Seed Collection Zones

for

State Forest Management

A report to the

Sustainable Forest Management Division

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Background

Appropriate strategies for collecting seed that will provide the raw genetic material for revegetation activities is an important issue for restoration or rehabilitation programs. Current approaches regarding seed collection tend to follow a restrictive precautionary principle that advocates the use of only ‘local’ seed or seed of ‘local provenance’ for revegetation. The Sustainable Forest Management Division of the Department of Environment and Conservation has adopted this precautionary approach regarding the collection of seed for forest rehabilitation purposes. This is a response to the ‘local’ requirement regarding the collection of seed that is stipulated in the Forest Management Plan 2004-2013. The term ‘local’ has not been defined although anecdotally, highly geographically restricted or ‘local’ seed collection zones of around 15 km are used by both the Forest Products Commission and the Department of Environment and Conservation.

Considerations

Traditional arguments for the use of ‘local provenance’ seed have included

- assumption of strong local adaptation associated with genetic divergence over restricted geographic areas in plant species,
- concerns about the production of hybrid progeny that display outbreeding depression among genetically divergent populations, and
- concerns about other ecological interactions, such as invasiveness and displacement of the local form.

Defining appropriate seed collection zones is a difficult task, and in many cases assigning a specific geographic scale or ‘local’ seed collection zone will not be possible nor may it be the most appropriate approach to collecting seed for revegetation. For most Western Australian understorey species used in current forest rehabilitation operations there is little information available regarding patterns of local adaptation and genetic diversity, and the likelihood of hybridisation among genetically divergent populations, the likelihood of invasiveness or other ecological interactions.

Delineation of seed collection zones will vary for given taxa and for a given restoration program, and should be based on a number of considerations including:

- the aim of the restoration or revegetation program,
- characteristics of the site requiring restoration,
- patterns of local adaptation in species used for revegetation,
- partitioning of genetic variation in species used for revegetation, and
- availability and quality of seed sources.

Recommendations

A key recommendation of the report is that an eco-geographic approach, where seed is collected from a number of large healthy populations at sites matched for environmental, edaphic and climatic variables with less regard to their geographic distance from the restoration site, may be a more appropriate strategy for seed collection than the exclusive use of material from geographically restricted areas.

The report recommends that studies be undertaken to examine the genetic diversity of a selection of Western Australian understorey species in combination with field studies such as reciprocal transplant and common garden experiments in order to more accurately reveal patterns of local adaptation.

This report also makes a number of specific recommendations regarding the collection of seed for forest rehabilitation operations:

- Populations to be used as seed collection sites must be accurately identified at the subspecies level.
- Seed collection sites and rehabilitation sites should be matched for climatic, edaphic and other environmental variables regardless of geographic distance between them.
- The requirement for rehabilitation with ‘local’ seed sources becomes reduced as levels of disturbance at the restoration site increase and the size of the restoration site decreases.
- The requirement for rehabilitation with ‘local’ seed sources increases as the level of disturbance at the restoration site decreases, the size of the restoration site size increases, if inter-fertile local populations are present, and if local adaptation is recognised.
- The likely partitioning of genetic variation within specific species should be evaluated to gain insight into the possible patterns of local adaptation.
- All seed sourced for rehabilitation operations should be collected from healthy stands of sufficient size to ensure the quality of the seed supply.

Introduction

Regeneration in forest regions is a key restoration activity in Western Australia and is based on sound scientific principles. Appropriate strategies for collecting seed that provide the raw genetic material for restoration activities is an important issue for forest regeneration, as for other revegetation programs. Traditional approaches regarding seed collection tend to follow a restrictive precautionary principle that advocates the use of only 'local' seed or seed of 'local provenance' for revegetation. This approach has been adopted in the Forest Management Plan that prescribes the use natural regeneration followed by 'locally' sourced seed:

> '*Allowing natural seed drop from a perimeter influence remains a primary objective in revegetation where reasonable and practicable, and where the area is too large to rely on perimeter influence seed drop alone, the Forest Products Commission and the Department of Environment and Conservation will undertake their revegetation or rehabilitation operations by using seed collected locally, or plants propagated from seed collected locally*' (Conservation Commission of Western Australia 2004).

The term 'local' has not been defined although anecdotally, 'local' seed collection zones of around 15 km are used by both the Forest Products Commission and the Department of Environment and Conservation. This restriction relates simply to geographic distance and does not take into consideration other factors relevant to seed supply for revegetation.

