Chapter 12
Functional Traits of Boreal Species and Adaptation to Local Conditions

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Abstract Species continuity under the harsh climatic conditions of the boreal forest requires trees to ensure the functioning of two main life processes, namely growth and reproduction. However, species survival becomes a challenge when environmental conditions become unstable and reach the taxa's ecological tolerance limit. Survival in an unstable environment is possible through the concurring processes of phenotypic plasticity and local adaptation; each process has its advantages and shortcomings. Local adaptation allows attaining the best possible fitness under conditions of limited gene flow and strong directional selection, leading to specific adaptations to the local environment; however, there is a risk of maladaptation when conditions suddenly change. In turn, phenotypic plasticity provides trees an advantage when weather events change rapidly and enables a response expressed by the production of different phenotypes by the same genotype. However, this process is expensive in terms of costs in maintenance and causes developmental instability within the individual. Boreal trees utilize both processes as reflected in variations in their functional traits within the same species. In this chapter, we address the main life processes, presenting the variability of functional traits of flowering and seed production, xylem conductivity, bud and cambium phenology, as well as transpiration and photosynthesis, as a consequence of the interaction of genotype and environment. We describe the practical consequences of a variation in functional traits, as expressed in chemical and mechanical wood properties. Finally, we outline applications and perspectives for managing boreal forests in a context of heterogeneous and changing environmental conditions.

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12.1   Introduction

12.1.1   *Populations and Local Adaptations*

To understand how functional traits vary across ecotypes, we first define an ecotype, explain how the concept has evolved, and identify the main drivers of its variation. The terms *ecotype* and *provenance* are often used in parallel, especially in forest sciences, because the phenotypic variation within tree species has been used in forestry for centuries. The Swedish researcher Olof Langlet, who focused primarily on forestry, was one of the early pioneers in provenance research, although there had been considerable work conducted since the mid-eighteenth century in Europe (Langlet, 1971a). Since most of this early work was undertaken in France, it is not surprising that the word provenance is the French term meaning "origin." We can better understand the term origin (and provenance) from a simple experiment by the French Navy in the middle of the eighteenth century. As *Inspecteur Général de la Marine* (Inspector General of the Navy), Henri Louis Duhamel du Monceau (b. 1700–d. 1782) became responsible for improving the quality of ship masts for the French Navy. To find more suitable pylon material, he collected seeds from pines growing in various locations (Scotland, Latvia, and central Europe) and planted them in the same site in France, the precursor of a common garden. At that time, it was thought that the seeds belonged to individuals from different species because of their miscellaneous appearances. However, a nephew of Duhamel du Monceau continued the work of

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his uncle and reported, 40 years later, that they were rather varieties of one species, namely Scots pine (*Pinus sylvestris* L.) (Langlet, 1971b). This early and ground-breaking experiment served as the starting point for many other investigations across the globe that led to significant improvements in our understanding of how genetics and the environment shape the geographic variation of plant phenotypes.

There are two major interacting forces, genetic and environmental, involved in creating the geographic variation in tree traits. Genetics define what is intrinsic to the tree and create heritable variations that can be passed to successive generations. The unit of observation is usually defined as the gene, which is the carrier of all essential information at the DNA level, often resulting in an expressed amino acid and subsequent complex molecular organic compounds (Pearson, 2006). The environment represents all abiotic and biotic agents conditioning a tree during its lifetime. Genecology, the interaction between genetics and environment, is the research of provenance variation or, more precisely, the discipline analyzing the environmental effects on the spatiotemporal variation of genotypes and phenotypes. Although our definition differs slightly from that of Langlet (1971b), we aim to provide a handy and intuitive description of this term for applied ecologists rather than provide an exhaustive and incontestable theoretical definition.

Going back to the abovementioned French experiment from 1745, we raise the question as to what factor caused the Scots pine trees to differ greatly in form despite growing in the same environment in Duhamel's French garden. The answer is simple: the gene expression under specific environmental conditions. The genetic background of the transplanted seeds still matched their original locations and represented an assembly of well-adapted genes developed under specific environmental pressures. Thus, the trees grew as per the environmental conditions at their site of origin. Thus, variation at the trait level for a given species, i.e., growth or frost resistance, usually coincides with the variation in allele frequencies at the DNA level among provenances. The relationship between changes in mean trait values such as bud flush or height growth across environmental gradients, e.g., per degree of mean annual temperature or degree of latitude, is named a cline. The steepness and general shape of these provenance clines can vary considerably among species, traits, and geographical scales (Alberto et al., 2013). In an extensive literature review, Alberto et al. (2013) analyzed genecological clines for several tree species, including those of the boreal forest. They described evident clines between the timing of bud burst and origin, i.e., the latitude of seed sources, in Norway spruce (*Picea abies* Karst.) and sessile oak; however, they found weak clines among white spruce (*Picea glauca* (Moench) Voss) provenances. This demonstrates that tree species can be differentiated unequally, a factor that must be accounted for when intraspecific variation is used in seed transfer. Important genecological features associated with boreal tree populations are frost hardiness, timings of bud set, and early survival of seedlings, as growing conditions are characterized by harsh winters and short growing seasons. In Scots pine, for example, these traits show a strong adaptive divergence even at moderate geographical scales. Thus, the traits of Scots pine populations from northern Finland are easily distinguished from populations originating from southern Finland (Savolainen et al., 2004).

The field of genecology and provenance research has recently started to attract scientists because of its putative usability in adaptive forest management (Aitken et al., 2008). Consequently, provenance research combined with improvements in molecular genetics and climate modeling has already resulted in revised seed source zonations and novel recommendations for forest genetic resources when climate is considered.

12.1.2   Inter- and Intrapopulation Variability

We can define historical gene flow among populations as being related to the exchange of genetic information—through sexual reproduction—during the postglacial recolonization of newly accessible and suitable habitats. The traits of populations originating from glacial refugia, e.g., the Iberian Peninsula and the Carpathian Mountains, often differ from those of populations at the leading edge of the northern boreal zone when analyzed using neutral genetic markers. For instance, Scots pine (*Pinus sylvestris* L.) populations from southern Spain and Norway spruce (*Picea abies* (L.) H. Karst.) populations from the Carpathian Mountains differ in their genetic structure from Scandinavian and Baltic populations of both taxa (Sinclair et al., 1999; Tollefsrud et al., 2008). To explain this diversity pattern, we should consider the tree populations as islands that frequently exchange a certain number of migrants with each other. The rate of exchange, i.e., the number of exchanged migrants or gene copies per generation, consequently determines the similarity of populations. This can be expressed by using common F-statistics, such as F_{ST} (Wright, 1943). The maximum value of F_{ST} is 1 and indicates no exchange of genetic information over a sufficiently long period among populations. An F_{ST} of 0 raises questions about whether we are observing different populations because they exchange so much genetic information that divergence in space or time would be extremely unlikely. For Scots pine and Norway spruce, F_{ST} reaches 0.8 and 0.6, respectively (Sinclair et al., 1999; Tollefsrud et al., 2008), suggesting that most neutral variability is indeed found among, rather than within, populations.

Another common phenomenon leading to variability in space is the stochastic loss of gene variants through founder events during colonization. This random loss of alleles in space and time, also known as genetic drift (Lande, 1976), is generally portrayed as a bottle filled with differently colored beads representing alleles or genotypes. Each time a subsample of these beads is removed through the bottleneck, i.e., the founder event, the relative proportions of colors can change unpredictably. Colors that initially appeared at lower probabilities, i.e., rare alleles, are more likely to disappear after such a bottleneck. Hence, it is thought that boreal tree populations are often genetically less diverse than southern populations because they have experienced more removals before their arrival to the boreal regions—the *southern richness but northern purity* paradigm of Hewitt (2000). A closer look at Norway spruce and Scots pine reveals, however, that this pattern is only partly true, as both species appear to have maintained their intrapopulation variability in the boreal portion of

their distribution despite the extensive distance from glacial refugia (Savolainen et al., 2011; Tollefsrud et al., 2008).

