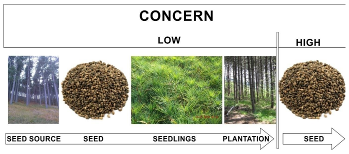
Concerns and evidence on genetic diversity in planted forests

Vladan Ivetić✉, Jovana Devetaković

University of Belgrade, Faculty of Forestry, Kneza Višeslava 1, 11030 Belgrade, Serbia

✉vladan.ivetic@sfb.bg.ac.rs



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Abstract

Planted forests are an important source of various services (economic, environmental, and social) with increasing portion in the total world's forest area. Genetic diversity is fundamental for success and sustainability of planted forests. Facing the concern of the reduction of genetic diversity in planted forests, this study offers a review of evidence on comparisons between the levels of genetic diversity in forests established by different regeneration methods. A total of 34 papers comparing genetic diversity in natural forests versus various regeneration methods of 24 tree species examined by the range of markers are reviewed. In most cases, there are no significant differences in genetic diversity between natural and planted forests, followed by an almost equal number of cases with decreased and increased level of genetic diversity. The loss of rare alleles, but also new alleles are reported in planted forests. Although the origin of planting material in the most cases are unknown, the size of parental population is determinant for the level of genetic diversity in the new forest, with the provenancing and seed collection strategy as the most important management practices in planting projects.

Keywords

Planted Forests; Genetic Diversity; Reforestation; Afforestation; Forest Reproductive Material

Contents

1 Introduction: Planted forests and genetic diversity

1.1 Planted forests (PF)

PF are a vital resource for future green economies (ICPF 2013), as recognized at the 3rd International Congress on Planted Forests. Beside wood, PF provide many other services such as: fresh water, clean air, bioenergy, carbon sequestration, biodiversity, or recreation (Payn et al. 2014). As the primary objective of forest restoration switches from historical to functional perspective (Stanturf et al. 2014), PF will become more important.

The new forests can be established by natural regeneration (unmanaged or managed) or by artificial regeneration (by sowing or planting), (Skroppa 1994). PF are a result of afforestation, reforestation and artificial regeneration (Ivetić and Devetaković 2016). PF are forests predominantly composed of trees established through planting and/or deliberate seeding (= the planted/seeded trees are expected to constitute more than 50 percent of the growing stock at maturity), including coppice of such forests and excluding self-sown trees of introduced species (FAO 2012). The concept of PF covers a wide range of forest conditions (Ivetić and Vilotić 2016). In this sense, there is a distinction between artificial regeneration aimed to replace the felled stand with new, well-stocked and improved quality stock (Skroppa 1994) and tree plantations aimed for commercial purposes (Lindermayer 2003). Since 2005, in global Forest Resources Assessment, both plantations and the planted component of semi-natural forests are considered as PF (Evans et al. 2009). PF range from highly protected conservation forests to productive short rotation plantations (ICPF 2013), and there is a gradient of forest conditions between extremes of the planted or seeded mixture of native species, managed for non-consumptive uses, such as biodiversity enhancement on the one side, and forest plantation concept of a monocultures on the other side (Zhang and Stanturf 2008). Establishment of PF is an important component of forest restoration strategies, such as: rehabilitation, reconstruction, reclamation and replacement (Stanturf et al. 2014).

Increasing areas of the world's forests are composed of planted, as opposite to natural forests (Ratnam et al. 2014). Tree planting has a long history, for thousands of years for food or other non-wood forest products (Evans 2009), with constant increase of PF. Currently, PF covers 6.95% of total global forest area or 277.9 million of hectares (FAO 2015). However, global increase in area of PF has slowed down in 2010-2015 to a current rate of 1.2% - only half of the 2.4% rate suggested to supply the world's demands (Payn et al. 2015).

