

Revegetation with Australian native grasses – a reassessment of the importance of using local provenances

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Abstract. Many restoration guidelines strongly recommend the use of local sources of seed in native plant revegetation projects. These recommendations are based on assumptions that the species used for revegetation are cross-pollinated and woody, as they were developed for overstorey vegetation from the northern hemisphere. Their validity is challenged with respect to replacing or enhancing the native Australian grass component of degraded ecosystems. First, far from being the dominant pollination mechanism, obligatory cross-pollination has not been recorded in any Australian native grasses except for a few dioecious species. Indeed, the common Australian native grasses so far studied have revealed complicated breeding systems that provide the evolutionary resilience necessary for coping with the variable Australian climate as well as with future climate change. It is suggested that a key feature of this flexibility is polyploidy and its implications for sourcing seed are discussed. Second, it is argued that the genetic dissimilarity among populations of a species is not proportional to the distance between them but is more related to the environmental stresses that have been placed on those populations in the past. This is illustrated by different scales of ecotypic variation that are often trait-dependent. Evidence for this can be found in several translocation experiments, where populations of native grasses from a great distance away survive and often perform better than local populations. It is concluded that there is little justification for the recommendation that only local sources of seed of Australian native grasses should be used for revegetation projects, and particularly in large-scale programs. Instead, it is argued that studies on Australian native grasses provide clear evidence that distinct adaptive advantages may be gained by sourcing non-local provenance seed, which is matched to the environment of the revegetation site, and which contains appropriate stress tolerance genes, or by mixing populations from several locations to increase the genetic diversity of seed sources. Some general guidelines are provided for deciding whether or not to use local provenances depending on the purpose of the revegetation, the degree of environmental modification of the site and the characteristics of the species of choice.

Additional keywords: apomixis, genetic introgression, inbreeding depression, outbreeding depression, polyploidy.

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Introduction

Many restoration guidelines strongly recommend the use of local sources of seed in native plant revegetation projects because of an assumed local adaptational advantage and lower risk of unwanted hybridisation, particularly outbreeding depression (Jones *et al.* 2001; Volis *et al.* 2002; Potts *et al.* 2003; Lenssen *et al.* 2004; Capelle and Neema 2005; McKay *et al.* 2005; O'Brien *et al.* 2007; Byrne *et al.* 2011). Local provenance requirements for seed sourcing in many revegetation projects remain current in Australia. For example, at almost all levels of government, sourcing local seed (or as close to the restoration site as possible) is still widely promoted over the use of non-local sources. The Australian Federal Government recommends that best practice within the mining sector be based on sourcing local seed (Anon. 2006a); the South Australian (DPTI 2008)

and Victorian (Anon. 2006b) state governments both recommend seed to be collected from a limited distance (local provenance or regional); and Catchment Management Authorities in eastern Australia also support the use of local provenance seed sources (HCCMA 2007; HNCMA 2008). Many of these recommendations and other similar provenance requirements, reference back to publications by Mortlock (1999, 2000) setting the standard for provenance collection zones for seed sourcing and these continue to be promoted by Greening Australia (2012).

In this review, we are concerned with the revegetation of the grass components of grasslands or woodlands, and not the woody nor the non-grass herbaceous plants in these communities. Such revegetation occurs at different scales. Large-scale revegetation occurs following open-cut mining, after major highway

construction or during regeneration of native pastures following large-scale grazing mismanagement or drought (Whalley *et al.* 2005). Smaller-scale projects involve replacing specific native grasses that have disappeared from grasslands or woodlands through weed invasion or past mismanagement and potentially involve the use of a larger number of grass species than in large-scale revegetation projects. These smaller-scale projects often occur on public land (National Parks, Travelling Stock Reserves, council managed areas, etc.) and may also involve saving rare and endangered grass species. The risks involved with the use of different seed sources in large- and small-scale grass revegetation projects will vary and will also be influenced by the revegetation objectives (Waters *et al.* 2007). This means that a blanket application of The Precautionary Principle to the sourcing of native grass seed is an inappropriate policy (Whalley *et al.* 2003).

The greatest risk in large-scale revegetation projects with native grasses is that the seed does not germinate or the seedlings do not become properly established (Semple *et al.* 1999; Whalley *et al.* 2005; Paterson 2011). Species of grasses that have remained common or have increased in their populations since European settlement in Australia are the species mostly used in this type of revegetation. These are the species that have been the most studied, their breeding systems are mostly well understood (Groves and Whalley 2002) and we propose that the risks of unwanted genetic effects involving local communities are small. These are the species for which large quantities of seed are required and may be met through commercial seed supply where seed quality (purity and viability) can be assured through independent testing. Waters *et al.* (2000) list 11 such species and

Chivers and Raulings (2009) list 23 species for which seed is commercially available – a very small proportion of the Australian native grass flora. Mallett and Orchard (2002) list ~1400 species of grass as occurring in Australia and perhaps 400 of these are introduced species that have become naturalised.