Historical gene flow and genetic drift are neutral processes, and their contribution to the cold-climate adaptations of Norway spruce and Scots pine is probably marginal. In Scots pine, adaptation to cold environments in the boreal north has likely been happening by directional selection from standing genetic variation within populations (Savolainen et al., 2011), which is a necessary process to consider in the context of adaptation to climate change. Nevertheless, neutral processes, such as gene flow and drift, harbor critical implications for adaptive forest management, e.g., defining conservation goals for rear-edge tree populations, because the adaptation to novel environmental conditions, such as climate change, requires certain thresholds of minimum genetic diversity to allow the populations to adapt (Fady et al., 2016). This awareness has also led to legal frameworks, e.g., national forest policies, that recommend a minimum number of mother trees for seed harvesting or establishing clonal seed orchards. Rather than the result of adaptive processes, gene flow and drift have partly shaped the current diversity patterns, providing the raw material for evolution and selection.

The environment remains an important factor affecting variation within and among populations. Contrary to gene flow and drift, selection is targeted, shifting mean phenotypic values toward specific directions, the phenotypic optimum. One of the fundamentals of natural selection is based on the idea of Darwin (2003) that individuals exhibiting a phenotype conferring greater survival and reproduction in a particular environment contribute to the next generation with more offspring (and hence more gene copies). We can identify several adaptive phenotypes in boreal species, such as greater cold hardiness or specific bud set, as observed for Scots pine (Savolainen et al., 2004) and Norway spruce (Oleksyn et al., 1998) populations. The term adaptive indicates that a certain amount of the phenotypic variation is heritable and provides a fitness advantage to the individual. A commonly used measure for the degree of heritable variation in a trait is the narrow-sense heritability (h^2). Only traits showing significant heritability within populations can improve breeding to obtain more resilient genotypes (Louzada & Fonseca, 2002). As for the abovementioned F_{ST}, we define a measure partitioning quantitative or adaptive variability within and among populations by including heritability. This measure is named Q_{ST} (Q represents quantitative and implies that the variability in the studied trait is adaptive). It relates the total heritable variation to the heritable variation found among populations (Spitze, 1993). Where an F_{ST} of 0.9 suggests a limited exchange of genetic information between populations because of limited gene flow, e.g., a mountain cascade, a similar Q_{ST} suggests that populations experienced spatially varying selection pressures and hence differ markedly in their average values for a certain trait, e.g., cold hardiness, between southern and northern provenances. Whereas heritability can be used as a broad surrogate for breeding success, Q_{ST} may inform on the success of applying assisted gene flow in adaptive forest management. Only populations with a significant Q_{ST} for a specific trait can assure adaptation success by transferring putatively preadapted genotypes. Traits related to adapting to cold environments usually

show strong quantitative trait differentiation among populations, underlining their evolutionary importance in species with boreal distributions (Savolainen, 1996).

Inter- and intrapopulation variability can also exist for the ability of phenotypes to adjust rapidly to a changing environment, referred to as *variation in phenotypic plasticity* or *genotype-by-environment interaction*. Variation in plasticity is also the result of a targeted process, although not necessarily an adaptive one (Merilä & Hendry, 2014). Variation in plasticity is much more challenging to assess, particularly for trees, and therefore its contribution to climatic adaptation remains largely uncertain.

In this section, we have seen that both inter- and intrapopulation variability in boreal tree species are important features for the current diversity from neutral or adaptive points of view. However, neutral and adaptive processes are not mutually exclusive but simultaneously affect variability, sometimes making it difficult to disentangle the two forces to estimate the evolutionary outcome of a species. Figure 12.1 provides a simple framework to understand the two forces and their implications for the adaptive management of boreal tree populations.

Fig. 12.1 Overview of inter- and intrapopulation diversity measures (*pink column*), the underlying evolutionary processes (*green column*), whether the evolutionary process in neutral *(horizontal black arrow)* or targeted *(angled green arrow)* types of assessment (*yellow column*), and some implications for adaptive forest management (*blue column*)

12.2 Functional Traits

12.2.1 Ecophysiological Responses to Short Growing Seasons and Harsh Winters

In the previous section, we discussed the interaction between genetics and the environment. In this section, we focus on how boreal trees respond to the environment during their lifespans and how these functional and structural responses are coordinated. This area of research is called tree ecophysiology. In more detail, we discuss how boreal trees respond to an environment characterized by short growing seasons and harsh winters in terms of photosynthetic production, growth, wood anatomy, water transport, and frost tolerance. Understanding these responses is important because boreal forests are typically temperature limited and are thus considered especially sensitive to climate warming.

Compared with trees in most temperate and tropical ecosystems, boreal trees are small relative to their age and have a relatively low net primary production of about 270–540 g C.m^{-2}.yr^{-1} (Kolari et al., 2009; Luyssaert et al., 2007). In boreal forests, 80%–95% of gross primary production is used for ecosystem respiration, and soil processes are responsible for a large share of total ecosystem respiration (Kolari et al., 2009; Luyssaert et al., 2007). The annual solar radiation and temperature cycle regulate the photosynthetic processes and timing of tree growth, i.e., the time between the spring thaw and the autumn freeze determines the amount of annual tree growth (Jarvis & Linder, 2000).

The light-saturated rate of photosynthesis is affected by air temperature because enzymatic processes involved in photosynthesis are temperature driven (Farquhar et al., 1980). In addition, the physiological state of the photosynthetic machinery follows changes in temperature with a time lag of a few days (Kolari et al., 2014). There are, however, other indirect responses of photosynthesis to temperature. When plants take in CO_2 for photosynthesis through stomatal openings in leaves, they lose water to the atmosphere. Xylem transport and water uptake by roots must provide sufficient water supply for transpiration because otherwise, stomata will close to prevent excessive dehydration of the plant. Hölttä et al. (2017) developed a whole tree–level theoretical framework to explain stomatal behavior and presented a model linking carbon source (leaf gas exchange), carbon sink (sugar utilization), and soil water uptake relations through xylem and phloem transport. The model simulations showed that when sink strength decreases with lower ambient temperatures—as per the well-known temperature dependence of plant respiration—this leads to a higher leaf sugar concentration and further limits photosynthesis (Hölttä et al., 2017). In addition to air temperature, soil temperature is also critical for photosynthesis. Stomatal conductance and photosynthesis decrease sharply when the soil temperature is less than approximately 8 °C in boreal conifers (e.g., Mellander et al., 2004). Under these conditions, insufficient water is available for trees because the cold soil limits the capacity of trees to extract and transport water from the soil to the canopy, thereby reducing canopy conductance and photosynthesis (Lintunen et al., 2020).

Although the boreal climate is typically rather moist, soil moisture could become a critical factor for boreal trees in the future. Reich et al. (2018), in a three-year open-air warming experiment with 11 temperate and boreal tree species, showed that an increase of 3.4 °C increased light-saturated net photosynthesis in moist soils only. Therefore, low soil moisture reduces or even reverses the potential benefits of climate warming for photosynthesis in boreal environments during drought and regularly occurring modestly dry periods.