1.2 Importance of genetic diversity (GD) in planted forests

GD is a fundamental component of biodiversity. The term GD refers to the phenomenon that individuals of a given species do not have the same genotype, and consequently differ in appearance and behavior (Koski 2000). GD define the tree population potential of evolutionary flexibility, adaptability, and resistance to biotic and abiotic disturbance. Without GD, evolution is impossible. GD includes interspecific and intraspecific variation. Intraspecific variation (within species) includes variation between populations (races, ecotypes, and provenances), within populations (families) and between individual trees (genes). GD is an important resource for any tree breeding program.

Low GD results to a higher and more unpredictable interaction with the environment, while high GD result in a higher and safer biological production (Lindgren 2016). Targeted level of GD in PF depends on management goals, rotation and breeding level (Ivetić et al. 2016). A high level of GD is needed to maintain in conservation forests with long rotations, especially if these PF will be used as seed sources for next generations by planting or by natural regeneration. Targeted level of GD is also species dependent. For example, large GD must be incorporated into oak populations, more than other species, in order to maintain the ability to adopt to heterogeneous environments (Muller-Starck et al. 1993). Opposite to this, in commercial plantations established by improved forest reproductive material (FRM), planned for clear cutting in short rotations, genetic gain is imperative over GD, which is usually narrow. A product is more valuable if it is uniform and that could be the reason for low GD (Lindgren 2016).

1.2.1 Species diversity in planted forests

Although interspecific diversity in PF complicate forest management, there is a number of advantages (Kelty 2006; Mason and Connolly 2014). Mixing tree species upon planting increases the number of ecological niche, decreases the risks of failure, associated with pests and diseases, and forest fires and strong winds (Larjavaara 2008). Mixing of tree species can result in a faster growth rate and better wood quality (Tani et al. 2006; Pelleri et al. 2013). Different species have different needs, and use site resources in different ways, meaning that competition between individuals of different species is less intense than competition between individuals of the same species.

1.2.2 Population (provenance) diversity in planted forests

Forest tree species are highly heterozygous, with the most of total genetic variation within populations and spatial structuring of GD. Results of long term provenance tests shows that existing tree populations have a high level of GD, which is constantly renewed by geneflow; adaptive traits show large differences between populations, despite gene flow; and clinal patterns for differences between populations along climate geographic variabilities are the same for all species (Kremer et al. 2012). Provenance researches also show that most tree species have a high level of phenotypic plasticity and that this differs among populations (Koskela et al. 2014). Variation between populations maybe clinal or ecotypic and knowledge of pattern of variation is important in cases of FRM transfer for artificial regeneration (Ivetić et al. 2016).

1.2.3 Family diversity in planted forests

The number of families (half-sib lines) in reforestation determines the degree of GD and adaptability of the new stand or plantation. The initial number and ratio of families (half-sib lines) in PF depends on FRM production outcome (seed source, collecting and processing, and nursery production), and this number and ratio can be changed with time by different responses to selection pressure or hazardous events (Ivetić et al. 2016). Except in industrial plantations, the initial number of families in reforestation should not be less than 40 (OECD 21013), but other numbers are recommended as well. Pacalaj et al. (2011) found that 20 seed trees are minimum to reduce a difference in GD between mother and progeny stand of *Picea abies* (L.) Karst. Ferreira et al. (2012) found that at least 133 seed trees of *Araucaria angustifolia*

(Bertol.) Kuntze are needed to retain an effective population size of 500. Saenz-Romero et al. (2003) found that approximately 4,660 trees of reproductive age are needed for maintaining a heterozygosity level of 0,16 in a pine population. Since the loss of additive variance (genetic variation) is 1% per generation in population of 50 parental trees, this number can be used as the upper threshold value (Eriksson 2014), having in mind that the genetic structure of seeds collected from the same stand differs from year to year (Konnert and Ruetz 2006).

