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The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change



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ABSTRACT

The current distribution of forest genetic resources on Earth is the result of a combination of natural processes and human actions. Over time, tree populations have become adapted to their habitats including the local ecological disturbances they face. As the planet enters a phase of human-induced climate change of unprecedented speed and magnitude, however, previously locally-adapted populations are rendered less suitable for new conditions, and 'natural' biotic and abiotic disturbances are taken outside their historic distribution, frequency and intensity ranges. Tree populations rely on phenotypic plasticity to survive in extant locations, on genetic adaptation to modify their local phenotypic optimum or on migration to new suitable environmental conditions. The rate of required change, however, may outpace the ability to respond, and tree species and populations may become locally extinct after specific, but as yet unknown and unquantified, tipping points are reached. Here, we review the importance of forest genetic resources as a source of evolutionary potential for adaptation to changes in climate and other ecological factors. We particularly consider climate-related responses in the context of linkages to disturbances such as pests, diseases and fire, and associated feedback loops. The importance of management strategies to conserve evolutionary potential is emphasised and recommendations for policy-makers are provided.

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1. Introduction

Forests cover approximately 30% of the world's total land mass (FAO, 2010) and are an integral part of life on earth, providing a range of services at local, national and global levels. Projected changes in climate, both gradual and extreme events, pose a serious threat to forestry (IPCC, 2011). As such, international organizations are currently engaged in actions to address the interconnected challenges of deforestation, forests degradation and desertification in a changing environment. Not only does climate change pose a threat to forests themselves, but also to the millions of people who depend

on them directly for their livelihoods (Dawson et al., 2014, this special issue), and to the billions who are supported by forests through the provision of environmental services that are vital to humanity (UNEC, 2009; FAO, 2010).

Global climate change projections depend on future rates of greenhouse gas emissions, but expected temperature increases range from 1.1 °C to 2.9 °C by 2090–2099 (compared to 1980–1999) for a low (B1) emissions scenario, 1.7 °C to 4.4 °C for a medium (A1B) scenario and 2.0 °C to 5.4 °C for a high (A2) scenario (Solomon et al., 2007). Even a change at the lower end of this range is significant for forests and trees. Considerable changes in precipitation are also projected, with locations that are currently dry receiving generally less precipitation and locations that are currently relatively wet receiving more (Solomon et al., 2007). Evidence for negative effects of climate change on forests globally is mounting (Allen et al., 2010). In North America, for example, whitebark pine (*Pinus albicaulis* Engelm.) is dying due to a combination of drought-induced stress, mountain pine beetle attack (*Dendroctonus ponderosae* Hopkins) and blister rust (*Cronartium ribicola* A. Dietr.) that is attributed to climate change (Campbell and Antos, 2000; Smith et al., 2008; Zeglen, 2002). Other negative effects attributed to climate change include: the massive die-off (on 12,000 km²) of *Pinus edulis* (Engelm.) in the southwestern USA (Breshears et al., 2005); the sudden decline of *Populus tremuloides* (Michx.) in the USA's Rocky Mountains (Rehfeldt et al., 2009); the decline in *Cedrus atlantica* ([Endl.] Manetti ex Carrière) in the Middle Atlas mountains of Morocco (Mátyás, 2010); the decline of *Fagus sylvatica* L. in southwest Hungary (Mátyás et al., 2010); and the replacement of *F. sylvatica* by more drought-tolerant *Quercus ilex* L. in Catalonia, northeast Spain (Peñuelas et al., 2007).

Although in this paper our focus is the challenges in responding to anthropogenic climate change, it should be noted that human-included environmental alteration also carries some potential benefits for forest production in particular regions, where net productivity may be raised due to increases in CO₂ levels and temperature (in contemporary cold regions), if drought stress does not become limiting. For crops, modelling shows that drought often becomes constraining despite elevated CO₂ levels acting as a 'fertilizer' (Parry et al., 2004). In cold climates, it is not unusual for natural tree populations to be located under sub-optimal conditions, with the discrepancy between the inhabited and the optimal climate increasing with the severity of climate (Rehfeldt et al., 2004). In such locations, an increase in temperature, coupled with at least stable precipitation, may result in increased wood yields in the short- to medium-term. Projected examples of such increases include: *Pinus banksiana* in the North American Great Lakes region (Mátyás and Yeatman, 1992; Mátyás, 1994); *Pinus contorta*, *Pinus sylvestris* and *Larix sibirica* in Siberia (Rehfeldt et al., 1999, 2001, 2004); *Picea glauca* in southern Quebec (Beaulieu and Rainville, 2005); and *Pseudotsuga menziesii* in western North America (Leites et al., 2012a,b). In the longer-term, however, declines are expected as adaptive and plastic capacities to respond to change are exhausted (Mátyás et al., 2010).

Here, we address the role that forest genetic resources (FGR, the genetic variation in trees of present or potential benefit to humans; FAO, 1989) can play in responding to anthropogenic climate change. The present distribution of FGR globally is the result of natural geological, ecological and genetic processes, which, over thousands of years, and along with the influence of man, have resulted in adaptation to local environments (Alberto et al., 2013). Included in this is adaptation to local disturbances, such as fire, insects and diseases. We review the pressures on FGR imposed directly by changing climate, as well as the indirect impacts on forests induced by changes in the biotic (e.g., insect and disease) and abiotic (e.g., fire, flood) disturbances that affect them. In particular, we consider

climate-related responses in the context of linkages to disturbances and associated feedback loops, an issue not widely addressed in previous reviews on climate change and tree genetic resources. We conclude by discussing the feasibility of various management options to utilize the genetic variation in trees to respond to climate change and present options for policy-makers.