This guideline reviews the scientific basis for use of local provenance germplasm in revegetation, with particular reference to forest rehabilitation. It makes recommendations for seed collection zones for forest management in Western Australia based on these scientific principles.

Germplasm collection zones

How are local seed collection zones defined for plant populations? Unfortunately, there exists no universal definition of 'local' when it comes to plant populations used as seed sources for restoration or revegetation programs. The term 'local provenance', which is often applied to seed collected 'locally' or of local origin, is largely undefined and is often used simply to describe the origin or source of specific genetic material. The concept of 'provenance' developed from observations that morphological and physiological variation in trees were associated with environmental factors as well as their evolutionary history (Boland 19865, Turnbull and Griffin 1986). Thus 'local provenance' arises from the assumption that seed from local plants are best adapted to local conditions. However, patterns of morphological and physiological variation may or may not be reflective of genetic adaptation to local environmental conditions and local adaptation can occur at a number of scales. Thus, there is no practical definition of 'local provenance' for plant populations, in the sense of referring to specific genetic adaptation to site conditions.

Recommendations for sourcing local provenance seed suggest small on-site seed collection areas in the first instance, and if difficulty arises in harvesting sufficient amounts of seed from these populations, the seed collection area should be extended to the next geographically closest viable populations (Mortlock 2000). This approach has been recommended particularly in the absence of information on the distribution of genetic diversity, in particular that which may confer adaptation to local environmental conditions for a given species (Mortlock 2000). There are a number of reasons that this precautionary approach has been advocated and adopted:

- It has been shown that material sourced from local populations will be best suited to a specific site, possessing adaptation to local climatic, edaphic, biotic and other environmental conditions (eg. Galloway and Fenster 2000, Montavlo and Ellstrand 2000; Joshi et al. 2001). Such 'local provenance' material has a 'home site advantage' in terms of maintaining ecological processes and long term population adaptation, viability and survival due to local adaptation. Conversely, material that is not adapted to local conditions may display reduced survival, growth, reproduction, and long-term persistence at revegetation sites, relative to locally adapted material (Potts et al. 2003).

- The use of local provenance material for revegetation reduces the risks associated with interactions between genetically divergent yet inter-fertile, introduced populations and local populations. When material that is not adapted to local conditions crosses with locally adapted populations, hybrid progeny that display outbreeding depression (reduced fitness in terms of growth, survival and reproduction) may be produced (Edmands 2007). If hybrid progeny fail to persist, the effective population size may be reduced to levels that affect the ability to adapt to long-term changes in environmental conditions and overall viability and persistence (Rhymer et al. 1996).

- The use of local provenance seed source material in revegetation may also reduce the risk of negative effects associated with ecological interactions between introduced non-local populations and local populations and their broader communities. These negative impacts may include invasiveness, displacement of the local form and changes to the surrounding community structure. The relative risks of such impacts will be dependent on species and site specifics.

These are the traditional arguments in support of 'best practice' in the use of locally sourced material for restoration and revegetation. However, opinions differ on the appropriate strategy for selecting plant material for revegetation (Montalvo et al. 1997; Lesica et al. 1999; Hufford et al. 2003; McKay et al. 2005) and locally sourced material may not always be the most appropriate. Non local genetic material may not necessarily be maladapted, outbreeding depression may not occur in hybrid progeny of inter-fertile yet divergent populations, and if it does, maladapted alleles may be readily purged by selection, leading to only a short term decrease in fitness (McKay et al. 2005). Ecological interactions may not be an issue with the use of native species. A restrictive approach toward local seed collection zones may also have its drawbacks. If seed for revegetation is collected from a restricted area there is a risk that it will have limited genetic diversity and will not possess enough adaptive potential to respond to changes that have already occurred at the revegetation site, or to future changes such as climate change. The use of geographically restricted seed collection zones may also encourage the selection of inbred or genetically depauperate seed sources.

Ideally, in making decisions on an appropriate strategy for geographic scale of seed collection zones and deployment of material at revegetation sites, a range of factors should be assessed, including:

- the aim of the revegetation program,
- current and future aspects of the site requiring revegetation,
- patterns of local adaptation in species to be utilised,
- the partitioning of genetic variation in the species to be utilised, and
- the availability and quality of target species seed.