1.2.4 Individual diversity in planted forests

Similar genotype interacts more intensively in competition for resources and can suffer more from pests or environmental changes (Lindgren 2016). GD within individuals depends on outcrossing and gene dispersal efficiency, and the use of FRM from outcrossing maintain a wide GD. Lee (2000) found lower rates of outcrossing in artificial forests (AF) and seed orchards (SO) of *Dryobalanops aromatic* Gaertn.f., nom cons., compared to primary forests. He explained this with lack of flowering synchrony and insufficient number of pollinators.

There is no GD within a monoclonal plantation, and in clonal forestry, the GD can be managed at estate level in the case of monoclonal plantations (Griffin 2014), or at an individual level in the case of polyclonal plantations. The number of clones or genotypes used in PF should balance genetic gain and GD (Ivetić et al. 2016).

1.3 What is the impact of PF on biodiversity?

There are some concerns that PF, especially monocultures, represent so-called “green deserts” in biodiversity. However, there is no single or simple answer to the question of effect of PF on biodiversity (Carnus et al. 2006). There is abundant evidence that PF can provide valuable habitat, even for some threatened and endangered species, and may contribute to the conservation of biodiversity by various mechanisms (Brockerhoff et al. 2008). The PF of non-native conifers in UK seems to provide suitable habitat for a wide range of native flora and fauna and make a positive contribution to biodiversity conservation (Humpherey et al. 2001). Assessment of the actual or potential impact of PF on biodiversity should consider biodiversity status of planting site and neighboring landscape before establishing PF, as well as the likely alternative for land-use options for the site (Carnus et al. 2006). Although this is a speculation with no evidence presented in this review, once the forest is removed for any reason, it is better to have some than no vegetation and it is better to have a managed tree culture than unmanaged, possibly invasive vegetation.

2 Concerns

Artificial regeneration, as the most obvious silvicultural practice, can drastically change genetic structure (Finkeldey and Ziebe 2004), and there is a concern on reduction of GD in PF (Laikre et al. 2010). However, various regeneration practices can result in high GD (Lefèvre 2004), and there is little evidence that planting forests leads to a reduction of GD at stand level, regardless of the seedlings origin: natural stands, seed stands or seed orchards (Koski 2000).

The importance of maintaining the level of GD depends on the goals of establishing the new forest (Fig. 1). On one hand, in forests planted with the predominant goal being timber production, the level of GD is not a concern, because they are in most cases clear-cut and regenerated by planting of seedlings or by direct seeding. On the other hand, maintaining GD during artificial regeneration increases the chance of natural regeneration of new forests (Larjavaara 2008) and the issue of maintaining GD is particularly important in PF intended for use of reproductive material, either by its natural regeneration or conversion to seed production area (Stefenon et al. 2008).