The position is different for small-scale revegetation or when saving rare and endangered native grasses. The species involved are generally less well studied and the genetic risks associated with the use of non-local seed are perhaps higher. When two common native grass species were compared with their rare congeners with respect to their breeding systems, the major differences were in the embryology and percentage viable seed produced in the inflorescences (Yu 1999; Yu *et al.* 2000, 2003) with the less common species having lower seed production. There could well be a case for the use of local seed in any revegetation project using these two less common species (*Bothriochloa biloba* and *Dichanthium setosum*) but not for *Bothriochloa macra* and *Dichanthium sericeum*, the two widespread and common species. (Botanical nomenclature for grasses in this paper is according to Mallett and Orchard 2002.) However, harvesting seed from small, remnant populations may have a significant impact on their survival, particularly for species with rapid population turnover times. Seed collection from such populations often results in poor quality seed with few florets containing viable seeds (Yu 1999; Yu *et al.* 2000, 2003). A better strategy is to increase the seed supply in a seed production nursery from a small quantity of seed or transplanted intact plants (Whalley and Brown 1973). This is an expensive exercise (Fig. 1), often technologically difficult and in practice

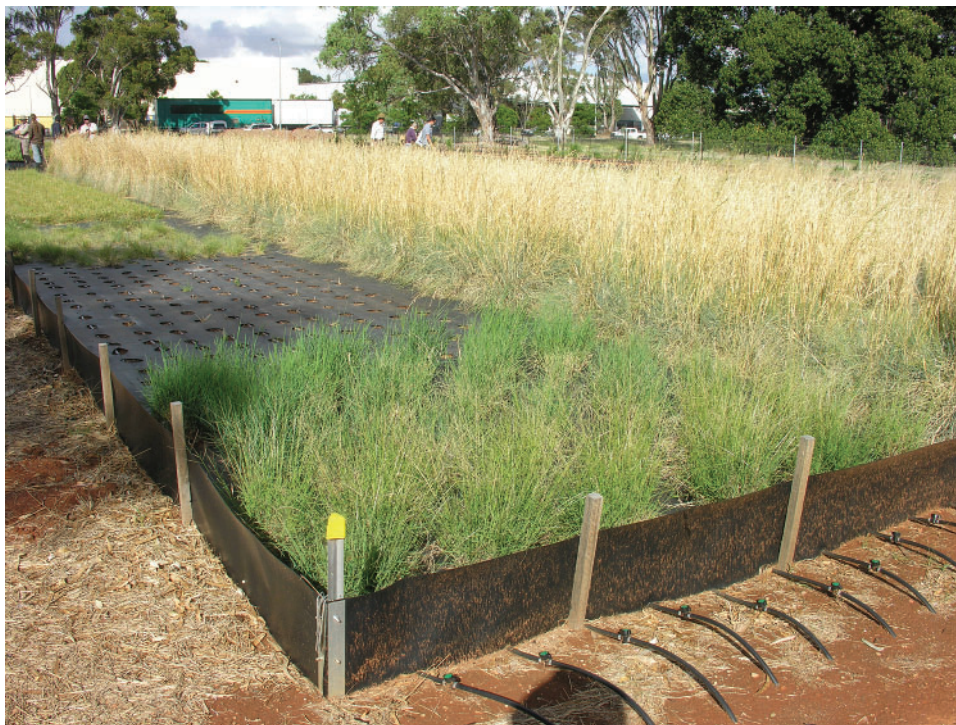


Fig. 1. Initial nursery for multiplying seed of local provenances of native grasses in South Australia. The next stage is to plant the seed collected into larger field sites for further seed production under irrigation. Photography by Wal Whalley.

takes several years before seed is available for use. It is important that the initial collection be from at least 50 plants when the breeding system of the species concerned is unknown (Buza *et al.* 2000; Broadhurst *et al.* 2008). Sgrò *et al.* (2011) suggest considerably larger numbers but their data are based on obligate outcrossing species.

In this review, we examine the impact of recent geological history on the breeding systems of Australian native grasses compared with those of the temperate grasslands of the northern hemisphere. This history underpins the development of a range of breeding systems and ploidy levels in important Australian genera and species. We examine the implications for the genetic risks involved in revegetation using different native grasses and conclude with some general guidelines for the selection of native grass seed sources for grassland and woodland revegetation at different scales.

Evolution of some modern native grasslands

Self-incompatibility mechanisms ensuring cross-pollination in the northern hemisphere temperate grasses were favoured by the rapid revegetation following the Pleistocene glaciations and mass species extinctions some 25 000 years ago in northern Europe and North America. These mechanisms provided an increased potential for creating novel genotypes capable of adaptation to new environments (Richards 1997; Mithen 2003). The temperate grasses of these areas evolved the S-Z self-incompatibility system, which involves two separate genes (S and Z), each with multiple alleles (Baumann *et al.* 2000; Groves and Whalley 2002). When pollen lands on the stigma, germination of the pollen grain will only occur if there are no matches between the alleles of the pollen and the stigma at both the S and Z loci. This S-Z self-incompatibility system is mostly confined to grasses worldwide and is a mechanism to ensure cross-fertilisation. Knowledge of this self-incompatibility system in the temperate native grasses in the northern hemisphere has underpinned the historic recommendation to only use local seed sources. All of the literature supporting the use of local provenances for revegetation referred to earlier, assumes that the species being sown are cross-pollinated and that resultant inbreeding or the use of non-local provenances will lead to several deleterious outcomes.

