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European Forest Genetic Resources Programme (EUFORGEN)

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IPGRI
Via dei Tre Denari, 472/a
00057 Maccarese
Rome
Italy

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Summary

This Technical Bulletin aims to contribute information and provide guidance for the *in situ* conservation and management of European black poplar (*Populus nigra*). It is the result of the collaborative activities of European countries within the *Populus nigra* Network of the European Forest Genetic Resources Programme (EUFORGEN).

P. nigra is a typical pioneer tree species of the riparian forest ecosystem. Therefore, the *in situ* gene conservation strategies and methods developed for other forest tree species are not always suitable. In fact, successful *in situ* conservation strategies for black poplar need to consider the current status and management of existing populations as well as the physical dynamics of the natural habitat formed by the river. Furthermore, conservation relies heavily on the potential to restore entire floodplain ecosystems, as well as the development of appropriate strategies for the management of restored sites. These factors not only determine the objectives of designated *in situ* conservation units, but also the methods and costs of the approach that is ultimately adopted. The flow chart in Figure 1 is intended to assist in the selection of the most appropriate type of *in situ* conservation strategy for each given situation. As black poplar naturally forms metapopulations rather than small, isolated stands, *in situ* conservation activities should not consider local sites or conservation units in isolation but should rather consider them as part of the complete network of inter-linked local populations. It is proposed that a network of natural and managed *in situ* conservation units be established, covering the most important genetic resources of black poplar throughout the distribution area.

Black poplar is heavily dependant on the hydrological conditions of the riverside environment for its regeneration. For example, flood disturbances create ideal microsites for regeneration from seed. At the same time, the risk presented by flood disturbances, especially to the youngest cohorts, is to some extent avoided through the adoption of multiple regeneration strategies. The different regeneration strategies of the species are discussed and concrete measures are proposed to promote the survival of germinants and the balanced growth of seedlings. Knowledge of the timing and duration of seed release of a *P. nigra* population, for instance, will confer a distinct advantage in the successful *in situ* conservation at those sites where there is a lack of suitable microsites for natural regeneration. In these situations, it is advisable to intervene and manage the riparian area in such a way as to benefit seedling establishment, just prior to the period of maximum seed release. In those cases where it is not possible to introduce high flows, mechanical disturbance of the substrate will be necessary, followed by local flooding and regulation of water table levels. Full sunlight conditions are also critical for regeneration as they allow seedlings to achieve maximum

growth rates and attain sizes that will minimize their vulnerability to either drought stress or flooding.

As regeneration of *P. nigra* relies on a combination of ecosystem disturbance and migration events, restoration projects are required to create the suitable ecological conditions for seedling establishment. For situations where adult seeding populations are not intact, theoretical approaches to determining minimum viable population sizes in restoration plantings, and their practical consequences, are also outlined. It should be noted that for *P. nigra* numbers given refer to clones, this is in reference to clones, and not individual trees since populations sometimes comprise considerably fewer clones than trees. It is argued that the most effective way to counter genetic risks in ecological restoration projects is to allow for migration, i.e. the exchange of pollen and seed with neighbouring populations. A higher number of clones provides a safeguard against unwanted effects and the highest possible number of clones should be used for planting in each given area. On the other hand, if the number of clones is limited, but plenty of space available, planting many trees of each clone will minimize the risk of losing a clone altogether. Repeated plantings at 10-year intervals would mimic natural processes that produce patchworks of even-aged cohorts. Recommendations on type, origin and mixture of genetic material to be used in restoration plantings are provided.

A set of ecological, demographic, and genetic indicators to monitor and evaluate gene conservation is proposed, with particular emphasis on two principal types of conservation strategies: natural *in situ* conservation units and managed *in situ* conservation units (Table 5). These indicators will be used to evaluate the impact of management practices on *P. nigra* diversity. All the indicators proposed are considered as realistic and practical, although they might require different technical capacities. Indicators are informative through their instant value, but most of them may also change over time and these changes are also informative: a 5-year period of re-evaluation can be recommended in order to adjust management practices.

Contact details of authors

Nadia Barsoum
Department of Geography
University of Cambridge
Downing Site
Cambridge CB2 3EN
United Kingdom
E-mail: nb204@cus.cam.ac.uk

Berthold Heinze
Institute of Forest Genetics
Federal Forest Research Centre
Hauptstrasse 7
1140 Vienna
Austria
E-mail:
berthold.heinze@fbva.bmlf.gv.at

Davorin Kajba
Faculty of Forestry
Svetosimunska 25
10000 Zagreb
Croatia
E-mail: davorin.kajba@zg.tel.hr

François Lefèvre
Unité de recherches forestières
méditerranéennes, INRA
Avenue A. Vivaldi
84000 Avignon
France
E-mail: lefevre@avignon.inra.fr

Peter Rotach
Department of Forest Sciences
Chair of Silviculture
Swiss Federal Institute of
Technology
Rämistrasse 101
8092 Zürich
Switzerland
E-mail: rotach@fowi.ethz.ch

Jozef Turok
Regional Office for Europe
International Plant Genetic
Resources
Institute
Via dei Tre Denari, 472a
00057 Maccarese (Fiumicino)
Rome, Italy
E-mail: j.turok@cgiar.org

Sven M.G. de Vries
ALTERRA Green World Research
PO BOX 47
6700 AA Wageningen
The Netherlands
E-mail:
s.m.g.devries@alterra.wag-ur.nl

Introduction

***Sven M.G. de Vries*[1] *and Jozef Turok*[2]**

[1] *ALTERRA Green World Research, Wageningen, the Netherlands*

[2] *International Plant Genetic Resources Institute, Rome, Italy*

A young cohort (8-12 years old) in a quiet derivation of the river Loire (central France).

