

Chapter 7

Genetic Effects



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Abstract

- Genetic effects of continuous cover forestry (CCF) are not well known. We need more research, especially on the genetics of spruce-dominated CCF sites. Levels of relatedness are of interest, as are estimates of safe limits for the intensity and duration of CCF practices that secure genetic potential for good growth and quality.
- With even-aged forestry, genetically improved regeneration material can be used to mitigate climate change-related risks through breeding and deployment recommendations. In CCF, currently based on natural regeneration, we assume that enough seedlings establish, and that sites contain enough genetic variation to enable natural selection and evolutionary processes.
- Based on research in other regions, the number of reproducing trees must be kept large to avoid excessive levels of relatedness and inbreeding and to maintain sufficient levels of genetic diversity.

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- In some well-documented long-term experiments in other regions, intensive high-grading has led to slower growth rates, which could partly be due to genetic degradation of the stand. If contemporary recommendations for selection cutting are followed, negative genetic effects should be unlikely.

Keywords Continuous cover forestry · Genetic diversity · Inbreeding · Selection · Growth potential

7.1 Research on Genetic Effects of CCF Is Difficult But Important

There is a clear knowledge gap about the genetic effects of CCF in northern, conifer-dominated forests. This issue is further complicated by the diversity of CCF management methods (Fady et al. 2016). Under the umbrella of CCF methods, trees can be harvested by selection cutting, gap/group cutting, or shelterwood cutting (see Chap. 2). The genetic effects of seed-tree cutting with Scots pine and other light-demanding species have been well studied (e.g., Savolainen and Kärkkäinen 1992; García Gil et al. 2015). However, the reproduction patterns and genetic effects of harvesting in spruce-dominated uneven-aged stands in the Nordic region have not received much attention.

Heavy high-grading (see Chap. 2, Sect. 2.2.3), commonly practised in the past, involved harvesting all the large and high-quality trees without considering the condition or future of the remaining stand. Although high-grading was common in Nordic forests until the early 1900s, there has been no genetic research on the effects of these exploitative practices. Some observers noted the degraded state of heavily high-graded sites in Finland and Sweden (e.g., Lindqvist 1946). CCF is currently uncommon in Nordic forests (see Fig. 7.1, Mason et al. 2022) and genetic studies on CCF study sites have only recently begun. Therefore, our evaluation of the genetic effects of CCF is based only on research from regions where CCF has been practised for a long time, but where species and management methods differ from those in Nordic forests.

From a human perspective, the genetic effects of forest management methods manifest very slowly, making them hard to study. It is fairly easy to assess the rate of matings between related trees that can lead to inbreeding depression or reduced molecular genetic diversity, by using contemporary DNA-marker or sequencing techniques (e.g., García Gil et al. 2015). It is more difficult to estimate whether repeated selection cutting diminishes the growth potential of the stand. Multiple generations of growth and genetic data would be needed to fully understand the dynamics. To some extent this can be estimated with simulations.

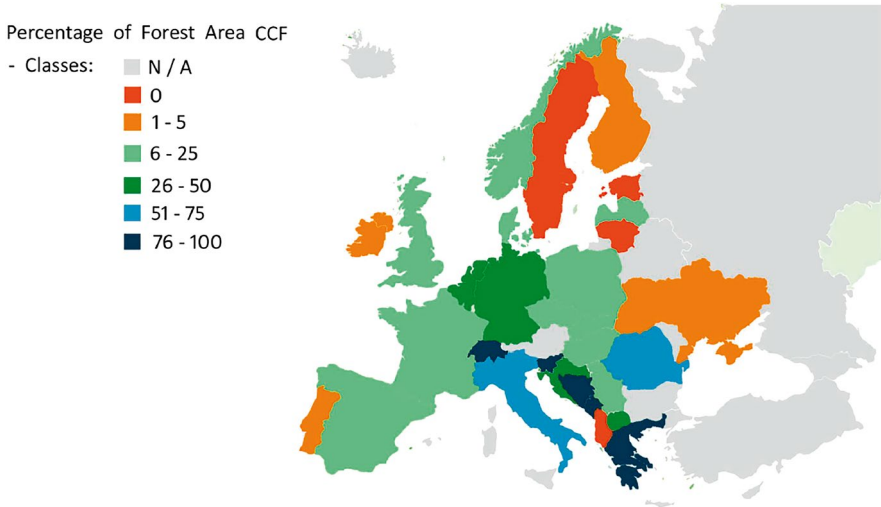


Fig. 7.1 The percentage of total forest area managed under continuous cover forestry (CCF) in different European countries (Fig. 1 in Mason et al. 2022; CCBY 4.0, link to the license: creativecommons.org/licenses/by/4.0/)

7.2 Does CCF Affect Genetic Diversity, Levels of Inbreeding and Adaptive Potential of Forests?

Genetic variation in essential traits of trees is a prerequisite for adapting to climate change. The amount of genetic variation in traits like growth, quality, cold tolerance, and pest/pathogen resistance can be estimated in specific trials. This is, however, rather laborious, and it is difficult to know exactly which traits are most important for adapting to future biotic threats and climate (e.g. new pests and pathogens, drought). Therefore, levels of genetic variation are often approximated by assessing overall genetic diversity using DNA markers or sequence data. These markers or sequenced genome areas do not necessarily control adaptive trait variation, but can be used to estimate within- and between-population genetic diversity, and how they are affected by forest management practices.