How then are growth and photosynthesis linked to wood anatomy? Trees scale leaf and xylem areas to couple transpiration and photosynthesis with xylem water transport, and some species are known to acclimate their leaf to xylem area ratio in response to climatic conditions. Petit et al. (2018) analyzed climate effects on the scaling of leaf and xylem areas in branches of Scots pine, Norway spruce, silver birch (*Betula pendula* Roth), and common aspen (*Populus tremula* L.) sampled across a continental transect in Europe. They found that the scaling of cumulative leaf and xylem areas axially from the branch apex down along the main branch axis is constant irrespective of species across Europe. Trees in the cold boreal region and dry southern Europe keep their functional balance between water transport and transpiration by maintaining their biomass allocation to leaf and xylem areas according to their growth rate. Specifically, allocation to leaf area is relatively higher for reduced growth rates because older growth rings are kept functional to maintain xylem conductance.

Cold temperatures in the boreal region limit photosynthesis and tree growth. Moreover, coping with cold winter periods is crucial for trees to survive at these latitudes, as these trees experience frequent freeze–thaw events during the winter. The freezing of xylem sap has several consequences for trees. The first is freeze–thaw-induced embolism. Gases dissolved in the xylem sap form bubbles during freezing, and these bubbles are at risk of expanding and creating embolisms upon thawing under tension (Sperry & Sullivan, 1992). Embolism prevents water transport and decreases xylem conductivity and is thus harmful to trees, although some tree species can restore the hydraulic system in spring (Mayr et al., 2020). The second important consequence of freezing for trees is frost-induced cellular damage, i.e., extreme winter dehydration or cell membrane rupture caused by ice crystal formation within the living cells (Thomashow, 1998). Living cells either avoid freezing by deep supercooling or tolerate subzero conditions by extracellular freezing. Extracellular freezing is visible, e.g., as shrinkage of woody tissues (Lintunen et al., 2017), and is typical in boreal species that experience temperatures colder than − 40 °C (Fujikawa & Kuroda, 2000). In extracellular freezing, water is withdrawn from the cells into the apoplast, increasing the intracellular solute concentration and protecting the cell sap from freezing.

Winter acclimation is essential for frost tolerance. Winter acclimation is how plants prepare themselves for winter conditions and become hardy. During the winter acclimation stage, protective downregulation of photosynthetic light reactions in boreal Scots pine and Norway spruce are stronger in spring than in autumn (Linkosalo et al., 2014). Relative to spruce, pine down-regulates photosynthetic light reactions earlier in autumn and reactivates them later in spring. This pattern suggests that spruce benefits more than pine from warm spring temperatures by increasing photosynthetic

production during warm spells; however, spruce is more vulnerable to frost damage if the temperature cools markedly after a warm spell (Linkosalo et al., 2014).

12.2.2   *Flowering and Seed Production*

The reproduction process of tree species is conditioned by cyclical timings of flowering and seed production, i.e., masting. The published literature provides many definitions of masting, including the synchronous production of seeds over long intervals by a plant population and the episodic synchronous production of large seed crops by plant populations (Janzen, 1976; Kelly, 1994). In general, masting occurs at the population level when abundant seed production is synchronized among individuals (Kelly, 1994). Masting is variable between years and synchronous among populations (Kelly, 1994; Poncet et al., 2009). The main evolutionary advantage of masting for wind-pollinated species, e.g., boreal taxa, is an improved pollination efficacy (Moreira et al., 2014; Nilsson & Wastljung, 1987). There are limited data regarding the masting frequency of boreal species (Ascoli et al., 2017). The masting pattern may vary from one to two years for eastern hemlock (*Tsuga canadensis* (L.) Carrière) (Ruth, 1974), three years for jack pine (*Pinus banksiana* Lamb.) (OECD 2010), two to six years for black spruce (*Picea mariana* (Mill.) BSP) (Viereck & Johnston, 1990) and seven to eight years for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco.) (Stein & Owston, 2002). Norway spruce and Sitka spruce (*Picea sitchensis* (Bong.) Carrière) produce cones sporadically, with four years between mast crops. During this nonmasting period, cone density is very low or cone production is absent (Broome et al., 2007). In Sitka spruce populations in Norway, mast years occur at three- to five-year intervals in western Norway, whereas in the northern regions, mast years occur on a far more irregular basis (Nygaard & Øyen, 2017). Multiple hypotheses have been proposed to explain masting patterns (Pearse et al., 2016). In the following section, we detail the two most common hypotheses explaining masting for boreal species—weather conditions and resource budgets.

Environmental conditions are the drivers of pollen and seed production. Geburek et al. (2012) investigated pollen production of some boreal species (*Picea, Larix*, *Abies*, *Betula*, *Populus*, and *Alnus*) and distinguished masting and nonmasting pollen producers. Trees of the first type produce high amounts of pollen only before a masting event; they only mast when the pollination period is synchronized with favorable weather conditions. Nonmasting species produce pollen every year. Some boreal North American and European species show intraspecific spatiotemporal synchroneity in masting over vast areas (Koenig & Knops, 1998), with synchronous masting for the same boreal species occurring over distances of 500 to 1,000 km between sites (Gallego Zamorano et al., 2016; Koenig & Knops, 1998).

A relationship between masting and ecological parameters permits predicting cone production, and multiple authors have investigated potential correlations between specific environmental conditions and masting years. Gallego Zamorano et al. (2016) studied four boreal species in Finland—silver birch, downy birch (*Betula pubescens*

Ehrh.), Norway spruce, and rowanberry (*Sorbus aucuparia* L.). Flowering was affected positively by May temperatures but negatively by previous-year temperatures. The spatial synchrony covered up to 1,000 km owing to synchronous weather conditions. The influence of larger-scaled events caused by global climate changes can also affect masting; for example, the El Niño-Southern Oscillation (ENSO) and Atlantic Multidecadal Oscillation (AMO) influence masting in species such as white spruce (Ascoli et al., 2019).

There is evidence that masting reduces the radial growth of trees. Selås et al. (2002) observed a negative correlation between tree-ring width and seed masting for Norway spruce. Hacket-Pain et al. (2019) found the same results but only for *super producers*, i.e., trees having exceptional masting, and Ascoli et al. (2019) observed a positive correlation between drought events and masting in white spruce.

Wildfire strongly influences masting patterns (Charron & Greene, 2002). The environmental prediction hypothesis holds that some wood boreal species produce abundant seed after the first year of wildfires, which ensures a high survival rate of young trees (Peters et al., 2005; Wirth et al., 2008). This hypothesis applies primarily to plant species in fire-prone regions, whereby woody plants produce serotinous fruits, which release their seeds after wildfires (Kelly, 1994; Pearse et al., 2016). The projected increased occurrence, amplitude, and severity of fires across the boreal ecosystems will likely increase seed production in the boreal zone (Shvidenko & Schepaschenko, 2013).

Other hypotheses of masting behavior are based on the physiological aspects of plant life. The resource budget model illustrates that masting requires more resources than plants can secure over a single year, hence the resulting periodicity in fructification. There is little empirical support for the commonly stated hypothesis that plants store carbohydrates over several years to expend in a high-seed year. Plants can allocate carbohydrates from growth in high-seed years, and seed crops are more probably limited by nitrogen or phosphorus (Pearse et al., 2016). The source depletion hypothesis describes the occurrence of masting years through the accumulation and storage of resources. Masting occurs once a specific threshold is reached. This hypothesis agrees with some of the abovementioned results, which also support spatial synchronism through environmental factors caused by large-scale weather conditions. According to this hypothesis, mast seeding leads to resource depletion, and the threshold must be reached again through resource accumulation to produce the next masting.

12.2.3   Wood Properties

The marked variability in wood properties is the complex result of genetics, stand-level conditions, and short-term weather events. Wood properties, such as tracheid or fiber length, strength, stiffness, and density, are not only important for the tree as a living organism but are also essential for the use of wood as a material.