The S-Z self-incompatibility mechanism has not yet been recorded for any native Australian grass species, nor, to our knowledge, for the tropical grasses of the southern USA. Those studied all appear to be self-compatible (Baumann *et al.* 2000; Groves and Whalley 2002). An important feature of the evolutionary history of Australian grasses is that they were not subjected to the relatively recent massive extinction and recolonisation that occurred in the northern hemisphere during and after the Pleistocene glaciation. These differences in glaciation between the northern and southern hemispheres have probably been repeated many times in the past. This has meant that the Australian environment, with its diverse range of ecological niches, has only been subject to slow changes over recent geological time. Under such conditions, taxa with obligate outcrossing waste reproductive energy producing a wide range of genotypes during every reproductive event (Groves and Whalley 2002). Therefore, plant taxa with the capacity to rapidly

reproduce genotypes that are successfully growing in each environment would have had an evolutionary advantage. We suggest these taxa have various methods of reproduction, which allow for the rapid reproduction of 'successful' genotypes in a variety of ecological niches, including various forms of self-pollination, and that there should be a lower proportion of obligate outcrossing grass species in the Australian environment than in the much younger grasslands of the North American and European continents (Groves and Whalley 2002). Taxa with these flexible reproductive systems would have an increased evolutionary resilience as described by Sgrò *et al.* (2011). To our knowledge, no obligate outcrossing species of Australian native grasses (except for four dioecious genera) have been described. These general differences in the breeding systems of temperate North American grasses compared with their Australian counterparts have been emphasised in Smith and Whalley (2002).

Breeding systems

A wide range of breeding systems have been described for Australian native grasses, each having implications for choices about the germplasm used for revegetation.

Dioecism (the production of male and female flowers on separate individuals) ensures cross-fertilisation but appears rare in Australian grasses. Four genera (*Distichlis*, *Pseudochaetochloa*, *Spinifex* and *Zygochloa*) are reported as dioecious (Groves and Whalley 2002). The majority of these are distributed close to shorelines (either present or geological) and in all but *Pseudochaetochloa*, clonal reproduction is much more common than seedling recruitment (Connor and Jacobs 1991; Maze and Whalley 1992).

Globally, the flowers of most grass species are hermaphroditic, producing both male and female parts. Grass flowers (florets) may be cleistogamous (closed) and the pollen is shed directly on to the stigma (Campbell *et al.* 1983). On the other hand, they may be chasmogamous in which case the florets open and the anthers and styles are exerted and the pollen is shed externally allowing for cross-pollination. It is usually assumed that most grasses are chasmogamous and cross-pollinated but this assumption appears flawed for Australian grasses. For example, Brock and Brown (1961) reported predominantly inbreeding systems for *Danthonia* spp. (later *Austrodanthonia* spp.; Mallett and Orchard 2002; and now *Rytidosperma* spp.; Linder *et al.* 2010) although limited intra- and inter-specific hybridisation did occur. For all the *Rytidosperma* spp., and many other Australian native grass species, the common method of self-fertilisation is autogamy where the anthers dehisce before the florets open and the anthers and stigmas are exerted (Richards 1986). This evidence suggests that reproductive effort may be spread between self- and cross-fertilisation with a predominance of selfing or clonality. This ensures that large numbers of locally fit individuals adapted to prevailing conditions are produced, but that a smaller percentage of cross-fertilised individuals can result. This may act as a kind of insurance for the potentially changed or changing environmental conditions.

The production of both cleistogamous and chasmogamous florets within the same inflorescence is a mechanism that supports mixed mating and has been demonstrated for several

Australian grasses. Cleistogamous florets have the same micro-evolutionary impact as self-fertilisation and chasmogamy can result in cross-fertilisation. Yu *et al.* (2000) studied the reproductive biology of four closely related species *Bothriochloa biloba*, *B. macra*, *Dichanthium sericeum* and *D. setosum*. In this study, while *D. setosum* was entirely chasmogamous, the other three species had varying proportions of both types of florets within one inflorescence and the proportions of floret type appeared to be under both environment and genetic control (Yu *et al.* 2000).

Microlaena stipoides predominantly produces inflorescences bearing only cleistogamous florets and occasionally produces inflorescences bearing only chasmogamous florets (Clifford 1962). Different populations of *Microlaena stipoides* have been reported to have different proportions of each type of inflorescence when grown in a comparison nursery (Huxtable 1990). This species also produces cleistogenes, a different type of cleistogamous flower (Fig. 2). These are mostly produced from the lower axillary buds of the grass culms located inside

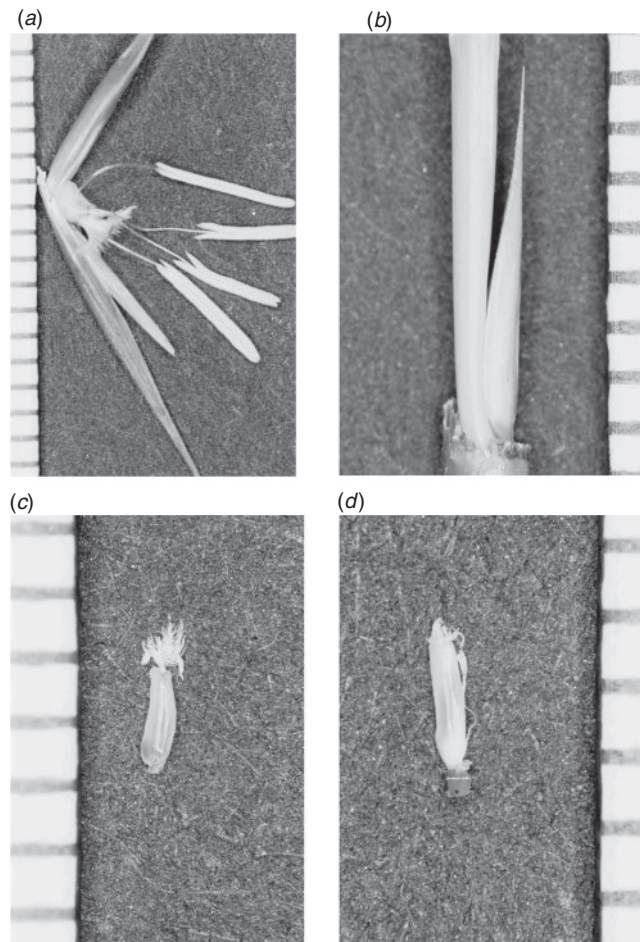


Fig. 2. The three types of *Microlaena* flowers. (a) A chasmogamous spikelet showing four large anthers and a feathery style. (b) A cleistogene with the leaf sheath removed. (c) A dissected cleistogamous flower showing two tiny anthers and a small style. (d) A dissected flower of a cleistogene showing two tiny anthers and a tiny style. The scales are in mm and photography is by Chris Cooper.

