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Santiago C. González-Martínez, Juan José Robledo-Arnuncio, Peter E. Smouse

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# Issues on gene flow and germplasm management

**M. Carmen de Vicente (editor)**



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# III. The consequences and implications of introgression in the conservation of forest trees

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## Introduction

‘Introgression’ is defined as “...the permanent incorporation of genes from one differentiated population into another” (Anderson 1949; Rhymer and Simberloff 1996). It is an important evolutionary process in plants (Rieseberg and Wendel 1993) that may operate at either the species or subspecific (population) level. Its potential effects include changes of genetic variation and the appearance of novel adaptations (Abbott et al. 2003).

Introgression is a long process, involving many steps and several generations of genetic segregation (Stewart et al. 2003). Evaluation of the precise biological significance of natural introgression is difficult because, for example, the relationship between spontaneous hybridization (a first step for natural introgression) and long-term local adaptation is still largely unknown (Barton 2001). Compounding the difficulties are the consequences of introgression derived from planting exotic seed sources or species (i.e. human-mediated introgression), including those from genetically modified organisms (GMOs). These consequences require additional economic, aesthetic, philosophical and political considerations.

A broad spectrum of opinion exists on introgression, ranging from the view that it poses a serious threat to the genetic integrity of plant genetic resources (e.g. Rhymer and Simberloff 1996) to the viewpoint that genetic engineering could be part of the conservation effort itself by introducing new genes into native plant populations (e.g. Adams et al. 2002).

Generalizations are difficult, and any objective appraisal of the implications of introgression requires a case-by-case analysis. We intend to provide a comprehensive general overview of the role of human-mediated introgression in the particular context of the conservation of forest tree species.

## Trees: how do they differ from crops?

Trees are long-lived organisms, generally spread in continuous stretches (forests) that can cover hundreds or thousands of hectares. They represent the dominant life form in many ecosystems. Forests, even those that are periodically harvested, are best viewed as multi-purpose ecosystems and not only as crops. Societal perception of the natural aesthetic value of ‘the forest’ highlights the list of non-economic ecological values attributed to large forested expanses; however, the overriding ecological imperative is to simultaneously preserve local adaptation to the environment and the evolutionary potential, i.e. the genetic variability, of the resident native species.

As yet, most forest-tree species have not been subjected to consistent domestication or plant breeding efforts. Any serious efforts have been restricted to only a few fast-growing and easy-to-propagate species (Campbell et al. 2003, Appendix). Until about 50 years ago, most domestication efforts focused on choosing the right seed source for different localities. For a few heavily used species, breeding concentrated on the selection and establishment of superior trees in seed orchards. The use of tools from biotechnology is expected to accelerate the domestication of forest trees in the near future (Campbell et al. 2003), thus heightening our interest in conserving native germplasm and the adaptive variation it carries.

The characteristics of the life history and reproductive system can play major roles in determining specific patterns of introgression in trees. First, trees have a long life span and many woody perennials are able to propagate vegetatively. These factors extend the time scale over which any potential introgression can be expected to operate in tree populations, making the assessment of its long-term effects difficult. Recurrent gene flow over several reproductive cycles, from the crop into the native species, may be sufficient to overwhelm any slight fitness disadvantages of the hybrid or exotic seed (Haldane 1931).

Second, trees outcross considerably more than annual crops (Barrett 1998). Many plant taxa with higher frequencies of interspecific introgression are outcrossing perennials (Ellstrand et al. 1996). In plants, gene flow is a complex process; it involves propagule dispersal and subsequent interbreeding with individuals in the recipient population. In general, successful gene flow into native populations via pollen from gardens and roadside ornamentals, from restoration and commercial plantations or even from transgenic tree plantations into native forests is likely to initiate introgression. Because tree plantations of exotic or 'improved material' are often located in close proximity to native stocks, opportunities for introgression involving forest trees are frequent.

Forest-tree genera include major crop species such as pine (*Pinus* L.), spruce (*Picea* A. Dietrich), fir (*Abies* Miller), oak (*Quercus* L.), eucalyptus (*Eucalyptus* L'Hérit.) and poplar (*Populus* L.); widespread horticultural genera that include major crop species are junipers (*Juniperus* L.) and cypresses (*Cupressus* L.) and fruit crops. Most of these genera hybridize naturally with wild congeners, creating a steady supply of genetic novelty on which evolutionary processes can operate. Also, over the last 50 years tree breeders have developed highly successful artificial hybrids, for example, *Pinus caribaea* var. *hondurensis* (Sénécl) Barrett et Golfari  $\times$  *P. elliottii* Engelm. var. *elliottii*, *P. rigida* Mill.  $\times$  *P. taeda* L., *Castanea crenata* Siebold & Zucc.  $\times$  *C. sativa* L. These hybrids frequently involved allopatric species, as in the example of *Populus*  $\times$  *euramericana*, using North American *P. deltoides* Bartram ex Marshall and European *P. nigra* L.