Tracheid, or fiber, length varies within a single tree ring, between juvenile and adult wood, and among individual trees and species. It is under strong genetic control but can also be influenced by silvicultural practices. Tracheid length increases from pith to bark (Bannan, 1967), and changes in growth rates (and the available time for growth) cause intra-annual differences that result in longer tracheid lengths toward latewood. Tracheid length influences various hydraulic parameters of living trees (Choat et al., 2008); it also has technological implications, e.g., paper quality (Wimmer et al., 2002). More important, however, is the microfibrillar angle, which is associated closely with tracheid length (Donaldson, 2008). Low microfibrillar angles are associated with high wood strength and stiffness. Environmental factors influence the produced angles, although the angles do show significant heritability (Donaldson, 2008).

Adequate mechanical wood characteristics are needed to support the tree architecture and the use of wood products. Whereas there are many different measures, such as hardness and tensile, bending, compression, and impact strength, these parameters are all strongly tied to wood density. In addition to ring width, wood density is the most commonly studied parameter of wood. Wood density measures the total amount of cell wall material per volume (Wimmer, 1995). A higher density in softwood results mainly from a greater presence of latewood within the tree ring (Kort, 1993), which can vary in Scots pine, for example, from 19 to 50% (Wimmer, 1995). Ring width, which affects the latewood percentage, strongly affects wood density, with the higher latewood proportions observed in smaller tree rings (Rathgeber, 2017). There are, however, exceptions to this general assumption. Rossi et al. (2015) found a higher density, associated with a higher latewood percentage and higher values for mechanical traits, in the wider rings at a lower latitude site of boreal black spruce. Under the shorter vegetation periods at more northern latitudes, cell wall deposition and latewood formation—two processes related to temperature—are reduced (Cuny & Rathgeber, 2016). Therefore, lower temperatures at higher latitudes may reduce carbon allocation in latewood, leading to a lower wood density, even when small tree rings are produced (Rossi et al., 2015).

Usually, ring width decreases with age, whereas the latewood percentage and wood density of softwood increases. The effect of climate on earlywood density is of particular interest (Grabner et al., 2010) owing to its close link with plant hydraulics. A potential consequence of low earlywood density is that negative water pressure exceeds the fracture limits of the wood, and radial cracks or stem cracks can therefore occur (Grabner & Wimmer, 2006). Unfortunately, information regarding earlywood density, using X-ray densitometry, is rare in dendrochronological studies. Maximum density at high-altitude or high-latitude sites is mainly affected by summer temperature, the period when the wood is formed.

In addition to the environmental influences, wood formation and, therefore, wood quality are under strong genetic control (Cuny & Rathgeber, 2016). The analysis of different species of *Abies* (and particularly *Abies alba*) provenances growing in

eastern Austria demonstrated the influence of species and provenance on wood-quality traits (George et al., 2015). The observed variation of wood traits and their responses to drought revealed that the genus (*Abies*) explains between 10 and 20% of the variance in wood density but only a negligible amount of the ring-width variance. In contrast, provenances (of *A. alba*) are responsible for 10–15% of the variation in ring width. Nonetheless, provenance explains only a nonsignificant proportion of the variance of ring density (George et al., 2015).

Wood quality is also influenced by ecological parameters and forest management decisions (Jaakkola et al., 2006). Pamerleau-Couture et al. (2019) found differences in wood properties dependent on stand structure and forest practices, e.g., partial cutting, in the boreal forest (Montoro Girona et al., 2016).

12.2.4   Anomalies in Xylem Structure

In boreal climates, abnormally low temperatures may damage the tissues surrounding the cambium, disrupting cell division and differentiation; this damage can manifest itself as deformed and collapsed tracheid or traumatic parenchyma cells. When frost events occur in the middle or at the end of the growing season, before the ending of lignification, incompletely lignified earlywood or latewood tracheids are formed to produce what is termed light rings or frost rings (Gindl et al., 2000). Anomalies in xylem structure also appear when trees are subjected to high spring and early summer temperatures when the latewood-like cells in earlywood are formed. Moreover, rainfall following drought periods may stimulate the formation of earlywood-like cells in the latewood ring zone. These xylem anomalies are classified as intra-annual density fluctuations (IADF) and can be formed in both temperate and boreal species (George et al., 2019; Klisz et al., 2019).

Although the main drivers of anomalies in xylem structure are extreme climatic events, there is evidence that the predisposition of trees to the formation of IADF, frost rings, and light rings is, to some extent, genetically controlled and can lead to the adaptation or maladaptation of genotypes to drought and frost (Battipaglia et al., 2016; Birgas & Colombo, 2001). Moreover, intraspecific variation in growth reaction to climatic anomalies has been demonstrated for several gymnosperms growing in boreal and temperate climates, e.g., lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Douglas fir, European larch (*Larix decidua* Mill.), silver fir, and Norway spruce (George et al., 2019; Klisz et al., 2016; Montwé et al., 2018). For example, boreal provenances of Douglas fir originating from cold-climate areas in Canada had lower IADF frequencies in latewood than temperate provenances when trees had been growing in a warm and dry common garden where drought occurred more frequently (George et al., 2019). This pattern for IADF strongly suggests that the formation of IADF has a genetic origin and results from a long-term adaptation of provenances to different climatic conditions. Assessment of IADF in regard to adaptive forest management will probably become more critical in the future, as boreal species are vulnerable to frequent drought periods (Isaac-Renton & Montwé 2018).

