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Genetic effects of forest management practices: Global synthesis and perspectives

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ABSTRACT

Understanding the genetic impacts of forest management practices is crucial for conservation and management of forest genetic resources. Forest management practices based on selective and clear cut systems followed by natural or artificial regeneration can impact population structure and mating patterns, thus gene flow and genetic diversity. Survival and productivity of both tree and non-tree species can be compromised or, possibly, enhanced. The extent of genetic impacts depend on the management system applied, stand structure as well as species' distribution, demography, biological attributes and ecology. The impact of management practices is reviewed and synthesized for temperate, boreal and tropical forests based on experimental and simulation studies. In addition, the effects of genetically improved planting materials and establishment of large scale plantations on natural forests are examined. Recommendations are made for genetically sustainable forest management practices.

1. Introduction

1.1. Forest management practices

Forest management aims at the sustainable provision of multiple goods and services from forests (Mendoza and Prabhu, 2000). Wood is often the most important product and its management is the subject of this review. Non-timber forest products and the provision of ecosystem services also need to be considered in sustainable silvicultural systems (Pearce et al., 2003). Long generation times of forest trees and rotation cycles often preclude the rapid adoption of changed management regimes on large forested areas. However, the role of biodiversity in forest ecosystems (Bengtsson et al., 2000) or impacts of global change and climate warming and the role of forests in this context (Bolte et al., 2009; Schlamadinger and Marland, 1996) are eventually reflected in forest management guidelines and recommendations (Lindner, 2000).

Forest management systems are manifold even though they do not fully reflect the enormous biodiversity within and among forest ecosystems (Günter et al., 2011). Different societal demands and different public pressures are important drivers creating a variety of silvicultural approaches to manage forests (Kimmins, 2008). The most important and universal aspects related to the regeneration, stand development and harvesting of managed forests which impact genetic diversity are described in this section.

Regeneration is the basic process that maintains forest ecosystem dynamics and, as such, is a key aspect of any sustainable forest management system (Ackzell, 1993). The fundamental distinction between natural regeneration based on seed and seedlings or vegetative propagules and artificial regeneration by planting or, less frequently by direct seeding is particularly important for forest

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genetic resources (FGR). Artificial regeneration disrupts the continuous evolution of tree populations at a given site, but opens opportunities for increasing genetic diversity and enhancing productivity through the selection of superior provenances (White et al., 2005). Natural regeneration allows the transmission of genetic information to the next generation, but does not preclude adaptive and non-adaptive changes of genetic structures during the regeneration phase (Rajora and Pluhar, 2003). Silvicultural treatments such as enrichment planting, that mainly aim to enhance the value of secondary tropical forests (Schulze et al., 2008) by planting seedlings in patches where natural regeneration failed, exemplify options that combine artificial and natural regeneration in flexible silvicultural systems. However, the issue requires careful study since Schwartz et al. (2013) indicate positive effects when post-harvest silvicultural treatments are applied to increase the number of valuable trees. Another example that combines natural and artificial regeneration is the conversion of pure stands into mixed forests. The admixed species is frequently introduced by planting seedlings or direct seeding, whereas the species to be converted contributes to the next generation by natural regeneration (Ammer et al., 2008).

Thinning operations are the main silvicultural techniques used for increasing the commercial value of forest stands during their development (Rötzer et al., 2010; Zeide, 2001). The growth of the most valuable trees within the stand is promoted and their spatial distribution optimized by removing trees of inferior quality. Since selective thinning is based on a phenotypic assessment of the trees in a stand, changes at a genetic level are expected when quantitative (e.g. height or diameter growth) and qualitative (e.g. stem form) traits used for selecting trees are at least partially under genetic control (Finkeldey and Ziehe, 2004).

Harvesting operations start after trees attain their target dimensions. Clear cutting after a stand reaches its rotation age followed by artificial regeneration is the most simple and widespread system. Partial harvesting systems such as shelterwood systems, seed tree cut, single or group selection or target diameter tree cuttings need to be combined with specific measures to enhance reproduction and survival of the next generation or to maintain pre-existing regeneration if economical or ecological reasons call for natural regeneration (Pommerening and Murphy, 2004). The number, spatial distribution and phenotypic criteria used for the selection of seed trees potentially influence the genetic structure of the next generation (Finkeldey and Hattemer, 2007).

