

Forest genetic resources and adaptation to climate change

J. Loo



© BIOVERSITY INTERNATIONAL/R. KHALLI

Genetic resources determine the adaptive potential of trees and influence the long-term value of tree-planting efforts for climate change mitigation.

Judy Loo works for Bioversity International (Rome, Italy) as Science Domain Leader, Forest Genetic Resources and Restoration.

Trees are essential components of adaptation and mitigation strategies to counter impacts of climate change. On the one hand, trees play a vital role in adaptation of landscapes and human communities to tolerate climatic changes, including hotter and drier conditions; and, on the other, expanding forest cover increases the carbon sequestration capacity of landscapes, mitigating the negative impacts of emissions. Genetic resources determine the adaptive potential of trees as well as influencing the long-term value of tree-planting efforts for mitigation purposes. Thus genetic resources of trees are

A desert tree that shows both the extent of soil erosion and an ability to tolerate such changes

critical for effective adaptation and mitigation responses to climate change. In spite of this, among natural resource managers, restoration practitioners and conservation agents, little attention is paid to the importance of forest tree genetic resources and their vulnerability to impacts of climate change if not properly managed.

Genetic diversity comprises the heritable differences among individuals within a species, and forest genetic resources refers

to the genetic diversity in trees that is of current or potential importance to people. From a biological perspective, adaptation is a genetic response to changes in environmental conditions (in a broad sense) through natural or human-mediated selection. The term has taken on a much broader meaning in climate change discourse, but in this article, the focus is on the biological definition: the process by which tree populations or species change to become better suited to their environment.

Rapid adaptation may occur as a response to strong selection pressure (i.e. high mortality as a result of an environmental shift) that favours survival and reproduction of individuals having particular adaptive trait values, combined with high phenotypic variability and high heritability. This means that the values or forms of traits necessary for survival are present in the population and are passed on from parent to offspring (Alberto *et al.*, 2013). The key

question is whether genetic variation in adaptive traits is sufficient to equip populations of tree species to survive in the face of climate change. The answer, of course, is “It depends”: it depends on how rapidly change is occurring and whether it is directional; the amount of both plasticity (the ability of an individual organism to change its phenotype in response to environmental changes) and genetic diversity within populations; the pollination mechanisms and dispersal patterns of the tree species in question; and the degree to which populations are isolated and fragmented across landscapes. Scientists’ opinions vary; for example, Yanchuk and Allard (2009) were pessimistic in their assessment of the potential of classical tree improvement programmes to respond to climate change quickly enough; Hamrick (2004) was more optimistic regarding the potential for rapid adaptation within natural populations of trees.

Several reviews (Loo *et al.*, 2015; Alfaro *et al.*, 2014; Koskela, Buck and du Cros, 2007) have dealt with this subject during the past decade; this article provides additional information and examples of the role of forest genetic resources in adapting to climate change.

VULNERABILITY OF FOREST TREE GENETIC RESOURCES TO CLIMATE CHANGE

Climate change threatens forest genetic resources through the potential loss of unique genetic diversity when populations of trees are extirpated or severely diminished. In the most obvious and dramatic instance, trees of all ages, including mature ones, may exhibit high mortality after extreme events such as drought or flooding or the invasion of previously unknown or sporadically occurring insects or diseases. Alternatively populations may fail to regenerate and climate-sensitive



Residual patch of forest, Sri Lanka

tree species may be replaced gradually by others that are more suited to the changed conditions (Walck *et al.*, 2011). Regeneration failure may result from factors such as loss of pollinators or loss of synchrony in the timing of flowering and pollinator activity (Broadhurst *et al.*, 2016). Climate change can affect wind patterns so even wind-pollinated trees may exhibit reduced reproduction as a result (Kremer *et al.*, 2012). In northern climates mid-winter warming followed by sub-zero temperatures can destroy flower buds and, in extreme cases, cause tree mortality. In fact, large-scale tree die-off has already been reported in North America and Eurasia, and counter-intuitively, tree damage or death from cold stress as well as heat stress is expected by some to increase as a result of climate change in coming decades (Harfouche, Meilan and Altman, 2014). In either case, trees' reproductive capacity is compromised. Among other factors, the severity of the impacts of climate change depends on topography, recognizing that climate changes more rapidly over a given distance in mountainous topography than on flat land. Populations at or near mountaintops are likely to be highly vulnerable (Aitken and Bemmels, 2016).