the leaf sheaths and often ripen after the inflorescence seeds have fallen (Connor and Matthews 1977). In this species, cleistogamous florets only produce two tiny anthers whereas chasmogamous florets produce four (or sometimes five) large anthers (Fig. 2). Therefore, the pollen/ovule ratio is much smaller in the cleistogamous florets and so the energy cost of seed production is lower than in chasmogamous florets. This difference is a common feature of cleistogamous grass taxa (Campbell *et al.* 1983).

Apomixes, or agamospermy, involves the production of viable seeds without the union of gametes and is widespread among grasses (Fryxell 1957) but its prevalence in Australian grasses has yet to be determined. Many grass taxa have polyploid races and it is often these lines that are apomictic (Connor 1987) and involve diploid/polyploid cycles combining sexual and apomictic reproduction (de Wet 1968; de Wet and Harlan 1970; Yu *et al.* 2003). The successful combination of sexual and apomictic reproduction in some species of grasses can minimise the high cost of sexual reproduction while retaining the capacity for adaptive polymorphism and the rapid reproduction of fit genotypes in specific environments (i.e. evolutionary resilience, Sgrò *et al.* 2011). These same traits would be of value in coping with climate change. Such systems have been described for several Australian native grasses such as *Themeda triandra (australis)* (Woodland 1964) and different species of *Elymus* (Murphy 2003).

In summary, the breeding systems of all the Australian native grasses that have been studied in any detail suggest that breeding mechanisms generally ensure a high degree of inbreeding, together with occasional outcrossing opportunities resulting in limited gene flow from one population to another, even when the populations are in close proximity. The species most commonly used in large revegetation projects are the ones which have been studied in the most detail.

Ploidy levels

Polyploidy is common among the Poaceae and at least 80% of species globally are of polyploid origin (de Wet 1987). Polyploid series within individual species are common and often the diploid races reproduce sexually and the polyploid races apomictically (de Wet and Harlan 1970). *Themeda triandra* is an Australian example with the diploid race ($2n=20$) reproducing sexually and a tetraploid race at least sometimes reproducing apomictically (Hayman 1960; Woodland 1964; Evans and Knox 1969). Polyploidy is more often the result of the union of gametes, of which at least one is unreduced, than of true autopolyploidy. It is often the result of hybridisation and the production of complex groups, sometimes with several ploidy levels and different forms of reproduction in the different groups (Taliaferro 2003; Jewell *et al.* 2010; Waters *et al.* 2011). The higher ploidy level populations within a species often behave as functional diploids and can revert to lower ploidy levels with the formation of embryos from unfertilised but reduced ovules. This is often associated with a return to sexual reproduction from an apomictic race (de Wet 1968; de Wet and Harlan 1970). We suggest that the higher ploidy levels are to some degree a protection against inbreeding depression (e.g. Dewey 1969) but it may also provide the key to the ongoing evolutionary

development of species. Polyploidy appears common within grasses worldwide and its importance cannot be overstated because of its role in past and ongoing evolution (Ramsey and Schemske 1998; Soltis *et al.* 2004).

A recent study of *Rytidosperma* (*Austrodanthonia*) spp. illustrates the importance of different ploidy levels in native grass populations. Waters *et al.* (2009, 2010) systematically collected 28 natural populations across 75 000 km² at roughly 50-km intervals in central New South Wales. A total of 343 plants from five species were included in the collections with the majority identified as *R. caespitosum*. Traditional chromosome counts as well as flow cytometry were used to determine the ploidy levels of these populations (Waters *et al.* 2011). The chromosome counts confirmed that the majority of *R. caespitosum* plants were tetraploid or diploid ($2n=48$ or $2n=24$) with $x=12$. The flow cytometry revealed three ploidy races ($2x$, $4x$, $6x$) and two intermediate cytotypes ($1x$, $3x$), but importantly revealed that co-existent cytotypes were common within any population for *R. caespitosum* (and also within four related species). The authors concluded that in *R. caespitosum* co-existent cytotypes and the absence of a relationship between cytological races and environmental variables suggests these grasses are predominantly self-fertilised with some cross-fertilisation, and have as well a potential for intra-specific hybridisation between cytological races. Similar complicated cytological races and ploidy levels have been detected in populations of *Cynodon dactylon* (Jewell *et al.* 2010). Additional molecular studies support this notion and provide evidence for historic and on-going intra-specific hybridisation between chromosome races (Waters 2007). In other words, these populations are evolving, have high evolutionary resilience (Sgrò *et al.* 2011), and will continue to evolve and so cannot be preserved in their present state, even if this were considered desirable.