New knowledge on tree genomes is expected to promote, in the decades ahead, the domestication of forest trees to the level of herbaceous crops, for instance, through the commercial use of transgenic trees (Campbell et al. 2003). This will increase interest in conserving native germplasm and the adaptive variation it harbours.

## Human-mediated introgression: risks and consequences

The occurrence of introgression into native forests may have ecosystem-wide effects. For example, hybridization in eucalypts affects the abundance of associated herbivorous insects and pathogenic fungi (Whitham et al. 1994), potentially affecting higher trophic levels.

Global changes in genetic diversity can also take place, depending on the levels of allelic diversity in the exotic plantations and the native populations.

Introgression may also have important adaptive consequences for single local populations. On the one hand, reduced adaptation to local conditions can arise because of gene immigration from distant populations (i.e. 'migrational load'). On the other hand, introgression can both

increase the genetic variability available for the evolution of adaptation in marginal populations (the 'rescue effect') and reduce the deleterious effects of inbreeding in small populations (Lenormand 2002).

### Interspecific hybridization

One type of human-mediated introgression derives from the possibility of hybridization with related species that have been planted beyond the range of their original distribution. Simulation analysis has shown that, for high levels of introgression to occur between two hybridizing populations, there must be high levels of interfertility and limited immigration of pure individuals from nearby populations of one or the other parent species into the hybrid zone (Ferdy and Austerlitz 2002). The same study suggests that when interfertility is moderate, relative to immigration from the monospecific, an initial population size difference between the two species will ultimately result in the probable extinction of the rarer species. It can be expected, however, that when selection pressure against (or in favour of) the hybrids is strong, the process of introgression will be delayed (or enhanced) substantially.

The risk of hybridization and rate of introgression with exotic species also depend on the taxonomic distance between the species involved. In *Eucalyptus*, for instance, Potts et al. (2003) found 0.03% to 3.90% of native forests were first generation ( $F_1$ ) hybrids. The potential for hybridization and the viability of  $F_1$  hybrids was higher among species belonging to the same section of the genus. However, despite the scarcity of crosses between species of greater taxonomic divergence, their impact on native genepools is potentially greater than that produced by crosses between less divergent species. For example, introgression of genes from the exotic *Populus deltoides* into the European black poplar (*P. nigra*), caused by gene flow from cultivated hybrid poplars (*Populus* × *euramericana*), is considered a major threat to the native species, even though estimates of introgression levels are low (<5%) (van Dam and Bordács 2002; Storme et al. 2004).

Other concerns regarding tree species artificially moved beyond their original locations are (1) the fact that allopatric species may lack barriers to hybridization, which would make cross-fertilization easier when the two species are artificially brought together (Potts et al. 2001); and (2) the fact that hybrids produced via advanced reproductive technology (e.g. the use of pollen solvents for pollen extraction) can circumvent natural barriers to interbreeding, allowing backcrosses to the parental species. Thus, widespread planting of exotic species or artificial hybrids might, when they hybridize with local stocks, deeply affect native populations and, in some cases, lead to the assimilation of the native stock by the exotic.

### Exchange among seed sources or provenances

At the intraspecific scale, reproductive barriers with local conspecific populations are not expected and, as a consequence, a high level of genetic exchange exists. The global impact of seed transfer varies according to the origin of the material transplanted, the destination environment and the local population size (Figure 2 in Lefèvre 2004).

Lack of domestication in many tree species implies that the only possible breeding of these trees is done by selection among available seed sources, which, in some cases, involves the movement of plant material over large geographic distances. Long-distance transplantations may be significant because variation in adaptive traits among seed sources may be substantial, as in the example of the Mediterranean pine (Alía et al. 1999). Consequently, valuable adaptive traits and/or gene complexes developed in a particular local environment may become diluted or eventually lost through admixture with commercial exotic seed sources.

