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TREE SEED SOURCING FOR LANDSCAPE RESTORATION UNDER CLIMATE CHANGES

SELEÇÃO DE SEMENTES DE ESPÉCIES ARBÓREAS PARA A RESTAURAÇÃO DE PAISAGENS EM MEIO ÀS MUDANÇAS CLIMÁTICAS

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ABSTRACT

If climate change proceeds as predicted, plant stock well matched under current climate will be growing in sub-optimal conditions. Forest restoration projects should be based on scientific knowledge especially under climate change. Revegetation with native species is identified as a partial solution for many landscape and biodiversity problems linked to restoration. Plant material can be either sourced locally or from more distant locations within the species range. In the recent decades, genetic material for revegetation projects has been quite often collected locally. However, seed sourcing for ecological restoration is a highly complex issue. Plants that are locally adapted now may not be locally adapted in the future. Adaptation strategies resulting from climate change may not always be possible through a simple shift of seed sources along environmental gradients. Restoration by establishing tree populations genetically diverse and appropriate to ecosystem stability has not been frequently evaluated. This review intends to assess the relevant aspects of tree seed sourcing for future restoration projects. We searched peer-reviewed articles dealing with seeds from tree species published during the last two decades, regardless of continents.
Keywords: seed germination; native species; plant adaptation; seed genetics.

RESUMO

Se as alterações climáticas prosseguirem como previsto, as plantas bem adaptadas ao clima atual estarão crescendo sob condições subótimas. Projetos de restauração florestal devem ser baseados no conhecimento científico especifico sob mudanças climáticas. A revegetação com espécies nativas é identificado como uma solução parcial para muitos problemas de paisagem e da biodiversidade ligados à restauração. O material vegetal pode ser selecionado localmente ou em locais mais distantes dentro da ocorrência das espécies. Nas últimas décadas, o material genético para projetos de revegetação foi, muitas vezes, coletado localmente. No entanto, a seleção de sementes de espécies lenhosas para a restauração ecológica é uma questão altamente complexa. As plantas atualmente adaptadas ao local poderão futuramente não se readaptarem. As estratégias de adaptação resultantes das alterações climáticas nem sempre poderão ocorrer através de simples mudança de fontes de sementes ao longo de gradientes ambientais. A restauração através do estabelecimento de populações de espécies lenhosas geneticamente diversas e adequadas à estabilidade do ecossistema não tem sido frequentemente avaliada. Esta revisão pretende discutir aspectos relevantes da seleção de sementes de espécies lenhosas para futuros projetos de restauração. Utilizaram-se manuscritos abordando sementes de espécies arbóreas revisados e publicados nas últimas duas décadas independentemente dos continentes.
Palavras-chave: germinação de sementes; espécies nativas; adaptação vegetal; genética de sementes.

INTRODUCTION

Among the major initiatives to address environmental challenges of the 21st century, rehabilitation

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and restoration of degraded landscapes are well accepted as necessary and achievable (BOZZANO et al., 2014). Restoration is a process of implementing recovery of a degraded, damaged or destroyed ecosystem (SERI, 2004) and must be based on scientific knowledge, especially under climate change. Restoration can occur from a number of perspectives, but frequently begins with seed.

The compounding effects of seed germination on the entire life cycle of long-lived plants such as trees imply that investigations of plant adaptation would benefit from explicitly considering the interactions between germination and post germination traits such as survival and early growth.

The objective of this review was to present and discuss the relevant aspects of tree seed sourcing for restoration projects under conditions imposed by future climate changes. This review will cover published peer-reviewed articles of tree species during the last two decades, regardless of continents focusing on the dilemmas of seed collection from wood species to capture high quality and genetically diverse propagules in order to establish self-sustaining and evolutionarily adaptive tree populations.

Vegetation under the influence of climate change

If climate change proceeds as predicted, plant stock well matched under current climate will, in certain cases, be growing in sub-optimal conditions within the next 20 to 50 years (MCKENNEY; PEDLAR; O'NEILL, 2009). Climate change will alter site and ecological conditions. Furthermore, it will increase instability in many ecosystems and will increase the value of forest carbon and wood energy (SCHOENE; BERNIER, 2012). Under that scenario, adaptation in restoration shall include adjustments in practices, processes or structures, which can moderate or offset the potential for damage or take advantage of opportunities (INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE, 2007).

