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Seed collection for revegetation: Guidelines for Western Australian flora

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Abstract

Current approaches to seed collection for revegetation tend to follow a precautionary principle that advocates the use of seed of 'local provenance' from geographically restricted areas. In many cases however, assigning 'local' seed collection areas for specific taxa is not possible due to a lack of available information regarding local adaptation and patterns of genetic variation, the possibility of hybridisation among genetically divergent populations, and the possibility of invasiveness or other ecological interactions. We suggest that strategies for determining appropriate seed collection areas should be based on a number of considerations including: the aim of the revegetation program, characteristics of the site requiring revegetation, known or inferred patterns of local adaptation and genetic differentiation, and the availability and quality of seed sources in taxa used for revegetation. We review the limited information available regarding patterns of local adaptation and the partitioning of genetic variation for plant species commonly used in revegetation in south-west Australia. We suggest that the presence of local adaptation and partitioning of genetic variation may be inferred by assessment of a number of species-specific traits, and that adherence to restricted seed collection areas may not be the most appropriate approach for seed collection strategies for all taxa particularly common widespread species often targeted in restoration programs. In some cases, an ecogeographic approach where seed is collected from a number of large healthy populations at collection sites matched for climatic, edaphic and other environmental variables at the restoration sites, with less consideration given to geographic distance between them, may be a more appropriate strategy for seed collection.

Key words: revegetation, seed collection, provenance, local adaptation, genetic differentiation

Introduction

Determining appropriate strategies for collecting seed is an important issue for revegetation programs. Current approaches regarding seed collection tend to follow a precautionary principle that advocates the use of seed of 'local provenance'. The term 'provenance' is frequently used simply to describe the geographic origin or source of specific genetic material and is often applied when variation is observed in morphological and physiological traits over a species natural range (Coates & Van Leeuwen 1996). More specifically 'local provenance' is applied to seed collected locally or of local origin although 'local' is often not clearly defined. Where it is defined strictly in terms of a geographic distance between source and restored populations it is generally applied to all plant species regardless of their biological attributes, breeding system, geographic distribution and demographics.

Traditionally, seed collection guidelines recommend seed for revegetation be collected from 'local provenance' material, or from natural populations as local as possible. These guidelines advocate initial small on-site seed collection areas that may be gradually extended to the next geographically closest viable populations if seed supply is limited (Mortlock 2000a). This approach is generally recommended in the absence of information on the distribution of genetic diversity, in particular that which may confer adaptation to local environmental conditions (Mortlock 2000a).

There are a number of reasons that this precautionary approach has been adopted. (i) It is assumed that material sourced from local populations will be best suited to a specific site, possessing local adaptation to climatic, edaphic, biotic and other environmental conditions. Such 'local provenance' material may have a 'home site advantage' with enhanced long term population adaptation, viability and survival (Coates & Van Leeuwen 1996; Joshi *et al.* 2001). Conversely, material that is not adapted to local conditions may display reduced survival, growth, reproduction, and long-term persistence at revegetation sites (Potts *et al.* 2003). (ii) Local provenance material is considered to reduce the risks of outbreeding depression arising from crosses between genetically divergent yet interfertile, introduced populations and local populations. Outbreeding depression, a significant reduction in offspring fitness that may be expressed over a number of generations, can lead to low population viability and a substantial decrease in the likelihood of population persistence (Rhymer & Simberloff 1996). (iii) Local provenance seed is also considered to prevent negative ecological interactions such as changes to breeding systems, invasiveness, displacement of the local form and changes to the surrounding community structure;

however the relative risks of such impacts will be species and site specific.

There is now some debate on the most appropriate strategy for selecting plant material for revegetation, and whether locally sourced material is always the most appropriate (Montalvo *et al.* 1997; Lesica & Allendorf 1999; Hufford & Mazer 2003; McKay *et al.* 2005; Broadhurst *et al.* 2008). Bussell and Hood (2006) suggest that the importance of achieving successful revegetation and maintaining ecosystem integrity should override issues of spatial proximity of seed sources and revegetation sites. Arguments against restrictive seed collection strategies stress that non local genetic material may not necessarily be maladapted (for example when local adaptation is not present), hybrid progeny of interfertile yet divergent populations do not always display outbreeding depression and maladapted alleles may be readily purged by selection, (leading to only a short term decrease in fitness). Indeed there are relatively few studies in plants that have clearly demonstrated outbreeding depression (Edmands 2007). A restrictive approach toward local seed collection areas may also result in seed that is inbred, has limited genetic diversity and lacks potential to respond to past or future environmental changes. Thus this precautionary approach may be suitable for some species targeted for restoration but for other species it may be unnecessary and even counter productive.

