Avoiding failure in forest restoration: the importance of genetically diverse and site-matched germplasm

E. Thomas, R. Jalonen, J. Loo and M. Bozzano

The likelihood of success of forest restoration can be improved by choosing genetically diverse forest reproductive material that is well adapted to the planting sites.

Evert Thomas is Associate Scientist with Bioversity International, Cali, Colombia.
Riina Jalonen is Associate Scientist with Bioversity International, Serdang, Malaysia.
Judy Loo is Scientific Domain Leader with Bioversity International, Maccarese, Italy.
Michele Bozzano is Scientist with Bioversity International, Maccarese, Italy.

INTRODUCTION

While the international community and individual countries have committed to restoring hundreds of millions of hectares of degraded forest landscapes,[1] the successes and failures of past restoration efforts remain poorly documented and communicated. This is a missed opportunity to learn from past experiences and to improve practices for better success

rates and more efficient resource use in future restoration projects. Case studies demonstrate that failures may have been much more common than successes (Wuethrich, 2007; Godefroid *et al.*, 2011). The causes of restoration failures can be manifold. One reason that is often overlooked is inadequate consideration of the source and genetic quality of forest reproductive material (FRM) (Godefroid *et al.*, 2011; Le *et al.*, 2012). Genetic diversity is positively related not only to

Above: Nursery seedlings produced for the establishment of a progeny trial with native species from tropical dry forest in Colombia

---

[1] https://www.cbd.int/sp/targets.http://www.un.org/climatechange/summit/wp-content/uploads/sites/2/2014/07/New-York-Declaration-on-Forest-%E2%80%93-Action-Statement-and-Action-Plan.pdf.

The result of restoration of a gold mine spoil in Cáceres, Colombia, 12 years after initiation (same site, before and after). The site was originally planted with diverse seed mixtures of 20 tree species (Moscoso Higuita, 2005) and now contains over 120 different native tree species and diverse wildlife, including jaguars, boa constrictors, sloths and several species of primates. This project has successfully attained certification for several standards such as the Verified Carbon Standard (VCS), Climate, Community and Biodiversity Standard and the gold standard, and it is currently trading verified carbon units (>400kt) on the international carbon market. With this, it became the first VCS project in South America, and the first ever in the world, with over 100 native tree species generating carbon credits (Thomas, 2014)

the fitness[2] of tree populations (Reed and Frankham, 2003; Schaberg *et al*., 2008) but also to wider ecosystem functioning and resilience (Gregorius, 1996; Reusch *et al*., 2005; Sgrò *et al*., 2011). Adequate attention to the genetic quality of FRM is particularly important for forest restoration, including tree-planting activities that aim to ''reinstate autogenic ecological processes by which species populations can self-organize into functional and resilient communities that adapt to changing conditions while at the same time delivering vital ecosystem services'' (Alexander *et al*., 2011).

The origin and genetic diversity of FRM significantly affect the survival, growth, and productivity of trees as well as the adaptive capacity and hence self-sustainability of tree populations (Reed and Frankham, 2003; Schaberg *et al*., 2008). In a meta-analysis of almost 250 plant species reintroductions worldwide, Godefroid *et al*.

(2011) found that knowledge of the genetic diversity of the species introduced, and integrating that knowledge in seed sourcing, significantly enhanced the survival rate from the first year after reintroduction, and that this effect increased over time. The importance of using appropriate germplasm was recently highlighted by the 12th meeting of the Conference of the Parties to the Convention on Biological Diversity, which called for "due attention to both native species and genetic diversity in ecosystem conservation and restoration activities…" (Decision XII/19, 2014).[3]

CONSEQUENCES OF LOW GENETIC DIVERSITY OR INAPPROPRIATE ORIGIN OF FOREST REPRODUCTIVE MATERIAL

Two main considerations in the selection of FRM are crucial for bolstering the resilience of restored forests: planting material should be: (i) well-matched to the (present and predicted future) conditions of the

planting site to ensure adaptedness; and (ii) sufficiently genetically diverse to avoid the adverse effects of inbreeding, provide sufficient genetic variants for natural selection to occur, and enhance the resistance of established populations to acute and chronic stressors, such as pests and diseases, as well as drought and other effects of progressive climate change.