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 has been the rapid restoration of degraded land achieved via the establishment of plants of only a few species, often exotics (Lesica et al. 1999). Other revegetation goals include the re-establishment of select ecological functions, the provision of specific habitat, the restoration of biodiversity and the prevention of invasion by exotics. These programs have raised awareness of the use of native species for restoration and revegetation. Some rehabilitation 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, restoration or revegetation programs is the re-establishment of fully functional and biodiverse, self-sustaining ecosystems that persist well into the future (Coates et al. 1996; Lesica et al. 1999). This is largely thought to be best achieved by conserving or restoring genotypes of the original local populations of native vegetation.

The aim of regeneration operations in forest regions of Western Australia is '*to rehabilitate or regenerate forest that has been disturbed to sustain in the longer term the range of flora composition and structural attributes consistent with relevant biological diversity objectives*' (Conservation Commission of Western Australia 2004). Therefore the use of local provenance germplasm is appropriate for forest rehabilitation.

Site characteristics

An assessment of the site requiring restoration or revegetation will allow some broad generalisations to be made on the most appropriate strategy for the selection of seed sources for revegetation. Lesica and Allendorf (1999) recommend that both the degree and extent of disturbance at a site requiring revegetation and the site situation, or level of isolation with regard to nearby local populations, should be taken into consideration when the requirement for local provenance material for revegetation is being assessed.

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. Thus, seed from these sources, if of suitable quality, may be a first choice for revegetation. An example of this may be logged over forests where post harvest treatments are minimal and where the soil structure remains intact (Lesica et al. 1999).

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 and may no longer be the most appropriate material for use in revegetation (Lesica et al. 1999). Indeed, more diverse seed collections of varying genetic material may provide the higher levels of genetic variation required for adaptation to the novel environment thus facilitating 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 eco-geographic approach to restoration where seed comprised of a mixture of genotypes from climatically, edaphically and ecologically matched populations is utilised. 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, areas that have been previously used for agriculture and mine sites where the topsoil has been removed.

The scale of disturbance at the site requiring revegetation should also be considered as it will dictate how much genetic material will need to be introduced for revegetation purposes and therefore give some indication of the scale of 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 existing surrounding vegetation and natural populations of species used in revegetation occur nearby (Lesica et al. 1999). In this case the use of locally collected material will reduce the risk of negative impacts that may occur via hybridisation or 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 by introduced non-local material. If the site requiring revegetation 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 survival of revegetation in the short term is more dependant on demographic, environmental and anthropogenic events at the revegetation site than genetic diversity of the germplasm (Coates et al. 2001). However, genetic diversity may be extremely important for survival through future long-term environmental conditions at the revegetation site, such as those caused by climate change. 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 the new conditions thus increasing the chances of long term restoration success and population persistence.

Forest rehabilitation in Western Australia generally occurs in relatively small sites that have low levels of disturbance, suggesting that local germplasm may be appropriate, but it also aims to restore long term ecological function therefore genetic diversity in seed supply will be important for long term survival.

Local adaptation

The presence of local adaptation is the main reason for a restrictive approach to seed collection zones, but local adaptation is difficult to assess. It is best investigated using an approach that assesses quantitative 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.

Currently, genetic data can be obtained more rapidly and cost effectively than ecological and reciprocal transplant studies, and it has been suggested that genetic approaches can be applied to defining provenance for seed collection for revegetation purposes (Coates et al. 1996; Bussell et al. 2006). Genetic approaches that utilise molecular markers can be used to detect any significant divergence in allele frequencies among populations. Analysis of populations from across the species range provides an assessment of the geographic partitioning of genetic variation among populations for the given taxon. Genetic structuring among populations may then indicate independently derived lineages, provide insights into the historical levels of isolation among populations and reflect the actions of natural selection in shaping local adaptation. The patterns of genetic diversity measured by molecular markers primarily reflect the impacts of past gene flow and genetic drift and are not necessarily correlated to the current forces of selection that are largely responsible for conferring local adaptation. Hence, there is no theoretical basis for assuming neutral (in terms of natural selection) markers are an effective means of defining scales of local adaptation for quantitative traits (Reed et al. 2001; McKay et al. 2005).

Despite their limitations, neutral genetic markers are potentially useful in describing possible evidence of local adaptation as they do indicate population genetic divergence due to restricted gene flow (Bussell et al. 2006). Such marker-based predictions of genetic differentiation should ideally be combined with field studies to confirm that genetic differentiation reflects adaptive variation. Measuring quantitative and heritable ecologically important traits in plants from different source populations grown at a common site allows assessment of environmental adaptation as a cause of phenotypic variation. However, studies that combine marker based analysis of genetic variation and field based assessments of quantitative traits are unlikely to be conducted for a range of endemic non-commercial understorey species. Jarrah is the only native Western Australian species for which a combined study has been undertaken (O'Brien 2007; O'Brien et al. 2007).