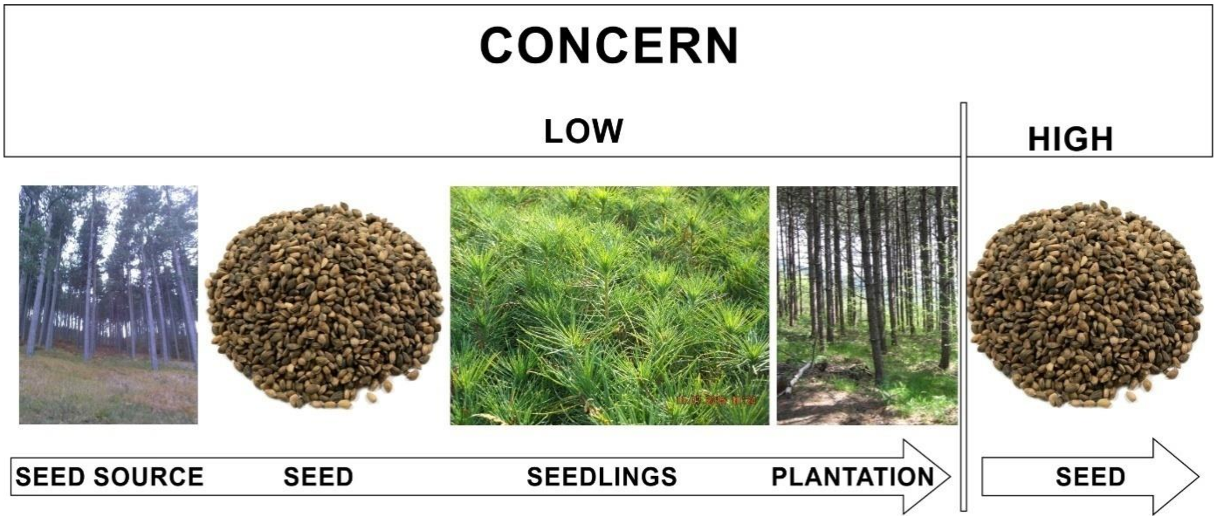

Figure 1. The level of GD in PF is much more important if the new population will be used as the seed source, compared to plantations which will be clear-cut and regenerated by planting of seedlings.

2.1 Risk of GD reduction in PF

Regeneration is a key stage affecting GD in natural forests (Ratnam et al. 2014), and even more in PF. Although artificial regeneration disrupts the continuous evolution of tree populations at the given site, it also provides opportunities for increasing GD and enhancing productivity throughout the selection of superior provenances (White et al. 2005), or by the use of the seed mixtures (Fig. 2). For an excellent review on genetics effect of forest management see Ratnam et al. (2014).

The GD in PF depends on seedling stock and can be controlled at different levels: it is at its maximum during seed collection, bearing in mind that correct choice of collecting methods, with appropriate phenotypic selection and effective population size is indispensable (Ivetić et al. 2016). A common problem in germplasm collection practices are mismatching site conditions and genetic bottleneck, with source population either declining or collecting practices failed to capture GD (Thomas et al. 2014). If seeds used for reforestation are collected from a limited number of trees, a founder effect is likely to occur (Hufford and Mazer 2003). The probability of an allele being lost during a bottleneck rises with the reduction of effective population size. Rare alleles are lost first during bottlenecks. Loss of heterozygosity occurs due to the loss of alleles, but occur more slowly, particularly compared to rare alleles.

The level of GD in PF can be reduced with time. Planting material produced in homogenous conditions in nurseries have a wide GD and may be drastically reduced after planting when exposed to heterogeneous field conditions (Finkeldey and Ziehe 2004).

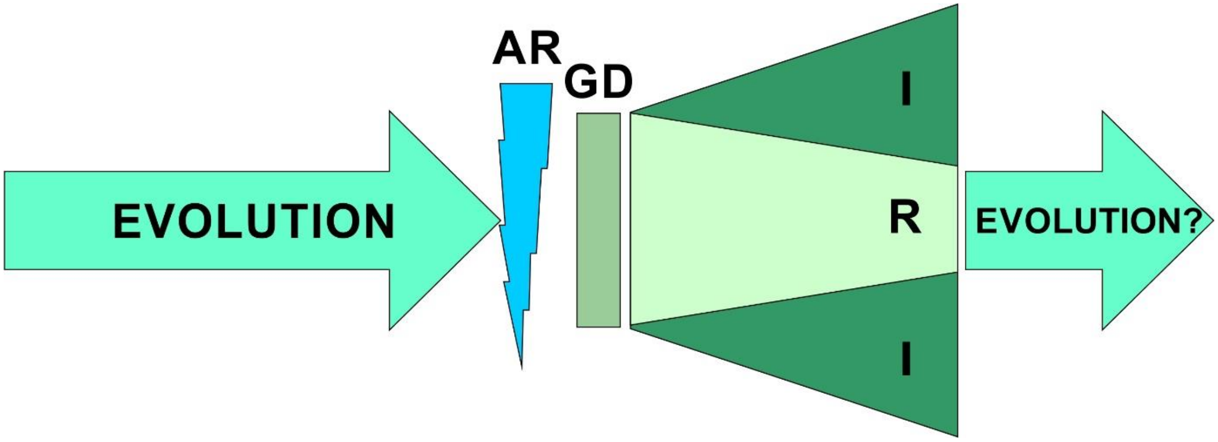

Figure 2. GD of population at given site is the result of evolutionary processes, which are interrupted by artificial regeneration (AR). Whether the GD in planted forests will be reduced (R) or increased (I) in comparison to the old forest at given site, depends on seed collecting strategy and level of GD captured in reproductive material. Whether the evolution will continue at given site depends on the final use of PF.