An interesting case is provided by the Scots pine. *Pinus sylvestris* var. *nevadensis* H. Christ is a relict variety of this widespread species. It is found only in the Sierra Nevada National Park



(Spain), which lies at the southernmost extremity of the pine's range. The entire population of the relict variety is found as scattered stands over an area of about 120 hectares. This area is surrounded by plantations of Scots pine of unknown origin (about 18 000 ha) that show clear divergence from the native local stock, according to molecular marker studies by J.J. Robledo-Arnuncio (unpublished data).

Because both mtDNA (Sinclair et al. 1999) and quantitative growth studies (Alía et al. 2001) have shown the uniqueness of *P. sylvestris* var. *nevadensis*, introgression from the exotic conspecifics may result in the loss of genetic variation of potentially high local ecological value. We are currently assessing the actual risk of introgression, testing whether effective pollen migration from the plantations into the relict population is taking place and whether the resulting progeny are successfully establishing and backcrossing with the local trees.

## Transgenic movements

In the last decade, serious concerns have arisen regarding the use of biotechnological tools. These tools could lead to the production of genetically modified trees for a wide range of traits such as insect and herbicide resistance, lignin composition and content, salinity and drought tolerance and reproductive sterility (Coventry 2001; Campbell et al. 2003). Introgression of neutral transgenes into native populations is probably not important, but major risk is associated with introducing transgenes with significant fitness effects such as insect resistance (e.g. poplar or spruce engineered to produce Bt toxins) or herbicide tolerance (e.g. reduced sensitivity to glyphosate).

Risk assessment studies of the impact of gene flow from transgenic trees into native poplar stands, using the Simulation of Transgene Effects in a Variable Environment (STEVE) model (DiFazio 2002), showed low neutral transgene flow (about 1.4%) over 25 years. The flow, however, became significant over 100 years (9.50%), with continuous increase over time for an insect-resistance transgene conferring growth benefits in the wild.

Because of the potential for widespread escape of transgenes into natural forests and the difficulty of assessing their long-term evolutionary consequences, several authors have suggested the development of male sterility in transgenic trees as an advisable prerequisite for their commercial use (Potts et al. 2001 and references cited therein). Male sterility is not sufficient, however, because transgenic plants can serve as seed parents, receiving pollen from the natural population and subsequently dispersing hybrid seeds (carrying both the transgene and the male-sterility gene) into wild populations. Moreover, male sterility would not remove the other risks associated with transgenic releases. For example, in trees engineered for pest resistance, strong selective pressures may be exerted on pest populations, thus fostering the evolution of genetic resistance in the pest to those same chemicals in the transgenic tree.

## Introgression and management strategies for the genetic reserves of forest trees

The conservation of local adaptive variation and interest in the preservation of local genetic identity of forest tree populations (frequently through the establishment of genetic reserves) are recent developments, dating back only a few decades. In contrast, germplasm movements and tree breeding have been documented from much earlier times; examples are the massive propagation across western Europe of an English elm clone by the Romans (Gil et al. 2004) and the successful introduction of *Pinus radiata* D. Don into Australia in the 1850s. For most forest trees, however, a complex mosaic of native populations is commonly found, including

forests proposed as *in situ* conservation areas, and plantations of exotic seed sources (often of unknown origin) or even exotic species.

Although our knowledge of the ultimate evolutionary consequences of introgression in the wild is limited, preventing introgression of exotic genes into genetic reserves may well be an appropriate measure to fulfil a customary objective, which is to preserve the natural evolutionary processes in the local ecosystem. In particular cases, however, the introduction of novel genes into genetic reserves, in the form of individuals from other locations, may be required to preserve the viability of small inbred populations. Empirical evidence exists to support the assertion that this action may increase the fitness of endangered plant populations (Heschel and Paige 1995; Richards 2000).

In other cases, the viability of the endemic species may be severely threatened by introgression. A classic example, reported by Frankham et al. (2002), is the Catalina Island mountain-mahogany (*Cercocarpus traskiae* Eastw.), a small endangered tree from Catalina Island (California, USA). Hybridization with a closely related species (*C. betuloides* Nutt.) affected about 40% of the remaining trees so that, by 1996, only 11 mature individuals existed from a population of 40.

Management strategies to limit gene flow into genetic reserves of forest trees involve one or more of the following actions (Adams and Burczyk 2000): (1) controlling the location, size and isolation of the reserves; (2) maximizing pollen production within reserves, relative to surrounding stands; and (3) controlling mating within the reserve. Particular attention is needed to design conservation units sufficiently large and isolated from genetic pollution sources.