Genetic variation

For many native species, generalisations will have to be made about the partitioning of genetic variation and levels of gene flow among populations. This can be done by assessing a range of biogeographical, ecological 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 et al. 1996; Nybom 2004). These generalisations can be used as a first indication of the likely levels of genetic differentiation to aid the broad delineation of possible seed collection zones in the absence of specific information on local adaptation.

Gene flow in plant species is a function of pollen and seed dispersal, thus these mechanisms, in combination with the breeding system, have a major influence on the distribution of genetic variation among plant populations (Hamrick et al. 1996). High levels of gene flow are generally observed for obligatory or highly outcrossing species and those with mechanisms for long distance pollen and seed dispersal. These species tend to have lower levels of among population genetic differentiation than predominantly selfing species, species where the opportunity for long distance pollen dispersal is reduced, and species where seed dispersal is limited. For outbreeding species local adaptation may be limited or occur over broad geographic distances and seed collection zones for revegetation may possibly be extended to intermediate or regional ranges. Life history traits and life form have also been shown to be good predictors of spatial scales of genetic differentiation, 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 (Nybom 2004). For example, *Allocasuarina fraseriana* pollen is wind dispersed and the dioecious trees have an obligatorily outcrossing breeding system. Levels of gene flow in this species would be expected to be high as it has a widespread and relatively continuous distribution, and local provenance seed sources may cover regional areas. Indeed, little adaptive genetic variation was detected in a study comprising a number of populations of *Allocasuarina fraseriana* (O'Brien 2007). Other woody species of *Allocasaurina*, *Banksia*, and *Agonis* and bird-pollinated species such as *Xanthorrhoea* and *Angiozanthos* may also be expected to exhibit little adaptive genetic variation among populations, which suggests that seed collection zones may cover relatively large areas.

However, the majority of Western Australian understorey species tend to be predominantly small insect pollinated shrubs, factors which, when coupled with disjunct population distributions, would be expected to result in low levels of gene flow and high levels of genetic differentiation among populations. This would suggest sourcing seed for use in revegetation programs from more local populations. Coates (2000) showed that many rare species of fragmented south-west flora (e.g. *Acacia anomala*, *Banksia cuneata*, *Eucalyptus caesia*, *E. crucis*, *Gelezenowia verrucosa*, *Lambertia orbifolia*, *Stylidium coronifirme and S. nungarinenese*) exhibit high levels of genetic differentiation between populations. Disjunct and restricted populations are typical of many species of the southwest forest understorey, such as *Gastrolobium bilobum*, *Hardenbergia comptoniana*, *Kennedia coccinea*, *K. prostrata*, and some subspecies or variants of *Acacia browniana, A. pulchella,* and *A. saligna*. These species would be expected to exhibit high levels of genetic differentiation between populations. High levels of genetic structuring among different populations, variants or subspecies may reflect high levels of adaptive variation among populations and suggest that the most germplasm for revegetation should be derived from more restricted seed sources.

The most obvious barriers to gene flow in plant populations may be components of the physical environmental such as rivers and large areas cleared of native vegetation. These physical barriers may produce abrupt genetic differentiation among populations and form boundaries for seed collection zones. Other environmental factors that may contribute to local adaptation, such as climatic (e.g. temperature, day night cycles, light, frost, rainfall) and edaphic conditions (e.g. soil texture, water holding capacity, chemical composition), as well as ecological processes (e.g. mycorrhizal associations, pollinator abundance, seed dispersers), will vary across a landscape. Thus, consideration of these factors may also assist in defining seed collection strategies. Indeed, the establishment of seed collection zones 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 et al. 1998).

Significant correlations between geographic distance and levels of genetic variation have been found in some plant genera (Hamrick et al. 1996), including eucalypts (Moran et al. 1983), although for other species with relatively continuous distributions over wide geographic areas, geographic distance alone is an unreliable guide to patterns of genetic diversity. Nonetheless, some generalisations can be made with regard to patterns of genetic differentiation in terms of the geographic distribution of species. Species with widespread or regionally continuous distributions and common, non-fragmented environments, with no natural physical barriers, are expected to have more opportunity for gene flow and therefore less genetic differentiation between populations.