Typically, northern pine and spruce forests show abundant molecular genetic diversity. This variation is mostly shared between populations, meaning that at the overall genomic level the forest sites are not differentiated (Tollefsrud et al. 2009; Tyrmi et al. 2020). In many adaptive traits, however, the populations differ from each other. As an example, northern trees stop their yearly growth earlier than southern trees when tested under common conditions (e.g. Savolainen et al. 2007), triggered by the local temperature, day length (e.g. Heide 1974) and light quality (e.g. Ranade and García-Gil 2021). Although clearly different on average, the populations seem to maintain plenty of within-population variation that can facilitate adapting to different conditions (Savolainen et al. 2011). The maintenance of genetic

variation in Nordic conifer species is due to their large populations, vast distributions, and effective gene flow through wind pollination (Savolainen et al. 2007).

Maintenance of genetic diversity depends on the choice of forest management practices (Ledig 1992; Savolainen and Kärkkäinen 1992; Ratnam et al. 2014; Kavaliauskas et al. 2018; Aravanopoulos 2018). The number of reproducing individuals is central; with a large reproductive population, good levels of overall genetic diversity are maintained. However, it is hard to conclude generally about the effect of different forest management practices on the levels of variation, since the response depends on the tree species' biology and the forest stand's history. These issues must be studied in Nordic boreal forests.

Fennoscandian forests were overexploited in the eighteenth and nineteenth centuries, followed by extensive clearcuttings and even-aged forestry, with an increasing proportion of commercial plantations with improved material after World War II. As a result, most Nordic forests have experienced periods of human activity, although the genetic effects of forest management on genetic diversity or inbreeding have so far been quite small (Savolainen and Kärkkäinen 1992; Aravanopoulos 2018).

Some have suggested that CCF could induce more family structures (increased frequency of genetically related trees) and therefore increase the rate of inbreeding among close relatives (Finkeldey et al. 2002). However, many such studies are done with tropical tree species experiencing selective cutting, and are therefore not applicable to boreal forests due to differences in the trees' biology (animal-pollinated tropical trees with small, sparse populations vs. wind-pollinated boreal trees with large, continuous populations; Ratnam et al. 2014). In boreal forests, Boyle et al. (1990) detected more relatedness in an uneven-aged black spruce site than in an even-aged stand naturally regenerated after a forest fire. According to Sagnard et al. (2011), spatial clustering and distances between reproducing trees and seedlings within sites influences the level of relatedness. In theory, high relatedness can lead to more inbreeding, in turn reducing growth and quality. However, pollen arriving from outside the stand reduces the frequency of between-relative mating in wind-pollinated species. Inbreeding depression in conifers is strong, as seen in the high mortality of self-pollinated embryos during seed development (Savolainen and Kärkkäinen 1992; Kärkkäinen and Savolainen 1993) and early seedling stages (Koelewijn et al. 1999). Milder levels of inbreeding could, however, result in non-mortal defects, such as reduced growth (Williams and Savolainen 1996; Wu et al. 1998).

Rapidly progressing climate warming creates many opportunities and challenges for our forests. Growing seasons lengthen, but frost damage due to temperature swings may increase, new pests and pathogens will emerge, and droughts will become more frequent and severe. How will CCF forest sites react to these changes compared to sites regenerated with genetically improved material from forest breeding? The possibility of assisted adaptation by regenerating sites with improved seed or seedling material with genetic properties likely to match future needs (e.g. Koralewski et al. 2015; Gómez-Pineda et al. 2021) is currently being studied.

In the Nordic countries climate change is taken into account in tree breeding and deployment by considering observed climate changes (Berlin et al. 2016) and

climate forecasts (Hallingbäck et al. 2021). In joint analyses between Finland and Sweden, national deployment area recommendations have already been updated concerning climate warming (<https://metsainfo.luke.fi/fi/vilpas>). This kind of assisted adaptation is not possible in strictly naturally regenerated CCF sites.