2. The impacts of climate change on FGR

Impacts are experienced through several demographic and genetic processes (Kremer et al., 2012; Savolainen et al., 2011). Some are directional and gradual, such as trends in increasing temperature and reducing rainfall, while others involve abrupt change, including drought, flood, fire and sudden pest invasions (in this paper we refer to these as catastrophic events; Scheffer et al., 2001; Scheffer and Carpenter, 2003). If environmental change is directional and continuous, fast-maturing trees in particular may have the potential to adapt genetically (Hamrick, 2004). At the receding edge of species distributions in particular, however, the magnitude and speed of projected anthropogenic climate change is likely to surpass adaptive capacity in many cases, resulting in local extirpations (Davis and Shaw, 2001). As climate changes, species and genotypes within species that are mal-adapted may be replaced by fitter ones that are already present at a site or by genotypes migrating from elsewhere. At the ecosystem level, the result will be a change in the relative abundance of species and genotypes in the landscape. Such changes may be unpredictable, with significant changes in net ecosystem productivity possible (Thornley and Cannell, 1996; Wang et al., 2012). Extirpation of ecologically important keystone species will have critical impacts on coexisting organisms and their adaptation.

Climate change may also result in high variability in temperature and precipitation, with an increase in incidence of extreme events, such as flooding, late frosts and intensive summer droughts, amongst other events (IPCC, 2011) (Table 1). In some areas, such as the Mediterranean and the Neo-tropics, an increase in seasonality is also expected (Alcamo et al., 2007; Meir and Woodward, 2010). Under such conditions, natural selection may not result in efficient adaptation because selection pressures are multi-directional, involving traits that may be inversely correlated at the gene level (Jump and Peñuelas, 2005). The standing genetic variation in populations may then not be large enough to create the rare new genotypic combinations that are required. Ecosystems affected by abrupt change may sustain rapid and widespread transformation as ecological tipping points are exceeded (Lenton, 2011). Given the pivotal role of trees in ecosystem function, abrupt climate change impacts on them may thus have profound consequences for forests as a whole (Whitham et al., 2006). Irreversible loss of ecosystem integrity and function may follow, with replacement by new non-endemic ecosystems (Gunderson and Holling, 2002; Mooney et al., 2009).

3. Responses of tree populations to environmental change

3.1. Adaptation and 'standing' genetic variation

Tree populations rely on three interplaying mechanisms to respond to environmental change: adaptation, migration; and phenotypic plasticity (Davis and Shaw, 2001; Jump and Peñuelas, 2005). Genetic adaptations that make a population more suited for survival are achieved through gene frequency changes across generations (Koski et al., 1997). Many tree species have high genetic variability in adaptive traits and can therefore grow under a wide range of conditions (Gutschick and BassiriRad, 2003). Indeed, phenotypic traits of adaptive importance, such as drought

Table 1
Forest genetic resources under pressure: climatic drivers of change.

Direct effects of changing climate	These include high tree mortality through extreme climatic events, particularly drought in combination with widespread regeneration failure (IPCC, 2011). Malhi et al. (2009), for example, examined the evidence for anthropogenic climate change leading to future large-scale “dieback” in Amazonian rainforest. Analysis suggested that dry-season water stress is likely to increase in eastern Amazonia over the 21st century, with the region tending toward a climate more appropriate to seasonal forests. Due to their deep roots, trees are able to persist under extreme weather events such as droughts for longer periods than many non-woody taxa can, but this persistence should not be over-estimated. For example, in an experiment in the Amazon in which rainfall was restricted to mimic savannah conditions, Nepstad et al. (2007) demonstrated that there was a lag of only three years before the increased mortality of mature trees due to limited water availability
Effects of changing climate on organisms associated with trees	In particular, changes in the biology of insect pests and diseases may make ecosystems more susceptible to tree mortality (Alfaro et al., 2010). Because of improved environmental conditions for the pest and reduced tree resistance due to increased stress, pests may react to climate change with range expansions and/or increases in attack severity (Raffa et al., 2013). Since many pests have short generation times, large populations and strong dispersal abilities, they may adapt to environmental change more quickly than host trees (Harrington et al., 2001)
Changes in abiotic disturbance regimes	These include changes in fire regimes, flooding, landslides and/or hurricanes. Fire and climate are closely linked and are also associated with changes in land use (Piñol et al., 1998; Pausas, 2004). Coupled climate and fire-risk models (Moriondo et al., 2006) suggest not only an increase in the frequency of fires but also in fire size and length of the fire-risk season, with some areas subject to risk that were not before. Malhi et al. (2009) considered how tipping points may be reached in Amazonian rainforest by a combination of increased dryness and an increased incidence of fire events
Invasion by organisms foreign to local ecosystems	This includes the increased risk of establishment by invasive species which accidentally arrive into ports of entry, through globalized commerce. By making new niches available, climate change will facilitate the survival of mammals, insects, diseases and/or weeds foreign to endemic ecosystems. These include invasive exotic trees introduced for production and amenity purposes that are more precocious, have higher seed dispersal distances, are more fecund and/or are more adaptable than existing species, or that are better suited to new environmental conditions (Peterson et al., 2008)

tolerance, cold-hardiness, resistance to pests and diseases, and flowering and fruiting period, have been shown to vary across ecological and geographic gradients to an extent that may be as important as the differences observed amongst species (Alberto et al., 2013; Petit and Hampe, 2006). The result is local adaptation along these gradients (Alberto et al., 2013; Savolainen et al., 2007). Navarro et al. (2002, 2005), for example, found that *Cedrela odorata* L. populations sampled from areas with long dry periods were more adapted to drought than those collected from wet areas. In relation to pests, Alfaro et al. (2013) indicated that populations of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) with resistance to *Pissodes strobi* Peck were more common in areas with intense pest pressure than in areas where the pest was absent. The process of adaptation to climate change is influenced by migration and genetic drift, with fitness trait values shifting over generations to track environmental change and to ensure the survival of tree populations, with the emergence of endemic populations and speciation (Futuyma, 2010; Kremer et al., 2012; Savolainen et al., 2011).

