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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.

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, forest degradation and desertification in a changing environment. Not only does climate change pose a threat to forest 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).

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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 km^2) 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 also 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 CO_2 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 CO_2 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 *Pseudostsuga 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 of 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 incidence of extreme events, such as severe drought or 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 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