When seed production is successful, seed still may not germinate or seedlings may not survive under changed temperature and moisture conditions (Walck *et al.*, 2011). The seedling stage is the most vulnerable in the survival and growth of tree species (Gaspar *et al.*, 2013). In the absence of successful regeneration, a population of trees may be doomed, in spite of apparently healthy mature trees that may live on for decades. Reported incidences of tree die-back are increasing, even though Walck *et al.* (2011) hypothesized that populations of many species could be buffered from the effects of climate change thanks to generally high local intraspecific genetic variation and phenotypic plasticity in seed dormancy and germination traits, occurring over small distances (both elevational and latitudinal). The examples from around

the world, provided by Allen (2009) when *Unasylva* last undertook the task of summarizing adaptation to climate change in the forest sector, can be supplemented now by numerous additional ones. See, for example, Hartmann *et al.* (2015); however, the authors caution that much uncertainty remains regarding global trends in tree mortality and potential ecological effects.

Hartmann *et al.* (2015) stated that we still do not have answers to basic questions like: (1) whether tree mortality is increasing globally; (2) why some trees survive and others die under similar drought conditions; (3) which physiological characteristics of trees are critical for understanding and modelling tree mortality; and (4) which features of droughts are the most important in predicting tree mortality. The second question can be answered, at least in part, by knowledge of genetic variation in adaptive traits, which influences the differential survival of trees when faced with drought and other serious environmental challenges (Alberto *et al.*, 2013). Finding an answer to the third question, as well as better understanding the genetic control of physiological traits involved in drought resistance, could lead to better management responses to counter the underlying causes of tree mortality.

In general, when environmental conditions change, tree populations have two possible alternatives to avoid extirpation: (1) adapt in place through a combination of phenotypic plasticity and genetic variation in relevant traits; or (2) migrate via seed and/or pollen to more suitable habitats (Aitken *et al.*, 2008). Franks, Weber and Aitken (2014) summarized evidence of evolutionary and/or plastic responses to climate change for a number of tree species. Although many of the temperate and boreal species included in their review exhibited apparent adaptation or plastic responses, less than half of them were judged to have sufficient response to keep pace with climate change. However, Kremer *et al.* (2012) pointed out that rarely would adaptation or migration occur independently of each other and concluded, based

on evaluation of the role of long-distance gene flow, that migration itself could be sufficient in many cases. The authors summarized results of mainly European tree species but it should be noted that tropical or subtropical species may have shorter gene flow distances (animal-mediated instead of wind pollination) and tropical and sub-tropical tree populations are often subject to greater landscape fragmentation than temperate ones.

As noted by Alberto *et al.* (2013), more data are available for trees than for many other plant species with respect to effects of climate change; field trials established decades ago are extremely useful now for assessing and predicting responses of tree populations to climate change. However, with a few notable exceptions, this information is limited to northern temperate and boreal species and much less is known about tropical or subtropical species.

Epigenetic effects can influence how some tree species respond to environmental change. Although not well studied or understood for many species, it is known that a handful of temperate and boreal conifer tree species exhibit these effects through permanent changes in regulation of phenological traits, such as timing of bud burst, that are triggered during the zygotic or embryo phase (Yakovlev *et al.*, 2014). The "epigenetic memory" is maintained throughout the lifespan of the affected trees, via modified protein transcription at particular gene loci, and is passed to offspring, although there is no change in primary DNA sequence (Yakovlev *et al.*, 2014). This complicates the interpretation of the clinal patterns of adaptation that are frequently observed across the range of tree species. However, as noted by Aitken and Bemmels (2016), the size of the epigenetic effects is itself subject to genetic variation among families.

Tree populations must be large (at least several hundred reproductively mature trees) to maintain inherent adaptive potential and ideally they should have uninhibited gene flow with other populations to facilitate adaptive responses to



Naturally drought-resistant trees in the mountainous landscape of Tajikistan

environmental stimuli or stress. Most tree species are both highly diverse and have high fecundity; millions of seeds may be produced over the lifetime of one single tree and only one offspring has to survive to replace each parent tree to maintain the population. Thus nature offers a huge potential for selection. In order for such directional selection to be successful, however, a second condition is that changes in climatic conditions must be directional and consistent. It is much less likely that trees can adapt to survive extreme events than to accommodate gradual directional change.