A range of factors should be assessed when making decisions on appropriate geographic scale of seed collection areas and deployment of material at revegetation sites, including the aim of the revegetation program, current and future aspects of the revegetation site, patterns of local adaptation and the partitioning of genetic variation in the species to be utilised, and the availability and quality of seed. We discuss each of these factors below and how they influence seed collection strategies with reference to the flora of south-west Western Australia that is commonly used for revegetation.

Aim of the revegetation program

Restoration and revegetation programs operate at varied geographic scales and are conducted with a range of goals. The goal of many early revegetation projects was the rapid restoration of degraded land achieved via the establishment of plants of only a few species, often exotics, with a high survival rate (Lesica & Allendorf 1999). Other revegetation goals include the provision of specific habitat, the prevention of invasion by exotics, the re-establishment of select ecological functions and the restoration of compositional biodiversity. These programs have raised awareness of the use of native species for revegetation. Some revegetation programs aim to restore populations of specific endangered species and focus necessarily on the reintroduction of only those species, often at small scales. However, the aim of many present day, often large scale, revegetation programs is the re-establishment of fully functional and compositionally biodiverse, self-sustaining ecosystems that persist well into the future (Coates & Van Leeuwen 1996; Lesica & Allendorf 1999). Each of the factors affecting the choice of seed collection strategy is discussed below in the context of these large scale revegetation programs.

Site characteristics

Lesica and Allendorf (1999) recommend that the degree of disturbance at a revegetation site, as well as its size and proximity to local populations, should be taken into consideration. The degree of disturbance at a revegetation site may vary from slight degradation to total transformation. If the severity of disturbance is low and the abiotic environment has not altered significantly, nearby populations should still be well adapted to the environmental and ecological conditions at the revegetation site and seed from these sources, if of suitable quality, may be a first choice for revegetation (Lesica & Allendorf 1999). Examples of these sites may be logged forests where post harvest treatments are minimal and where the soil structure remains intact.

At highly disturbed revegetation sites, environmental conditions may be significantly altered and completely novel compared to the original state. Where there have been large changes to edaphic and ecological conditions, locally sourced genetic material may no longer be well adapted to the site (Lesica & Allendorf 1999). Indeed, more diverse seed collections of varying genetic material may provide the higher levels of genetic variation required for adaptation, population survival and long-term population persistence. In highly disturbed sites, matching for environmental factors may be more critical for successful revegetation than simply minimising the geographic distance between seed source populations and the site requiring revegetation, and the 'coarse selective tuning' or 'habitat matching' approach of McKay and Christian *et al.* (2005) may be more appropriate. This advocates an ecogeographic approach to revegetation with seed lots comprised of a mixture of genotypes from climatically, edaphically and ecologically matched populations. This approach would limit the introduction of highly maladapted genotypes and still provide enough genetic variation within the restored populations for further adaptive 'fine tuning'. Examples of severely disturbed sites may include roadsides, ex-agricultural land, and mine sites where the topsoil has been removed.

The size and proximity of the revegetation site to local populations should also be considered as it influences the risk posed to local populations via the potential introduction of non-local material. This is particularly relevant when the area to be revegetated is large in comparison to nearby native vegetation (Lesica & Allendorf 1999), where the use of locally collected material will reduce the risk of hybridisation or negative ecological interactions between local and non-local populations. If the area to be regenerated is small or isolated, there is little chance locally adapted genotypes will be swamped out by introduced non-local material. If the site is highly disturbed and also small or isolated in area, the 'coarse selective tuning' approach, using material from more diverse seed collections may be the best approach (McKay *et al.* 2005).

There is general recognition that for survival over the short term, genetic variation within populations is often less critical than stochastic demographic, environmental and anthropogenic events at the revegetation site (Coates & Atkins 2001). These events are by definition difficult to predict. However, there are also likely to be long-term changes to future environmental conditions, such as those caused by climate change. While increased temperature and decreased rainfall are predicted for south-west Western Australia, some of these future changes are also likely to be unpredictable, and suggest that the use of material of diverse origins where genetic diversity is maximised will be an advantage for revegetation programs (Harris *et al.* 2006). Seed collection strategies that sample seed from an increased number of more widely sourced populations will maximise genetic variation and increase the likelihood of capturing adaptive genes required for future conditions. Such approaches to seed collection should provide greater opportunity for evolutionary development in revegetated populations thus increasing the chances of long-term population persistence and revegetation success.