   From the assumption that genetic and environmental components control xylo-
genesis, we can conclude that abnormal xylem structures, namely frost and light
rings, result from gene expression under extreme climatic events. Confirmation of
this hypothesis involved studies of the cold adaptation in 20 lodgepole pine prove-
nances growing in a common garden located in southern interior British Columbia,
Canada (Montwé et al., 2018). Provenances adapted to colder environments with
larger temperature amplitudes and shorter growing seasons show less susceptibility
to frost damage preceding meristem activity; however, they are more susceptible to
frost damage at the beginning of the growing season (Fig. 12.2). In general, a strong
geographic cline for frost damage and incompletely lignified tracheids is noticeable,
suggesting the importance of considering cold adaptation when long-distance seed
transfer is introduced to minimize risks in assisted migration (Bansal, 2015).
   From a functional point of view, IADF is a consequence of an adaptive strategy
to maximize water-use efficiency (earlywood-like cells) or avoid hydraulic failure
(latewood-like cells) (Pacheco et al., 2016). Considering the evidence of genetic vari-
ations in the morphofunctional adaptation of xylem structure manifested in IADF
(George et al., 2019; Klisz et al., 2016, 2019), there are solid premises for incor-
porating xylem functional traits into assisted migration strategies. Studies on tree
species from cold (Norway spruce) or alpine climates (European larch) note a clear
geographical trend in IADF formation, which may be even more noticeable in the
northern regions under boreal climate conditions (Fig. 12.3a–d). A general latitu-
dinal trend is evident for Norway spruce in the frequency of earlywood-like (IADF
E) and latewood-like (IADF L) cell structures, with more frequent IADF L in the
southern part of the transect than in the north and an opposite trend for IADF E
(Fig. 12.3c, d). This observed gradient confirms the abovementioned findings for
the non-native Douglas fir, where boreal provenances had a lower IADF L frequen-
cies compared with warmer provenances from more southern regions (George et al.,
2019; Fig. 12.3e, f). A similar pattern can be observed for European larch, although
in this case, the incomplete representation of the species distribution prompts greater
caution when drawing general conclusions (Fig. 12.3a, b).
   Furthermore, a higher frequency of IADF types testifies to a more pronounced
genetic determination of IADF frequency, which can be clearly seen in Norway
spruce and European larch growing under marginal conditions (Klisz et al., 2016,
2019); however, this is almost imperceptible under conditions close to the optimal
species requirements (George et al., 2019). Given that few observations of geograph-
ical clines in IADF formation are available, the variation between populations
increases as a function of the south-to-north dimension of the species occur-
rence. Nevertheless, this hypothesis requires thorough testing under boreal climate
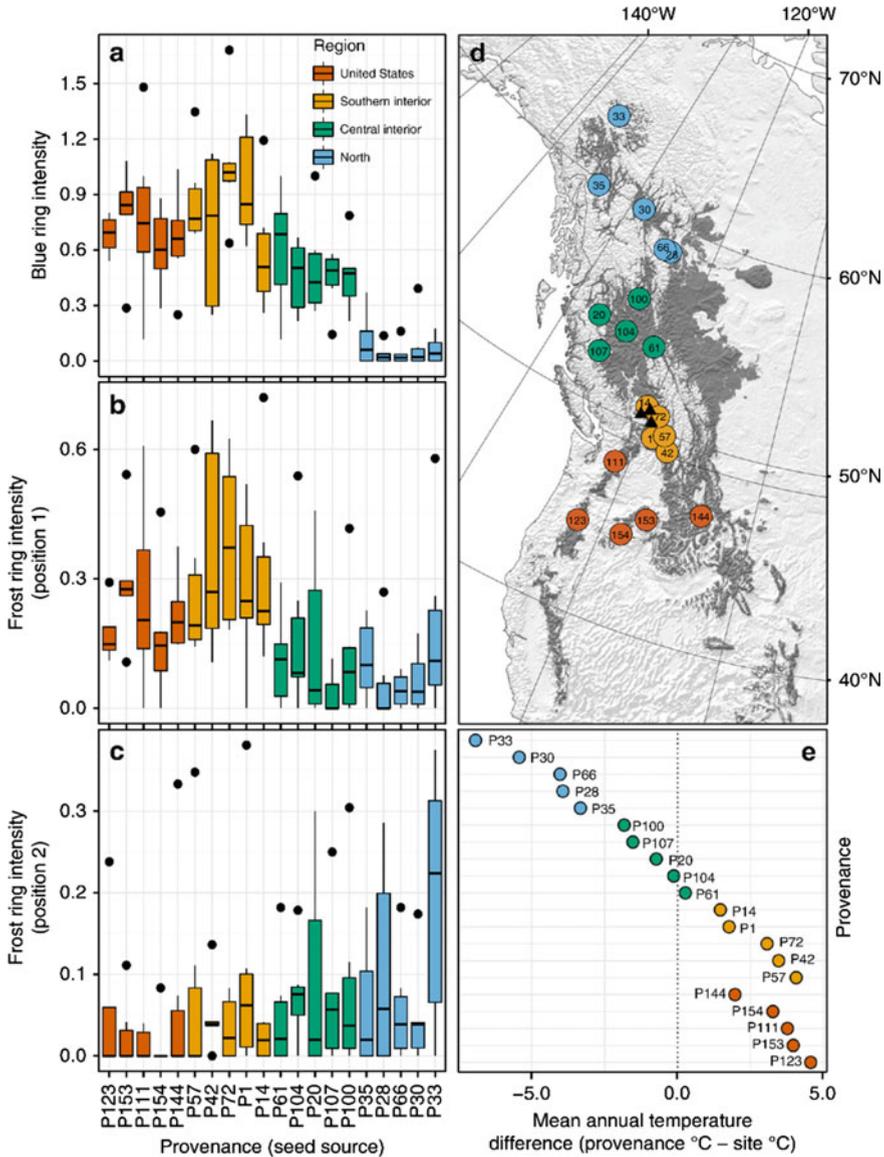conditions through multienvironmental provenance trials.

Fig. 12.2 Blue- and frost-ring intensities by provenance. Blue-rings **a** frost-rings position 1 (first cells of earlywood indicative of fall frost damage), **b** frost-rings position 2 (later in the earlywood indicative of spring frost damage), **c** the distribution and medians of light-ring and frost-ring intensities, where provenances are sorted by the mean annual temperature of their source climate (*warmest to the left*, n = 117). Provenances are colored according to their region (United States and regions of British Columbia, Canada) and labeled by identification number. (*Column right side*) **d** Location of provenances and regions as well as the range of lodgepole pine (*dark gray shading*) and the location of test sites sampled in this study (*black triangles*); **e** the difference of the provenance source climate to the average climate of the test sites indicates the degree and direction of climate transfers. Modified from Montwé et al. (2018), CC BY license
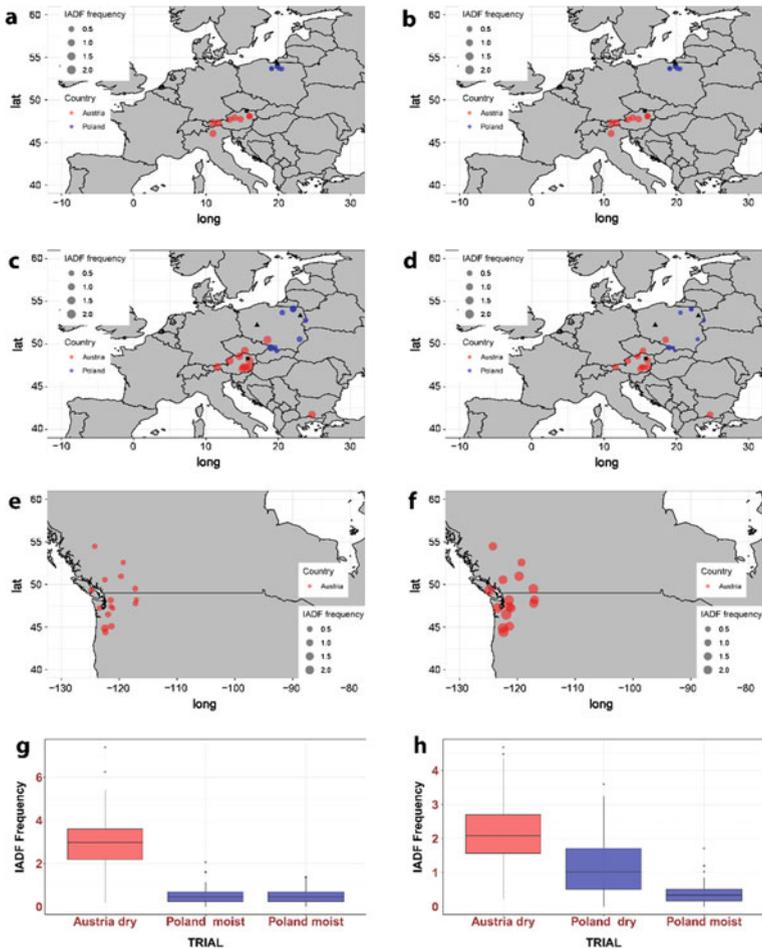
Fig. 12.3 Within-species variation in intra-annual density fluctuations (IADF) for three boreal conifers: **a**, **b** European larch (*Larix decidua*) **c**, **d** Norway spruce (*Picea abies*), and **e**, **f** Douglas fir (*Pseudotsuga. menziesii*). The *left* panels (**a**, **c**, **e**) display earlywood IADF, and the *right* panels (**b**, **d**, **f**) show latewood IADF. The *bottom* panels present overall IADF frequencies (earlywood + latewood) per trial site for **g** European larch and **h** Norway spruce. Douglas fir data were obtained from a provenance trial in eastern Austria (Traismauer); therefore, no trial site is shown in **e** and **f**. The illustrated data were compiled from two different data sets. Data set 1 is from George et al. (2019), Federal Research and Training Centre for Forests (BFW), Vienna, Austria. Data set 2 is from the Forest Research Institute (IBL), Poland. *Black symbols* show the trial sites (*triangles*: IBL; *squares*: BFW). *Red* and *blue circles* indicate the mean IADF frequency for each analyzed provenance. Data from the Austrian trial sites were reanalyzed to provide stabilized IADF frequencies for comparability, following Osborn et al. (1997). Boxplots show the combined IADF frequencies per trial site (earlywood + latewood) for each species. We kindly acknowledge the help of Michael Grabner, Konrad Mayr, and Filipe Campelo for IADF detection in the Austrian data. Modified from Klisz et al., (2016, 2019) CC-BY license and with permission from Elsevier, respectively, and George et al. (2019), CC-BY license

12.2.5   Phenology: The Case of Boreal Black Spruce

In boreal climates, most physiological processes of plants occur during a short lapse of time when the temperature is favorable to growth. The activity of meristems involves a sequence of multiple stages of development or maturation of primary and secondary growth; these stages last from a few days to several months (Perrin et al., 2017). The meristems of plants alternate between periods of activity and rest, following an annual cycle. The beginning and end of the growing season are the key times involving a trade-off between environmental constraints and resource availability. They mark the period of the year when resources can be acquired and used, reflecting an optimization between frost avoidance and carbon assimilation (Allevato et al., 2019).