Modelling approaches to predicting impacts of climate change focus on range expansion and migration of species to fill climatic niches created by changing conditions. They assume homogeneity within species, i.e. all individuals within a species are treated as if they were adapted

to the same climatic envelope (Alberto *et al.*, 2013). In fact, tree populations may be specifically adapted to local climatic conditions and their tolerance is typically much narrower than for the species as a whole (Kremer *et al.*, 2012). For tree species which have been studied in provenance trials or along climatic clines, approaches that take into account complex trait interactions such as that described by Liepe *et al.* (2016) may be used. Also commonly overlooked is the fact that other factors besides climate determine suitability of habitat and that species may not be able to migrate across highly modified landscapes to a suitable habitat, even if it exists.

Considering what is currently known, there is no clear answer for most species with regard to their ability to adapt sufficiently or migrate rapidly enough to survive and regenerate in climates of the future.

HOW CAN FOREST GENETIC RESOURCES BE HARNESSSED TO RESPOND TO CLIMATE CHANGE?

Understanding diversity in adaptive traits

Where they exist, provenance trials can provide very useful information about the degree of local adaptation to environmental conditions as well as the amount of plasticity within species. Provenance trials are common garden field tests that are established using samples of planting stock that originate from (usually) a large number of populations across all or a substantial portion of a species' natural distribution. They are established following an experimental design that allows

separation of population-level genetic from environmental effects by statistical analysis. Kremer *et al.* (2012) summarized some provenance trial results that are relevant to climate change responses. Results from large numbers of provenance trials indicate that: (1) populations of tree species contain high levels of genetic variation that are maintained by gene flow; (2) in spite of high rates of gene flow, adaptive traits are strongly differentiated between populations; (3) different species exhibit similar population-level clinal patterns, especially for phenological traits along climatic or geographical variables, suggesting that many species have similar adaptive responses to directional selection; and (4) the current distribution of between vs. within population differentiation for fitness-related traits (at least for several temperate broad-leaved species) developed rapidly with the process of post-glacial recolonization. The term “fitness” is used here to mean the number of surviving offspring left by an individual.

The mechanisms by which tree populations are known to cope with rapidly changing environmental conditions can be harnessed to speed up the process of adaptation and migration in species that are under active management. Genetic improvement of trees increasingly focuses on adaptive traits in addition to production (see e.g. Harfouche, Meilan and Altman, 2014). Yanchuk and Allard (2009) reviewed the potential for tree improvement to keep pace with climate change from the perspective of forest health and concluded that the standard approach of breeding trees for resistance to individual pests when they begin to pose a threat has significant limitations. The time required for results from classical tree breeding is prohibitive considering the surge in the pace of appearance and degree of damage caused by new insect pests and diseases. Our inability to predict the next big insect or disease challenge adds to the difficulty. The authors recommended seeking general or generic resistance that could be deployed as a pre-emptive strategy. They pointed out

that ensuring tree vigour and productivity is the first line of defence, but breeding for tougher, less palatable foliage, for example, could develop a form of general resistance. Numerous studies have shown genetic variation in adaptive traits, holding out the promise of breeding trees to match new environmental conditions. For example, Kreyling *et al.* (2014) described evidence for local adaptations to winter and spring frosts in seedlings of European beech (*Fagus sylvatica*) and they reported that adaptation was stronger in marginal than central populations. Identifying populations with the greatest variation in the traits of interest or which have the desired “preadapted” variants is feasible for some species. However, improvement in adaptive traits may come with a cost. As Harfouche, Meilan and Altman (2014) noted, some tree species exhibit great variation in tolerance to environmental stresses, and in some cases, the metabolic cost of stress tolerance has negative impacts on tree growth.

Montwé, Spiecker and Hamann (2015) studied Douglas-fir (*Pseudotsuga menziesii*) provenances in western Canada, using dendrochronology to evaluate the productivity response to climate change. They studied how mature Douglas-fir provenances differ in their tolerance to drought conditions and examined trade-offs with long-term productivity. Their study showed that it is possible to select planting stock that shows drought tolerance, but there would be an associated reduction in productivity. The generality of such trade-offs between productive and adaptive traits is not known.