Failure related to the use of poor-quality FRM may lead to high initial mortality, poor growth, susceptibility to biotic and abiotic stressors, and low reproductive success after the trees mature. High initial mortality is often witnessed within the planting or maintenance period of restoration projects and may be dealt with by replanting. However, the success of replanting depends on the underlying causes of mortality and how well these are addressed in further planting efforts. Most other types of failure become apparent later, often long after the project maintenance periods have ended, and are more difficult to mitigate. For example, poor growth or survival because of mismatched FRM or low genetic diversity may become increasingly apparent over decades. Delayed mortality resulting from susceptibility to biotic or abiotic stressors may manifest itself only after certain exceptional events. An example is the case of 30 000 ha of *Pinus pinaster* plantations, which were established in the Landes region of France with planting material from the Iberian

---

[2] For a definition of "fitness", see for example http://www.fao.org/DOcREP/003/X3910E/X3910E09.htm#TopOfPage.

[3] http://www.cbd.int/doc/decisions/cop-12/cop-12-dec-19-en.pdf.

peninsula that was susceptible to frost, and were destroyed during the exceptionally cold winter of 1984/1985 (Timbal *et al.*, 2005).

The diversity of the first generation of trees plays a key role in the success of subsequent natural regeneration at a site. First-generation trees that are established by using FRM from genetically diverse source populations where the reproductive material is collected but from only one or a few genetically diverse mother trees will grow normally. However, many of the planted trees will be full or half siblings, resulting in inbred offspring in the next generation which may lead to reduced fitness (Reed and Frankham, 2003; McKay *et al.*, 2005). The first signs of the deleterious effects of mating among relatives often become apparent when the trees reach reproductive age, with a drop in seed quality and quantity as well as decreased germination and seedling survival rates. In subsequent generations it may jeopardize the long-term viability and resilience of restored forests. For example, significantly reduced growth was observed in inbred second- and third-generation seedlings of *Acacia mangium* as compared to the mother trees that were originally introduced to Sabah (Malaysia) using FRM from Australia in 1967, and which had a very narrow genetic base (Sim, 1984). Inbreeding depression is more commonly expressed in more stressful environments, such as those characterized by the degraded soils found at most restoration sites (Fox and Reed, 2010). In the absence of an influx of new genes (e.g. through natural or human-influenced gene flow), this may lead to cascading effects over generations, increasing the risk of population and ecosystem collapse in the longer term owing to reduced vigour of trees, and a higher vulnerability to pests, pathogens and the effects of climate change. Similar problems occur when planting material is vegetatively propagated and originates from just a few trees.

In spite of these risks, insufficient consideration is given to the selection of appropriate planting material by restoration practitioners around the world (Bozzano *et al.*, 2014). In the future, use of inadequate planting material may be an even more likely consequence of the limited restoration experience of many new actors emerging in response to major international commitments to restoration goals. Avoiding this will require the availability and mainstream use of user-friendly knowledge-based tools and protocols to guide restoration practitioners' choices of species and seed sources. If such tools and protocols are not followed, the choices can be expected to be predominantly opportunistic (i.e. focused on using easily accessible and available planting stock), at least in the short term. A survey of 23 restoration researchers and experts showed that species selection was more frequently based on the availability of planting material than, for example, on the conservation status of the species or their functional traits (Bozzano *et al.*, 2014).