A number of native Western Australian overstorey species such as jarrah (*Eucalyptus marginata*), marri (*Corymbia calophylla*), tuart (*E. gomphocephela*) and karri (*E. diversilcolor*), occupy wide, virtually continuous, geographic distributions. Although these dominant tree species may exhibit morphological variation across their distribution, a lack of natural physical barriers, in combination with highly mobile insect, bird and mammal pollinators should result in the maintenance of high levels of gene flow, and low levels of genetic differentiation among populations. Genetic studies in these dominate tree species do indicate little geographic partitioning of genetic diversity throughout the main species range (Coates et al. 1989; Coates et al. 2002; Wheeler et al. 2003; Wheeler and Byrne 2006; O'Brien 2007; O'Brien et al. 2007), suggesting that broad regional seed collection zones may be used for these species.

In jarrah an extensive genetic study designed to investigate historical influences has revealed some significant geographic structuring that is related to a natural barrier to gene flow, the Darling Scarp (Fig 1). Populations on the Swan Coastal Plain show historical genetic divergence from those found on the lateritic Darling Plateau (Wheeler and Byrne 2006). This indicates that seed collections for rehabilitation should be conducted separately for each of these areas.

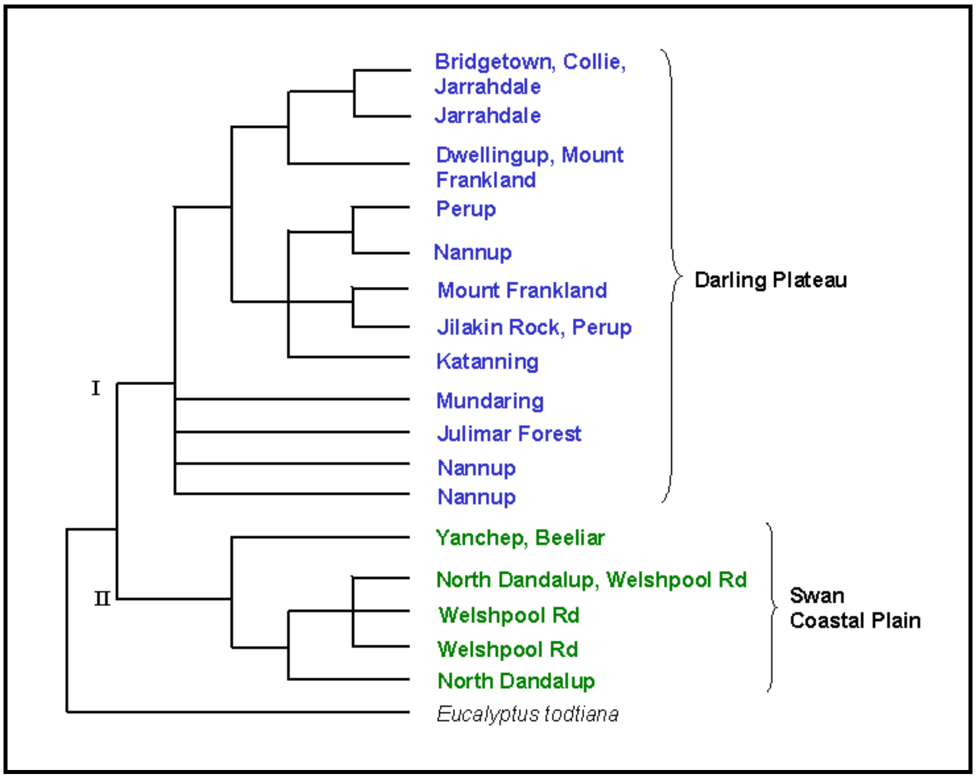

Figure 1. Phylogenetic tree showing the distribution of variation in chloroplast haplotypes for jarrah (*Eucalyptus marginata*). There are two major clades, one from the Darling Plateau and one from the Swan Coastal Plain, indicating long-term historical isolation of populations from these regions. Modified from Wheeler and Byrne, (2006).

Breeders and foresters have traditionally recognised the northern and southern jarrah forest as separate. Assessment of provenance trials has indicated the existence of adaptive variation in traits such as survival, stem diameter and growth rate among provenances from the northern forest and the southern forest (O'Brien et al. 2007) despite little molecular genetic variation within the main jarrah forest on the Darling Plateau (Wheeler et al. 2003). At a common low rainfall northern site, trees from northern sites produce smaller stem diameters, but survive well, possibly reflecting selection for slower growth, and trees from high rainfall southern sites display fast growth but poor survival (O'Brien et al. 2007). Some adaptation is also observed in latitudinal variation for flowering time. This evidence for local adaptation in relation to climatic and ecogeographic conditions, namely rainfall and latitude, supports the argument for habitat matching between northern and southern forest populations, and seed collected for rehabilitation should be matched to sites with similar rainfall and latitude.