Planting to restore forest ecosystems: the challenge of climate change

Tree-planting efforts are increasingly urgent as natural forest cover recedes under a battery of human-mediated impacts, including changing climatic conditions. Forest and landscape restoration through natural regeneration is highly successful in some areas, but planting is necessary where natural regeneration is not sufficient. However, success rates of forest restoration

based on planting trees have been patchy, partly because of lack of attention to the source of planting material. As explained by Thomas *et al.* (2014), the successful establishment of self-sustaining restored forest depends on using sources of planting material that is already adapted to the often tough conditions of the planting sites and that has sufficient genetic diversity to continue to respond to changing conditions. Genetic considerations are obviously not the only determinants of success but without appropriate genetic material, failure is a foregone conclusion.

Commercial forestry plantations often consist of exotic, short-lived species and they are not intended to be self-sustaining over generations. Thus matching adapted planting material to the planting site needs to consider only the current or near future conditions and as such, is not likely to be as challenging as matching planting stock to site in landscape restoration. Restoration approaches that involve planting trees, and that are intended to restore ecosystem services as well as livelihood benefits, are likely to have a longer timeframe than commercial plantation forestry. The planting material must be adapted to planting sites that are often harsh, and capable of adapting to changing conditions in the future. To ensure adaptive potential in future generations, genetic diversity is essential. Breed *et al.* (2013) suggested that creating mixtures of seed from different sources (provenances) might maximize the adaptive potential, although it introduces the danger of outbreeding depression. “Outbreeding depression” is said to occur when breeding between individuals from different populations produces offspring that have lower fitness than progeny from crosses between individuals within either population.

Importance of marginal populations

Marginal populations of trees, meaning populations that are at the edges of a species’ range, may hold particular importance in the context of adaptation to climate change. Kreyling *et al.* (2014) noted that

local adaptations are sometimes especially strong in marginal populations. This implies that the asymmetrical gene flow from the higher-density centre of species ranges to the relatively sparse periphery (as discussed by Aitken and Whitlock, 2013) does not prevent the occurrence of local adaptation in these populations. Although rapid climate change may pose threats to locally adapted marginal populations, high selection intensity (high level of climate-induced mortality) combined with isolation may have the opposite effect, resulting in rapid adaptation (Jump *et al.*, 2006). Where adaptation to extreme conditions at distribution range edges occurs, these populations may have high value for planting both in other parts of the species range and in new habitats. Such populations may be subject to greater threat levels than populations in other parts of species' ranges, however, because of the likelihood of weather events that are stressful to edge populations and often a high degree of fragmentation with respect to the target species. Thus there is an urgent need to characterize and conserve marginal populations of useful tree species for their importance in countering impacts of climate change.

CONCLUSIONS

Although genetic resources of trees often receive relatively little attention in forest management, restoration and conservation, they are essential for a successful response to the impacts of climate change. This is true whether the concern is for continued adaptation of forest tree species to changing climatic conditions or mitigation of the negative effects of climate change through expansion of carbon-sequestering forest cover. The two are linked because as conditions change over time, the evolutionary potential of tree species must be maintained to allow for their continued adaptation; where trees are not well-adapted to local conditions, they do not sequester carbon efficiently. Evidence for the ability of tree species to withstand and adapt to changing environmental conditions is growing, but it is also

clear that there are limits. Understanding the limits to adaptation of tree populations *in situ* and the potential for moving planting material to new suitable habitats is increasingly important. Population size is one of the most important factors in maintaining evolutionary potential but tree populations continue to be subject to loss and fragmentation. ♦