Populus nigra L., the European Black poplar, has a wide distribution area, from the Mediterranean in the south to 64° latitude in the north, and from Ireland and the British Isles to western Asia. It is a principal pioneer tree species of floodplain ecosystems. Being strictly heliophilous it forms metapopulations by colonizing open areas through seeds, stems fragments and sprouting from the roots and stems of damaged plants (Zsuffa 1974, Herpka 1986). *P. nigra* is characterized by a great diversity of population types, from isolated trees to large pure or mixed stands. The species is dioecious and anemophilous. Depending on the local circumstances, seeds have a relatively short viability (Muller and Teissier du Cros 1982), they are disseminated through wind and water, and need very specific water-soil conditions for germination. Although seed yields on mature trees are impressive, regeneration is generally poor within old established stands and consequently the riparian forest naturally evolves towards hardwood formations (Barsoum, this volume).

Populations of *P. nigra* face severe threats. Three main factors have been recognized in Europe (Lefèvre *et al.* 1998). The first one is the alteration of riparian ecosystems throughout the species' distribution area. Agriculture and urbanization of floodplain areas have displaced native poplar stands while other human activities including regulation of floods through hydraulic engineering practices have favoured later successional hardwood forests over poplar stands in the remaining wild areas. Second, faster growing hybrid poplars have been planted to replace the autochthonous black poplar resources or they have just been removed due to overexploitation. Finally, there is the potential threat of introgression from cultivated poplars such as the male clone 'Italica', distributed all over continental Europe (Cagelli and Lefèvre 1995).

Populus nigra is predominantly used as a parent pool in breeding programmes in many parts of the world, sometimes as a pure species, but mostly as a parent for Euramerican hybrids, providing adaptive properties for various soil and climate conditions, rooting ability, high resistance to *Xanthomonas populi,* fair resistance to *Marssonina brunnea* and to poplar mosaic virus (Cagelli and Lefèvre 1995). In fact, poplar breeders initiated genetic conservation of black poplar since the 1950s, and breeding institutes in many European countries have carried out substantial work for *ex situ* conservation of genetic diversity.

The interest to strengthen collaboration among national activities and programmes specifically addressing gene conservation of this species was affirmed by signatory countries of the Strasbourg Ministerial Resolution S2 (Conservation of Forest Genetic Resources). In fact, *P. nigra* was selected as one of the four pilot species for collaborative networks within the European Forest Genetic Resources Programme established in 1994.

Unlike many other forest tree species, *P. nigra* lacks a high direct commercial use. However, it has tremendous ecological value in riparian floodplain ecosystems. The high overall biological diversity in floodplains is a result of a high diversity of habitats, the structural complexity of the floodplain environment and frequent, dynamic changes; a mosaic of habitats, varying water levels and frequent disturbances maintain a high diversity of vegetation types and forests of significant horizontal and vertical structural complexity at various stages of development (P. Rotach pers. comm., Naiman *et al.* 1993, Décamps and Tabacchi 1994, Naiman and Décamps 1997). While results of experimental work on the species' ecological requirements, physiology, morphology, reproductive biology, population dynamics and genetic variation are available for significant parts of the distribution area, information on practical experiences with the conservation of genetic resources is still scarce. Also, the scientific knowledge is often not accessible to local forest officers and national or regional authorities responsible for the genetic conservation of forests.

In order for gene conservation programmes to be undertaken efficiently and safely, a substantial knowledge base is required. Even though the level and amount of information available on *P. nigra* is high compared with many other broadleaved trees and conifers, more scientific and practical knowledge is still needed for well-informed decisions to be taken.

Waiting for all scientific uncertainties to be solved would, however, delay taking action for the conservation of valuable, and in many cases severely threatened, genetic resources. Furthermore, a general framework is also important to identify key gaps in research and facilitate the practical implementation of research results. This Technical Bulletin aims to contribute information and provide guidance for the *in situ* conservation and management of *P. nigra.* It results from the collaborative activities of European countries within the EUFORGEN *Populus nigra* Network.

The Network (Lefèvre and de Vries 1997, Lefèvre *et al.* 1998) has emphasized the need for an integrated strategy incorporating *ex situ* and *in situ* conservation of the species. Initially, the collaborative work resulted in a number of joint outputs to facilitate and standardize *ex situ* conservation in European countries, including a database of clones and core collection (Cagelli *et al*. 1999, Vietto 2000), as well as guidelines for field collections (de Vries 1996) and for the storage of seed and pollen (Maestro 1995, Cagelli 1997). However, since 1997 *in situ* conservation strategies have been increasingly on the agenda of the Network. The International Poplar Commission also recommended that a strategy for *in situ* conservation for all *Populus* species be developed without delay (Steenackers 1996). As black poplar populations are highly dependant on the dynamics of natural physical processes in the floodplain ecosystem, *in situ* conservation of genetic diversity concerns both population and ecosystem management practices. Black poplar, indeed, is a model for gene resource conservation in forest ecosystems (Lefèvre *et al*. 2001).

This Bulletin focuses on *in situ* conservation of black poplar and is divided into four chapters. It starts with general considerations and basic strategies; followed by a discussion of the conditions and measures required to promote regeneration of black poplar. This is followed by further discussion of the theoretical and practical aspects of the *in situ* restoration genetics of riparian populations, and finally by an outline of indicators for monitoring the evolution of *P. nigra* genetic diversity.

Because of the unsolved threats to *P. nigra* genetic diversity, and the value for breeding programmes, the importance of international collaboration is becoming more and more apparent, both for exchange of genetic material and exchange of experience. The aim of this Bulletin is, therefore, to also contribute towards raising awareness about the often-neglected task of conserving the genetic resources of our forests.