Phenology, the study of seasonal biological cycles, results from climatically driven gene expression manifested by a specific phenotype (Man & Lu, 2010; Perrin et al., 2017). As natural selection favors those genotypes better adapted to local conditions, specific adaptive traits, which include the timing of growth, develop according to the gradual changes occurring with latitude (Morgenstern, 1969).

The reactivation of primary growth is well known and studied in black spruce both in natural stands and common garden experiments (Fig. 12.4); this trait varies among populations with latitude (Blum, 1988). Having a broad geographic distribution, boreal tree species show substantial phenotypic variations at a regional scale in response to variations in climatic factors (Andalo et al., 2005); this response arises from a combination of phenotypic plasticity and genetic variation. In common garden experiments, black and white spruce originating from higher latitudes have an earlier bud break (Rossi & Isabel, 2017). The earlier growth reactivation observed in northern provenances reflects an adaptation to colder environments. It allows the meristems to be active early in spring to lengthen the growing season as much as possible. Trees from higher latitudes or altitudes require less heat accumulation for bud break (Blum, 1988). Buds of boreal species reactivate in late spring (Antonucci et al., 2015) when the day length is relatively long, nights are short, and frost events are unlikely. At high latitudes, the trees are adapted to colder conditions, and bud development is more rapid than for southern provenances under similar thermal conditions (Körner, 2003). The genotypes originating from colder climates have developed a high metabolic activity and strict developmental regime (Körner, 2012). This evolutionary strategy maximizes safety. An early and quick growth ensures favorable conditions for photosynthesis, especially at higher latitudes where the photoperiod changes markedly between the equinoxes compared with the photoperiod at lower latitudes (Rossi et al., 2006).

For evergreen conifers of cold climates, the dates of growth reactivation of cambium and buds are closely correlated (Antonucci et al., 2015; Rossi et al., 2009). Perrin et al. (2017) observed that black spruce provenances with early bud flush have an early reactivation of cambial activity and xylem cell differentiation. Similar trends
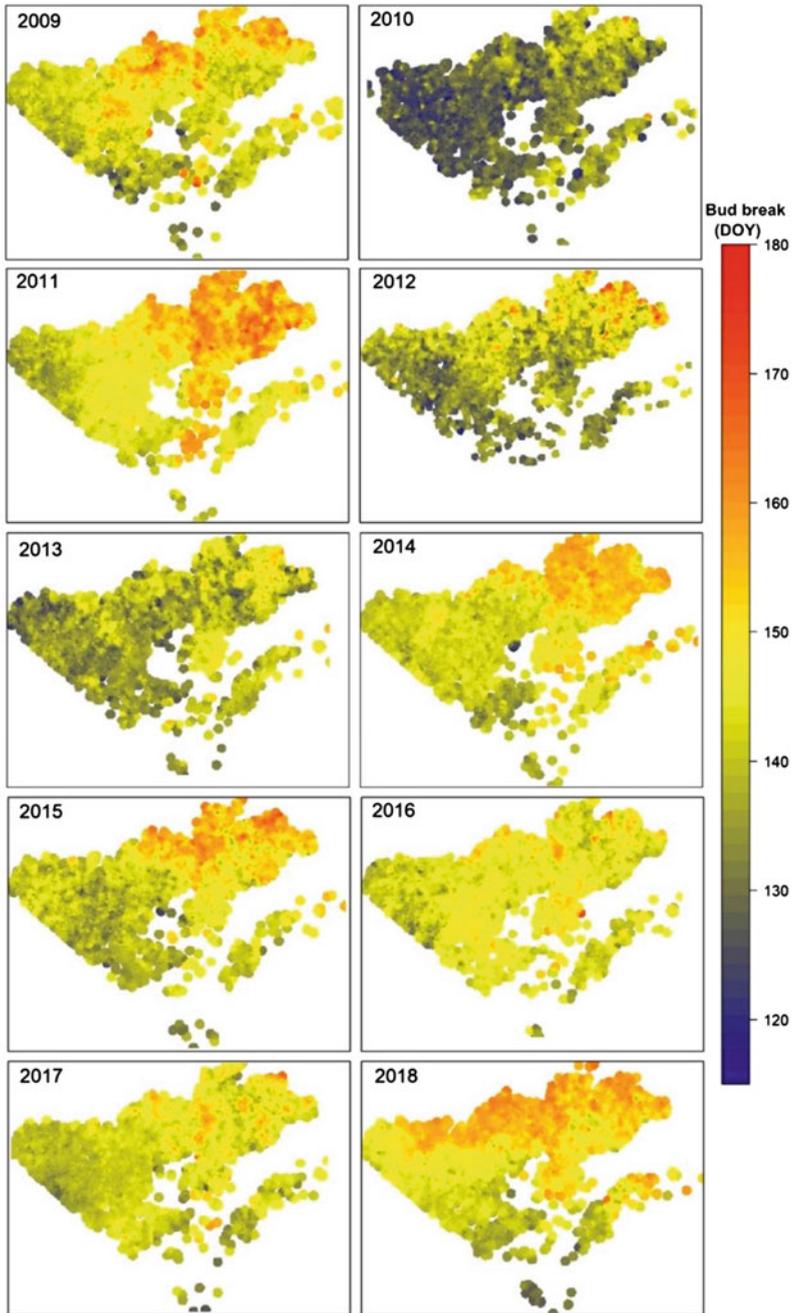
Fig. 12.4 Spring reactivation of the primary meristem represented by bud break dates (day of the year, DOY) across boreal black spruce stands in Québec, Canada. Reproduced from Khare et al. (2019), CC BY license

are reported for the end of the growing season. These results diverge for Norway spruce, where xylem phenology among provenances does not differ (Kalliokoski et al., 2012).

Both environmental and genetic factors affect cambium phenology (Fukatsu & Nakada, 2018), although with different contributions (Perrin et al., 2017). The environment is more critical for spring events, whereas autumnal events and dormancy are controlled mainly by genes (Cooke et al., 2012). Moreover, genetics most control the timing of the final enlarging and wall-thickening of cells. Perrin et al. (2017) observed that provenance, family, and individual tree explained a high proportion of the variability in cambial phenology during the summer and autumn, which indicated that endogenous factors are strongly involved in growth cessation. In conifers, growth cessation is genetically predetermined, and environmental effects on this phenological event are marginal (Cooke et al., 2012).

Differences in bud set among provenances mirror the dynamics of bud break (Johnsen & Seiler, 1996). The provenances classified as early spring also complete their growth early, resulting in a similar growing season duration (Silvestro et al., 2019). Xylem cell production in black spruce is mainly affected by growing season length (Rossi et al., 2014). Thus, no difference in annual tree-ring growth occurs among black spruce provenances growing in a common garden. All trees produce the same amount of xylem, regardless of their respective timing of flushing.