Naturally regenerated forests may contain abundant genetic variation that can be used for adaptation, provided that the number of reproductive individuals is kept high and effective seedling establishment is secured (Brang et al. 2014; Fady et al. 2016). The adaptive potential of CCF sites depends on existing genetic variation and variation arriving by gene flow, mainly through pollination. It is also crucial that the new, better-adapted trait combinations can take hold in the forests; the speed of adaptation is also affected by the available space for seedling establishment (Savolainen et al. 2004). In CCF sites, the reproducing trees and some of the understorey trees established decades ago, and the climate has already changed significantly since then. For long-term adaptive potential, it is important to consider the role of low-frequency variants in populations (e.g., Kastally et al. 2022), as some of them can be useful in the future climate. Concerns about losing low-frequency variants in CCF were raised by Finkeldey and Ziehe (2004), especially where variants are correlated with growth rate. The loss of low-frequency variants can be mitigated to some extent by keeping the number of reproducing individuals high, both in naturally regenerating forests and in the breeding population.

7.3 Does Selection Cutting Lower Genetically Controlled Growth Potential?

The concern about CCF practices lowering genetic growth potential arises from the history of heavy high-grading practices in Finland, which were detrimental to forests. All big trees qualifying as logs were harvested, leaving only small trees of poor quality, without considering the stand's future development. This kind of harvesting was practised outside Finland, too, and its genetic effects are unclear.

In theory, genetic changes in growth rates could be induced by high-grading or, in broader terms, selecting trees that are left to grow and reproduce. The reverse is also possible, in which the fastest-growing and best-quality trees are selected as plus trees. These plus trees are grafted into seed orchards to breed improved forest regeneration material. This material has been shown to have enhanced growth and quality compared with unimproved plants (Haapanen et al. 2016, 2020). This shows that selection of reproducing individuals can make significant changes in the genetic growth potential in only one generation. This genetic change has been due to high-intensity selection—only a very small fraction of trees qualified as plus trees (Oskarsson 1972). Tree breeding in the Nordic countries has improved growth considerably, with ~20–37% gains in spruce volume growth (Haapanen 2020; Liziniwicz et al. 2019), and over 20% better mean annual yield of pine stands (Haapanen et al. 2016). These estimates of the genetic gains from breeding are

based on rather young experiments (20–30 years). However, the genetic gains in older experiments abroad have remained similar through later life stages, for example radiata pine experiments in New Zealand (Kimberley et al. 2015). Note that these estimates reflect the genetic potential for better growth in even-aged forestry and cannot be used as reverse estimates under uneven-aged CCF practices. Nevertheless, they clearly show that selection based on tree phenotypes can affect forest growth.

One example of the impact of harvesting method was seen in a long-term red spruce experiment in Maine, USA (Sokol et al. 2004). Over a period of 50 years, fixed diameter-limit harvesting (FDL), removing all trees above ~23 cm in diameter, was repeated twice on one site. On a second site, nine selection cuttings every 5 years were performed without diameter-limit prescriptions. The diameter-limit harvested site had poorer growth in the residual trees compared to the selection-cutting site. However, this experimental setup may be problematic, since management caused variation in residual stand density, which can lead to biased results if not considered in analyses. When estimating genetic effects of CCF practices, intensity and duration (in generations) of phenotypic selection are important factors. Ledig (1992) describes two harvesting scenarios in the history of North American forest usage: harvesting the finest and largest white pines for masts, versus harvesting nearly all trees for buildings and fuel, leaving only the very poorest trees to re-establish the stands. According to Ledig (1992), the latter practice harmed the growth potential of the remaining forest more than the selective logging. The severity of the effect depends mostly on the selection intensity (low intensity in the selective logging as most trees were spared vs. high intensity when leaving only a small proportion of poor trees alive). By quantitative genetic assessments (e.g. Cornelius et al. 2005) or simulating effects of forest management (e.g. Schaberg et al. 2008) we may assess the possibility of unintentional selection on growth or quality in CCF.

7.4 Conclusions and Knowledge Gaps

In the case of the CCF methods applicable to Scots pine (gap and shelterwood cutting), it is not likely that genetic growth potential is decreased by forestry practices. In those cases, there is no artificial selection in regeneration but big canopy trees next to the gaps are reproducing. In spruce-dominated forests, selection cutting of big and good-quality trees is used, but some of these large trees should be left to ensure efficient regeneration, coupled with careful maintenance of the remaining forest. Furthermore, if natural regeneration is limited in the stand and relies on a few reproducing trees, additional artificial regeneration via seeding or planting with genetically improved regeneration material could not only produce sufficient and spatially even seedling establishment, but also mitigate possible genetic worries. Overall, the lessons learned from the cases described above in other countries suggest that CCF practices are unlikely to lower the genetic growth potential, at least not during the first or second rounds of harvesting (Ledig 1992; Cornelius et al.

2005; Ratnam et al. 2014). It is, however, important to pay attention to the regenerative potential of the tree stands.

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