Adjoined to the four chapters, is a selected bibliography offering a list of references relevant to the genetic resource conservation and management of *P. nigra.* In addition to the literature cited in the Bulletin, the bibliography includes some important published results of research carried out during the past four decades, as well as recent review articles and proceedings of specific meetings. The selected bibliography provides suggestions for further reading, and should not be considered as an exhaustive bibliographical source. A brief glossary of terms used in the Bulletin is also provided. The definitions attempt to facilitate the reading of the text by describing the essence of terms, which are widely used but often have an ambiguous meaning or lack overall acceptance.

We thank all members of the *Populus nigra* Network and the reviewers of the individual chapters for their input to this Bulletin.

General considerations and basic strategies

Peter Rotach

Department of Forest Sciences, Chair of Silviculture, Swiss Federal Institute of Technology, Zürich, Switzerland

The ultimate aim of *in situ* conservation of a species is to maintain a broad genetic diversity so that it can retain its potential to adapt to changes in the environment. Hence, the objective is to use a dynamic approach to conserve genetic diversity rather than to concentrate on the conservation of individual genotypes. A successful *in situ* gene conservation programme must fulfil three basic requirements (Koski *et al.* 1997): (1) regeneration of the population must be assured and the new generation of trees must predominantly result from mating within the conserved population, (2) the number of genotypes in the conserved population must be large enough to include most of the common alleles, and (3) the network of conserved stands must be distributed in such a way as to cover the spatial genetic variation present in the species.

European black poplar (*Populus nigra* L.) is a typical pioneer tree species of riparian forests. Therefore, the traditional *in situ* conservation methods developed for other tree species (Koski *et al.* 1997, Teissier du Cros and Bilger 1995) are not always suitable. For successful seedling germination and establishment, black poplar requires sites where there are recent deposits of sand and shingle, free of vegetation and with optimal water/soil conditions (see Barsoum, this volume). Such conditions do not exist in mature stands and, therefore, regeneration is restricted to new sites where there are no mature trees.

As a pioneer species, black poplar shows a natural dynamic over space and time. It forms metapopulations of inter-linked local populations that undergo extinction complemented by recolonization of new locations elsewhere within the metapopulation. Natural populations of black poplar are thus characterized by a constant "turnover" and a highly dynamic demography. Likewise, the natural habitat of black poplar needs to be highly dynamic in order to provide a constant supply of suitable sites for recolonization. These are typically found in dynamic floodplains where sediments are periodically turned over during flooding events in localized sections of the floodplain, creating the microsites required for natural regeneration of black poplar. Successful *in situ* conservation strategies consequently need to consider both the nature and management of existing populations as well as the physical dynamics of the natural habitat formed by the river (Peterken and Hughes 1995). Today, successful *in situ* conservation of black poplar in Europe primarily depends on the location and degree of protection afforded to the functional status of its natural habitat. Consequently, genetic, demographic and ecological factors must be considered in order to devise the most appropriate *in situ* conservation strategy for each particular site. Furthermore, conservation strategies for black poplar are highly reliant on the potential of sites for restoration of floodplain ecosystems as well as the development of appropriate strategies for their management. These factors not only determine the objectives of designated *in situ* conservation units, but also the methods and costs of the approach that is ultimately adopted.

Depending on the demographic and ecological situation, five different types of *in situ* conservation strategies can be distinguished:

- natural *in situ* conservation units (reserves);
- managed *in situ* conservation units;
- temporary *in situ* conservation units;
- temporary *pseudo in situ* conservation units;
- artificial *in situ* conservation units (restored sites).

In a strict sense, only the first two represent true *in situ* conservation strategies, as they allow for the dynamic conservation of a broad genepool and contribute to maximizing adaptive potential. Artificial *in situ* conservation units may eventually serve dynamic conservation objectives, provided one of the following conditions prevails. Firstly, the habitat conditions must support periodic or sporadic natural regeneration and the number of introduced, unrelated clones must be sufficient to avoid genetic drift. Alternatively, they may serve as founder populations for new establishments or as sources for gene flow into neighbouring populations. Temporary *in situ* conservation units may make some contribution to dynamic conservation through gene flow and migration during the remaining life expectancy of the individuals, provided that they are part of a network of *in situ* conservation units. Temporary *pseudo in situ* conservation units cannot contribute to dynamic conservation; they merely allow for a static conservation of genotypes during their remaining lifetime.

The choice of the most appropriate *in situ* conservation strategy for a given site is based on demographic and ecological considerations. These are summarized in Table 1. Figure 1 provides a flow chart to assist in the selection of the most appropriate type of *in situ* conservation strategy for any given situation.

Natural *in situ* conservation units are the first priority for dynamic conservation because their demographic and ecological conditions allow for dynamic gene conservation totally controlled by the natural disturbance of the ecosystem. Technical or silvicultural interventions are thus unnecessary. In such situations *P. nigra* and its genepool could be 'self-sustaining' provided that natural physical processes and the population are preserved in their present state. Protection of the unit itself may, however, be insufficient as it might be necessary to protect the entire river system with natural fluctuations in its hydroperiod in order to guarantee floodplain dynamics in the future. In addition, demographic, genetic and ecological conditions need to be carefully monitored over time in order to anticipate and prevent unfavourable developments. Lefèvre and Kajba describe key indicators for this purpose in this volume.

Managed *in situ* conservation units are of lower priority for dynamic conservation. This type of strategy applies to native populations in a state of transition. While the number of flowering individuals is still sufficient for conservation purposes, dynamic evolution of the population is not guaranteed without management, mainly due to changes in habitat conditions. Natural regeneration is no longer assured as a natural process but may be favoured, supported or initiated. This may either be achieved by managing the water regime in such a way that natural disturbance patterns are at least partially or episodically restored, or by technical measures such as removal of weeds and using artificial disturbance measures over a period of several years. Interventions may also be necessary in order to remove unwanted genotypes such as planted hybrid poplars or non-local material. *In situ* conservation in these sites will be successful only if the following conditions prevail: the area and the population are fully protected; all the institutions that are concerned in any way are supportive; a management plan with clear objectives and measures has been established and the development is closely monitored over time so that the management may be continuously adapted to the actual situation.