Seed collection provenances for revegetation activities using karri have historically been based on major river catchments (Coates et al. 1989). However, there is little evidence of genetic structuring in populations from different catchments within the main forest (Coates et al. 1989) or of adaptive variation at this scale from provenance trials (Mazanec et al. 1993). Some outlying populations do exhibit a low level of genetic divergence, and also slower growth that may indicate adaptive variation. Variation in growth rate may be an adaptive response to rainfall similar to that seen in jarrah and indicates that suitable seed collection zones for rehabilitation may be broadened beyond major river catchments although habitat matching especially for climatic conditions, such as rainfall, will still be important.

Generalisations in describing patterns of genetic differentiation using information from breeding systems do become more complex where ploidy levels, chromosome number changes or chromosomal rearrangements occur. The fragmented population systems of native Western Australian flora, such as *Stylidium crossocephalum* and *Isotoma petraea*, may be associated with complex cytoevolutionary patterns (Coates 2000). If the presence of polyploidy or chromosomal rearrangements is identified in a given taxon, it is important that seed collected for use in revegetation is sourced from populations of the same ploidy level or chromosomal types as populations local to the revegetation site. Hybrid progeny produced as a result of breeding between populations of differing ploidy levels or chromosome arrangements may be sterile, contributing to failure of revegetation in the long term (Coates et al. 1979; James et al. 1981).

It is also worth noting that the accurate identification of the correct taxonomic entities represents an essential first step in defining seed collection zones 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. The correct identification of populations of newly described subspecies may be an issue for seed collection in a number of understorey species, such as the acacias *A. browniana, A. pulchella,* and *A. saligna*. High levels of morphological variation are found in these species complexes, and a number of subspecies are described (Fig 2). However, population identification in the field is often difficult as morphological differences used to distinguish subspecies 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 Koojong (*A. saligna*). Genetic studies in Koojong have revealed high levels of genetic divergence between the subspecies indicating that specific local adaptation is likely to be expressed in this species (Millar et al. 2007). Koojong seed should be collected and treated separately for each subspecies and used for revegetation only within the natural range of that subspecies. As suggested by Coates and Van Leeuwen (1996) the first step for seed collectors is to keep abreast of reviews of the relevant taxa to ensure accurate population identification.

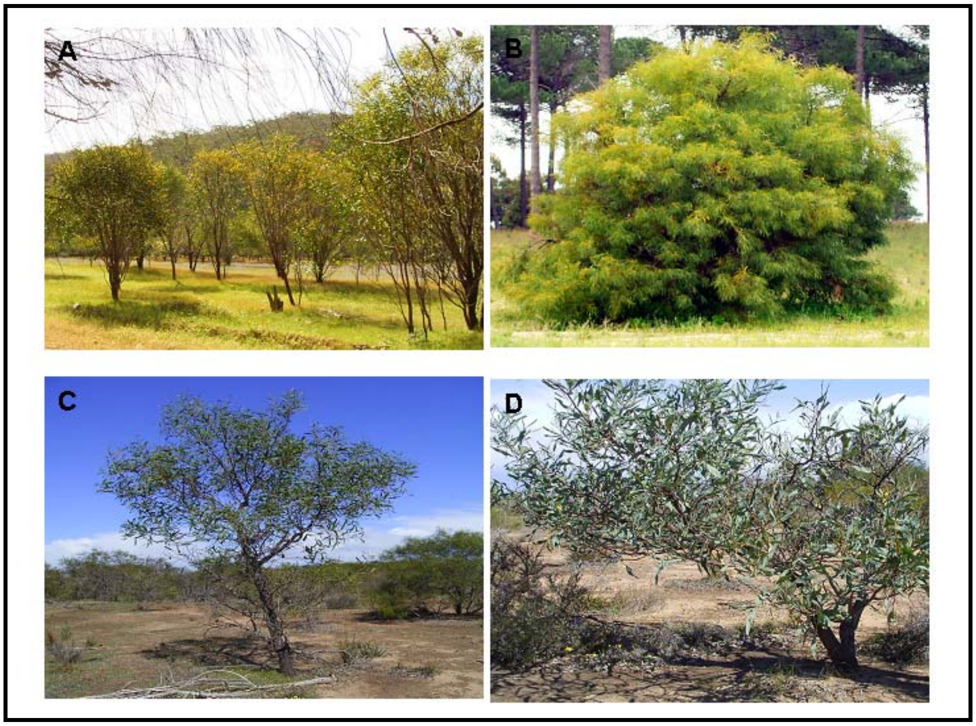

Figure 2. The four main proposed subspecies of *Acacia saligna* showing mature specimens of subspecies (A) *lindleyi* (B) *saligna* (C) *stolonifera* and (D) *pruinescens*.