ENSURING THAT FRM IS GENETICALLY DIVERSE

Adaptation to changing site conditions occurs through natural selection. Effective natural selection depends upon: (i) genetic diversity in the traits that influence survival, growth and reproduction; (ii) the heritability of these traits; and (iii) large population sizes. When the intention is to establish self-sustaining forest ecosystems through restoration, it is pivotal that sourcing or collection of FRM is carried out in such a way as to capture a broad diversity in adaptively important traits for the target species. This means collecting seed from sufficiently large populations and from many unrelated mother trees, i.e. a minimum of 30–60 widely spaced trees or more if vegetative propagules are used (Kindt *et al.*, 2006; Basey *et al.*, 2015). Efforts should be made to avoid the successive use of seed collections from planted stands with low genetic diversity (Lengkeek *et al.*, 2005), as this may exacerbate the effects of a narrow genetic base in subsequent populations. Also, where restoration relies mainly on natural regeneration, seed sources near the restoration site must be genetically diverse.

Guidelines for tree seed collection that aims to ensure a minimum level of genetic diversity exist, but appear to be largely unknown or overlooked by restoration practitioners or those who supply germplasm (Bozzano *et al.*, 2014; Godefroid *et al.*, 2011). This is probably partly because their implementation can be both time- and resource-demanding and partly because genetic homogeneity is not immediately visible while its negative effects become so only over time (Rogers and Montalvo, 2004; FAO, 1987; FAO, 2003; Palmberg, 1983).

An additional argument for the use of genetically diverse germplasm is that restored forests may later become seed sources for future restoration activities. Furthermore, if properly designed, restoration efforts offer cost-effective opportunities for conserving native tree species and their genetic variation (Sgrò *et al.*, 2011). This is particularly useful for rare, endemic or endangered species for which the availability of suitable germplasm is often very limited. Maintaining records of the sources of FRM is essential to inform decisions about future collection and management. Such records will also provide valuable information about the adaptability and viability of the original FRM used as the restored forests mature and their fitness can be evaluated (Rogers and Montalvo, 2004; Godefroid *et al.*, 2011; Breed *et al.*, 2013).
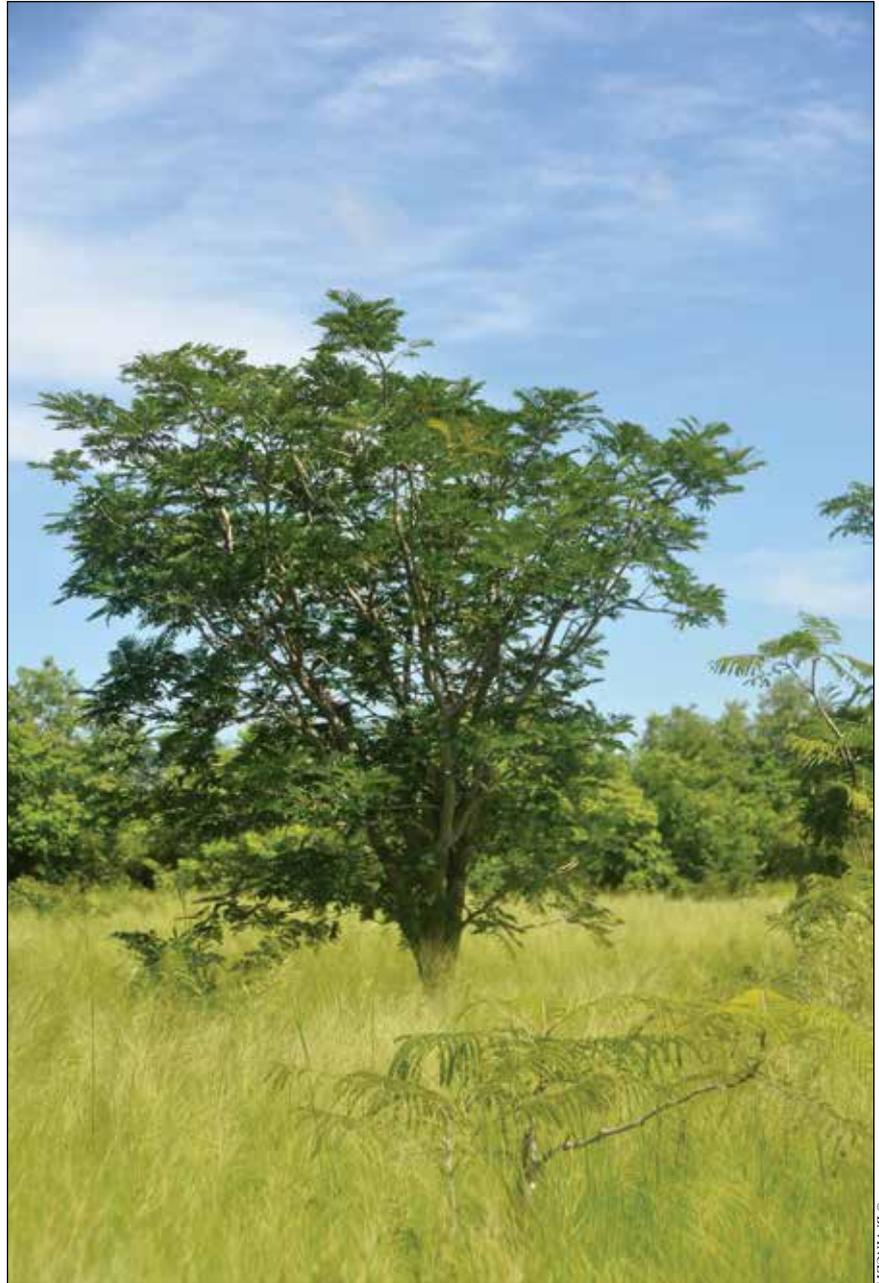
ENSURING ADAPTATION TO PLANTING SITE