A small area of *P. nigra* in a landscape of extensive agriculture: river Allier (central France).

In order to meet the third requirement for *in situ* conservation that was stated above, a network of natural and managed *in situ* conservation units, covering the most important genetic resources of black poplar throughout the whole distribution area, needs to be established. Although both types of populations are now rare (mainly due to the loss of suitable habitats or alterations of the riparian ecosystems), they are the key to successful gene conservation of black poplar. Consequently, all suitable natural conservation sites should be designated as *in situ* conservation units, so that they will be protected and carefully monitored. In addition, potential areas in which an active management strategy can restore or support the natural dynamics of both population and habitat should be selected, protected and managed as *in situ* conservation units.

Because black poplar naturally forms metapopulations rather than small, isolated populations, *in situ* conservation activities should not consider local sites or conservation units in isolation but should instead consider them as part of a complete network of inter-linked local populations. Genetic diversity in a pioneer species can only be successfully maintained on the scale of the whole network (metapopulation) since both local extinction and recolonization are natural events in the dynamic demography of this species. Consequently, even populations that are smaller than the minimum viable population size and do not regenerate on the site itself may be very valuable as temporary *in situ* conservation units, provided that they are part of a network. Since pollen and seed of black poplar move over very large distances, even small populations may contribute to dynamic gene conservation through gene flow and migration. They may also serve as founder populations for new establishments of black poplar over rather large distances or as seed sources for reproductive material used for restoration. Temporary *in situ* conservation units should contain at least 40 individuals (Heinze 1998) and hybrids should be absent from the site and its immediate surroundings. Units with less than 40 individuals, which obviously do not contribute to gene exchange with other populations, or which have a high proportion of hybrids in or near the site, are not suitable for dynamic gene conservation. They may, however, serve static conservation purposes (temporary conservation of genotypes *in situ*) or may be valuable from an ecological or aesthetic point of view ("natural monuments"). Since the population size of such units is too low for dynamic gene conservation purposes and since they do not contribute through gene flow or migration, this category of temporary units may be called 'temporary *pseudo in situ* conservation units'.

Artificial *in situ* conservation units contain material of non-natural origin suitable for dynamic gene conservation. Depending on habitat conditions, these artificially created populations may serve various objectives. Ideally, populations should be newly established on sites that have the potential to support episodic natural regeneration. In such conditions, dynamic gene conservation will ultimately be achieved with a minimum of effort and investment. In undisturbed natural habitats of black poplar, restoration will normally not be necessary except in cases where the native population has been destroyed or drastically reduced through overexploitation, or where it has been replaced or "polluted" by hybrids. Restoration of black poplar populations for *in situ* conservation will also be most effective in areas where the floodplain ecosystem has been or will be restored, or where the river is managed to allow episodic flooding. In addition, restoration of artificial populations may also effectively contribute to dynamic conservation if the newly created populations are in genetic contact via pollen and seed transport with other existing *in situ* conservation units. Restored sites may help to bridge current gene flow barriers, linking existing populations.

Heinze and Lefèvre (this volume) provide theoretical considerations together with a practical approach for *in situ* restoration of the riparian populations of black poplar.

In situ conservation strategies need to be carefully selected on the basis of demographic, genetic and ecological conditions. Objectives need to be clearly defined and must be sensibly based on current knowledge since in most cases the implementation of these decisions often implies high costs.

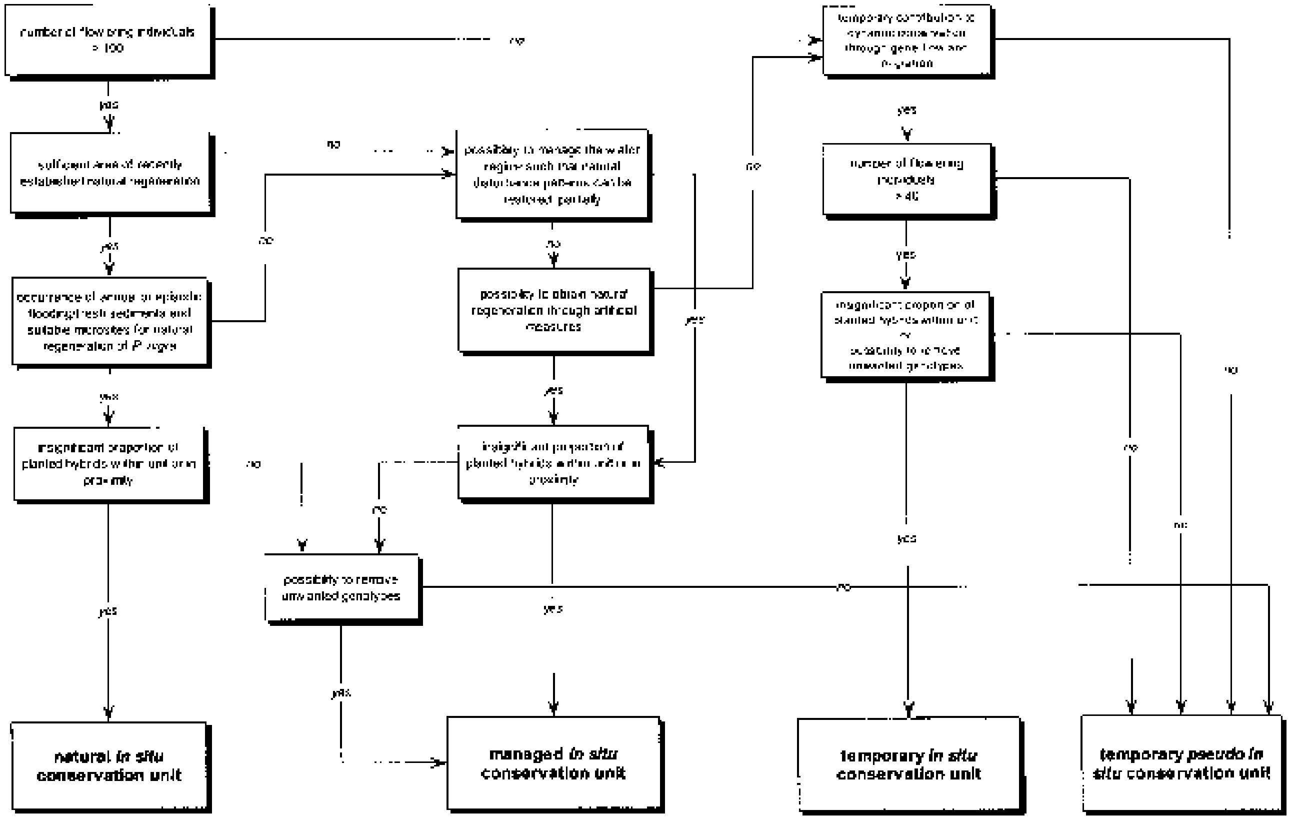
Table 1. The objectives and management principles of the five types of *in situ* conservation units along with a description of the demographic situation and ecological conditions, which prevail at each site.