Although a large amount of genetic diversity *per se* does not guarantee adaptation and adaptability (Gomulkiewicz and Houle, 2009), the high within-population genetic diversity observed in many forest tree species (but see Vendramin et al., 2008 for a counter example) can support an optimistic view that climate change challenges may be met by standing genetic variation in many cases (Hoffmann and Sgro, 2011). Many forest trees, for example, have high genetic diversity in important adaptive traits, such as tallness, longevity and defense mechanisms (Petit and Hampe, 2006). Trees also often have high fecundity (El-Kassaby et al., 1989), which creates a large gene pool to select from. The speed of adaptive response within populations also depends on the size of the population; the heritability of fitness-related traits; interconnectedness; and the intensity, direction and duration of the selection pressure.

Field trials have been central to demonstrating the extent and distribution of genetic diversity in fitness-related traits in tree species (Kremer et al., 2002; Savolainen et al., 2007). Experiments have been conducted mostly on boreal and temperate species and a few commercially important tropical trees (Aitken et al., 2008; Alberto et al., 2013). Recently, however, there has been a move to include a wider range of less commercial species in the tropics (Ræbild et al., 2011). New studies on indigenous African

fruit trees, for example, have specifically considered traits important in the context of climate change adaptation (see www.safrui-t.org). The information being obtained on the effects of different treatments on root development, seedling vigour and other important adaptive characteristics will inform the strategies by which planting material of these fruit trees is supplied to African smallholders (Sanou et al., 2007). In addition to common garden trials, recent molecular-level studies have demonstrated allelic shifts in genes related to drought and heat tolerance amongst tree populations, variables that are relevant for local adaptation (Grivet et al., 2011).

Evidence from field experiments suggests that a balance between divergent selection across contrasting ecological sites and reproductive contact has maintained enough genetic diversity to support adaptation to changing environments in the past (Kremer et al., 2010). Certainly, it has been demonstrated that maintaining high genetic diversity within and amongst tree populations can increase ecosystem resilience (Whitham et al., 2006; Thorsen and Kjær, 2007), especially when trees are keystone species (Barbour et al., 2009). Intra-specific diversity can promote both resilience to pest attack and the productivity of individual species; economic modelling has, for example, shown that in some cases more optimal production under climate change will be attained in plantations by “composite provenancing” from within a species’ range (Bosselmann et al., 2008; Hubert and Cottrell, 2007).

The fast pace of anthropogenic climate change and the comparatively long generation interval of many trees, however, mean that there may be insufficient time for natural selection to give rise to genotypes within populations that are adapted to new environments (Jump et al., 2006). When environmental conditions change at a rate beyond the point where they cause demographic declines, the adaptive challenges faced by populations are markedly different from those experienced during demographic expansions (Gomulkiewicz and Holt, 1995). In a race between decline and evolutionary change, if genetic change is too slow population extinction will be the result. Only when the pace and extent of environmental change is moderate, when a population is initially large, and when evolutionary potential is high, is a population likely to be rescued through adaptation (Gomulkiewicz and Holt, 1995; Gomulkiewicz and Houle, 2009).

3.2. Migration via pollen and seed movement

Pollen- and seed-mediated gene flow can facilitate adaptation to new environmental conditions by replenishing population genetic variation (Bridle et al., 2010; Le Corre and Kremer, 2003; Polechova et al., 2009), and by reducing the effects of genetic drift in small stands (Alleaume-Benharira et al., 2006; Lopez et al., 2009). Under climate change, the asymmetric gene flow from large central populations to small peripheral ones (Kirkpatrick and Barton, 1997; Lenormand, 2002) should prove beneficial for populations at the leading edge of migration fronts, but possibly maladaptive for populations at the rear edge (Hampe and Petit, 2005). Pollen is known on occasions to travel very long distances, particularly in wind-dispersed broadleaves and conifers (Liepelt et al., 2002), but also sometimes for animal-pollinated species (Jha and Dick, 2010; Kramer et al., 2008; Oddou-Muratorio et al., 2005; Ward et al., 2005). Paleocological reconstructions of the recolonisation of temperate zones during the Holocene have also suggested that seeds are capable of travelling long distances rapidly (Brewer et al., 2002; Nathan et al., 2002), in the range of several hundreds of meters per year. Landscape genetic approaches, macrofossil evidence and theoretical studies, however, indicate that cryptic refugia may have been overlooked, considerably reducing migration estimates (McLachlan et al., 2005; Roques et al., 2010; Willis and van Andel, 2004). In addition, modern estimates of contemporary seed dispersal, although pointing to the existence of long distance dispersal events, generally indicate that median migration rates are in the range of a few tens of meters per year (Amm et al., 2012; Clark et al., 1998; Sagnard et al., 2007; Willson, 1993).

Whereas such modest migration rates are enough to keep pace in mountain and tropical conifer biomes, migration rates of over 1 km per year may be needed, even under quite modest scenarios of temperature change, in tropical and boreal broadleaf biomes (Loarie et al., 2009). In addition, rates of natural migration are reduced by forest degradation and fragmentation, which therefore increase vulnerability to climate change (Kellomäki et al., 2001; Malcolm et al., 2002). Trees in agricultural land or planted in corridors can enhance pollen-mediated gene flow between forest patches (Ward et al., 2005), allowing more effective responses to change (Bhagwat et al., 2008; Thuiller et al., 2008). Mediterranean and other mountainous regions, where strongly contrasted topography on a meso- or micro-geographic scale prevail, may prove to be amongst the few biomes where climate change velocity will not outpace migration rates (Loarie et al., 2009), provided that land use change and man-made habitat fragmentation does not limit natural migration processes.