Inbreeding and outbreeding depression, genetic introgression

The terms ‘inbreeding depression’, ‘outbreeding depression’ and ‘genetic introgression’ occur frequently in the literature and are often used to support the use of local provenances. Thus definitions and some examples of their effects are provided below. These processes have been described many times in both natural and artificial populations of a wide range of both plants and animals but, to our knowledge, they have not been found in native Australian grasses even when small numbers of individuals have formed the bases for selected varieties or when native grasses have been introduced into existing grasslands (Lodder 1989; Lodge 1993; Lodge and Schipp 1993; Johnston *et al.* 1999; Semple *et al.* 1999).

Inbreeding depression is a general decline in vigour of the resultant progeny compared with the parents and can occur when a normally cross-fertilised plant crosses with itself (selfing) or a close relative (Fenster and Dudash 1994). While it is generally accepted that inbreeding depression occurs in some field crops and northern hemisphere pasture grasses, there are few studies indicating its importance in natural populations of grasses, and those that have been undertaken, generally document the short-term consequences of extreme inbreeding (Fenster and Dudash

1994). We know of no such studies involving Australian native grasses because the only ones that are known to be self-sterile are the dioecious grasses.

Outbreeding depression is defined by Frankham *et al.* (2011) as ‘... a reduction in reproductive fitness (reduced ability to mate [pollinate], fertilise, produce offspring, survive, or reproduce) in the first or later generations following attempted crossing of populations.’ Templeton (1986) described outbreeding depression in several species of animals and quoted experimental data showing that it can sometimes be rapidly eliminated from a population by natural selection provided that the population turnover time of the species in question is relatively short, say several years. Frankham *et al.* (2011) produced a decision tree for predicting the probability of outbreeding depression between two populations of normally outbreeding populations using quantitative genetic models. These models are based on animal data where the degree of inbreeding is determined by the population size and the ultimate inbreeding, that is, self-fertilisation, is impossible. Fenster and Galloway (2000) studied both inbreeding and outbreeding depression in *Chamaecrista fasciculata* (Fabaceae), a mostly outcrossing but self-compatible annual, using interpopulation crosses of populations from 100 m to 2000 km apart, spanning its range in eastern North America. They found almost universal F₁ superiority over the parents but the F₃ hybrids suffered a loss of fitness compared with the F₁ hybrids. We question whether the same result would be obtained with normally self-pollinating Australian native grasses. Templeton’s (1986) paper, perhaps because of the paucity of appropriate studies on Australian plants, is quoted as the authoritative source of the importance of outbreeding depression in the use of Australian local provenances of plant species in revegetation projects in the Australian literature including Broadhurst *et al.* (2008) and Byrne *et al.* (2011).

Genetic introgression is the introduction of alien genes into a local population of a species by the establishment of plants from an alien population of the same species (Keller *et al.* 2000). These genes may be a threat to the local population because of their poor adaptation to local conditions or have ‘possible destabilising effects on the genetic integrity of native populations’ (Keller *et al.* 2000). These ‘destabilising effects’ are not specified. Alternatively, it could be suggested that the alien genes introduced into the native population may enhance its ability to survive and further evolve under the changed ecological conditions that inevitably will occur in the future. In addition, because the common Australian grasses that have been studied in detail are mostly self-pollinated, gene exchange with surrounding populations appears to be relatively minor.

These three processes (inbreeding depression, outbreeding depression and genetic introgression), therefore, might be important in revegetation using trees when the planted population could live for several hundred years but would be less important with Australian native grasses in which the population turnover times are relatively rapid (Williams 1966; Williams and Roe 1975) and self-pollination is the most common mode of reproduction. Furthermore, any deleterious effects of these three processes that did occur following the introduction of native grass species from distant provenances

would rapidly disappear if they resulted in less fit individuals because of these rapid population turnover rates.

Alternative scales of adaptive and genetic variation

Another central argument for using local provenances of all native species in revegetation projects is based on the notion that the genetic dissimilarity among individual subpopulations of a species is proportional to the distance between them (e.g. Keller *et al.* 2000). This notion follows logically from the assumption that the organisms in question have simple sexual breeding systems. With animals, the extent of the effect of distance on the genetic dissimilarity depends on the mobility of the animals and the distance the young travel in their search for a mate. Most cross-pollinating grasses are wind-pollinated and the distances that pollen travels is usually quite short, but can occasionally be substantial. Even so, steep environmental gradients can produce distinct ecotypes of grass species in England within 2–3 m in mine dumps with localised metal toxicity in the soil (Bradshaw 1960). Even when such steep environmental gradients are not present, genetic dissimilarities have been detected within short distances among lines of the predominantly cleistogamous *Microlaena stipoides* growing in association with different companion perennial grasses within one small paddock on the Northern Tablelands of New South Wales (Magcale-Macandog and Whalley 2000, 2007).

Waters *et al.* (2003) collected 11 species of native grasses from 51 sites throughout western New South Wales and southern Queensland and examined the genetic variability among the different populations of the different species. They found a strong relationship between site of origin and plant morphological characteristics when the plants were all grown in a comparison nursery. That is, the location of a plant was strongly associated with a particular morphologically distinct population, providing strong evidence for local adaptation. However, the distance between sites could not be used as an indicator of morphological difference among populations (Waters *et al.* 2003). For some populations of *Digitaria coenicola* and *Austrodanthonia caespitosa* (now *Rytidosperma caespitosum*) phenotypic differences were sometimes detected over very short distances (<6 km), while in other cases the same phenotypes were found in populations separated by several hundred kilometres. The greatest influence over observable phenotypic traits was the difference between the environments from which they were collected, not the distance between those various environments (Waters *et al.* 2003).