Conservation strategy	**Natural *in situ* conservation units**	**Managed *in situ* conservation units**	**Temporary *in situ* conservation units**	**Temporary pseudo *in situ* conservation units**	**Artificial *in situ* conservation units (restoration)**
Objectives	dynamic conservation of broad genetic variation and adaptive potential of population over generations	- dynamic conservation of broad genetic variation and adaptive potential of population over generations	- temporary* contribution to dynamic conservation through gene flow and migration into neighbouring populations - temporary* static conservation of existing genotypes	- temporary* static conservation of existing genotypes *in situ*	- dynamic conservation of broad genetic variation and adaptive potential of population over generations or - temporary* contribution to dynamic conservation through gene flow and migration into neighbouring populations
Management	- protection of habitat and population - monitoring development of habitat and population using ecological, demographic and genetic indicators	- protection of habitat and population - management plan with clear objectives - monitoring development of habitat and population using ecological, demographic and genetic indicators	- protection of individuals - silvicultural interventions when necessary - monitoring population	- protection of individuals - silvicultural interventions when necessary - monitoring population	- protection of both habitat and population or population alone - management plan with clear objectives - monitoring development of both habitat and population or population alone using respective indicators
Demographic situation	- number of flowering individuals clearly greater than 100 - abundance of recently established natural regeneration from seed - abundance of juvenile stage (different cohorts - age classes)	- number of flowering individuals clearly greater than 100 - no or insufficient natural regeneration from seed - clearly unbalanced age structure - more or less balanced sex-ratio	- number of flowering individuals at least 40 but smaller than minimum viable population size - linked to other *in situ* conservation units by way of gene flow and migration - no or insufficient natural regeneration	- number of flowering individuals at least 20 - isolated populations where gene exchange with other populations is unlikely - no natural regeneration	- depending on the objective, the ecological situation, the management possibilities and available reproductive material

Conservation strategy	**Natural *in situ* conservation units**	**Managed *in situ* conservation units**	**Temporary *in situ* conservation units**	**Temporary pseudo *in situ* conservation units**	**Artificial *in situ* conservation units (restoration)**
Demographic situation *(continued)*	- more or less balanced sex-ratio - insignificant proportion of planted hybrids within unit or in proximity - contribution by the majority of the trees to seed production	- insignificant proportion of planted hybrids within unit or in proximity. Alternatively: possibility to remove unwanted genotypes	- clearly unbalanced age structure - insignificant proportion of planted hybrids within unit or in proximity. Alternatively: possibility to remove unwanted genotypes		
Ecological conditions	- occurrence of annual or episodic spring flooding - occurrence of natural lateral movement of riverbed - annual or episodic renewal of alluvial sediments and suitable microsites for natural regeneration	- no or insufficient natural dynamic of the river - lack of suitable microsites for natural regeneration - turnover rate of colonizable landforms is too frequent (e.g. channelized reaches) for recruits to reach maturity however either - possibility to manage the water regime such that natural disturbance patterns can be restored partially or - possibility to obtain natural regeneration through artificial measures	- no or insufficient natural dynamic of the river - lack of suitable microsites for natural regeneration - turnover rate of colonizable landforms is too frequent (e.g. channelized reaches) for recruits to reach maturity	- no or insufficient natural dynamic of the river - lack of suitable microsites for natural regeneration - turnover rate of colonizable landforms is too frequent (e.g. channelized reaches) for recruits to reach maturity	- possibility to manage the water regime such that natural disturbance patterns can be partially restored or - possibility to obtain natural regeneration through artificial measures or - no or insufficient natural dynamic of the river and lack of suitable microsites for natural regeneration - turnover rate of colonizable landforms is too frequent (e.g. channelized reaches) for recruits to reach maturity

* for the remaining life expectation

Figure 1. Overview and relationships between the conditions for selection of most appropriate *in situ* conservation strategy.