References

- Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S.** 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, 1(1): 95–111.
- Aitken, S.N. & Whitlock, M.C.** 2013. Assisted gene flow to facilitate local adaptation to climate change. *Annual Review of Ecology, Evolution, and Systematics*, 44(1): 367.
- Aitken, S.N. & Bemmels, J.B.** 2016. Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications*, 9(1): 271–290.
- Alberto, F.J., Aitken, S.N., Alía, R., González-Martínez, S.C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. & Savolainen, O.** 2013. Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, 19(6): 1645–1661.
- Alfaro, R.I., Fady, B., Vendramin, G.G., Dawson, I.K., Fleming, R.A., Sáenz-Romero, C., Lindig-Cisneros, R.A., Murdock, T., Vinceti, B., Navarro, C.M. & Skroppa, T.** 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *Forest Ecology and Management*, 333: 76–87.
- Allen, C.D.** 2009. Climate-induced forest dieback: an escalating global phenomenon. *Unasylva*, 231/232: 43–49.
- Breed, M.F., Stead, M.G., Ottewell, K.M., Gardner, M.G. & Lowe, A.J.** 2013. Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, 14(1): 1–10.
- Broadhurst, L.M., Jones, T.A., Smith, F.S., North, T. & Guja, L.** 2016. Maximizing seed resources for restoration in an uncertain future. *BioScience*, 66(1): 73–79.
- Franks, S.J., Weber, J.J. & Aitken, S.N.** 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications*, 7(1): 123–139.
- Gaspar, M.J., Velasco, T., Feito, I., Alía, R. & Majada, J.** 2013. Genetic variation of drought tolerance in *Pinus pinaster* at three hierarchical levels: a comparison of induced osmotic stress and field testing. *PLoS one*, 8(11): 79094.
- Hamrick, J.L.** 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management*, 197(1): 323–335.
- Harfouche, A., Meilan, R. & Altman, A.** 2014. Molecular and physiological responses to abiotic stress in forest trees and their relevance to tree improvement. *Tree Physiology*, 34(11): 1181–1198.
- Hartmann, H., Adams, H.D., Anderegg, W.R., Jansen, S. & Zeppel, M.J.** 2015. Research frontiers in drought-induced tree mortality: crossing scales and disciplines. *New Phytologist*, 205(3): 965–969.
- Jump, A.S., Hunt, J.M., Martínez-Izquierdo, J.A. & Penuelas, J.** 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency. *Fagus sylvatica. Molecular Ecology*, 15(11): 3469–3480.
- Koskela, J., Buck, A. & du Cros, E.T., eds.** 2007. *Climate change and forest genetic diversity: implications for sustainable forest management in Europe*. Rome, Bioversity International.
- Kremer, A., Ronce, O., Robledo-Arnuncio, J.J., Guillaume, F., Bohrer, G., Nathan, R., Bridle, J.R., Gomulkiewicz, R., Klein, E.K., Ritland, K. & Kuperinen, A.** 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, 15(4): 378–392.

- Kreyling, J., Buhk, C., Backhaus, S., Hallinger, M., Huber, G., Huber, L., Jentsch, A., Konnert, M., Thiel, D., Wilmking, M. & Beierkuhnlein, C.** 2014. Local adaptations to frost in marginal and central populations of the dominant forest tree *Fagus sylvatica* L. as affected by temperature and extreme drought in common garden experiments. *Ecology and Evolution*, 4(5): 594–605.
- Liepe, K.J., Hamann, A., Smets, P., Fitzpatrick, C.R. & Aitken, S.N.** 2016. Adaptation of lodgepole pine and interior spruce to climate: implications for reforestation in a warming world. *Evolutionary Applications*, 9(2): 409–419.
- Loo, J., Fady, B., Dawson, I., Vinceti, B. & Baldinelli, G.** 2015. Forest genetic resources and climate change. In FAO Commission on Genetic Resources for Food and Agriculture, ed. *Coping with climate change – the roles of genetic resources for food and agriculture*, pp. 41–53. Rome, FAO.
- Montwé, D., Spiecker, H. & Hamann, A.** 2015. Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. *Tree Genetics & Genomes*, 11(2): 1–11.
- Thomas, E., Jalonen, R., Loo, J., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P. & Bozzano, M.** 2014. Genetic considerations in ecosystem restoration using native tree species. *Forest Ecology and Management*, 333: 66–75.
- Walck, J.L., Hidayati, S.N., Dixon, K.W., Thompson, K.E.N. & Poschlod, P.** 2011. Climate change and plant regeneration from seed. *Global Change Biology*, 17(6): 2145–2161.
- Yakovlev, I.A., Lee, Y., Rotter, B., Olsen, J.E., Skrøppa, T., Johnsen, Ø. & Fossdal, C.G.** 2014. Temperature-dependent differential transcriptomes during formation of an epigenetic memory in Norway spruce embryogenesis. *Tree Genetics & Genomes*, 10(2): 355–366.
- Yanchuk, A. & Allard, G.** 2009. Tree improvement programmes for forest health – can they keep pace with climate changes? *Unasylva*, 231-232: 50–56. ♦