Populations of *Rytidosperma* spp. collected over a large geographic scale revealed strong adaptive variation in flowering and growth that was related to large-scale seasonal patterns of rainfall (Waters *et al.* 2011). However, in the same study other traits such as leaf morphology were related to both large- and small-scale site characteristics suggesting that environmental variation drives adaptive diversity at several scales. It appears overly simplistic to suggest that local seed sources are always the best site-adapted material. This evidence along with the predominance of inbreeding among native Australian grasses does not support the assumption that the genetic dissimilarity among individual subpopulations is proportional to the distance between them as it ignores the environmental patchiness of the

landscape. As a result, the evidence for Australian native grasses supports the recommendations of Broadhurst *et al.* (2008) to match environmental conditions at the seed collection sites with those of the restoration site and suggests that matching the local environmental factors is of greater importance than using locally collected seed sources. However, as is the case with *Cynodon* spp., adaptations to the environment are not always obvious and populations with high drought tolerance were not always found in dry environments (Zhou *et al.* 2013).

Self-fertilisation and the genesis of locally adapted genotypes

Both self-fertilisation and accompanying infrequent mutation events or cross-pollination along with polyploidy seem to be involved in the genesis of local genotypes in native grasses but it is important to recognise that the characteristics of these populations are not stable over time. When revegetating degraded communities, therefore, there may be little value in using restoration goals that aim to restore genotypes that occurred at some nominated earlier time. It is more important that the genotypes used in native grass revegetation, will, in fact survive in the environment in which they are to be established and have sufficient genetic capacity to survive future environmental change. Whether this will happen is often difficult to determine except by trial and error.

A broad-scale evaluation trial was conducted for 3 years during the 1990s comparing the survival, recruitment and herbage mass production of 31 accessions of a range of species of native grasses at eight sites spread across temperate Australia (Garden *et al.* 2005; Norton *et al.* 2005; Sanford *et al.* 2005; Waters *et al.* 2005; Whalley *et al.* 2005). Where multiple accessions of one species were compared, selected varieties of *Rytidosperma caespitosum* (*Austrodanthonia caespitosa*) and *R. bipartitum* (*A. bipartita*) sometimes outperformed their locally sourced progenitors in terms of herbage mass produced (Garden *et al.* 2005; Waters *et al.* 2005). In addition, the survival and recruitment of an accession of *Microlaena stipoides*, collected in Tasmania, was outperformed at most sites, including one in Tasmania, by accessions collected on the northern and southern tablelands of New South Wales (Garden *et al.* 2005; Waters *et al.* 2005). In general terms, the performance of individual accessions at particular sites could be predicted by comparing the environments of the sites in which they were collected with those of the sites in which they were tested. However, there were numerous exceptions when the performance (survival and growth) of individual accessions at particular test sites either exceeded or were very much worse than expectations of their performance at particular sites based on the assessed environmental similarity of the collection and test sites.

A recent study (Fitzgerald *et al.* 2011) showed that there was more variability at a molecular genetic level in *Microlaena stipoides* under conditions where environmental stresses were greater than those with fewer stresses. Genes for defence against stresses, such as diseases, were more varied on the drier and hotter plains of eastern Victoria than they were in the moister and cooler Victorian Alps. These results demonstrate the ability of this native grass (a mostly self-pollinating tetraploid) to evolve

to tolerate local stresses either through mutation or through gene activation/silencing, rather than through cross-pollination.

Bermudagrasses (*Cynodon* spp.) are a cosmopolitan group of warm season (C_4) grasses that are used throughout the world as forage and turfgrasses (Jewell *et al.* 2012a) and are common in Australia. Both deliberate and accidental introductions have occurred since European settlement but there is general agreement that there are populations of *Cynodon dactylon* that are native to Australia as well as more recent introductions (Lazarides 1972; Jewell *et al.* 2012b). A recent study of drought tolerance involved the collection of a large number of accessions of bermudagrasses throughout Australia and testing their drought tolerance using small lysimeters (Zhou *et al.* 2013). There was no relationship between drought tolerance and geographic origin, and drought-tolerant lines among the native Australian material could be found across a range of present climatic regions. In general, the commercial lines introduced from overseas had lower drought tolerance than the native lines (Zhou *et al.* 2013). As these taxa have predominantly vegetative reproduction, it is not at all clear how the high drought-tolerant populations arose. It is likely that similar situations occur in other native taxa because, to our knowledge, no other native grasses have been studied in such detail across Australia. These uncertainties lead us to suggest that mixing populations from several sources might enhance the probability of a successful revegetation outcome in most situations.

Choice of native grass species for revegetation

Dramatic changes have occurred in the relative abundance of different native grass species in Australia since European settlement (e.g. Moore 1953, 1970; Lodge *et al.* 1984; Lodge and Whalley 1989). Some species have become relatively more abundant in response to the vastly changed ecological conditions over the last >200 years, there has been a general migration of some species from more arid regions to more humid (Moore 1970) and other species have become less abundant and are now listed as rare and endangered. These differences have been little studied but one set of comparisons between species pairs, one abundant and the other less so, have revealed differences in their breeding systems perhaps related to their different responses to the changed ecological conditions (Yu 1999; Yu *et al.* 2000, 2003). It is the species that have not become rare and endangered that are generally chosen for broad-scale revegetation projects whereas rare and endangered grasses are those that are involved in recovery projects. The seed sources available are quite different for these two broad groups of species.