Quality and availability of local seed sources

The quality and availability of seed sources are also important in decisions on the appropriate geographic scale of seed collection zones and the deployment of germplasm at revegetation sites. In most revegetation situations, quality of the seed source is a more important consideration than sourcing from the nearest population. Seed collected from a range of climatic, edaphic and environmentally matched populations with 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. In addition, the practical aspects of availability and quality of local provenance seed will necessarily influence the most appropriate sources of seed for revegetation.

There can be a number of problems associated with the collection of geographically local seed for revegetation:

- locally sourced seed is often of limited supply and its availability is a persistent management issue for seed collectors and suppliers,
- local seed collection may be inefficient, difficult and costly, and
- the amount of seed available for harvest and the quality of that seed will depend on seasonal variation in rainfall and temperatures, masting, predation by insects and fauna and natural seed viability.

The quality of natural populations available for use as seed sources must be taken into account when determining whether local populations are a suitable option for revegetation purposes. Local sites may be unsuitable for collecting seed for revegetation if they are small, or of recently reduced size, because small, isolated populations may be suffering from inbreeding depression; the deleterious effects of increased mating among relatives (Edmands 2007). In this case, populations may already exhibit low fecundity, and sufficient amounts of seed may not be available for collection. For example, Yates et al (2007) found a decline in seed production with decreasing population size in the bird pollinated shrub *Calothamnus quadrifidus* (Figure 3). Small populations produced at least 50% less seeds per fruit than large population fragments. Small populations of less than a few hundred individuals should be avoided as seed sources, as seed crops may be genetically impoverished and a poor choice for revegetation (Coates et al. 2004). Additionally, harvesting of seed is likely to result in further inbreeding depression at the collection site thus reducing seed set and population recruitment.

When local source populations are small, and where the site to be revegetated is small, site disturbance is significant or there are few local populations with which introduced material may interbreed, an approach where seed is sourced from a number of large healthy populations located a greater distance from the site to be rehabilitated will be especially appropriate. Seed collections from a number of large healthy populations occurring across regions matched to environmental conditions at the revegetation site may provide the greatest opportunity for successful site restoration in the short and long term. Indeed, Bussell and Hood (2006) suggest that, in such cases, the importance of achieving successful restoration and maintaining ecosystem integrity should override issues of spatial proximity of seed sources and restoration sites.