Local adaptation

The presence of local adaptation is often proposed as one of the reasons for a restrictive or localised approach to seed collection areas. Local adaptation is best investigated using an approach that assesses quantitative ecologically important traits of heritable variation, and combines common garden studies, reciprocal transplant studies, and crossing experiments over a range of geographic distances. A limitation of these methods is that they are costly and time consuming and not likely to be conducted for a range of endemic taxa or for non-commercial species.

Some information on local adaptation is available for three tree species from the south-west forests. Assessment of provenance trials in Jarrah found evidence for adaptive variation in traits such as survival, stem diameter and growth rate between provenances from the northern jarrah forest, the southern jarrah forest, and the Swan Coastal Plain (Alcoa, unpublished data). Within the northern forest region adaptive variation was low although provenances from low rainfall sites on the eastern edge of the forest had poorer growth (O'Brien *et al.* 2007). This finding suggests an approach using regional seed collection areas with ecogeographic habitat matching for northern and southern populations. The difference in performance between Swan Coastal Plain and main forest provenances is also consistent with historic genetic differentiation between these provenances identified with molecular markers (Wheeler & Byrne 2006).

Provenance trials of Karri also showed little adaptive variation between major river catchments and little genetic differentiation was detected among catchments (Coates & Sokolowski 1989; Mazanec & Mason 1993). Some outlying populations exhibited slower growth that may indicate adaptive variation. These findings suggest that seed collection areas may be broadened beyond major river catchments to more regional collection areas although outlying populations should be treated separately. Similarly, little adaptive genetic variation was detected in a study comprising a number of populations of *Allocasuarina fraseriana* (O'Brien 2007) indicating that seed may be sourced at a regional scale.

Environmental factors such as climatic (*e.g.* temperature, day night cycles, light, rainfall probability, frost tolerance, germination temperatures) and edaphic conditions (*e.g.* soil texture, water holding capacity, chemical composition), as well as ecological processes (*e.g.* mycrorrhizal associations, pollinator abundance, seed dispersers), may vary across a landscape and contribute to local adaptation. Thus, consideration of these factors may also assist in defining seed collection strategies. Indeed, the establishment of seed collection areas based on broad ecological and geographical similarities between the seed collection site and the area undergoing revegetation has been recommended in the absence of more detailed data on patterns of local adaptation (Jones & Johnson 1998).

Genetic differentiation

Determinants and patterns of genetic variation

It has been suggested that population genetic approaches can be applied to defining provenance since genetic data can be obtained more rapidly and cost effectively than ecological and reciprocal transplant studies (Coates & Van Leeuwen 1996; Bussell *et al*. 2006). The patterns of genetic variation measured by molecular markers primarily reflect the impacts of past gene flow and genetic drift and are not necessarily correlated with the forces of selection that confer local adaptation (Reed & Frankham 2001; McKay *et al.* 2005). Despite their limitations, neutral genetic markers are potentially useful in describing possible evidence of local adaptation. They are used to indicate population genetic divergence due to restricted gene flow and as pointed out by Lynch (1996) significant molecular divergence provides strong evidence that adaptive divergence has the opportunity to occur but it is important to note that lack of any molecular divergence is likely to be uninformative. Such marker-based predictions of genetic variation should ideally be combined with field studies to confirm that genetic variation reflects adaptive variation.

For many native species, information about the partitioning of genetic variation among populations will not be available. However, some indication of the likely patterns of genetic variation may be obtained by assessment of a range of biogeographical, reproductive and species life history traits that have been shown to strongly influence gene flow and the subsequent partitioning of genetic variation among populations (Hamrick 1979; Hamrick & Godt 1996; Nybom 2004). Pollen and seed dispersal, in combination with the breeding system, have a major impact on patterns of genetic variation among plant populations (Hamrick 1979; Hamrick & Godt 1996). Species with high levels of gene flow through highly mobile pollinators or wind pollinated systems tend to have lower levels of genetic differentiation among populations than predominantly selfing species and species where the opportunity for pollen and seed dispersal is limited. Life history traits and life form can be good predictors of spatial scales of genetic variation, with trees and later successional stage long lived perennials generally having higher levels of gene flow than herbaceous, early successional stage annuals that tend to have restricted gene flow and high population differentiation (Hamrick 1979; Hamrick & Godt 1996; Nybom 2004). Thus, assessment of these traits may indicate the likely levels of genetic differentiation in the absence of specific information on the partitioning of variation.

Some generalisations can be made with regard to patterns of genetic variation in terms of the geographic distribution of species although there will always be exceptions. Species with widespread or regionally continuous distributions would be expected to have ample opportunity for gene flow and therefore little genetic differentiation between populations. In species with relatively low genetic differentiation local adaptation would be limited or occur over broad geographic distances and seed collection areas for revegetation may be extended to intermediate or regional ranges. The most obvious barriers to gene flow in widespread plant populations may be components of the physical environmental such as rivers, significant landforms and major edaphic differences. These physical barriers may cause genetic differentiation among populations and form boundaries for seed collection areas.