Local conditions for revegetation sites are not necessarily similar to those of previous decades and, given climate change scenarios, are unlikely to be the same in the future. Vegetation regenerators and landscape planners need to plan for landscapes into the future. Selection of common species of grasses, which have breeding systems that are flexible and have the capacity for rapid micro-evolution, will permit the continued growth and function of those plants in both the existing and future-modified environment. There is also a case for combining seed from several sources to ensure a wide range of adaptation in the future population. The evidence provided here supports the notion that local populations do not necessarily always provide

the best site-adapted material and that this material may not have sufficient adaptive capacity to accommodate future environmental changes. In many cases for broad-scale sowings, seeds produced commercially by professional seed growers and independently tested for purity and germinability provide the best chance of a successful outcome for revegetation using native Australian grasses. Semple *et al.* (1999) have emphasised the importance of adequate weed control and the use of high quality seed sources in the successful establishment of native grasses in regenerative sowings.

General guidelines

The choice of a seed source for revegetation plantings of Australian native grasses depends on the condition of the revegetation site (starting point) and the complexity of the desired outcome (Fig. 3). The degree of modification of the starting environment may vary from total, as in a highway verge or a mine site revegetation, to minimal where a once-abundant native grass species has become locally extinct and the objective is to restore the species. The complexity required may range from low in amenity plantings, such as lawns or golf-course roughs, moderate for native pasture or following highway construction, to high for revegetation after mining, or a conservation reserve or national park where the native grass component is depauperate and the aim is to restore complexity. We plot the general importance of using local seed by the diagonal arrow. Using local provenance is of greatest importance where a complex outcome is the goal and the starting environment has undergone little modification (Fig. 3).

The characteristics and breeding systems of the native grass species chosen for planting (Table 1) also affects the choice of seed source. For instance, if there are many ploidy levels within natural populations, then there is little justification for insisting on the use of local provenances where the complexity of the desired outcome is low. Again, when the ploidy level of the species and seed source is high (e.g. *Microlaena stipoides*, Table 1), there is little justification for insisting on the use of local provenances. There is also a range of degrees of clonal reproduction ranging from predominantly vegetative (*Spinifex* spp. and *Distichlis distichophylla*) through those that are frequently vegetative (e.g. *Paspalum distichum* and *Hemarthria uncinata*) through to

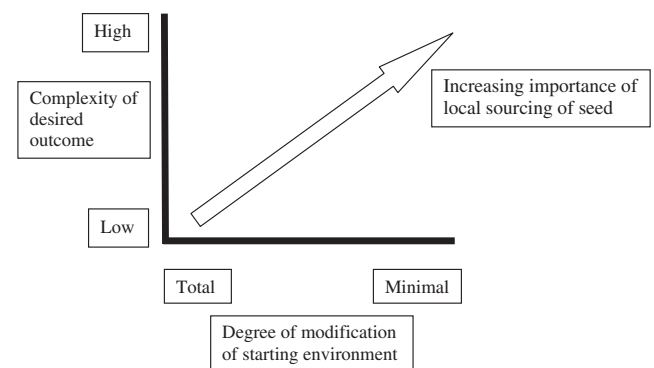


Fig. 3. The increasing importance of using local sourcing of seed when using Australian native grasses depending on the complexity of the desired outcome and the degree of modification of the starting environment.

Table 1. Some common native Australian grass species with base chromosome numbers (x) and ploidy levels recorded. The predominant breeding systems are listed where they are known together with mechanisms involved, frequency of vegetative reproduction and references

Distributions are shown below the name and are from Mallett and Orchard (2002) and abundance from the authors' experience. Gaps in the Table indicate that no information could be found