Regeneration - requirements and promotion measures

Nadia Barsoum

Department of Geography, University of Cambridge, Cambridge, United Kingdom

Introduction

The successful *in situ* conservation of a black poplar (*Populus nigra* L.) population that is capable of not only successful pollination, but also of regenerating within given conservation boundaries, requires an understanding of the regeneration requirements of the species, the hydrological and sedimentological characteristics of the conservation unit and an appreciation of the inextricable link between these. As illustrated in the life cycle flow chart (Figure 2), black poplar is clearly adapted to its riverside environment; it is affected at all stages of its life cycle by hydrological controls and it is, in fact, reliant on them for regeneration. Flood disturbances of particular frequencies and magnitudes create ideal microsites for regeneration from seed and the presence of a water table above critical depths prevents drought stress in each phase of the life cycle. The formidable risk presented by flood disturbances, especially for the youngest cohorts, is to some extent avoided through the adoption of multiple regeneration strategies, which play a compensatory role in the face of unpredictable flooding events. Where flood disturbances are removed from the system and/or natural patterns of river flow and water table levels are altered, the species is no longer capable of following its regeneration pathway. In this chapter a detailed account is given of both sexual and asexual reproduction in black poplar and the specific hydrological and sedimentological conditions that will promote the different regeneration strategies.

Sexual reproduction

Pollination, seed formation and seed dispersal

Black poplar trees reach reproductive age when they are 10-15 years old, but will not begin to produce remarkable quantities of seed until they are 20+ years old (Braatne *et al.* 1996, Stanton and Villar 1996). As a dioecious species, black poplar trees are either male or female. Approximately 1-2 weeks prior to leaf initiation in the early spring (March-April), during the flood peak period along rivers in temperate Europe, male and female trees produce flowers clustered in pendulous catkins. The catkins (< 10 cm long) tend to be borne in the upper tree crown and are reddish-purple in appearance on males and slightly larger and green on females. Wind-dispersed pollen landing on receptive stigma will fertilize ovules within 24 hours of arrival and the subsequent ripening and seed maturation process

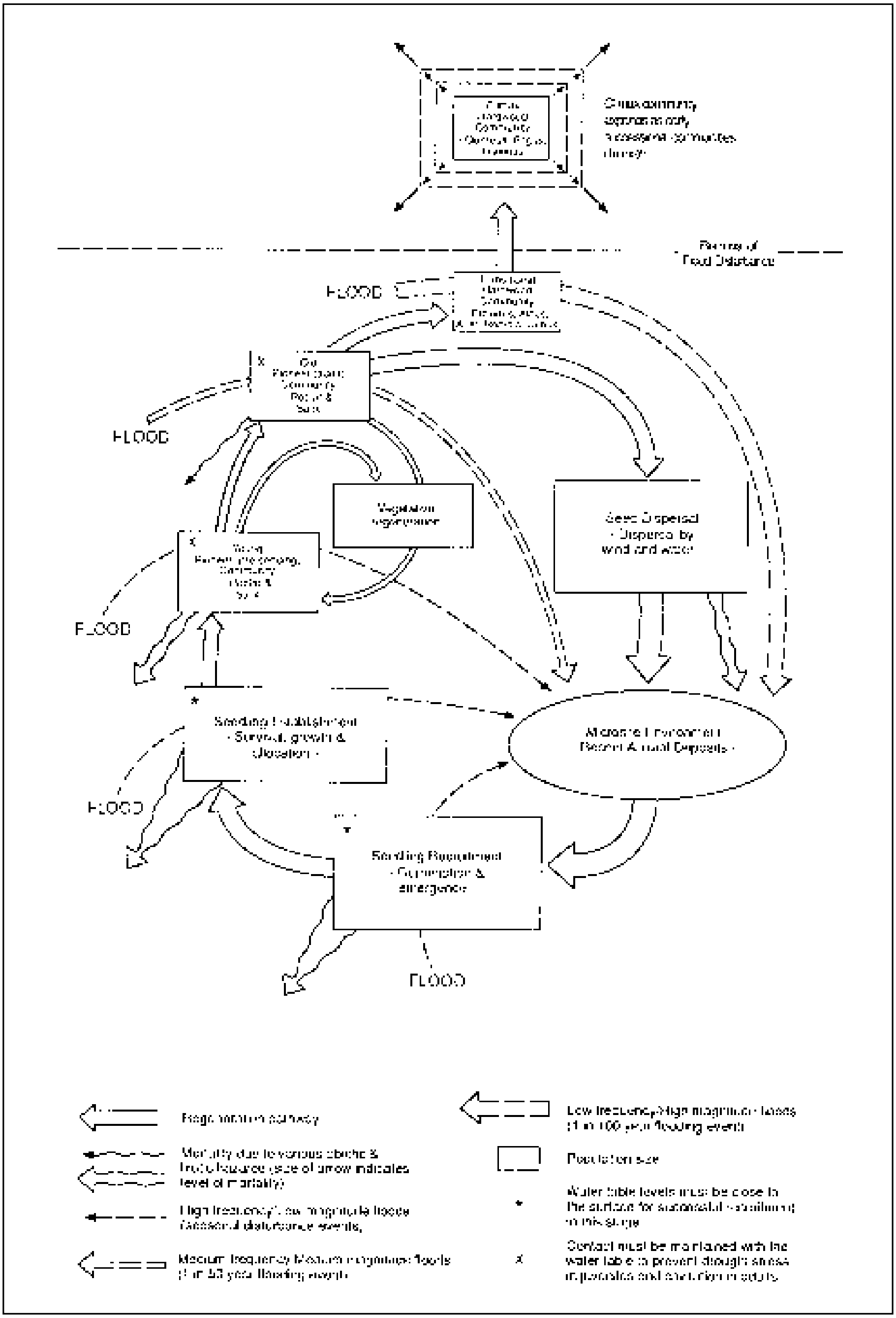


Figure 2. Conceptual model of the regeneration of Salicaceae woodland showing the importance of natural disturbance for rejuvenation.

lasts 4-6 weeks (Larsson 1976). During this period the female catkins lengthen and swelling green fruit capsules appear along their length. Approximately 20-50 fruit capsules will ripen on each catkin producing up to 225 seeds per catkin. When ripe, the fruit capsules will eventually split in warm dry weather, releasing tiny seeds (2 mm) embedded in significant quantities of *pappus*. The opening of fruit capsules and release of seed from catkins can be either gradual or very rapid (Guilloy *et al.* 2001). Nevertheless, seed yields on mature trees are impressive (i.e. a total of 25-50 $\times 10^6$ seeds per tree; Schreiner 1974 and Bessey 1904) and such productivity can be repeated more or less on an annual basis.