The dominant trees of the south-west forests are widely used in revegetation and are examples of species that occupy wide, virtually continuous, geographic distributions. Genetic studies in these dominant tree species do indicate little geographic partitioning of genetic variation throughout the main range (Coates & Sokolowski 1989; Coates *et al.* 2002; Wheeler *et al.* 2003; Wheeler & Byrne 2006; O'Brien 2007; O'Brien *et al.* 2007), suggesting that broad regional seed collection areas may be used for these species.

In contrast to species with continuous distributions, many common Western Australian shrub species that are used for revegetation have geographically widespread but naturally patchy distributions and exhibit low to moderate levels of genetic variation between populations (Byrne 1999; Hines & Byrne 2001; Broadhurst & Coates 2002; Byrne *et al.* 2003; Elliott & Byrne 2003; Broadhurst *et al.* 2004). The distribution of these species is related to the natural mosaic of habitats throughout much of the south west, although species with patchy distributions can also occur in the more continuous habitat of the forest ecosystems. Moderate levels of genetic structuring in such species may indicate the possibility of adaptive variation among populations. This suggests that germplasm for revegetation should consist of more localised seed sources when possible, although factors such as characteristics of the revegetation site and the quality of local seed sources should be also considered.

We note here that we are not considering other species of the south-west flora that are not generally targeted for revegetation as they are rare, have isolated populations or highly disjunct distributions. These species, and those occurring in highly fragmented environments, or where significant geographic barriers to gene flow occur, generally have high levels of genetic differentiation (Coates 2000, Byrne & Hopper 2008). Seed collections from these species may be for specialised restoration programs and reintroductions but would not be targeted for general revegetation.

Chromosome variation

Variation in chromosome number, ploidy level and chromosomal rearrangements may have an important influence on the expression of outbreeding depression through the development of chromosomal barriers to gene flow. In these cases crossing between chromosomally differentiated populations can result in seed abortion, partially or fully sterile progeny or hybrid breakdown in subsequent generations leading to restoration failure in the long term (Coates & James 1979; James & Hopper 1981). Complex cytoevolutionary patterns including polyploidy, chromosome number changes and other kinds of chromosomal rearrangements are evident in a number of species from south west Western Australian with extreme examples including *Stylidium crossocephalum* and *Isotoma petraea* (Coates 2000). Although there are relatively few species where such data is available if the presence of ploidy or chromosomal rearrangements is identified in a given taxon, it would be prudent for seed collections to be sourced from populations of the same chromosome type as those at the revegetation site.

Taxonomic considerations

It should be noted that the accurate identification of the correct taxonomic entities represents an essential first step in defining seed collection areas for revegetation. Many native species show high levels of morphological diversity across their range and the dynamic nature of taxonomy in Western Australian flora means species are often subject to taxonomic revision (see Gibson *et al.* 2007). The correct identification of populations of newly described subspecies and variants may be an issue for seed collection in species complexes with high levels of morphological variation such as many acacias, *e.g. A. browniana, A. pulchella*, and *A. saligna*. However, population identification in the field is often difficult as morphological differences used to distinguish subspecies or variants may only be present at certain times of the year and identification may be further hampered by variable juvenile growth forms, as is the case for *A. saligna* (Millar *et al.* 2008). Genetic studies in *A. saligna* have revealed high levels of genetic divergence between the subspecies (George *et al.* 2006; Millar *et al.* 2008) and specific local adaptation is likely. For species complexes such as these, seed collections should be treated separately, and seed should only be used within the natural range of that subspecies or variant. As suggested by Coates & Van Leeuwen (1996) a first step for seed collectors is to keep abreast of reviews of the relevant taxa to ensure accurate population identification.

Quality and availability of local seed sources

The availability and quality of seed sources are also important in making decisions on the appropriate geographic scale of seed collection areas and the subsequent deployment of material at revegetation sites. In most revegetation situations the quality of the seed source should be considered more important than sourcing from the nearest population. Seed collected over a range of populations covering a climatically,

Table 1

Factors to consider when determining appropriate seed collection strategies for flora of south-western Australian commonly used in revegetation.