Although, the reasons behind failures among restoration activities are not often known, Rogers and Montalvo (2004) pointed to either poor matching of planting material to target site or a narrow genetic base of the planting stock as areas of potential fault. Therefore, in order to avoid those drawbacks, it would be crucial that planting material represents a minimum level of intraspecific diversity to ensure that its progeny would not only be viable but also produce viable propagules.

Revegetation with native species is identified as a partial solution for many landscape and biodiversity problems linked to restoration. An integral component of any revegetation project is the decision as to where to obtain the genetic plant material. Plant material can be either sourced locally or from more distant locations within the species range.

Concepts and terminology

Restoration, sometimes referred also as ecological restoration, comprises the process of recovery of an ecosystem that has been degraded, damaged or destroyed (CLEWELL; ARONSON, 2007) with the return to a pre-disturbance state (SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL, 2004). Restoration may include an active approach by planting indigenous species, or a passive approach by removing pressures to enable natural regeneration to occur (BECHARA et al., 2016).

Aspiration of those involved in increasing sustainability and services of ecosystems drives restoration. Restoration strategies may involve terms or practices such as rehabilitation, reconstruction, reclamation, and replacement. Rehabilitation applies to restoring desired species composition, structure, or processes to an existing but degraded ecosystem, while reconstruction refers to restoring native plant communities on land used for crop production or pasture. Reclamation applies to severely degraded land (i.e. open pit mining), while replacement deals with new species or genotypes in response to climate change (STANTURF; PALIK; DUMROESE, 2014).

The decision with respect to planting material concerns to the species selection. In order to restore ecosystems and their services, native species are generally preferred over exotics (THOMAS et al., 2014), although exotic species may be useful or even necessary in some cases such as nurse crops to ameliorate the microenvironment on very degraded sites (NEWTON, 2011). The use of exotic species in restoration is typically met with stronger critiques compared to the use of native species.

The dilemma of seed sourcing

Given the expected environmental changes associated with changing climate, it will be necessary to predict the future climate conditions of a site to assess the potential of a seed source for adaptedness to that location. In recent decades, genetic material for revegetation projects has been quite often collected locally. The traditional reasons for using local provenance are relevant for long-term restoration success under stable environmental conditions. However, under a rapidly changing climate it is expected that local populations become more fragmented, land use is altered and exotic plants, animals and pathogens turn into invaders (DUKES; MOONEY, 1999).

Plants that are locally adapted now may not be locally adapted in the future. Additionally, if local populations are small and genetically impoverished, using seeds from these populations may ultimately be detrimental to the long-term success of the revegetation project via inbreeding depression (BROADHURST; YOUNG, 2007).

The burden of local plant populations has genetic fundamentals. Unless new genetic material is introduced to the population by pollen or propagule dispersal, the genetic diversity of small populations will eventually be reduced impacting the species capacity to adapt to a changing environment (WEEKS et al., 2011).

Common goals for restoration include rapid plant establishment, long-term plant persistence and restoration of functioning ecosystem (KETTENRING et al., 2014). In some cases, restoration projects use cultivars optimized for rapid plant establishment (LAMBERT; BAER; GIBSON, 2011), under highly disturbed conditions to achieve the first goal of native species establishment. Use of locally adapted propagules presumably increases long-term persistence of restored populations since they can tolerate biotic and abiotic site conditions (MCKAY et al., 2005).

Major bottlenecks faced by restoration professionals working with large or very disturbed sites are of low availability of propagules, restrictive timetable, cost constrains, shortage of funding and legal compliances (LESICA; ALLENDORF, 1999). Nowadays, several United States federal and state agencies either suggest or require the use of locally adapted and regionally appropriate native plant materials based on site characteristics and ecological setting. This means that plant germplasm should be adapted to current environments, yet possess ample diversity to adapt and respond to changing biotic and abiotic conditions.

Native plant restoration policy calls for the use of genetically appropriate native plant material on lands owned by the Bureau of Land Management and the Forest Service (JOHNSON et al., 2010). Therefore, the primary concern may to find enough propagules to be established on a site, which unfortunately does not ensure long-term persistence or restoration of a functioning ecosystem.

In the discussion concerning the genetic composition of seeds needed for native plant and landscape restoration, several authors suggested that if the site degradation has not been severe, then local seed sources are logical choices (JONES; MONACO, 2009; KRAMER; HAVENS, 2009). The above argument is based on common-garden and provenance studies, which demonstrated inferior performance of seed sources collected distant from the planting site (HEREFORD, 2009).