The timing and duration of flowering and the length of the seed maturation process are related to both the photoperiod and ambient temperatures and, therefore, will vary from one locality to the next with implications for the timing of seed release (Mahoney and Rood 1998). At higher latitudes and elevations, flowering will be delayed (usually until May), while under the warm and longer growing seasons of lower elevations and latitudes, flowering may have ceased by mid-April (Braatne 1996). Such climatic influences have equally been observed to affect the duration of *P. nigra* seed dispersal. For example, along the River Rhine in the Netherlands, seed dispersal is brief, occuring only during the first two weeks in June (Van Splunder *et al.* 1995). Similarly, along the Drac and Isère Rivers in France, in a humid Alpine environment, seed dispersal occurs for 2-3 weeks in late June and early July (Foussadier 1998). This is in contrast to an 8-week seed dispersal period (May-June) observed in the warm dry conditions along the Drôme River in the south east of France (Barsoum 1998) and a 9-10 week seed dispersal period (late April to mid-July) observed in the south-east of France along the Garonne River (Guilloy *et al.* 2001), where in both of these cases, there is a period of maximum seed dispersal in June. Short periods of seed release become especially critical where hydrological conditions offer an equally narrow window of opportunity for recruitment (Figure 3).

The period of seed release in black poplar is strategically timed to coincide with the abatement of floodwaters in the spring when, for a short period, ideal conditions for seed germination and seedling establishment are present. These conditions include mild climatic conditions and freshly disturbed bare alluvial deposits, saturated by gradually retreating flood waters. The abundant *pappus* surrounding *P. nigra* seeds, and in addition a tuft of hairs attached to each seed, ensure that as seeds are dispersed on air currents across the active alluvial plain, they have a very good chance of becoming instantly arrested on contact with any moist surface. Vast quantities of seed will also be dispersed by the river, extending the period of seed dispersal by 2-3 weeks (Johnson 1994).

Knowledge of the timing and duration of seed release of a *P. nigra* population will confer a distinct advantage in the successful *in situ*

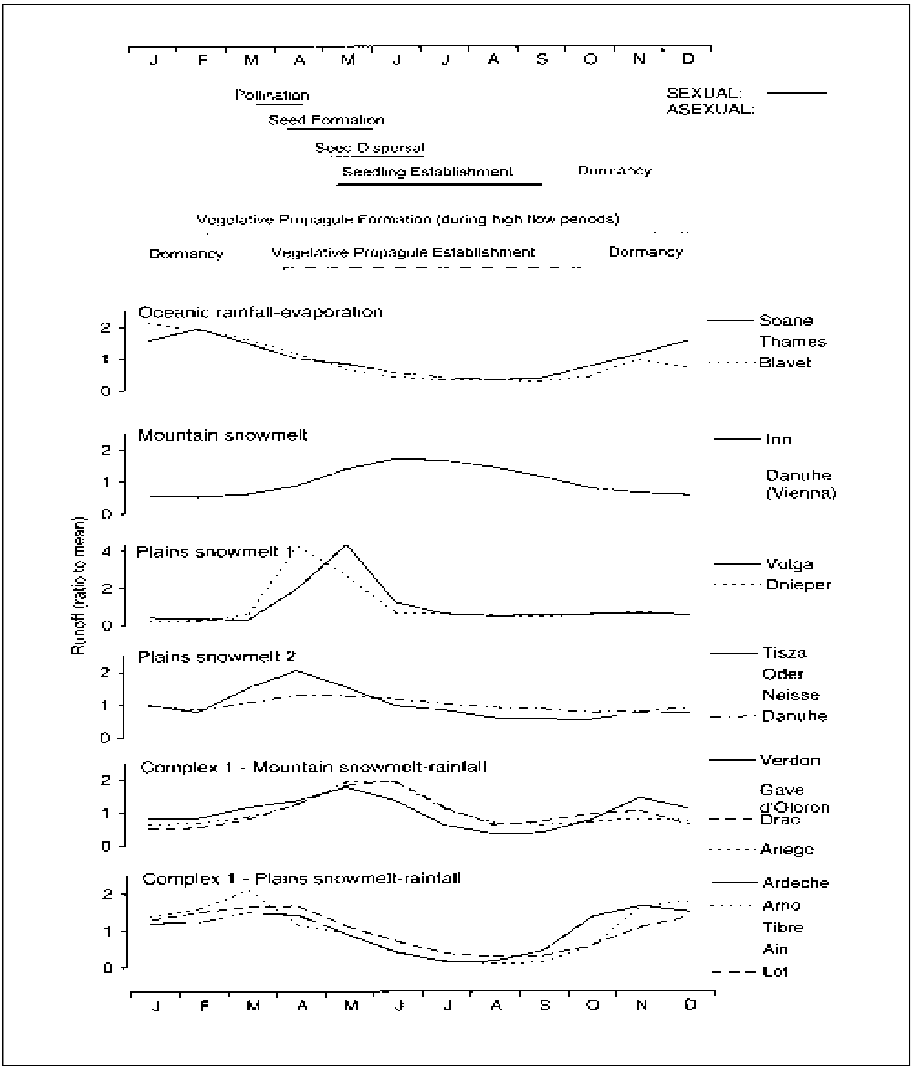


Figure 3. Timing and duration of *P. nigra* reproductive events in relation to annual patterns of stream discharge along European rivers. Six main river regimes are illustrated with examples of each of these (drawn from data in Pardé 1933).