Factor	Aspect	Scale	Effect on seed collection area and collection strategy
Aim of revegetation program	Highly specialised goals	–	May require specialised strategies
	Functional and compositional ecosystem restoration	–	Consider the factors below
Characteristics of revegetation site	Degree of disturbance	High	Broader, more diverse collections, attempt to habitat match collection and revegetation sites
		Low	Localised collections
	Size	Large	Localised collections
		Small	Broader collections may be used if required
	Proximity to native populations	Isolated	Broader collections may be used if required
		Nearby	Localised collections
	Future changes	Likely or unknown	Broader, more diverse collections, attempt to habitat match collection and revegetation sites
		Unlikely	Localised collections
Presence of local adaptation	Known	Present	Localised collections
		Not present	Broad to regional ecogeographic collections
	Unknown	–	Assess partitioning of genetic variation
Partitioning of genetic variation	Known	High divergence	Localised collections
		Low divergence	Broad to regional ecogeographic collections
	Unknown	–	Assess likely extent of gene flow
Likely extent of gene flow	Requires assessment of distribution, biogeography, life history traits, cytogenetics and taxonomy.	Extensive	Broad to regional ecogeographic collections
		Restricted	Localised collections
Availability and quality of local seed sources	Availability	Local sources available	Assess quality of seed sources
		Local sources not available	Broaden collection area
	Quality	Large healthy populations	Suitable for collection
		Small unhealthy populations	Not suitable for collection, broaden collection area

edaphically and environmentally matched regional scale that provides high levels of genetic diversity will almost always be more appropriate material for revegetation than seed collected from a restricted number of 'unhealthy', small or isolated populations on a local geographic scale.

Small local populations may also be unsuitable sites for collecting seed for revegetation due to genetic impoverishment. Small populations, especially those of recently reduced size, may be suffering from inbreeding depression due to the effects of increased mating among relatives (Edmands 2007). Germination may be reduced and progeny may display reduced growth and survival due to the accrual of deleterious recessive traits in seed collected from such populations. Small populations experiencing inbreeding may also exhibit low levels of seed production. For example, Yates *et al.* (2007) found a decline in seed production with decreasing population size in the bird pollinated shrub *Calothamnus quadrifidus* where populations produced at least 50% less seed per fruit than large populations. Harvesting of seed from such populations is likely to result in further reductions in seed set and population recruitment, and enhance inbreeding depression in the population.

Practical aspects of seed collection may need to be considered as there can be a number of problems associated with the collection of geographically local seed for revegetation, and its availability is a persistent management issue for seed collectors and suppliers (Mortlock 2000b). Often, locally sourced seed is of limited supply resulting in harvest activities being relatively inefficient and costly. Both the amount of seed available for harvest and the quality of that seed will depend on stand health, seasonal variation in rainfall and temperature, masting, predation, and natural seed viability.

Conclusion

Current strategies for collecting native seed of south-west Western Australian flora for use in revegetation tend to follow a precautionary principle that advocates collecting seed from geographically restricted areas located close to revegetation sites. Ideally, appropriate seed collection areas should be defined according to species-specific local adaptation to site conditions. Because of the paucity of information on local adaptation from genetic and field studies, recommendations for appropriate seed collection areas are not available for most species utilised for restoration and revegetation in this region. However, the likelihood of local adaptation and hence the requirement to utilise more locally collected seed in revegetation programs, may be inferred from patterns of genetic differentiation among populations. In the absence of genetic data probable patterns of genetic differentiation may in turn be inferred by assessment of species-specific traits such as geographic distribution, pollen and seed dispersal, breeding system, life history traits (successional stage, annual, short-lived or long-lived perennial) and life form (herbaceous, shrub or tree).

We have suggested here a strategy for determining appropriate seed collection areas for south-west Western Australian flora commonly used for revegetation. We recommend taking into consideration a number of factors including the aim of the revegetation program, the characteristics of the revegetation site, species specific local adaptation, partitioning of genetic variation, and the availability and quality of local seed sources (Table 1). In many cases, a seed collection strategy where seed is sourced from a number of large healthy populations located a greater distance from the site to be rehabilitated but habitat matched for regional edaphic, climatic and environmental variables at the revegetation site may be appropriate. Such a strategy aims to prevent the introduction of highly maladapted genotypes whilst maximising genetic diversity and the potential for adaptation at the revegetation site in both the short and long term. Such an approach is especially advocated for small revegetation sites where the degree of environmental disturbance is significant or future changes to the environment are likely, where there are few local populations with which introduced material may interbreed and when local adaptation is not present. Seed collection areas may also be broadened for species where information suggests local adaptation and outbreeding depression is unlikely and significant partitioning of genetic variation due to restricted gene flow is not expected. In situations where local seed sources are not available or are of poor quality, seed collection areas will also have to be broadened and collections from a number of healthy populations matched from ecogeographic variables are recommended.

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