Abundant seed production is needed for efficient migration (and local adaptation, see Section 3.1). Predicting how climate change modifies tree fecundity remains a formidable challenge, however, because flowering phenology and seed production are regulated by complex endogenous (e.g., hormonal) and exogenous (e.g. climate) factors that are not completely understood yet. Selås et al. (2002), for example, indicated that spruce seed production in Norway is subject to a negative autocorrelation that lags by 1 year, i.e., good seed years (mast years) are preceded by low seed years, a phenomenon common to many trees. These authors found that seed production during mast years was directly related to higher temperatures in the previous spring and summer, late spring frost and summer precipitation of the last 2 years. On the other hand, more recently, Kelly et al. (2013), analysing extensive data sets from five plant families, found that a warm spring or summer in the previous year had a low predictive ability for seed production. Kelly et al. (2013) developed a model for the prediction of seed production that was based on temperature differentials over several seasons. They concluded that mast seeding will be unaffected

by gradual increases in mean temperature, because this will have little effect on the temperature differential over multiple years. Instead, yearly climatic variability may determine the amount of seed produced. This model was recently found to be an accurate predictor of acorn production in valley oak, *Quercus lobata* Jeps (Pearse et al., 2014).

Increased mortality under climate change reduces tree density (especially at the receding edge), which will also affect the quantity (and genetic quality) of seed crops (Restoux et al., 2008). Changes in climate may also result in asynchronies between flower development and pollinator availability which, for trees that depend on animal vectors, may reduce the seed crop (Dawson et al., 2011), at least until new mutualistic relations are established between trees and pollinators (see Section 4.1). Many tropical tree species that are pollinated by insects, birds, or bats may be affected (Hegland et al., 2009).

3.3. The role of phenotypic plasticity

Phenotypic plasticity is defined as the capacity of a particular genotype to express different phenotypes under different environmental conditions (de Jong, 2005; Pigliucci and Murren, 2003). The concept is often extended to populations and species, with 'plastic' trees those with flexible morphology and physiology that grow at least reasonably well under a range of different environmental stresses without genetic change (Gienapp et al., 2008). A degree of phenotypic plasticity is found in most trees (Piersma and Drent, 2003; Rehfeldt et al., 2001; Valladares et al., 2005), but varies substantially amongst and within species (Aitken et al., 2008; Bouvarel, 1960; Skrøppa et al., 2010). Even in species with very little genetic diversity, such as *Pinus pinea* L. (Vendramin et al., 2008), strong phenotypic plasticity is expressed for growth-related traits, which may have helped the species colonise new environments (Mutke et al., 2010).

At least in the short term, high plasticity is likely to favour tree survival under changing environmental conditions, although trade-offs between traits can be expected. As processes related to phenotypic plasticity may oppose those related to genetic adaptation, however, in the longer term, survival may not be favoured (Aitken et al., 2008). Since phenotypic plasticity has a heritable basis and may be selected for under changing environments (Nicotra et al., 2010), complex interactions between traits are possible, depending on the magnitude and structure of change (Chevin et al., 2010). Selecting populations and genotypes that demonstrate good levels of phenotypic plasticity (based on multi-locational field trials and environmental data) may be an appropriate management response to climate change for plantation forestry and agroforestry, especially for regions where greater variation in weather conditions is anticipated. Multi-site field trials sometimes reveal that trees have more plastic responses than would be expected based on their existing geographic distributions (e.g., *Pinus radiata* D. Don., Gautam et al., 2003).

Epigenetic phenomena (modification of DNA expression but not the nucleotide sequence, e.g., through DNA methylation, histone modification and mRNA regulation) may affect phenotypic plasticity and adaptive potential (Hedhly et al., 2008). Epigenetic effects caused by environmental stresses can be maintained across several generations and vary across populations and individuals (Bossdorf et al., 2008; Yakovlev et al., 2010). Since epigenetic modifications can be reversed, they can be considered as relatively "plastic", providing for a rapid response to change while avoiding the need for additional genetic diversification (Lira-Medeiros et al., 2010). According to Aitken et al. (2008), the epigenome may provide a temporary buffer against climatic variability, providing time for the genome to "catch up" with change.

Epigenetic effects have been demonstrated in the phenology of bud set in *Picea abies* (L.) Karst. Progenies of this species whose embryos develop in warm environments are less cold hardy than those that develop at lower temperatures (Skrøppa and Johnsen, 2000; Johnsen et al., 2005, 2009). Similar effects have been observed in: progeny from *Picea glauca* and in *P. glauca* × *P. engelmannii* (Parry ex Engelman.) (Webber et al., 2005); in *Pinus sylvestris* L. (Dormling and Johnsen, 1992); and in *Larix* spp. (Greenwood and Hutchison, 1996). Epigenetic phenomena have also been hypothesised to explain the phenotypic plasticity of the genetically depauperate *Pinus pinea* (see earlier in this section, Vendramin et al., 2008). There is, however, a general lack of information on epigenetic effects in angiosperm trees (Rohde and Junttila, 2008).

4. Responses of tree populations to catastrophic biotic and abiotic disturbances

Tree populations have developed mechanisms to respond to naturally occurring disturbances within their range. North American conifers, for example, have adapted to outbreaks of the defoliating insect spruce budworm (*Choristoneura fumiferana* Clem.) that have recurred at periodic intervals (~every 35 years) at least since the middle of the Holocene, 6000 years ago (Simard et al., 2011). Climate change may however cause range expansions in herbivorous insects (Murdoch et al., 2013) and in diseases, causing increased mortality in non-adapted populations. This is illustrated by whitebark pine, where a warming climate has increased the access of stands to native bark beetles that are now able to reach higher elevations, resulting in high mortality due to low defenses in trees that have had little previous contact with this beetle (Raffa et al., 2013). Recent modelling supports the view that large areas of current whitebark pine habitat are likely to become climatically unsuitable over the coming decades (McLane and Aitken, 2012). Increasingly, warm winters and earlier springs, which cause greater drying of soils and forest fuels, are also predicted to increase the number of large wildfires and the total area burned in temperate and some tropical forests (Malhi et al., 2009).

