among and within populations of these closely related species.

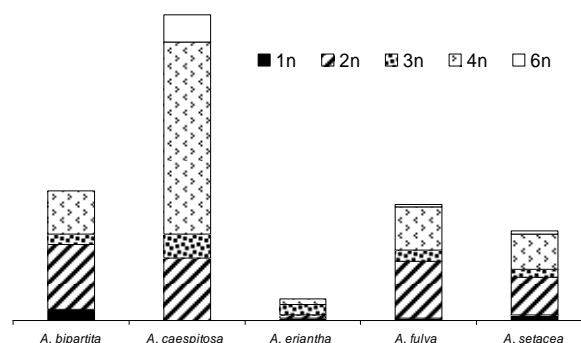
MATERIALS AND METHODS

Twenty eight natural populations of *Austrodanthonia* spp. were systematically sampled across a 75,000 km² collection area within central western New South Wales using 7 parallel east-west and 6 north-south transects at approximately 50 km intervals. Where possible, 20 plants were collected to represent a population. Large scale environmental characteristics included climatic, geological and soils data were collected from GIS coverage's. Small scale, site environmental characteristics, specific to the position in which the plant was growing were recorded in the field at the time of plant collection. These can be summarised into four broad categories – position in landscape, disturbance, soil and vegetation. Flow cytometry was used to screen 28 wild populations for polyploidy. A replicated common garden experiment conducted in a polyhouse was used to examine flowering patterns and quantitative traits of full siblings of parent plants. Data presented here are for flowering traits and dry matter production for *Austrodanthonia caespitosa* only. Analyses of variance were used to examine the main effects of species, ploidy and population. General linear models were used to examine the relationship between quantitative traits and environmental variables. Genomic DNA was analysed using Amplified fragment length polymorphism (AFLP) and patterns and genetic diversity within *Austrodanthonia caespitosa* of 13 populations are described here. The expected heterozygosity (H_e) and partitioning of total genetic variation was assessed by F_{st} using AFLPsurv 1.0. Details of techniques are described in detail in Waters (2007).

RESULTS

Almost all populations consisted of three or more species as well as coexistent chromosome races. *Austrodanthonia caespitosa* was the most common species and tetraploids were the most prevalent chromosome form for all species. Low frequencies of intermediate chromosome forms for all species provides evidence of hybridisation (Figure 1.) and the lack of clear habitat differentiation for different cytotypes provides additional evidence...

Figure 1. Proportion of chromosome races, 1n (monoploid), 2n (diploid), 3n (triploid), 4n (tetraploid) and 6n (hexaploid) for species of *Austrodanthonia* collected from central western NSW.



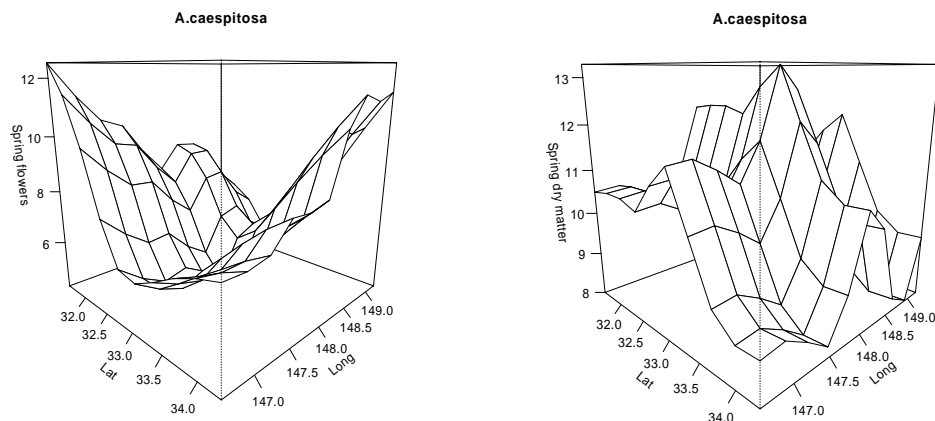
Most of the variation in morphological and flowering traits for all species occurred amongst populations suggesting strong ecotypic development (Table 1). Analysis of variance accounted for around 48 and 66% in flowering traits. Quantitative traits of *Austrodanthonia caespitosa* were related to a suite of environmental characteristics reflecting the adaptive nature of this variation. For example,

spring flowering was more protracted and growth rates faster in northern populations compared to southern populations (Figure 2.). This relationship was reversed in autumn. Small scale environmental characteristics such as shading influenced traits such as plant height and leaf width. Taller plants were associated with shading from the NW in spring. In autumn, plants growing in environments shaded from the NW had larger leaves but produced less dry matter than plants growing in more exposed sites.

Table 1. Variance components (%) and (df) for flowering characteristics of *A. caespitosa*

Source of Variation	Days to first flower		Number of flowers	
	Spring	Autumn	Spring	Autumn
Ploidy	3.18 (3) ***	6.51 (3) ns	<0.01 (3) ns	0.34 (3) ns
Populations	24.73 (23) ***	7.57 (22) ***	33.07 (23) ***	22.33 (23) ***
Population x ploidy	38.47 (18) ***	3.21 (17) ns	14.74 (18) **	19.99 (18) **
Error	33.61	82.71	52.18	57.33

Figure 2. Relationship between number of inflorescences in spring (left) and dry matter production in spring (right) for *Austrodanthonia caespitosa*.



Molecular studies revealed low levels of differentiation among populations suggesting background patterns of gene flow may be occurring (Table 2.).

Table 2. Estimated value (se) for total genetic diversity (H_t), within population (H_w), among population (H_B) diversity, the total genetic diversity that occurs among populations (F_{st}) and number of immigrants (N_m) for 13 populations of *Austrodanthonia caespitosa* generated from AFLP markers using 586 loci.

H_t	H_w	H_B	F_{st}	N_m
0.2181	0.1824 (000080)	0.0357 (0.012551)	0.1656 (0.098580)	1.259

CONCLUSIONS

The balance of this evidence suggests the current evolutionary architecture of the species is complex and is the result of overlaying and interacting effects of broad scale and probably ongoing gene flow among populations and perhaps between ploidy levels. This creates significant genetic variation for a

range of ecologically important traits that is subsequently acted on by directional selection in diverse environments across the range of these species.

This study also provides evidence of either intra-specific hybridisation (between chromosome races) or inter-specific hybridisation. Considerable overlap in flowering times (spring and autumn) was observed for all species providing a possible mechanism out-crossing. The role of different chromosome races in hybridisation was not clear. Whilst tetraploids were the most widespread chromosome form most populations also contained minor diploid forms. However, diploid individuals were generally absent from the centre of the collection area, localities where populations were confined to small roadside remnants, commonly within intensive croplands. These populations were also associated with lower number of inflorescences but higher dry matter yields, suggesting the reproductive performance of these populations may be compromised. Northern and western populations were collected from more extensive remnants or within pastures and diploid forms were found in all these populations. Therefore it may be possible that diploids play some role in maintaining viable populations.

This suggests it is over simplistic to always recommend using local seed sources as it ignores the complexities of the ecological processes of adaptation. In the case of *Austrodanthonia caespitosa* specifically, it may be more important to understand the nature and condition of seed source sites rather than its proximity to the revegetation activity. The formulation of broad recommendations for sourcing seed is more difficult but decision making tools that balance the benefits of different seed sources against ecological risks and economic costs may provide general guidance.

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