Germplasm should not only be genetically diverse but also matched to the current and future conditions of the planting site. There is commonly a preference for planting stock from local sources (McKay *et al.*, 2005; Sgrò *et al.*, 2011; Breed *et al.*, 2013). This is based on the assumption that local tree populations have undergone natural selection, thereby becoming optimally adapted to conditions of a nearby

*Individuals of **Parkia biglobosa** (Jacq.) G.Don (Leguminosae) in a provenance trial established by the National Tree Seed Center of Burkina Faso (CNSF) at the site of Gonsé in 1995. The trial included 15 provenances from across the range of the species. All trees were planted at the same time with planting material of different origin. The tree in the foreground shows signs of maladaptation to the environmental conditions at the planting site*

© B. VINCETI

restoration site, an assumption that is not always correct (McKay *et al*., 2005). Excessive emphasis on "local" germplasm may overlook the fact that geographical proximity to the restoration site is not necessarily the best indicator of the quality or suitability of germplasm. Local adaptation may, for example, be hindered by limited gene flow[4] or genetic drift[5] in small populations. In the degraded soils that often typify restoration sites, conditions may be very different from those under which local tree populations originally developed. Furthermore, environmental mosaics may result in geographically distant sites having similar conditions, while the conditions in nearby sites may be very different.

Ideally, the choice of the most suitable seed sources for a given restoration site is guided by provenance trials, if and when these exist. Provenance trials enhance our understanding of differences in responses by different genotypes grown in a particular environment. This is known as genotype by environment (GxE) interaction. Some genotypes may be very stable across a range of environments while others may perform much better in some environments

than in others. The magnitude and type of GxE influence the distances across which planting materials can safely be moved from their local environments.

Provenance trials can be particularly useful in informing restoration practitioners about the scale and extent of local adaptation in tree species. Although many current provenance trials were not intentionally designed to characterize adaptive traits

of different provenances, survival and growth are always assessed in such trials and these are basic measures of adaptation to the site where a trial is planted (Mátyás, 1994). They can help determine sources of planting material that are adapted to a particular site and the range within which reproductive material of a species can be moved without significant loss of adaptation (ecological tolerance limits).

---

[4] The exchange of genes between populations, usually through pollination and seed dispersal.