Most authors suggest isolation distances from exotic sources of pollen of about 1000 m (Potts et al. 2001 and references cited therein). Geographic isolation is probably insufficient for many cases, and the use of guard rows of inert genotypes or nonhybridizing species is advisable. For example, for the European black poplar large differences in introgression levels exist, depending on the presence of *P. nigra* males competing as pollen donors with the exotic hybrid *Populus × euramericana* (van Dam and Bordács 2002; Vanden Broeck et al. 2004). Establishing rows of male *P. nigra* trees surrounding hybrid poplar plantations might reduce the impact of the hybrids on native stands.

A very effective and feasible strategy to preserve the long-term genetic integrity of a population from undesirable introgression is to reinforce recruitment from the local (pure) forest, for example by planting offspring obtained by artificial crossing of pure individuals. This strategy can be more easily accomplished than removing hybrids or preventing hybridization (Ferdy and Austerlitz 2002).

Phenological differences among seed sources can also constitute a significant barrier to gene interchange. In fact, Burczyk et al. (2002), examining a *Eucalyptus regnans* F. Muell. seed orchard that included two different seed sources (Tasmania and Victoria, Australia), found crosses between trees from the same origin to be three times more frequent than between trees with different origins, primarily because of phenological differences (but see Chuine et al. 2000). Because timing and intensity of flowering seem to be under genetic control (el-Kassaby and Park 1993; Farmer 1993), deployment of plant material secondarily selected for delayed onset, different phenology, low flowering rate or even sterility may also help reduce genetic pollution of genetic reserves by commercial plantations.

## Conclusions

Forest trees are long-lived, largely undomesticated organisms that generally grow in wild multi-purpose ecosystems. Introgression is a natural process of great importance to plant species for creating novel and valuable variation. However, many effects are also potentially negative, especially when exotic species or transgenics are involved. A case-by-case analysis is therefore

necessary. Introgression in forest trees can be assessed at different levels of increasing potential impact: gene transfer among seed sources, interspecific hybridization and, most relevant, transfer from transgenic tree plantations.

We identified two major risks: (1) that associated with the introduction of transgenes with significant fitness effects; and (2) hybridization with exotic species or with exotic conspecifics when native local stocks have low effective population sizes. We also described methods to prevent introgression in genetic reserves.

Notwithstanding the available knowledge, the process of introgression in forest trees is still poorly understood and further research is urgently needed. Research priorities should include (1) the study of the precise spatial extent of pollen and seed flow, particularly the role of long-distance dispersal events in the dynamics of introgression; (2) differences in fitness of native and introgressed stocks, under both controlled and field experimental conditions; (3) risks of introgression into native populations of major tree crops, including those targeted for gene modification; and (4) the impact of human-mediated introgression on biodiversity at the ecosystem level.

## References

- Abbott RJ, James JK, Milne RI and Gillies ACM. 2003. Plant introductions, hybridization and gene flow. *Philos. Trans. Roy. Soc. Lond. Series B* 358:1123–1132.
- Adams JM, Piovesan G, Strauss S and Brown S. 2002. The case for genetic engineering of native and landscape trees against introduced pests and diseases. *Conservation Biology* 16:874–879.
- Adams WT and Burczyk J. 2000. Magnitude and implications of gene flow in conservation reserves. *In* Forest conservation genetics, principles and practice. (A. Young, D. Boshier and T. Boyle, eds.). Commonwealth Scientific and Industrial Research Organisation (CSIRO), Collingwood, Victoria, Australia. pp. 215–224
- Alía R, Galera R, Martín S, Agúndez D, de Miguel J and Iglesias S. 1999. Mejora genética y masas productoras de semilla de los pinares españoles. Monografías del INIA: Forestal num. 1. Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA), Madrid, Spain.
- Alía R, Notivol E and Moro J. 2001. Genetic variability of Spanish provenances of Scots pine (*Pinus sylvestris* L.): growth traits and survival. *Silva Fennica* 35:27–38.
- Anderson E. 1949. Introgressive hybridization. John Wiley & Sons, New York, USA.
- Barrett SCH. 1998. The evolution of mating strategies in flowering plants. *Trends in Plant Science* 3:335–341.
- Barton NH. 2001. The evolutionary consequences of gene flow and local adaptation: future approaches. *In* Dispersal (J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols, eds.). Oxford University Press, New York, USA. pp. 329–340
- Burczyk J, Adams WT, Moran GF and Griffin AR. 2002. Complex patterns of mating revealed in a *Eucalyptus regnans* seed orchard using allozyme markers and the neighborhood model. *Molecular Ecology* 11:2379–2391.
- Campbell MM, Brunner AM, Jones HM and Strauss SH. 2003. Forestry's fertile crescent: the application of biotechnology to forest trees. *Plant Biotechnology Journal* 1:141–154.
- Chuine I, Belmonte J and Mignot A, 2000. A modeling analysis of the genetic variation of phenology between tree populations. *Journal of Ecology* 88:561–570.
- Coventry P. 2001. Forest certification and genetic engineered trees: will the two ever be compatible? Occasional Paper 53. Oxford Forestry Institute, UK.
- DiFazio SP. 2002. Measuring and modelling gene flow from hybrid poplar plantations: implications for transgenic risk assessment. PhD diss., Oregon State University, Corvallis, OR, USA.