1.2. Importance of genetic diversity

Without genetic diversity, evolution is impossible. Without adaptation, population size eventually declines, which can result in local extinction (Keller and Waller, 2002). At the ecosystem level, genetic diversity of keystone species (those whose effect is disproportionately large relative to their population size, such as many forest trees, see Mills et al., 1993) can affect species diversity in associated communities (Vellend and Geber, 2005; Whitham et al., 2006). As described below, the genetic diversity of trees species is a key component of forest ecosystem functioning.

Tree species are among the most genetically diverse organisms on Earth (Hamrick and Godt, 1992; Savolainen and Pyhajarvi, 2007). Natural selection can foster rapid local adaptation and thus can explain some of this diversity, often expressed as clines or mosaics across the distribution range of the species for key fitness-related traits such as survival, growth, phenology of growth and flowering, resistance to drought and pests (Ducousso et al., 1996; Savolainen et al., 2007; Fallour-Rubio et al., 2009; Neale and Kremer, 2011).

Populations may also differ genetically for reasons other than responses to selection. Demographic processes, such as bottlenecks following catastrophic events or founder effects, and long distance migration during colonization, may imprint the genetic composition of populations just as (and often more) severely than natural selection (e.g. Magri et al., 2006; Liepelt et al., 2009; Conord et al., 2012 for Europe and the Mediterranean). Genetic drift may lead to extinction via inbreeding depression. Gene flow from other more diverse populations, via seed and pollen, can restore diversity, stop a decline to extinction and facilitate adaptation.

Thus, natural selection, genetic drift and gene flow collectively affect the genetic diversity of populations and either promote or hamper local and range-wide adaptation. In managed forests, silviculture can significantly modify the environment, and thus significantly affect both selection and demographic processes (Oddou-Muratorio et al., 2004; Hawley et al., 2005; André et al., 2008; Lacerda et al., 2008). Determining the thresholds and tipping points that truly affect FGR, however, remains a challenge.

1.3. Factors influencing genetic variability

Regeneration, from fecundation to seed dispersal and seedling recruitment, is a key stage affecting genetic diversity in natural forest tree populations. It is also a key stage in managed forests where foresters can modify the natural processes listed below. Demographic factors such as pollen and female flower quantity, flowering synchronicity, number, aggregation and density of congeners and their spatial distribution, act to modify the genetic diversity and structure of a forest population (Vekemans and Hardy, 2004; Robledo-Arnuncio and Austerlitz, 2006; Restoux et al., 2008; Oddou-Muratorio et al., 2011; Sagnard et al., 2011). The more adult trees are involved in reproduction, the higher the genetic diversity of the seed crop is likely to be. The mating system, whether it is predominantly outcrossed, mixed or selfed and whether long distance pollination is possible, also acts strongly on the genetic make-up of seedlings by supporting more or less gene flow into the population (Robledo-Arnuncio et al., 2004). Seed, whether they are dispersed near or far from seed trees, also affect gene flow among populations (Oddou-Muratorio et al., 2006; Bittencourt and Sebbenn, 2007). The higher the gene flow (via pollen and seed), the more genetically diverse populations will be. Consequently, different populations may also be more similar when gene flow is high, with a negative trade-off for local adaptation when ecological gradients are steep (Le Corre and Kremer, 2003, 2012). Although there are exceptions, habitat fragmentation, on the other hand, will most likely reduce gene flow and promote differentiation (Young et al., 1996).

Because trees are long-lived, detecting which environmental factors affect most their genetic diversity is not straightforward. Selection at germination and recruitment stages may affect traits differently than at the adult stage. For example, early-stage shade tolerance for seedlings may be favored in dense populations whereas light tolerance will be important at later stages for the same tree (Poorter et al., 2005). Similar trade-offs can apply to disease and pest resistance (which can be ontogenic-stage-specific) or water use efficiency. At the population level, selection for light will favor fast growing and vigorous seedlings in dense stands, whereas in marginal stands resistance to drought might be a desirable trait.

1.4. Potential genetic impacts of forest management practices

Forest management practices which modify tree density and age class structure, at different stages during a forest stand rotation, can have strong effects on genetic diversity, connectivity and effective population size (Ledig, 1992). In essence, and depending on its strength, the effect of silvicultural practices may be similar to that of natural disturbances which are known to affect both selective and demographic processes (Banks et al., 2013). At one