If local adaptation is the norm for plant species, under what conditions might local sources not be the best ones for restoration? Authors such as Jones and Monaco (2007), Broadhurst et al. (2008) and Jones and Monaco (2009) indicated that the most pressing cases for the use of non-locally adapted materials are those in which the target environment has been so substantially degraded or altered by natural or anthropogenic processes that it does not fit into the adaptive strategy of resident populations.

Because habitat distribution is patchy, plant populations from similar environmental conditions but distant habitats may have a greater number of similar adaptations than geographically close populations from distinct habitats (BISCHOFF et al., 2006). Consequently, someone seeking locally adapted propagules should collect them from sites that are environmentally similar to the area under restoration rather than relying on propagules that are simply close geographically.

A possible way to insure long-term ecosystem persistence of restoration practices is the application of the so-called genetic diversity (GD) approach. The importance of GD within plant species for ecosystem functions received less attention as reviewed by Kettering et al. (2014).

Sourcing within a seed zone or ecoregion

Tree species are genetically adapted to temperature or precipitation that directly or indirectly define their fundamental niche. The actual distribution range of a given tree species corresponds to its fundamental niche modulated by biotic interactions, human perturbations and historical factors.

Seeds from tree species with limited distribution also reveal geographic differences. Marchelli and Gallo (1999) reported significant variation in seed production, seed weight and proportion of seeds damaged by insects from 29 populations of *Nothofagus nervosa* in Argentina.

Most of the research dealing with seed zones occurred in the northern hemisphere (HUFFORD; MAZER, 2003). Seed zone was a term coined to indicate a mapped area with fixed boundaries in which seeds or plant materials could be transferred with minimal risk of maladaptation and loss of productivity as cited by Saint Clair (2014).

Sometimes seed zone is replaced by the term provenance. Provenance refers to origin or source. Provenance in forestry refers to the particular place where trees are growing or the place of origin of seeds or trees and may refer either to native or planted trees growing at that place, although its common use is in reference to native trees.

A reliable procedure to delineate seed zones is crucial because the underestimation of its size not only leads to redundant regulations, administration and legislation on seed sourcing, but may also increase levels of inbreeding among planted trees and decrease the potential to cope with global change (BROADHURST et al., 2008; KREMER et al., 2012).

Four types of studies have provided information on patterns of tree adaptive genetic variation across the landscape: long-term field provenance trials (LTPT), medium-term progeny tests (MTPT), short-term common garden nursery studies (STNS), and molecular markers. LTPT test different provenance collections over a variety of planting locations for periods longer than 20 years. MTPT uses offsprings from open-pollinated families, planted together at multiple sites for periods of 10 to 20 years. STNS goal is to examine the variation of adaptive traits across the landscape.

Molecular markers (MM) provenance zones describe the radius within which seed transfer is predicted to limit the risk for population fitness by defining the distance beyond which the significant genetic divergence among populations occurs (KRAUSS; KOCH, 2004). Unless MM are associated with or linked to a trait influenced by selection, variation in MM will be independent of the variation observed in quantitative traits. Therefore, seed zones established using MM should be considered tentative until confirmed by quantitative traits in a common environment (JOHNSON et al., 2004).

The application of ecoregions to inform seed transfer is particularly useful for the species for which little is known about adaptive genetic or molecular marker variation, or for which such information is missing across important parts of their ranges (POTTER; HARGROVE, 2012). Ecoregions have been used for seed transfer recommendations in Canada (HAMANN; GYLANDER; CHEN, 2011), the United States (VOGEL; SCHMER; MITCHELL, 2005) and Europe (VANDER MIJNSBRUGGE; BISCHOFF; SMITH, 2010).

Local versus non-local seed sourcing

Seed sourcing for ecological restoration is a highly complex issue. Revegetation with native species is identified as a partial solution for many landscape and biodiversity problems linked to restoration. Data for intraspecific variation in adaptive traits are difficult to obtain for most native, non-commercial species, especially at the scale of large restoration programs (SAVOLAINEN; LASCOUX; MERILÄ, 2013). As a result, seed sourcing guidelines for restoration are often limited to general "rules of thumb" to conserve genetic diversity and match environmental conditions between donor and restoration sites (LESICA; ALLENDORF, 1999; MCKAY et al., 2005). Reduced growth or mortality from maladaptation could reduce the success of restoration projects. In addition, gene flow from maladapted-planted trees into adjacent native populations could negatively affect the adaptation to local conditions (MCKAY et al., 2005).