Tree populations respond to abrupt, non-linear environmental changes through the mechanisms already outlined: natural selection favours genotypes with increased tolerance or resistance to disturbances, and phenotypic plasticity plays a role. It is well known, for example, that populations of *Pinus contorta* Dougl. ex Loud. and *P. banksiana* Lamb. from parts of North America more prone to natural fires have a higher proportion of serotinous cones than those from elsewhere. Serotinous cones remain tightly closed until a hot fire has destroyed standing trees, then releasing seed to initiate rapid post-fire regeneration. There is also evidence that in the Mediterranean ecosystem, fire selects tree species and individuals with a particular combination of functional traits including serotiny, thick bark and high water use efficiency (Fady, 2012; Budde et al., 2014). Populations of many Mediterranean plants persist after fire due to their capacity to form a resistant seed bank (Lamont et al., 1991; Keeley and Fotheringham, 2000). Although many tree species that grow in semi-arid regions have developed mechanisms that confer a degree of resistance to periodic fires, this may not be the case in more humid forests, where increased fire frequency due to climate change may eliminate fire-sensitive species (Verdu and Pausas, 2007). Regions that newly experience regular wildfires may evolve in close association with fire as the main driver, with rapid species and genotype transitions from fire-sensitive to fire-resistant (i.e., a rapid change in micro-evolutionary pattern may occur).

Large stand-replacing fires or widespread insect and disease outbreaks, although often resulting in large economic losses, do eliminate forests that were adapted to old climatic conditions

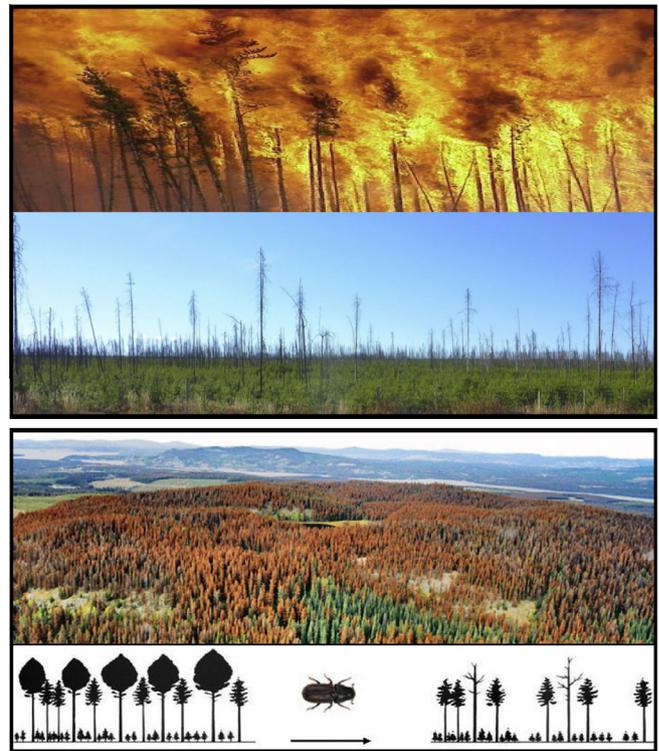


Fig. 1. Forest transformation by natural disturbances. For fire-adapted tree species in British Columbia, Canada, elimination of the old forest canopy by stand-replacing fire triggers massive forest regeneration (top two panes). The bottom photograph illustrates massive mortality of lodgepole pine by mountain pine beetle in British Columbia. The diagram shows the removal of the mature lodgepole pine canopy by mountain pine beetle (left) and forest transformation to a different species not affected by beetle (right). Canopy mortality by disturbances creates enormous economic losses, but at the same time provides conditions for forest regeneration. This provides new opportunities for natural selection to operate, resulting in a new generation of trees better adapted to new climatic conditions, and which eventually will replace old canopies born under the climate of over one hundred years earlier. Photographs: Canadian Forest Service.

and provide a ‘fresh start’ with new regeneration opportunities (Fig. 1). Such successional forests will eventually adapt to new climate through natural selection, particularly at the seedling stage. Selective shifts in traits related to fire resistance may, however, have negative effects on economically important associated traits. For example, Schwilk and Ackerly (2001) indicated that trees that embrace fire as a species survival strategy are more likely to favour traits such as short height, flammable foliage and no self-pruning.

4.1. Co-evolution and biotic disturbances

‘Co-evolution’ describes a situation where two (or more) species reciprocally affect each other’s evolution (Janzen, 1980; Pimentel, 1961), such as the classic case of host-pathogen interaction, where changes in *R*-gene resistance in the host lead to corresponding changes in *v*-gene virulence in the pathogen, triggering further rounds of change in one and then the other (Person, 1966). In trees, such gene-for-gene relationships have, for example, been found in a number of North American white pines in their interaction with blister rust (Kinloch, 2003; Kinloch and Dupper, 2002). Further important examples of co-evolution in trees include interactions with herbivores and pollinators. In the former case, a number of constitutive and induced defence systems, both mechanical defences (e.g., resin canals, sclereid cells and thorns) as well as chemical defences (e.g., the production of toxic phenols and

terpenoids), have evolved in response to herbivory (Alfaro et al., 2002; Cooper and Owen-Smith, 1986; Franceschi et al., 2005). Insects and pathogens have developed mechanisms to de-activate these defences and even utilize them for their own benefit; for example, some insects use tree terpenes as precursors for their communication pheromones (Erbilgin et al., 2014) or incorporate them into their own defence systems (Higginson et al., 2012).

The relationships between trees and associated herbivores, parasites and pollinators are strongly influenced by environmental factors. It is well known, for example, that drought stress reduces the ability of conifers to defend against bark beetles due to changes in plant defences (Ayres and Lombardero, 2000; Safranyik and Carroll, 2006). Climate change-mediated insect epidemics are already observed in Canada, where the mountain pine beetle has had severe economic consequences for forestry (Konkin and Hopkins, 2009; Fig. 1). In the Canadian province of British Columbia, an outbreak of mountain pine beetle, which began in the early part of the last decade and is only now (2014) abating, attacked more than 13 million hectares of *Pinus contorta* forests. The cause of this sustained outbreak is believed to have been a long series of unusually warm winters (Safranyik and Carroll, 2006). As with fire, however, large scale mortality does provide an opportunity for wide-scale regeneration (Axelson et al., 2010) and hence more rapid adaptation to changing climate.