3 Evidence - Comparisons of genetic diversity in natural and planted forests

There is no clear trend for reduction of GD in PF measured by heterozygosity (Fig. 1). In a total of 34 papers comparing genetic diversity in natural forests versus various regeneration methods of 24 tree species examined by the range of markers reviewed (Supplement 1), in the most number of cases there are no significant differences in genetic diversity between natural and planted forests, followed by an almost equal number of cases with decreased and increased level of genetic diversity.

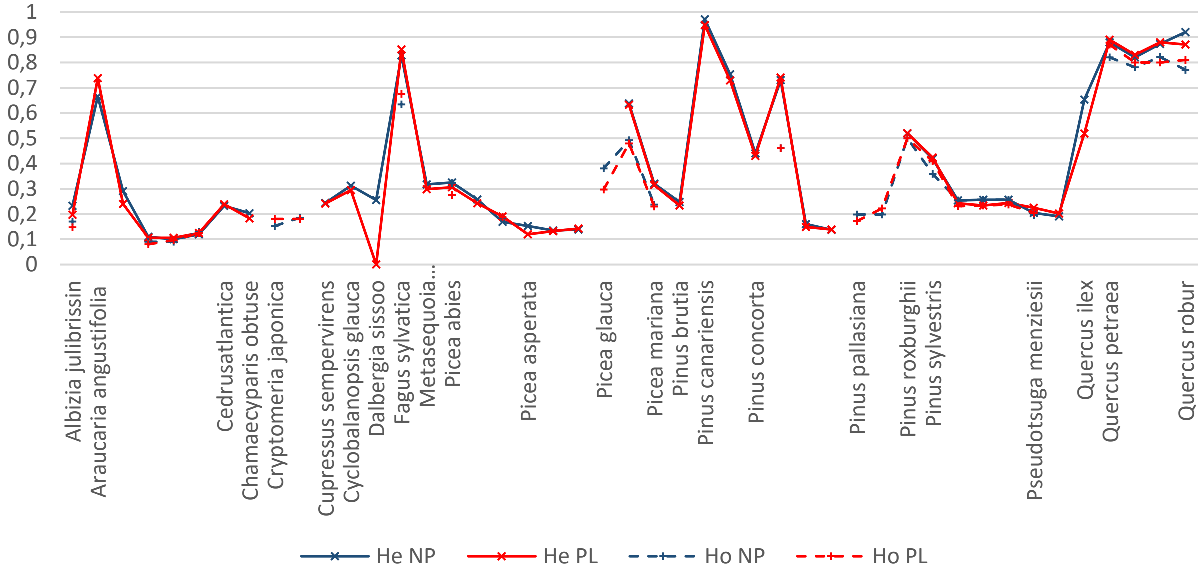

Figure 1. Expected heterozygosity (He) and observed heterozygosity (Ho) in natural populations (NP) and planted forests (PL).

Garcia Gil et al. (2015) found similar GD in both NP and regenerated population (plantation and seed-tree), "probably because regeneration practices did not decrease the population size to a point where random drift effects might be important". Adams et al. (1998) found a greater level of GD in seedling stock of *Pseudotsuga menziesii var. menziesii* used in artificial regeneration following three regeneration methods (group selection, shelterwood and clear-cut) than in seedlings from natural regeneration. This is explained the probably large initial GD, in the admixture of seeds originating from different natural stands. The high levels of GD in plantations may be related with the high allelic diversity of the natural stands where seeds were collected, or with the admixture of seeds that originated from different natural stands (Stefenon et al. 2008).