An integral component of any revegetation project is the decision as to where to obtain the genetic plant material. Plant material can be sourced either locally or from distant locations within the species range. Plants that are locally adapted now may not be locally adapted in the future. Additionally, if local populations are small and genetically impoverished, using seed from these populations may ultimately be detrimental to the long-term success of the revegetation project via inbreeding depression (BROADHURST; YOUNG, 2007).

Byrne and co-workers (2013), through a mixture of sources named “admixture” (a mixture that would also include other more distant but eco-geographically matched sources) emphasized the importance of future plant adaptability. The above author’s objective was to build evolutionary resilience into plantings by mixing a wide variety of provenances from sources across a species range without regard to the location of the planting site. Broadening seed sourcing that comprises environmental and climatic conditions will not only expand available seed sources, but also will provide a framework within which high quality seed sources will be targeted for restoration.

There are situations in seed sourcing for restoration where nonlocal provenance sourcing is warranted (BROADHURST et al., 2008; BYRNE; STONE; MILLAR, 2011; WEEKS et al., 2011; SGRO; LOWE; HOFFMANN, 2014). Those situations are based on composite provenance to maximize evolutionary potential and avoid potentially inbred seed from small fragmented source populations (BROADHURST et al., 2008) and restoring landscapes that are severely altered from their natural state (LESICA; ALLENDORF, 1999).

Impacts of climate change on restoration projects

Worldwide investments in ecological restoration are estimated at $ 2 trillion dollars per year (WILLIAMS; NEVILL; KRAUSS, 2014) in a scenario of accelerated climate change with significant implications for the long term success because the plant germplasm currently used is potentially poorly-adapted to future climates (PROBE et al., 2015). Early evidence suggested that tree species are already exhibiting changes in phenology and distribution in response to climate change (WOODALL et al., 2009). Adaptive evolution matters largely for plant persistence. A comparison of fifteen seed sources of *Pinus halepensis* from Spain in relation to the interaction between genotype and environment showed southern sources with better performance (survival and early growth) under dry conditions in spite of low plasticity for both traits (TAIBIA et al., 2015).

A promising opportunity for enhancing success of climate-resilience of restoration projects rest in the exploitation of natural genetic variability of the plant species which is only beginning to be explored (NICOTRA et al., 2010; HOFFMANN; AITKEN; WHITLOCK, 2013; SGRO; LOWE; HOFFMANN, 2014).

Numerous studies have documented variation in seed germination among and within taxa associated with habitat (BASKIN; BASKIN, 1998). Comparisons of native and introduced plant populations of the same species have shown differences in germination. The introduced populations have a wider range of conditions in which its seeds can germinate or they germinate faster (CERVERA; PARRA-TABLA, 2009; LORTIE et al., 2009) or yet are more dormant (HIERRO et al., 2009) by preventing germination under summer conditions. Additional evidence on the influence of long and short-term influence of climate upon seed dormancy was provided by Fernandez-Pascual et al. (2013), highlighting the potential of plants to adapt to fast environmental changes.

Other plant ecological processes such as seed production (MONTESINOS; GARCIA-FAYOS; VERDU, 2010) and early plant recruitment (SANZ; PULIDO; NOGUES-BRAVO, 2009; SANZ; PULIDO; CAMARERO, 2011) have also been altered by climatic constraints resulting from climate change. Long-lived, obligate-seeding species with limited dispersal ability and those that are already at the limits of their geographic range may be highly sensitive to changes in the environment (PARMESAN; YOHE, 2003).

Close et al. (2010), working with revegetation in Tasmania grazing areas, denuded of trees reported that average annual temperature at the seed-source, but the rainfall is not correlated with greater tree health and height growth, emphasizing the importance of temperature in matching species to site.

Past, present and future of seed sourcing for restoration

One of the most critical seed-related issues (COCHRANE, 2016) requiring investigation is how environmental variables that drive plant population performance will affect life-cycle events such as germination (COCHRANE et al., 2015). A systematic understanding of the inherent adaptive capacity of plant species within plant functional, taxonomic, and distributional types could play an important role towards the application of novel provenancing strategies (PROBE et al., 2015) for climate-resilient restoration.