Overall, pest-resistant tree genotypes occur more frequently in areas where climate is most favourable to the insect and the lowest resistance levels are found where the insect is absent (Alfaro et al., 2008). As global environmental changes influence the distribution of the insect, an associated adaptive response by the tree will be required.

The mutualistic relationship between trees and insect or vertebrate pollinators is of considerable interest in the context of climate change. The current view of ecologists recognizes that plant–pollinator relationships are not always a strict one-on-one co-evolutionary process; instead, there are many plant pollinator systems where diverse pollinator assemblages can lead to the maintenance of pollination services, plant reproduction and persistence, and relationships change over time and space (Burkle and Alarcón, 2011 and references therein). Under climate change, trees may be able to rely on new pollinators that shift their attention to them. According to Burkle and Alarcón (2011), the inherent plasticity of plant–pollinator interactions suggests that many species should be able to persist by responding to environmental changes quickly, even though their mutualistic partners may be different.

4.2. Responses to alien invasive species

Under climate change, FGR are likely to be increasingly threatened by alien invasive species i.e., more competitive trees, fungal and other diseases and herbivores that do not occur naturally in their local ecosystems, and to which they lack adequate defenses. The acceleration of global trade has increased the likelihood of cross-continental introductions of alien species, which may become more widely established in new ecosystem niches created by global warming (Koskela et al., 2009; Koskela et al., 2014, this special issue; Peterson et al., 2008). When forest ecosystems are already disturbed by other anthropogenic activities, they may have little resistance to invasive species, especially when climate change is also considered, with extreme results possible (Moore, 2005). There are, for example, numerous cases of exotic trees invading forest ecosystems (Richardson, 1998). Lack of resistance to alien invaders, especially in temperate forests, is more severe when the number of endemic species found in them is reduced (Petit et al., 2004; Simberloff et al., 2002). The consequences of exotic pest invasions may be a catastrophic elimination of FGR, such as the cases of chestnut blight and white pine blister rust (Kinloch,

2003). At a provenance level, exotic introductions may result in hybridisation and out-breeding depression in local tree populations already stressed by climate change, but, more positively, hybridisation may also introduce the new genetic variation required by trees to adapt to novel environments (Hoffmann and Sgro, 2011).

5. FGR-based strategies to respond to climate change

Isbell et al. (2011) stated that “many species are needed to maintain multiple functions at multiple times and places in a changing world”. From a forest management perspective, adapting to climate change requires the adoption of the “precautionary principle” and maintaining options in the form of inter- and intra-specific diversity (a form of insurance policy) (UNESCO, 2005). This should increase the resilience of natural and planted forests under environmental variability, especially if the component parts of systems and their interactions respond differently to disturbances (Fleming et al., 2011; Kindt et al., 2006; Steffan-Dewenter et al., 2007). As climate change progresses, poorly-performing trees will be naturally replaced by alternatives that are better suited to new conditions, altering the relative abundance of different species and genotypes in landscapes (Jump and Peñuelas, 2005). As resilience rests on the maintenance of genetic, species and ecosystem diversity, management strategies should support diversification at all three levels (Millar et al., 2007; Jump et al., 2008).

Although humans impacts on forests over time have often involved (genetic) resource depletion (e.g., in the Mediterranean, Fady et al., 2008), silvicultural interventions can provide opportunities to manage forests better under climate change. Several of the management interventions required to support natural and planted production forests in the context of climate change can be considered as good practice under ‘business as usual’ scenarios (Guariguata et al., 2012). Forest managers sometimes question, however, whether interventions specifically formulated to respond to climate change are economically justified, as tropical foresters are likely to consider commercial agriculture and unplanned logging more important production threats (Guariguata et al., 2012). Interviews of foresters in Europe indicate that they are sometimes similarly ambivalent in implementing specific management responses to climate change, partly reflecting uncertainties in climate impacts and appropriate responses (Milad et al., 2013).

As part of the toolkit that foresters can use to adapt forests to climate change, the distribution of FGR and their silviculture can be modified in space and time (Sagnard et al., 2011; Lefèvre et al., 2013). To date, few countries have however taken practical steps to reduce the risk of FGR loss due to climate change. Relevant steps are usually only indirectly incorporated into action plans for forest management under climate change. In France, for example, FGR are not explicitly mentioned in the national adaptation strategy (ONERC, 2007). They are, however, part of the action plan for forests, one of the sectors included in the national strategy for biodiversity, where recommendations for their conservation and sustainable use are explicitly mentioned (MAP, 2006).

5.1. Assisted migration

Assisted migration involves human movement of tree seed and seedlings from current locations to sites modelled to experience analogous environmental conditions in the future (Guariguata et al., 2008; McLachlan et al., 2007). Such movements may be latitudinal, longitudinal or altitudinal, and are designed to reduce extinction risks for those species not able to naturally migrate quickly enough, and to maintain forest productivity (Heller and Zavaleta, 2009; Marris, 2009; Millar et al., 2007). Assisted

migration may be undertaken over long distances, or just beyond the current range limit of particular genotypes and populations, or within the existing range (Winder et al., 2011). A gradual form of assisted migration could consist of reforestation of harvested sites with seed from adjacent locations likely to be better adapted to the planting site under future climate (e.g., in the Northern hemisphere, using seed from sources to the south; in mountainous regions using seed from lower elevations).

Aubin et al. (2011) and Winder et al. (2011) reviewed the pros and cons of the assisted migration approach. One problem is that the selection between different global climate models (GCMs) and the methods for downscaling to detailed geographic levels are still areas of active research and thereby introduce uncertainty in modelling, especially for marginal environments (Fowler et al., 2007). Clearly, areas of high probability for a given future environment, based on ensemble forecasting across GCM (and across the various statistical models available for determining species distributions) should be priorities for action (Rehfeldt et al., 2012).