Uchida et al. (1997) concluded that allozyme variation in natural populations of *Chamaecyparis obtusea* (Siebold & Zucc.) Endl. was mostly present even in the plus-tree groups, but with loss of rare alleles. Navascues and Emerson (2007) found higher proportion of rare alleles in PF (27.45%) than in NF (19.42%), probably due to possible origin mixing in seedling stock, or different seedlings origin for different reforestation phases. Raja et al. (1998) founded fewer alleles per locus and fewer polymorphic loci in artificial regeneration compared to natural regeneration treatments for *Pinus echinata* Mill. The new rare alleles appeared in progeny populations (more in planted than in natural) compared to maternal populations of *Pinus sylvestris* L., and this number differs between two planting events of reproductive material from the same maternal population (Kosinska et al. 2007). As for the heterozygosity, there is no clear trend for rare alleles in PF compared to natural forests in this review.

The type of markers used for measuring of GD can affect results. The significant reduction of GD in *Picea glauca* (Moench) Voss after different regeneration methods compared to natural old growth stands revealed by RAPD (Rajora 1999) was not confirmed when the same material was reassessed by microsatellites, although trends were similar (Fageria and Rajora 2014). Allelic richness and diversity were much higher for microsatellites (SSRs) than for RAPDs, although there was no significant difference in expected heterozygosity between different regeneration methods in *Pinus concorta* var "*latifolia*" (Thomas et al. 1999). Chloroplast microsatellites markers seem to have a higher sensitivity to bottlenecks compared to nuclear markers: in study of genetic diversity in reforested stands and two connecting natural forests fragments a little genetic differentiation was found for nuclear markers, while chloroplast microsatellites presented lower haplotype diversity in reforested stands (Navascues and Emerson 2007). More than one marker type should be used in studying impacts of forest management practices on genetic structure (Ratnam et al. 2014).

4 Can PF be used as seed sources?

Yes, they can. Tomaru et al. (1992) has found that allozyme variation in plus tree group of *Cryptomeria japonica* was comparable to artificial stands from which they have been selected, but phenotypically selected population preserved only 76% of the total number of alleles detected in 14 artificial stands. Authors explained these results by the so-called "sample size effect" (summed sample size of artificial stands was 1330, compared to 93 of plus tree group). However, using single-nucleotide polymorphisms (SNPs), Namroud et al. (2012) found that that neither the reduction in the sampling size nor the increase in selection intensity was sufficient to induce a significant change in the GD of the selected populations of *Picea glauca*. Even with largely uncontrolled production of forest reproductive material, genetic structure in most *Pinus roxburghii* plantations show no sign of reduced GD, inbreeding or other negative effects compromising the adaptedness or adaptability (Gauli et al. 2009). Authors concluded that plantations might qualify as gene conservation stands and that best phenotypically plantations should be developed into seed production areas. A similar conclusion was drawn for *Araucaria angustifolia* PF in southern Brasil (Ferreira et al. 2012). Wang et al. (2010) found that in the right conditions the recovery and maintenance of GD in the post-harvest *Picea asperata* stands may be achieved through either natural or artificial regeneration. So, PF can be used as future sources of forest reproductive material if properly designed (Thomas et al. 2014).

5 Conclusions

As the most obvious silvicultural practice, artificial regeneration can changes genetic diversity of the new generation population in two opposite directions: reduction and increasement. The direction of this change depends on level of parental population genetic diversity captured in the reproductive material. The use of reproductive material originating from well-designed seed orchards, the use of seed mixtures from different seed sources and provenances, and the use of seed collection from trees of different ages, can increase the level of GD in planted forests. However, targeted level of GD, as well as concerns about this level in the PF depends on management goals and final use of new plantation. The size of parental population is determinant for the level of genetic diversity in the new forest, with the provenancing and seed collection strategy as the most important management practices in planting projects.

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