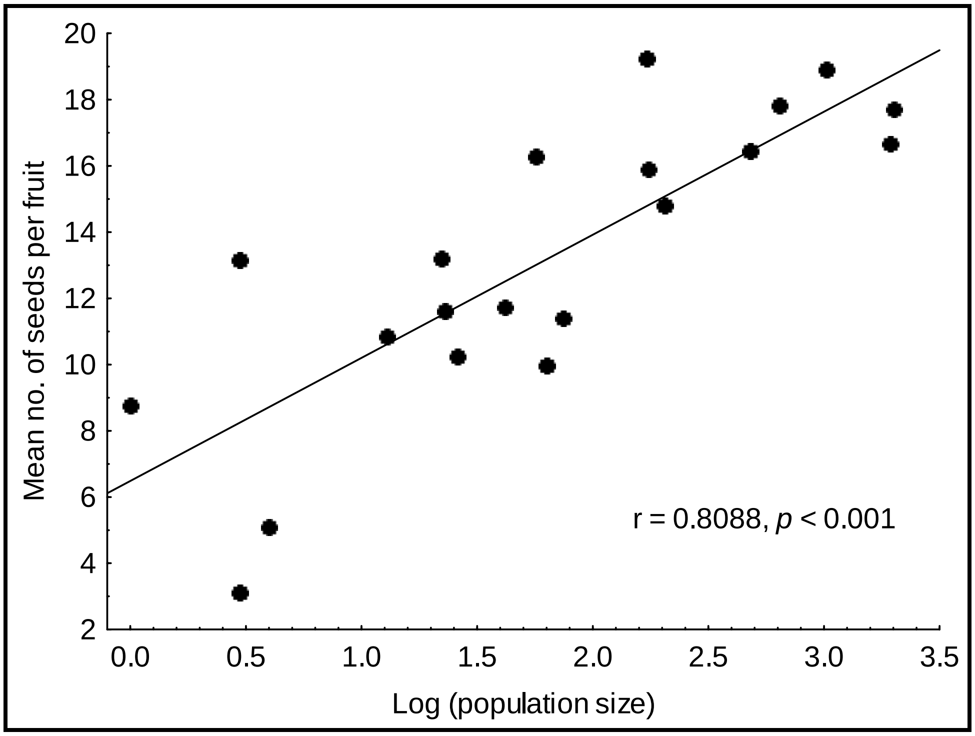

Figure 3. The relationship between mean number of seeds per fruit and log population size in 20 population fragments of *Calothamnus quadrifidus*. The significant positive correlation indicates the effects of inbreeding as reduced seed set in small populations. Populations are arranged in order of increasing size (number of reproductive plants). Values are means estimated from counts of seeds in 10 fruits on up to 20 plants in each population in each of three years (Yates et al. 2007).

Conclusions

Given the paucity of information from genetic and field studies on native Western Australian species, specific advice for appropriate seed collection zones is not available for many of the endemic understorey forest species required for rehabilitation of sites across south west Western Australia. However, it is suggested that a restrictive approach where seed collection sites are strictly limited to an arbitrarily set area not exceeding 15 km from the revegetation site will not be ideal. In many cases, when information on patterns of local adaptation is lacking, a 'habitat matching' approach where seed collection sites are matched for regional edaphic, climatic and environmental variables at the revegetation site, may be most appropriate. When multiple seed collection sites matched for habitat are used to source genetic material for revegetation, the introduction of maladapted genotypes will be prevented while genetic diversity and the potential for adaptation at the revegetation site in the long term is maximised.

Recommendations

The following recommendations are made in relation to seed collection practices for forest rehabilitation in Western Australia, based on the scientific principles outlined above.

Specific recommendations for seed collection zones can be made for the few taxa where genetic diversity and adaptive variation has been assessed. These recommendations are:

- Populations of jarrah on the Swan Coastal Plain should be treated separately from those on the Darling Plateau when seed is collected for revegetation purposes. Populations from the northern jarrah forest and the southern forest should also be treated separately. Within the northern or southern forests, matching sites of seed collection and revegetation for climatic and ecogeographic factors, such as rainfall and latitude, should be taken into consideration.

- Seed collection zones for karri may be broadened beyond major river catchments although outlying populations should be treated separately. Seed collection and revegetation sites should be matched for climatic and ecogeographic factors.

- Koojong seed collections should be treated separately for each of the four main subspecies and seed should be used for revegetation only within the natural range of the subspecies from which it was collected.

A number of guidelines can also be provided for seed collection zones for understorey species based on a range of characteristics related to the site requiring revegetation, the likely inferred patterns of genetic differentiation that may indicate local adaptation in the target species, and the availability and quality of local sources of seed for rehabilitation operations. These guidelines include:

- Ensure populations to be used as seed collection sites are accurately identified at the subspecies level.

- Match seed collection sites and revegetation sites for climatic, edaphic and other environment variables regardless of geographic distance between them.

- If the severity of disturbance at the revegetation site is high, the need to maximise genetic variation in seed sources increases. If the site is also small, the requirement for revegetation with local seed sources is reduced.

- If the severity of disturbance at the revegetation site is low, the site has large, inter-fertile local populations nearby, or local adaptation is recognised in the target species, material used for revegetation should be comprised mainly of more locally sourced material.

- If data is not available on local adaptation for a given species, assessment of distribution, breeding system, pollen and seed dispersal mechanisms, life history traits (successional stage, annual, short-lived or long-lived perennial) and life form (herbaceous, shrub or tree) should be made to gain insight into the likely patterns of genetic differentiation among populations.

- Germplasm should be comprised mainly of more locally sourced seed where greater levels of local adaptation may be expected. This includes species with limited distributions, highly disjunct populations, those that are predominantly selfing, have limited seed and pollen dispersal mechanisms, are of early successional stage, and are annuals or herbaceous short-lived perennials.

- All seed sourced for revegetation purposes must be collected from healthy stands of sufficient size that are not exhibiting low fecundity or suffering other effects of inbreeding depression.

- Revegetation programs should consider the potential for evolutionary adaptation to current and future impacts of long-term climate change. Given the projected impacts of climate change, such as increased temperature and decreased rainfall in south west W.A., the use of material of diverse origins where genetic diversity is maximised will also be an advantage for revegetation programs.

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