Much uncertainty is also due to the unknown future trajectories of greenhouse gas emissions in the longer term, as these will depend on technological developments that increase or decrease emissions (IPCC, 2011). For more immediate future scenarios, however, the variation amongst models is small; for México, for the decade centered on the year 2030, for example, it is only about ± 0.2 °C of mean annual temperature (Sáenz-Romero et al., 2010). Another difficulty in modelling is that the current distributions of tree species, which form the basic input data for determining likely future distributions, are often not well known (McLachlan et al., 2007; Rehfeldt and Jaquish, 2010), especially in the tropics, where sometimes complex topographies and high biodiversity paradoxically make accurate predictions even more urgent. In the light of uncertainties in modelling, the United Kingdom's Forestry Commission (2011) considers risk minimisation as the best approach, by maintaining existing genetic variation, promoting migration, encouraging natural regeneration and supporting provenance mixing in plantations (Hubert and Cottrell, 2007).

As already noted (see Section 4.2), interventions that involve moving tree species into entirely new areas is hotly debated because of potential disturbances to indigenous flora and fauna. There are also numerous commercial forestry examples where the introduction of ill-adapted genetic resources has resulted in massive production failures. For example, 30,000 ha of *Pinus pinaster* Aiton plantations were destroyed in the Landes region of France during the winter of 1984 to 1985 following the introduction of non-frost-resistant material from the Iberian Peninsula (Timbal et al., 2005). Careful thought to all environmental factors should therefore be given before climate-related assisted migrations are undertaken. In mountain regions, upwards associated translocations may not be an option if populations are already at or near the summit (translocation must then be to different mountains), or if edaphic conditions are unsuitable (Lauer, 1973). Certainly, the establishment of viable populations at extremely high altitudes would be very challenging (Sáenz-Romero et al., 2010, 2012).

Another challenge to assisted migration that is specific to long-living perennials is that, where climate is changing quickly, large differences in conditions may be observed over an individual tree's lifespan. To find species or genotypes well adapted to conditions at establishment and at productive maturity (e.g., for some species, perhaps a century later) may therefore be difficult. In order to achieve a proper balance, the interval to production/maturity needs to be considered, and multiple stepped translocations over time may be required (Soto-Correa et al., 2012). In addition, changes to pest outbreak risk could simultaneously occur as a result of climate change, and this should be factored into assisted migration decisions (Murdock et al., 2013).

Another useful approach is to conduct assisted migration on assemblages of species with positive interactions that reduce climate risks. For example, a "first-stage" species may be planted as a nurse crop to provide protection from temperature extremes for a second tree. Such an approach has been applied to *Abies religiosa* (Kunth) Schlttd. et Cham., using the leguminous shrub *Lupinus elegans* Kunth as a nurse plant for seedlings (Blanco-García et al., 2011). Within species, assisted gene flow, where genes are exchanged between populations by moving individuals or gametes, has also the potential to control and reduce mal-adaptation (Aitken and Whitlock, 2013).

5.2. Selection and breeding

Climate change-related traits including plasticity and adaptation to increased drought need to be incorporated more actively into breeding programs (IUFRO, 2006). Many existing provenance trials were established before the need to respond to large scale anthropogenic environmental change was considered an important research issue and the traits measured have therefore often not been the most important ones from this perspective. Nevertheless, information from old trials can be reinterpreted in the context of climate threats (Aitken et al., 2008; Alberto et al., 2013). New trials established to assess explicit responses to climate change are being established in a number of countries (see, e.g., <http://treebreedex.eu/>).

Traits needed to respond to different climatic conditions not often considered previously in breeding include:

- **Pest and disease resistance:** As noted above (Section 4), climate-change-mediated increases in pest and disease attack are a crucial issue in commercial forestry. To date, one of the most extensive programmes to develop trees with resistance to insect pests in temperate regions is in British Columbia (Alfaro et al., 2013; King and Alfaro, 2009). Using a conventional breeding approach, *Picea sitchensis* genotypes with resistance to the white pine weevil were screened and deployed in reforestation programmes (Alfaro et al., 2013; Moreira et al., 2012). Such traits may be controlled by only a few loci as a result of gene-for-gene co-evolution (*sensu* Thompson and Burdon, 1992), as already described (Section 4.1), making breeding easier.
- **Drought resistance:** For many tree species, such as in the Mediterranean and parts of the tropics, altered moisture regimes will be of greater concern than temperature changes (Santos-del-Blanco et al., 2013). Drought stress induces a range of physiological and biochemical responses in plants and an assortment of genes with diverse functions are induced or repressed in organ-specific changes (Kreps et al., 2002; Shinozaki and Yamaguchi-Shinozaki, 2007), which may make breeding more difficult. Perdiguerro et al. (2013), for example, using microarray analysis, detected that up to 113 genes were significantly induced by drought in two Mediterranean pine species. Species-dependent features shape the transcriptome response; for example, almost none of the 27 genes reliably responsive to water stress in *Arabidopsis thaliana* (L.) Heynh., differentially regulated under drought in poplar and pine (Polle et al., 2006). Candidate genes for drought tolerance include those involved in the synthesis of abscisic acid, transcriptional regulators of drought-inducible pathways, and late embryogenesis abundant proteins; shifts at such loci have been linked to global warming (Hoffmann and Willi, 2008).
- **Fire resistance/tolerance:** Since fire incidence and severity will increase in many regions under climate change, breeding for features such as serotiny, thicker bark and higher water use efficiency may all be required (e.g., Jump et al., 2008).