- El-Kassaby YA and Park YS. 1993. Genetic variation and correlation in growth, biomass and phenology of Douglas-fir diallel progeny at different spacings. *Silvae Genetics* 42:289–297.
- Ellstrand NC, Whitkus R and Rieseberg LH. 1996. Distribution of spontaneous plant hybrids. *Proceedings of the National Academy of Sciences USA* 93:5090–5093.
- Farmer RE. 1993. Latitudinal variation in height and phenology of balsam poplar. *Silvae Genetics* 42:148–152.
- Ferdy JB and Austerlitz F. 2002. Extinction and introgression in a community of partially cross-fertile plant species. *American Naturalist* 160:74–86.
- Frankham R, Ballou JD and Briscoe DA. 2002. *Introduction to conservation genetics*. Cambridge University Press, UK.
- Gil L, Fuentes-Utrilla P, Soto A, Cervera MT and Collada C. 2004. English elm is a 2,000-year-old Roman clone. *Nature* 431:1053.
- Haldane JBS. 1931. A mathematical theory of natural selection, VI: Isolation. *Trans. Cambridge Philos. Soc.* 26:220–230.
- Heschel MS and Paige KN. 1995. Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). *Conservation Biology* 9:126–133.
- Lefèvre F. 2004. Human impacts on forest genetic resources in the temperate zone: an updated review. *Forest Ecology Management* 197:257–271.
- Lenormand T. 2002. Gene flow and the limits to natural selection. *Trends in Ecology and Evolution* 17:183–189.
- Potts BM, Barbour RC and Hingston AB. 2001. The risk of genetic pollution from farm forestry using eucalypt species and hybrids. Rural Industries Research and Development Corporation, Barton, ACT, Australia.
- Potts BM, Barbour RC, Hingston AB and Vaillancourt RE. 2003. Genetic pollution of native eucalypt gene pools—identifying the risks. *American Journal of Botany* 51:1–25.
- Rhymer JM and D Simberloff. 1996. Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics* 27:83–109.
- Richards CM. 2000. Inbreeding depression and genetic rescue in a plant metapopulation. *American Naturalist* 155:383–394.
- Rieseberg LH and Wendel HF. 1993. Introgression and its consequences in plants. *In* *Hybrid zones and the evolutionary process* (R.G. Harrison, ed.). Oxford University Press, New York, USA. pp. 70–109
- Sinclair WT, Morman JD and Ennos RA. 1999. The postglacial history of Scots pine (*Pinus sylvestris* L.) in western Europe: evidence from mitochondrial DNA variation. *Molecular Ecology* 8:83–88.
- Stewart CN, Halfhill MD and Warwick SI. 2003. Transgene introgression from genetically modified crops to their wild relatives. *National Review of Genetics* 4:806–817.
- Storme V, Vanden Broeck A, Ivens B, Halfmaerten D, Van Slycken J and 22 others. 2004. *Ex situ* conservation of black poplar in Europe: genetic diversity in nine gene bank collections and their value for nature development. *Theoretical and Applied Genetics* 108:969–981.
- Van Dam BC and Bordács S (eds.). 2002. *Genetic diversity in river populations of European black poplar; proceedings of an international symposium*. Csiszár Nyomda, Budapest, Hungary.
- Vanden Broeck A, Storme V, Cottrell JE, Boerjan W, Van Bockstaele E, Quataert P and van Slycken J. 2004. Gene flow between cultivated poplars and native black poplar (*Populus nigra* L.): a case study along the river Meuse on the Dutch-Belgian border. *Forest Ecology Management* 197:307–310.
- Whitham TG, Morrow PA and Potts BM. 1994. Plant hybrid zones as centers of biodiversity: the herbivore community of two endemic Tasmanian eucalypts. *Oecologia* 97:481–490.



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