[5] A change in allele frequency from one generation to another within a population, due to the sampling of a finite number of genes that is inevitable in all finite-sized populations. The smaller the population, the greater is the genetic drift, with the result that some alleles are lost and genetic diversity is reduced. See for example http://www.bioversityinternational.org/uploads/tx_news/Forest_genetic_resources_conservation_and_management__overview__concepts_and_some_systematic_approaches__Vol._1_1018.pdf

Globally, some 700 tree species are subject to improvement programmes of some level, such as selection and provenance and/or progeny testing (FAO, 2014). While the oldest provenance trials were of temperate species, established both within and outside their natural ranges for industrial plantations, trials have also been established more recently for tropical species, including those that are important for the provision of non-wood forest products. Even if provenance trials do not exist at the time of planting, it is worth investing in their establishment, particularly in light of expected climate change, as they provide information about the adaptedness of the provenances to changing climate conditions over the lifespan of the planted trees. Ideally, provenance trials should cover the range of environments in which a species

Emerging seedlings of the critically endangered tree species Cariniana pyriformis *Miers (Lecythidaceae)*

occurs and where it may be planted. The site conditions in a restoration area are often substantially different from those of the surrounding forests. Degraded sites may be more prone to drought, suffer from nutrient-depleted soil or lack other species that would normally be part of a functioning forest ecosystem. The establishment of future provenance trials should therefore also consider incorporating these factors.

In the absence of provenance trial data, suitability modelling and ecogeographical analyses of the environmental conditions at the planting site, as well as at the possible sites from which germplasm may be obtained, provide an alternative approach for selecting well-matched seed sources. If available, the genetic characterization of potential source populations through the application of molecular markers can provide complementary information on the genetic diversity profiles of these populations, as well as on the degree of genetic differentiation among them (Soldati *et al*.,

2013; Azpilicueta *et al*., 2013). Recent advances in suitability modelling and the increasing availability of ever cheaper genotyping[6] techniques make it possible to better design restoration efforts at the landscape level, not only for matching FRM to restoration sites, but also for optimizing the connectivity of populations (McRae and Beier, 2007).

IMPROVING RESILIENCE TO CLIMATE CHANGE
Climate change will have a strong impact on many restoration sites. Yet currently few restoration practitioners appear to consider climate predictions in their design and implementation (Bozzano *et al*., 2014). Degraded forest sites typically constitute tough environments for seedling establishment and growth. When the climate

---

[6] The characterization of biological populations on the basis of DNA sequences through the use of molecular tools.

© EVERT THOMAS

simultaneously becomes harsher, natural or planted propagules experience even stronger selection pressure. Tree species generally have high genetic variation in adaptive traits, constituting latent adaptive potential which is expressed only when conditions change (Gamache and Payette, 2004; Alfaro *et al.*, 2014). However, in many cases this may not be sufficient to ensure the long-term viability of local tree populations. The introduction of germplasm collected from more distant populations may therefore be necessary.

A growing number of studies recommend the use of seed from mixed sources to anticipate the potential impacts of climate change (Broadhurst *et al.*, 2008; Sgrò *et al.*, 2011; Breed *et al.*, 2013). Decision trees have been developed to select the most appropriate seed-sourcing approach, depending on the evidence and confidence limits surrounding climate distribution modelling, and the knowledge of population genetic and/or environmental differences between populations (Breed *et al.*, 2013; Byrne *et al.*, 2011). If both GxE and expected climate change are known and expected to be low, a mix of germplasm obtained from local healthy tree populations may suffice. In the more usual cases where either GxE or climate change are unknown, *composite provenancing* has been proposed as a strategy to increase the adaptive potential of planting stock (Broadhurst *et al.*, 2008; Sgrò *et al.*, 2011; Breed *et al.*, 2013). *Composite provenancing* aims to simulate natural gene flow dynamics by mixing: (i) a high proportion of material sourced locally from a range of environmental conditions in the same or neighbouring seed zones with (ii) a medium proportion of material that is sourced from intermediate distances and is ecologically matched (e.g. including planting material from warmer rather than cooler environments) and (iii) a low proportion of germplasm from distant populations that are ecologically diverse. For situations where there is a high probability of substantial climate change, but where the GxE interaction is less well known,

an *admixture provenancing* approach has been proposed (Breed *et al.*, 2013). In admixture provenancing, seed collection is focused on capturing a wide selection of genotypes from large populations occurring in various environments, with no spatial bias towards the revegetation site and no regard to gene-flow dynamics (Breed *et al.*, 2013). This is intended to create a large, highly diverse gene pool so that natural selection can "choose" the best-adapted genotypes.