- *Cyclone resistance/salt tolerance*: Rising sea levels and an increase in the frequency of storms have the potential to wreak heavy damage on coastal forests, with low elevation islands at particular risk. Differential abilities to withstand storms and salinity are found more commonly amongst, rather than within, species, but the possibility of intra-specific selection should be further explored. Increasing storm frequency in the Pacific due to climate change has led to efforts to identify cyclone-resistant species such as *Endospermum medullosum* L.S.Sm. for large-scale planting. In Vanuatu, for example, the establishment of 20,000 ha of plantations of this species is planned over the next 20 years.
- *Phenotypic plasticity*: Important but generally poorly understood, the plasticity of particular tree species and populations is vital for responding to climate change, and can be studied in common garden tests (Rehfeldt et al., 1999, 2002; Vitasse et al., 2010). Plasticity across environments can be quantified and response functions for particular populations generated, which describe the change in a trait as a function of the transfer distance or the change in an environmental factor (Rehfeldt et al., 1999, 2002). Populations vary in their response functions: in *Pinus contorta*, for example, some populations have a high growth rate over a much wider range of climatic conditions than others do (Wang et al., 2006).

At a strategic level, the feasibility of classical breeding approaches as a response to climate change needs to be considered. Yanchuk and Allard (2009) reviewed 260 activities for pest and disease breeding in trees, and found relatively few examples where resistant or tolerant material had been developed and deployed operationally. They concluded that future programs to tackle increased pest and disease incidence caused by rapid climate change were likely to have limited success if they relied on conventional breeding approaches (but see the case in this section above on *P. sitchensis* and white pine weevil). The long life cycle, large size, and (generally) poorly characterised genetics of trees all make breeding responses to climate change more costly and slower than for annual species. Indeed, in the neo-tropics, Guariguata et al. (2008) were unable to identify any changes to industrial tree breeding approaches that were aimed specifically to this end.

A breeding response to climate change requires agile and accurate methods that can deliver the needed genetic improvements but with substantially reduced time and resources. More than ever, breeding programs need to target several traits simultaneously, while conserving large genetic bases for unpredictable adaptation needs (Eriksson et al., 1993). The recent development of Next Generation Sequencing and Genotyping by Sequencing approaches offers an unlimited number of genetic markers, creating opportunities for new developments. These include pedigree reconstruction, so the breeding phase of tree improvement can be by-passed (e.g., “Breeding Without Breeding”; El-Kassaby and Lstiburek, 2009), with additional simplifications in testing (El-Kassaby et al., 2011); the use of pedigree-free models that can deliver genetic assessments with unprecedented precision, with the added advantage of applicability to unstructured natural populations (El-Kassaby et al., 2012; Klápšte et al., 2013; Korecký et al., 2013); and selection methods that utilize information from the entire genome (Meuwissen et al., 2001). Additionally, new methods for bulking-up and delivering the improvements of breeding are needed for commercially important species, as traditional methods (e.g., seed orchards) are slow. Renewed efforts are needed for improving and simplifying vegetative propagation methods, starting from the conventional production of rooted-cuttings through to somatic embryogenesis.

6. Conclusion

Forest resilience and ecosystem stability are required to ensure the future flow of ecosystem services over space and time in the support of world societies (FAO, 2010). These depend on maintaining genetic diversity, functional species diversity and ecosystem diversity (beta diversity) across forest landscapes and over time. Only adapted and adaptable genetic material will, for example, efficiently mitigate global carbon emissions. From a forest management perspective, adapting to climate change (and mitigating its effects) requires the adoption of the “precautionary principle” and maintaining options including intra-specific diversity (UNESCO, 2005). Tree species generally contain high genetic diversity in many of the traits and genes analysed, which supports this principle (Jump et al., 2008), but the potential of trees to respond to climate change should not be over-estimated (Nepstad et al., 2007).

In determining human responses to climate change for the forestry sector, there needs to be good supporting evidence if the active engagement of forest managers is to be obtained to support management interventions that proceed beyond good ‘business as usual’ practice (Guariguata et al., 2012; Milad et al., 2013). This evidence includes reliable science-based estimates of risks and the benefits of management for the mitigation of climate change impacts. Responses based on assisted migration need to include the consideration of all environmental factors, as the consequences of only partial consideration (response to a single or a few variables only) may be catastrophic (cf. Timbal et al., 2005), with such measures then losing credibility with forest managers. For assisted migration, modelling should consider potential damage by biotic and abiotic disturbances; for example, potential increases in pest and fire risk as a result of stress in the new area (Murdock et al., 2013).

Assisted migration responses to climate change that are based on greater dependency on the trans-national exchange of forest genetic resources require an appropriate policy and legislative environment to support transfer, including by the harmonisation of phytosanitary requirements, as noted by Koskela et al. (2009). At a national level, policies defining seed zones will need to be modified to allow the assisted migration of genetic material within nations. Countries developing national forestry action plans should also be encouraged to specifically include genetic level responses to climate change in their plans, which has sometimes, but not always, been the case to date (Hubert and Cottrell, 2007).

Designing proper responses to climate change requires a greater understanding of the extent of phenotypic plasticity in trees for important traits, the adaptive significance of plasticity, the differences in phenotypic plasticity amongst different genetic levels (genotypes, families, populations, etc.), and the trade-offs between plastic and adaptive responses (Aitken et al., 2008). Also required is further research on epigenetic effects, especially in angiosperm trees (Rohde and Junttila, 2008). Plastic and adaptive responses can be studied in multi-locational common garden experiments that specifically consider climate-related traits in measurement and design (Rehfeldt et al., 2002; Vitasse et al., 2010). For animal-pollinated species in particular, research is also needed on the effects of climate change on tree reproductive capacity, such as how elevated temperatures may affect mutualisms with pollinators, and how the changed availability of mutualistic partners influences the persistence of interacting species (Hegland et al., 2009).

As in previous climate change episodes, forest genetic resources will recombine to produce new variants, which through natural or assisted selection will produce the genotypes required to continue providing the ecosystem services that societies need from forests.

But, as climate change progresses it will be important to monitor the adaptation of trees, stands and ecosystems, and to intervene with efforts to support adaptation where needed.

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