Climate change is likely to alter the seasonality and severity of cold and drought plant stresses in the future. Drought hardiness has become a greater concern than it was historical in response to variable precipitation patterns and drought-related mortality due to hydraulic failure or carbon starvation (CHMURA et al., 2011).

Ecoregions may be appropriate for some plant species (MILLER et al., 2011) as seed transfer zones in the absence of genetic data to improve the efficiency, economy, and genetic diversity of seeds produced for restoration. Bower and Aitken (2008) analyzed the geographic variation and the genetic differentiation in phenotypic seedling traits in a common-garden experiment of whitebark pine (*Pinus albicaulis* Engelm). The authors recommended that seed transfer for restoration favor movement from milder to colder climates to avoid maladaptation to current conditions yet facilitating adaptation to future climates.

The application of molecular markers for assessment of the population genetic structure can make a vital contribution to determine how much local is of important practical application (BUSSELL et al., 2006). Molecular markers (MM) can be used to analyze the population genetic variation. In addition, MM can also make useful contribution to the delineation of local genetic provenance of various species such as *Banksia menziesii* (KRAUSS et al., 2013).

Adaptive variation in wood species is usually continuous across the landscape. Several traditional methods are employed to investigate and predict plant adaptation under climate change. Reciprocal transplant and common garden experiments were used to determine the degree of plastic versus heritable variation in clinical traits. It must be recognized though that such experiments for long-lived species like trees are costly, time consuming and sometimes unfeasible.

How much of the adaptive variation is plastic or heritable? Bresson et al. (2011) demonstrated through common garden experiments that genetic differences in European oak and beech accounted for only a small percentage (0–28 %) of phenotypic variation, therefore suggesting that trait plasticity is responsible for the majority of the observed variation. Frei et al. (2014) used reciprocal transplant experiments of grassland species along an increased gradient and reported no indication of local adaptation due to plasticity observed in all three species studied.

Adaptation strategies resulting from climate change may not always be possible through a simple shift of seed sources along environmental gradients. Recent work by Liepe and collaborators (2016) concluded that a relatively small number of uniquely adapted populations from British Columbia and Alberta, Canada (11 out of 254 populations of *Picea glauca* [Moench] Voss and *Picea engelmannii* Parry ex Engelm complex and 9 out of 281 populations of *Pinus contorta* Dougl. ex Loud. ssp. latifolia [Engelm.] Critchfield) may be used to manage adaptive variation under expected future climates.

Recent advances in molecular genetic studies provide an alternative or complementary way to study adaptation over latitudinal or altitudinal gradients. It is important to note, however, that the use of molecular markers as a measure of a population's adaptive potential can be unreliable (MITTELL; NAKAGAWA; HADFIELD, 2015). Therefore, the identification of levels of genetic variation among genetic markers should not be taken as evidence for future adaptive potential of a population (CHRISTMAS; BREED; LOWE, 2016).

Increasing the understanding of the ways that plant species are likely to respond to climate change is an important part of human attempts to elucidate adaptive responses. Mijangos and associates (2015) in a survey of 160 articles dealing with genetics in restoration reported that 58% applied genetics to support decision-making processes including to identify source populations and to delimit seed transfer zones.

Population genomics can be an accurate and time-efficient resource to promote decisions of seed sourcing (DE KORT et al., 2014) as can novel applications such as large-scale statistical clustering technique proposed by Potter and Hargrove (2012) and the next generation sequencing technology discussed by Williams, Nevill e Krauss (2014).

FINAL REMARKS

As restoration targets grow and if the emphasis on local seed sources remains a priority, localized negative impacts through unsustainable practices may occur as result of collecting large amounts of seed crop or fruit from the local plant population.

The potential impacts of predicted climate warming underscore the importance of understanding genetic structure and adaptation of plant populations to their local environment. Interest in restoration of ecosystems is increasingly translated into strong political commitment to large-scale tree planting projects.

For the species threatened by pests and diseases in addition to climate change, minimizing maladaptation may mean the difference between establishing or maintaining viable populations and local extinction. While the issues surrounding ecological restoration in relation to climate change are being articulated, little empirical understanding of how to select seed to meet these challenges is available.

The success of restoration by means of established tree populations that are genetically diverse and appropriate to ecosystem stability has rarely been evaluated. Self-sustainability of tree populations depends on the adaptive genetic variation, combining the potential for survival, growth and resistance to changing biotic and abiotic stresses.

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