The variation in bud phenology within black spruce provenances is also relevant (Perrin et al., 2017; Rossi & Bousquet, 2014; Silvestro et al., 2019). A wide variability within populations is confirmed in other boreal species, such as silver birch (Rousi & Heinonen, 2007), Scots pine (Hurme et al., 1997), and Douglas fir (Li & Adams, 1993). Each local population is constituted by genetically heterogeneous individuals showing both earlier and later phenology. This heterogeneity allows a part of the population to endure unexpected, unfavorable climatic events, thereby ensuring the survival of some individuals under changing environmental conditions (Hurme et al., 1997). Such a reservoir of genetic variation within populations is highly valuable for the adaptive capacity of local populations. The richness in genetic variation ensures that populations evolve in the next generations according to changes in the environmental conditions that might exceed the limits of physiological plasticity.

12.3   Applications and Perspectives

Functional traits act as templates through which the basic components of a plant's life history (e.g., growth, reproduction, and survival) operate. Hence, functional traits have attracted much attention for understanding the mechanisms governing plant community assembly (HilleRisLambers et al., 2012), the interactions between trait variation and environmental conditions (Matías et al., 2018; Wainwright et al., 2019), and how inter- and intraspecific variation in functional traits connect with

those mechanisms maintaining biodiversity (Chesson, 2000, 2012). Such an understanding is crucial for formulating strategies for adapting forests and associated plant communities to climate change (Pérez-Ramos et al., 2012).

12.3.1 Climate Adaptation

Decades of scientific research have provided convincing evidence of observed and likely impacts of human-induced climate change on forest systems. In Europe, the effects of climate warming on forests include changes in forest productivity (Reyer et al., 2014), tree species distribution, and the economic value of forests (Dyderski et al., 2018; Hanewinkel et al., 2013), as well as intensified disturbance regimes (Seidl et al., 2017) and droughts.

Over the millennia, the boreal forest has adapted to short growing seasons, low summer temperatures, and a limited nitrogen supply (Kellomäki & Väisänen, 1997; Mäkipää et al., 1999). Warmer temperatures and increases in nitrogen supply could potentially lead to greater forest growth and productivity in the northern boreal regions, whereas the higher requirements for water in the southern boreal regions may limit such a productivity increase (Briceño-Elizondo et al., 2006; Peng et al., 2011). Moreover, a warmer climate and longer growing period combined with water stress should promote the propagation of insects and other parasites (Wermelinger, 2004). These factors will likely produce novel conditions to which the tree species and populations are poorly adapted. Current forest management must incorporate adaptive strategies that aim to reduce forest vulnerability and enhance forest resistance and resilience (Bolte et al., 2009).

Adaptation is an adjustment of natural or human systems as a response to actual or expected climate changes or their effects. Adaptive capacity is the ability of the system to adjust to novel conditions, take advantage of opportunities, or respond to consequences. Adaptation can be classified as either *autonomous* or *planned* (Schoene & Bernier, 2012). Autonomous adaptations are usually reactive and rely on existing knowledge and technology to respond to changing climate conditions, whereas planned adaptations are anticipatory responses aiming to alter the adaptive capacity of forests (Schoene & Bernier, 2012).

A portfolio of different adaptive management strategies has been discussed at the stand level. These strategies include (1) the conservation of forest structures, (2) active adaptation, and (3) passive adaptation (Bolte et al., 2009; Schoene & Bernier, 2012). The conservation of forest structures aims to maintain the current structural and compositional status of forests. This strategy is believed to increase the vulnerability of the forests to catastrophic disturbance events (Harris et al., 2006; Jandl et al., 2019) but may enable the manager to attain the original management targets. Active adaptation refers to the use of silvicultural measures to alter stand structures and composition to increase the adaptability of the forests to climate change. Such measures may include adjusting the rotating period, changing species composition, and using adapted provenances (Kellomäki et al., 2008). Passive adaptation

uses spontaneous adaptation processes in natural succession and species migration (Aitken & Bemmels, 2015). Other adaptive measures have received much attention in recent years and are currently subjects of intense debate; they include assisted migration (Marris, 2008) and assisted gene flow (Aitken & Whitlock, 2013). Whereas assisted migration aims to facilitate the colonization of forest tree species within new habitats having a suitable climate, assisted gene flow aims to manage the translocation of individuals within the current species range to facilitate a rapid adaptation to climate change and improve the long-term prospects of trees and related communities.

For the boreal forest, there exists a variety of adaptive management strategies, such as promoting species mixtures, reducing the rotation length of current stands, planting alternative genotypes or new species in anticipation of future climate, minimizing the fragmentation of habitat, and maintaining connectivity (Gauthier et al., 2014). In particular, the boreal forest is currently experiencing new disturbance regimes, including stand-replacing fires and the outbreak of herbivorous insects, e.g., the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) and the spruce bark beetle (*Dendroctonus rufipennis* Kirby) (Bernier et al., 2016). The conversion of vulnerable stands from coniferous to mixed stands (with broadleaf species) has been suggested as a major adaptive management option to respond to such disturbance agents (Astrup et al., 2018). Forest management solutions focused only on wood volume and productivity risk failure in a rapidly changing climate because they ignore the trade-offs between productivity and traits such as cold tolerance and drought tolerance. Therefore, forest managers should resort to diverse strategies of adaptive management accounting for diverse functional traits and their trade-offs (Park et al., 2014).

It is increasingly understood that climate change adaptation is intricately related to forest sustainability and the principles found within the Montreal Process (Ogden & Innes, 2007) and now the global sustainability goals (Hazarika & Jandl, 2019). Effective adaptation of the forest management system will revolve around including risk management in planning processes, selecting robust and diversified adaptation actions, and adopting an adaptive management framework. Monitoring is always regarded as an action that is central to implementing adaptive forest management (Gauthier et al., 2014).

12.3.2 Assisted Migration

Forest tree populations are likely to respond to climate change in three possible ways: (1) they migrate to track their ecological niche; (2) they adapt to the new conditions in their current locations; and (3) they go locally extinct (Aitken et al., 2008). The evidence suggests that tree species have undergone range shifts, migration, and extinction during past glacial and postglacial periods. Such changes continue today with the warming-related poleward and altitudinal migration of tree species and populations (Dyderski et al., 2018).

Natural migration over long distances is a slow process and often requires several generations and centuries for long-lived trees. Migration rates during the postglacial age are estimated at 100–500 m · y^{-1} (Williams & Dumroese, 2013). Ongoing climate change is expected to occur at a much faster rate, requiring tree populations to migrate faster than tree migration during the glacial period to remain within the species' environmental envelope. According to Tchebakova et al. (2006), some boreal populations of Scots pine would need to move 700–1,500 km north to track the climate projections for 2100. Geographic barriers and habitat fragmentation pose additional challenges to the intrinsic ability of trees to migrate, making some species vulnerable to extinction (Sáenz-Romero et al., 2012).

Forest trees have evolved at the species and population levels to adapt to the local environment in which they grow (Aitken & Whitlock, 2013; Kreyling et al., 2014). Such local adaptations lead to genetically diverse populations, with traits that enable these taxa to adapt to their local environment's biotic and abiotic factors (e.g., growing season and outbreaks of fire and insects). Examples of such adaptive traits include the timing and rate of growth, resistance to frost damage or drought stress, masting patterns, and dispersal distances and timings. Climate change will disrupt the link between climate and the local adaptation of forest tree populations, thereby creating physiological stresses that can lead to mismatches between the population and climate, known as the adaptation lag (Aitken & Whitlock, 2013). Thus, climate change will produce novel conditions to which the tree populations may not adapt. Phenotypic plasticity or the ability of the plant to respond to environmental change may mitigate the impacts of this decoupling to a certain extent, although it may be ineffective in cases of stress induced by extreme environmental events (Mátyás et al., 2010; Neuner et al., 2015).