In some cases, habitat conditions are expected to be altered to such an extent by climate change and interacting factors, such as fragmentation due to land-use changes, that deliberate movement of FRM along environmental gradients, beyond the maximum distance of natural dispersal or pollen flow, may be necessary (Aitken *et al.*, 2008; Sgrò *et al.*, 2011). Ideally, translocation decisions should be based on solid field trial data. Provenance transfer based purely on climate distribution modelling is still controversial (Seddon, 2010; Sgrò *et al.*, 2011). This is due to the uncertainties associated with both species distribution models and future climate models (Alfaro *et al.*, 2014). In situations where no provenance trial data are available, the composite or admixture provenancing approaches described above may be more prudent (Breed *et al.*, 2013).

AVAILABILITY AND SUPPLY OF PLANTING MATERIAL

By far the most commonly used planting material for restoration consists of nursery seedlings, partly because this increases the chances of successful establishment (Godefroid *et al.*, 2011). As a consequence, the possibility of using optimal species combinations and germplasm that is both adapted to site conditions and genetically diverse is often limited in practice by what is available in commercial nurseries. Seed collectors and nurseries (private or public) are driven by economic considerations and produce what they expect to sell. Nursery managers often minimize the number of species they grow for reasons that may

relate to the accessibility and availability of seed sources, efforts to simplify management, the risk of unsold production, or the lack of appropriate protocols for additional species (e.g. dormancy breaking) (Lillesø *et al.*, 2011). A solution is to set up nurseries as a part of restoration efforts. This reduces the dependency of restoration practitioners on the vagaries and practicalities of supply from commercial nurseries, but requires adequate training of seed collectors and nursery staff to ensure that good-quality FRM is obtained.

Restoration practitioners who plan to obtain planting material from existing nurseries should communicate early with nursery managers to provide sufficient time for propagation of the desired species and to allow seed collection standards for genetic diversity to be met. Public authorities, for their part, should demand that nurseries and restoration practitioners demonstrate that they have applied due diligence in the collection and production of planting material to be used in restoration projects, which are often financed with public funds. Countries also need to invest more heavily in the establishment of functional seed distribution systems, to ensure the availability of appropriate planting material at any restoration site.

RECOMMENDATIONS
The targets for restoration should not only be quantitative. It is important that they also include qualitative aims to ensure that restored forest landscapes are resilient and self-sustaining. This means that adequate attention needs to be given to the origin and genetic diversity of FRM.

There is an urgent need for the further development, application and mainstreaming of user-friendly guidelines and protocols to assist emerging restoration practitioners with the choice of tree species and sources of FRM

There is also a need for strong political commitment to create a demand and ensure availability of seed from diverse, well-adapted sources of native species through regulatory frameworks and

resource allocations. Publicly funded restoration projects should demand that nurseries apply due diligence with respect to the collection and production of planting material that is best adapted to target planting sites.

It is time for countries, particularly in the tropics, to invest in the establishment of provenance trials with native species across different environmental gradients, as these trials generate the most reliable data on the adaptedness of germplasm to particular sites and for predicting how this may change as a consequence of global warming.

It will be crucial to apply adaptive management by documenting and sharing not only successes but also mistakes and failures in forest and landscape restoration, both to accumulate existing knowledge and to continuously integrate new knowledge as it becomes available.

Acknowledgements

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.