Species	Ploidy levels	Predominant breeding system	Mechanisms involved	Frequency of vegetative reproduction	References
<i>Astrelba lappacea</i> . Qld, NT, NSW, SA, WA. Common	$x = 20, 2n = 40$	Mostly inbreeding with a small degree of cross-pollination	Apomixis unlikely	Occasionally by short rhizomes	Jozwik (1969); Watson and Dallwitz (1992)
<i>Austrodanthonia</i> spp. (Now <i>Rytidosperma</i> spp.). The information for this group of grasses covers several species including <i>A. caespitosa</i> , <i>A. richardsonii</i> , <i>A. bipartita</i> , <i>A. fulva</i> and <i>A. tenuior</i> . NSW, Vic., Tas., SA, WA. Common	Complex, $x = 12$, usually $2n$ and $4n$. Multiple ploidy levels are found in some communities including $2x$, $4x$, and $6x$ races as well as intermediate cytotypes, $1x$ and $3x$ and interspecific crosses	Mostly inbreeding 80–85% with some outcrossing (intra- or inter-specific hybridisation)	Flowers are usually chasmogamous but autogamy is common with the pollen being shed before the anthers are exerted	Occasionally by short rhizomes	Brock and Brown (1961) Waters et al. (2009, 2010, 2011)
<i>Austrostipa densiflora</i> . NSW, Vic., SA. Common	Complex data for genus <i>Stipa</i>	Both cleistogamous and chasmogamous florets	–	Occasionally by short rhizomes	Vickery et al. (1986); Watson and Dallwitz (1992)
<i>Austrostipa scabra</i> subsp. <i>scabra</i> . All states. Common	Complex data for genus <i>Stipa</i>	Both cleistogamous and chasmogamous florets	–	Occasionally by short rhizomes	Vickery et al. (1986); Watson and Dallwitz (1992)
<i>Bothriochloa macra</i> . NSW, Vic., SA, Qld. Common	$x = 10, 2n = 20$	Variable, both within populations but among seasons and among populations in one season	Chasmogamy 90%, both cleistogamy 10%, both occurring in the same seasons and among populations in one season	Occasionally by short rhizomes	Yu (1999); Yu et al. (2000)
<i>Bothriochloa biloba</i> . NSW, Qld. Locally abundant	$x = 10, 2n = 20, 3n = 30, 4n = 40, 6n = 60$	Variable, both within populations but among seasons and among populations in one season	Chasmogamy and cleistogamy 50% each, pseudogamous apospory and adventive embryony. Reduced seed set	Occasionally by short rhizomes	Yu (1999); Yu et al. (2000, 2003)
<i>Chloris truncata</i> . NSW, Vic., SA, Qld, NT, WA. Common	$x = 10$, probably $2n = 20$	All types of reproduction recorded within the genus	–	Often by stolons	Watson and Dallwitz (1992)
<i>Chloris ventricosa</i> . NSW, Qld, Vic., SA. Common	$x = 10$, probably $2n = 20$	All types of reproduction recorded within the genus	–	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Cymbopogon refractus</i> . Qld, NSW, Vic., NT	$x = 5$ or 10 . Probably $2n = 20$	Some populations sterile	–	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Cynodon dactylon</i> var. <i>dactylon</i> . All states. Common	$x = 9, 2n = 39$, but many variations have been recorded	Self-fertile and slight reduction in seed set in artificially sowed florets compared with natural pollination	–	Sometimes by seed but always by stolons and/or rhizomes	Watson and Dallwitz (1992); Jewell et al. (2010)
<i>Dichanthium sericeum</i> subsp. <i>sericeum</i> . All states. Common	$x = 10, 2n = 20$, one tetraploid record, $2n = 4x = 40$	Self-fertile and slight reduction in seed set in artificially sowed florets compared with natural pollination	Chasmogamy 15%, cleistogamy 65%, both occurring in the same seasons. Good seed set. One record (tetraploid) with evidence of apomixis	Occasionally by short rhizomes	Jacobsen (1981); Yu (1999); Yu et al. (2000)

<i>Dichanthium setosum</i> . NSW, Qld, Tas. Uncommon	$x = 10, 2n = 20$	Low seed set and no difference in seed set between artificially selfed florets compared with natural pollination	Only chasmogamous florets and very high pollen to ovule ratio. Pseudogamous apospory and adventive embryony recorded; very low seed set	No vegetative reproduction recorded	Yu (1999); Yu <i>et al.</i> (2000)
<i>Digitaria brownii</i> . All states except Tas. Common	$x = 9, 15$ and complex ploidy levels recorded within the genus	All types of reproduction recorded within the genus	—	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Elymus scaber</i> . All states except NT. Common	Complex, $x = 7, 2n = 6x = 42$. Some populations, $2n = 9x = 63$	Mostly inbreeding and range from fully apomictic ($7x = 63$ populations) to fully sexual with reduced number of seeds per floret	Some populations completely apomictic	No vegetative reproduction recorded	Murphy (2003)
<i>Enteropogon acicularis</i> . NSW, Vic., Qld, SA, NT. Common	$x = 10, 2n = 20$	—	—	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Heteropogon contortus</i> . Qld, NT, NSW, WA. Common	Complex, $x = 10$ or $11, 2n = 20, 22$ or multiples	—	—	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Microlaena stipoides</i>	$x = 12$, mostly $4x. 2n = 48$	Mostly inbreeding	Most inflorescences cleistogamous with plants occasionally producing chasmogamous inflorescences. Can produce one cleistogeme from the lowest node of the flowering culm	Occasionally by short rhizomes. Some lines root at the nodes	Clifford (1962); Connor and Matthews (1977); Huxtable (1990); Parthasarathy (1939)
<i>Poa labillardieri</i> var. <i>labillardieri</i> . Vic., Tas., NSW, SA, Qld. Common	$x = 7, 2n = 14$ or multiples	—	—	Occasionally by short rhizomes	Watson and Dallwitz (1992)
<i>Spinifex sericeus</i>	$x = 9, 2n = 18$	Dioecious	—	Almost always by stolons or rhizomes	Maze and Whalley (1992); Watson and Dallwitz (1992)
<i>Themeda triandra/australis</i>	Complex, $x = 10, 2n$ and $4n$ races	$2n$ usually sexual and $4n$ often apomictic	—	Very occasionally by stolons	Hayman (1960); Woodland (1964); Evans and Knox (1969)

species of *Rytidosperma* and *Austrostipa* (Table 1) that infrequently reproduce vegetatively.

Conclusions

Figure 3 and Table 1 provide some general guidelines for deciding whether or not the use of local provenances is important depending on the purpose of the revegetation, the degree of disturbance of the regeneration site and the reproductive systems of the species of choice.

The changes in the Australian environment over recent geological time have meant that there have been no mass extinctions in the grass flora but rather more gradual changes at individual locations. The widespread occurrence of inbreeding systems in Australian grasses has produced a degree of local adaptations, some of which are not readily apparent in the populations in the field. The genetic similarity of populations cannot be measured simply by the distance between them or necessarily by the characteristics of the environment in which they are located. Therefore, the blanket insistence on the use of local provenances for revegetation using native grasses cannot be justified.

The widespread occurrence of polyploidy means that local populations contain considerable potential for ongoing evolution and that they cannot be conserved in their present state. Nor would this be desirable given the likely climate changes in the foreseeable future. The relatively short generation time for most native grasses would ensure rapid elimination of any unfavourable genotypes introduced by the use of non-local seed.

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