Because of the limited migration and slow adaptation rate of trees, human-facilitated realignment will be required to match populations to the environment to which the trees are adapted (Aitken et al., 2008; Pedlar et al., 2012; Williams & Dumroese, 2013). Such facilitated movement is commonly known as assisted migration, assisted colonization, assisted relocation, or facilitated migration (Fig. 12.5). In particular, assisted population migration (assisted genetic migration or assisted gene flow) refers to moving seed sources or populations to new locations within the historical species range. Assisted range expansion refers to moving seed sources or populations from their current range to suitable areas beyond the historical species range, facilitating or simulating a natural dispersal. Assisted species migration (or assisted long-distance migration) moves seed sources or populations to a location far beyond the historical species range, beyond the natural ability of dispersion of the species for crossing natural geographical barriers.

Researchers and foresters have revisited historical provenance trials of forest tree species to understand intraspecific variations in climate adaptation and to plan assisted migration worldwide. Such experiments involve planting different species populations in a common environment, acting as a space-for-time substitute to study climate change (Kapeller et al., 2013; Leites et al., 2012). Several studies based on such provenance experiments conclude that tree populations often grow in suboptimal conditions; thus, a facilitated movement of such populations may be desirable to

Fig. 12.5 Representations of the general concepts of assisted migration. Three main strategies are shown: assisted population migration, assisted range expansion, and assisted species migration
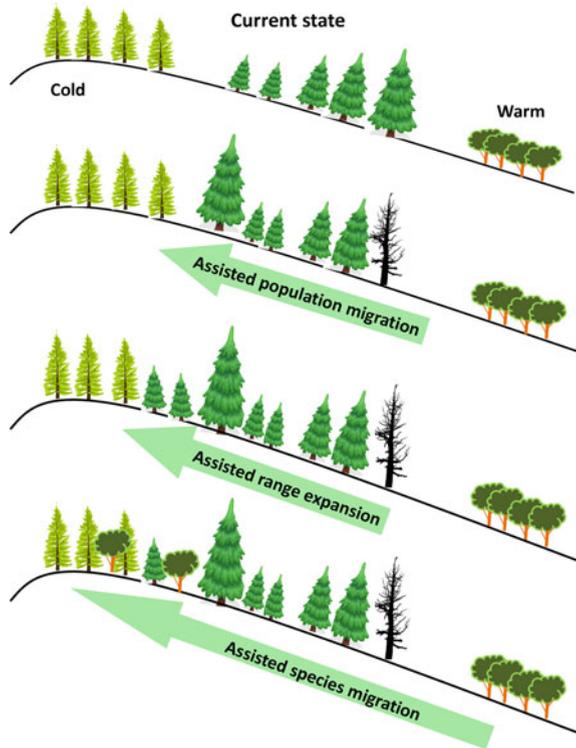
ensure their fitness under a changing climate (Chakraborty et al., 2016; Isaac-Renton et al., 2014; Rehfeldt et al., 2014; Wang et al., 2006). For example, whitebark pine (*Pinus albicaulis*) experiences better growth and germination when moved 800 km to the north of its current range, where seed sources from Oregon and Washington states performed well in locations in northwestern British Columbia (McLane & Aitken, 2012). Assisted migration is already incorporated into forest management policy in some countries, including Canada (Marris, 2009). A system similar to assisted migration, known as predictive provenance, is being used in the United Kingdom. This approach aims to match the current seed sources of native and non-native tree species to predicted climate in the future (Whittet et al., 2016).

Assisted migration does not necessarily need to be implemented widely. It should depend on a variety of criteria, such as the vulnerability of the native tree population, the provided ecosystem services, the current risks to stands, and the overall management goal of the landowner. A clear management strategy should be the first step for evaluating the need for assisted migration (Aitken & Bemmels, 2015). Assisted migration raises legal concerns about the trade and utilization of forest reproductive material. Seed and reproductive material for reforestation, traditionally sourced locally, may need to be adapted under climate change. However, legislation at the local and national levels may pose obstacles to such a transfer of plant material. In

some cases, the concept of assisted migration may lead to conflicts with conservation principles because of the likelihood of the increased use of non-native species and ecotypes, which may be potentially invasive (Aitken et al., 2008). The uncertainty in climate predictions over the century is another issue for assisted migration. Assisted migration may be more expensive than traditional regeneration practices, especially under conditions where natural regeneration is commonly practiced. Despite the uncertainties and challenges, it is often pertinent to evaluate the outcomes of inaction as a management option. There is no concrete evidence to believe that inaction would reduce the vulnerability of current tree populations to climate change. Although novel climates also can reveal the adaptive potential of populations, such adaptive variations will require time. However, if climate change causes the current forest populations to die or become too weak to produce healthy seeds, it might be impossible or unaffordable to assist their migration in the future.

12.4 Conclusions: The Importance of Ecotypes Under a Changing Environment

Climatic influences can modify many anatomical and chemical wood properties. Extreme events, such as droughts, heat waves, storms, late frosts, and flooding, substantially affect the metabolism of trees and lead to irreversible responses in wood formation in both its morphological and chemical structure (Bräuning et al., 2016; Grabner & Wimmer, 2006). It is difficult to determine the threshold for the triggering of certain modifications in wood anatomy or wood structure in relation to the occurrence of an extreme climatic event. Many stress factors induce complex responses, meaning that the measured effect has an unknown relationship with the stimulus; for example, storms may cause mechanical damage or bending in trees, inducing the formation of reaction wood or traumatic resin ducts. However, the susceptibility of trees to such events depends not only on the magnitude and frequency of these events but also on tree size, tree mechanical strength, and tree position within a stand.

The forest industry must become aware of the climatic influences on forest development and the related consequences on wood quality. The frequency and intensity of extreme climatic events are expected to increase (Salinger, 2005; Schär et al., 2004). In the worst-case scenario, the decline in wood quality because of extreme events may be so severe that it constrains the wood industry to find new provenances for their resources, replace wood by nonwood or nonsustainable raw materials, or develop new wood processing technologies.

Over the twenty-first century, the boreal forest will experience the greatest increases in temperature among all forest biomes worldwide. Projected temperature increases range between 4 and 11 °C, accompanied by a much less pronounced increase in precipitation; the combination represents a major threat to the health of this ecosystem (Gauthier et al., 2015). These changes will not only modify the

disturbance regime but also increase drought stress and drought-related mortality (Gauthier et al., 2015; Peng et al., 2011).

A strong influence of climate (drought) on earlywood density (besides mean ring density) can be seen by studying the influence of pointer years, such as drought years (Grabner et al., 2010). The microdensity profiles of Norway spruce trees grown in a dry region of Austria showed a slightly increasing trend of earlywood density. During drought periods (1992–1995, 2000–2003), these trees experienced an increased earlywood density (Grabner et al., 2010), a dramatically reduced ring width, and an increased mean ring density because of higher latewood percentages.

Climate change alters forest productivity through CO_2 fertilization and the lengthening of the growing season. In the boreal environment, these changes lead to the northward migration of the tree line and an increased tree and shrub cover (IPCC, 2019). Likewise, a significant increase in the annual growth of boreal forests in Finland has been found (Kauppi et al., 2014). However, Girardin et al. (2016) found no consistent growth response over 60 years in boreal forests across Canada. In high-latitude regions, warming will also increase drought, wildfire, and insect outbreaks (IPCC, 2019). Because of these environmental changes, foresters will need to develop new management strategies, and the wood industry may struggle to secure a resource that meets process requirements and market demands. Genetic improvement of wood-quality traits by selecting suitable tree provenances represents one option to alleviate the possible decrease in wood quality.

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