Alexander, S., Aronson, J., Clewell, A., Keenleyside, K., Higgs, E., Martinez, D., Murcia, C. & Nelson, C. 2011. Re-establishing an ecologically healthy relationship between nature and culture: the mission and vision of the Society for Ecological Restoration. *In* SCBD, ed. *Contribution of ecosystem restoration to the objectives of the CBD and a healthy planet for all people. Abstracts of posters presented at the 15th Meeting of the Subsidiary Body on Scientific, Technical and Technological Advice of the Convention on Biological Diversity*, pp. 7–11. Montreal, Canada, SCBD.

Alfaro, R.I., Fady, B., Vendramin, G.G., Dawson, I.K., Fleming, R.A., Saenz-Romero, C., Lindig-Cisneros, R.A., Murdock, T., Vinceti, B., Navarro, C.M., Skrøppa, T., Baldinelli, G., El-Kassaby, Y.A. & Loo, J. 2014. The role of forest genetic resources in responding to biotic and abiotic factors in the context of anthropogenic climate change. *Journal of Forest Ecology and Management*, 333: 76–87.

Azpilicueta, M.M., Gallo, L.A., van Zonneveld, M., Thomas, E., Moreno, C. & Marchelli, P. 2013. Management of *Nothofagus* genetic resources: definition of genetic zones based on molecular data. *Forest Ecology and Management*, 302: 414–424.

Basey, A.C., Fant, J.B. & Kramer, A.T. 2015. Producing native plant materials for restoration: 10 rules to collect and maintain genetic diversity. *Native Plants Journal*, 16: 37–53.

Bozzano, M., Jalonen, R., Thomas, E., Boshier, D., Gallo, L., Cavers, S., Bordács, S., Smith, P. & Loo, J. (eds). 2014. *Genetic considerations in ecosystem restoration using native tree species*. The State of the World's Forest Genetic Resources – Thematic Study. Rome, FAO and Bioversity International.

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: 1–10.

Broadhurst, L.M., Lowe, A., Coates, D.J., Cunningham, S.A., McDonald, M., Vesk, P.A. & Yates, C. 2008. Seed supply for broad-scale restoration: maximising evolutionary potential. *Evolutionary Applications*, 1: 587–597.

Byrne, M., Stone, L. & Millar, M.A. 2011. Assessing genetic risk in revegetation. *Journal of Applied Ecology*, 48: 1365–1373.

FAO. 1987. Information to be provided (to the extent possible) when ordering seeds for experimental purposes. *Forest Genetic Resources Information*, 15 (available at http://www.fao.org/docrep/006/s4009e/ S4009E10.htm#ch10).

FAO. 2003. *Forest reproductive material: an overview*. Forest Genetic Resources Working Paper FGR/72E. Rome (available at http://www.fao.org/docrep/005/AD093E/ AD093E00.HTM).

FAO. 2014. *The State of the World's Forest Genetic Resources*. Rome.

Fox, C.W. & Reed, D.H. 2010. Inbreeding depression increases with environmental stress: an experimental study and meta-analysis. *Evolution*, 65: 246–258.

Gamache, I. & Payette, S. 2004. Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology*, 92: 835–845.

Godefroid, S., Piazza, C., Rossi, G., Buord, S., Stevens, A.-D., Aguraiuja, R., Cowell, C., Weekley, C.W., Vogg, G., Iriondo, J., Johnson, I., Dixon, B., Gordon, D., Magnanon, S., Valentin, B., Bjureke, K., Koopman, R., Vicens, M., Virevair, M. & Vanderborght, T. 2011. How successful are plant species reintroductions? *Biological Conservation*, 144(2): 672–682.

Gregorius, H. 1996. The contribution of the genetics of populations to ecosystem stability. *Silvae Genetica*, 45: 267–271.

Kindt, R., Lilleso, J.P.B., Mbora, A., Muriuki, J., Wambugu, C., Frost, W., Beniest, J., Aithal, A., Awimbo, J., Rao, S. & Holding-Anyonge, C. 2006. *Tree seeds for farmers: a toolkit and reference source.* Nairobi, World Agroforestry Centre (available at: http://www.worldagroforestry.org/sites/default/files/Toolkit.pdf).

Lamb, D. 2012. Forest restoration – the third big silvicultural challenge. *Journal of Tropical Forest Science*, 24: 295–299.

Le, H.D., Smith, C., Herbohn, J. & Harrison, S. 2012. More than just trees: assessing reforestation success in tropical developing countries. *Journal of Rural Studies*, 28: 5–19.

Lengkeek, A., Jaenicke, H. & Dawson, I. 2005. Genetic bottlenecks in agroforestry systems: results of tree nursery surveys in East Africa. *Agroforestry Systems*, 63: 149–155.

Lillesø, J.-P.B., Graudal, L., Moestrup, S., Kjær, E.D., Kindt, R., Mbora, A., Dawson, I., Muriuki, J., Ræbild, A. & Jamnadass, R. 2011. Innovation in input supply systems in smallholder agroforestry: seed sources, supply chains and support systems. *Agroforestry Systems*, 83: 347–359.

Mátyás, C. 1994. Modeling climate change effects with provenance test data. *Tree Physiology*, 14: 797–804.

McKay, J.K., Christian, C.E., Harrison, S. & Rice, K.J. 2005. "How local is local?" A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, 13, 432–440.

McRae, B.H. & Beier, P. 2007. Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences USA*, 104: 19885–19890.

Moscoso Higuita, L. 2005. Reforestation: a natural process. Medellín, Colombia, Editorial Colina.

Palmberg, C. 1983. FAO guidelines for seed ordering. *Forest Genetic Resources Information*, 12 (available at http://www.fao.org/docrep/006/q5987e/Q5987E15.htm#ch15).

Reed, D.H. & Frankham, R. 2003. Correlation between fitness and genetic diversity. *Conservation Biology*, 17: 230–237.

Reusch, T., Ehler, A., Hammerli, A. & Worm, B. 2005. Ecosystem recovery after climatic extremes enhanced by genetic diversity. *Proceedings of the National Academy of Sciences USA*, 102: 2826–2831.

Rogers, D.L. & Montalvo, A.M. 2004. *Genetically appropriate choices for plant materials to maintain biological diversity.* Report to the USDA Forest Service. Rocky Mountain Region, Lakewood, University of California.

Schaberg, P., DeHayes, D., Hawley, G. & Nijensohn, S. 2008. Anthropogenic alterations of genetic diversity within tree populations: implications for forest ecosystem resilience. *Forest Ecology and Management*, 256: 855–862.

Seddon, P. 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology*, 18: 796–802.

Sgrò, C.M., Lowe, A.J. & Hoffmann, A.A. 2011. Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, 4: 326–337.

Sim, B.L. 1984. The genetic base of *Acacia mangium* Willd. in Sabah. In R.D. Barnes & G.L. Gibson, eds. *Provenance and genetic improvement strategies in tropical forest trees*, pp. 597–603. Mutare, Zimbabwe and Oxford, UK, Commonwealth Forestry Institute; Harare, Zimbabwe, Forest Research Centre.

Soldati, M.C., Fornes, L., Van Zonneveld, M., Thomas, E. & Zelener, N. 2013. An assessment of the genetic diversity of *Cedrela balansae* (Meliaceae) in northwest Argentina by means of combined use of SSR and AFLP molecular markers. *Biochemical Systematics and Ecology*, 47: 45–55.

Thomas, E. 2014. Forest devastated by mining is reborn. *Nature*, 511: 155.

Timbal, J., Bonneau, M., Landmann, G., Trouvilliez, J. & Bouhot-Delduc, L. 2005. European non-boreal conifer forests. *In* F.A. Andersson, ed. *Ecosystems of the world (6): Coniferous forests*, pp. 131–162. Amsterdam, Netherlands, Elsevier.

Wuethrich, B. 2007. Biodiversity. Reconstructing Brazil's Atlantic rainforest. *Science*, 315: 1070–1072. ◆