conservation of black poplar at those sites where there is a lack of suitable microsites for natural regeneration. In these situations, it is advisable just prior to the period of maximum seed release, to intervene and manage the riparian setting in such a way as to benefit seedling establishment. This can be achieved at those sites downstream of a dam and reservoir through prescriptive regulation of river flows. Moderately high flows will be necessary to create new bare surfaces followed by sensitive regulation of the flood attenuation hydrograph to favour seedling survival (Mahoney and Rood 1998 - see also following section). Where no more than 'fringe replenishment' of *P. nigra* stands and only minimal clearance along riverbanks is required, low to moderate flooding events (≥ 1 in 5-year floods, but probably no more than a 1 in 10-year discharge) should not be attenuated by dams at 5-10 year return intervals. For partial replacement of mature poplar stands and the creation of large colonizable surface areas, moderate to high magnitude flooding events should not be attenuated by dams (> 1 in 20 year flooding event) and should be allowed to recur at approximately 20 year intervals (Cordes *et al.* 1997, Mahoney and Rood 1998). Subsequent to a flooding event, during the period of seed release, exposed stream banks should be 0.6-2.0 m above base flow (Mahoney and Rood 1998).

In those cases where it is not possible to manipulate high flows, mechanical disturbance of the substrate (site scarification) will be necessary, followed by local flooding and regulation of water table levels, or regular irrigation of surface layers during the first growing season. Mechanical disturbance should involve clearing of vegetation and the removal of sod and litter in order to remove propagules of competing species and physical barriers to seedfall and seedling growth (Friedman *et al.* 1995). The removal of an organic top layer will also prevent any supplemental water and rainwater from being trapped at the sediment surface rather than draining freely into the mineral layers below; this will be especially important to avoid where the water table is deep (> 1 m), and there is a need to encourage rapid extension of tap roots towards the water table (Cooper and Van Haveren 1994). It might be advantageous, in those instances where some irrigation is necessary, to dig many small, widely spaced depressions (approximately 2 m in diameter and 30 cm deep in the centre) sloping gradually up to ground level at the edges. Such depressions would improve the efficiency of irrigation and would also minimize a reduction in growth and mortality rates through intra-specific competition (Friedman *et al.* 1995). Irrigation is otherwise recommended every 2-3 days with a fine mist sprayer for the first 3-4 weeks (Barsoum 1998) followed by watering at twice weekly intervals (~2 cm per dose) during dry summer periods in sediments that are within 1-2 m of the water table (Cooper and Van Haveren 1994).

Yet another alternative to periodic flood disturbance events is the use of well-timed and controlled levels of grazing by livestock. Ungulate grazing could play a compensatory role for a lack of flood disturbances by periodically exposing sections of the riverbank and thinning dense stands of vegetation (Cadbury 1998, Tucker and Leininger 1990, Van Splunder 1997). It is likely, however, that there will still be the need for occasional low to moderate flooding events to import fresh alluvial sediments and provide sufficient moisture to promote seed germination and seedling establishment.

Seed germination and seedling establishment

The diminutive size of *P. nigra* seeds reflects a minimum investment in stored energy reserves and there is consequently next to no dormancy period (Muller and Teissier du Cros 1982). Suitable sites must, therefore, be reached quickly before the seeds lose viability within 3-4 weeks (Van Splunder *et al.* 1995). To compensate for limited seed longevity, *P. nigra* seed viability at the time of seed release is typically very high (90%) and this is true over a broad range of temperatures (i.e. 5-25ºC) (Van Splunder et al. 1995, Foussadier 1998). Greatest levels of viability are observed during periods of maximum seed release (Guilloy et al. 2001), and when there are low ambient levels of humidity (Farmer and Bonner 1967, Moss 1938).

Within 24 hours of reaching a sufficiently moist site (water potential of no less than -0.25 Mpa according to Van Splunder *et al.* 1995, Foussadier 1998), *P. nigra* seeds will have imbibed sufficient water to germinate. Cotyledons and the radicle emerge at approximately the same time and appearing at the base of the hypocotyl is an adaptive feature in the form of a ring of 'root fibres'. Anatomically distinct from root hairs, these root fibres act to anchor the germinant to sand particles and maximize water absorption from the surroundings while the radicle slowly extends itself into the substrate. As there is a lack of endosperm, the growing seedling will be totally reliant upon photosynthate derived from cotyledons and first leaves for development. Full sunlight conditions are therefore critical in order for seedlings to achieve maximum relative growth rates and attain sizes that will minimize their vulnerability to inevitable stresses on the floodplain (i.e. inundation, burial and desiccation).

In addition to the need for full exposure to light, the survival of germinants is dependant on a continuously damp substrate in the first few weeks of establishment; this is distinct from waterlogged conditions, which will severely inhibit root extension into the substrate and result in a damping off of seedlings (Barsoum 1998).

Waterlogged conditions are most likely to evolve in fine textured sediments (clays, silts and fine sands) when the water table remains close to the sediment surface. In coarser sediments (coarse sands and gravel) there is less danger of saturated conditions developing, although the alternative risk of drought induced mortality will be high. The ideal substrate surface for establishment is a thin layer of fine alluvial sediments (1-10 cm) overlying a coarser substrate (Guilloy *et al.* 2001, Barsoum 1998), although where it is possible to manipulate water table levels *P. nigra* seedling growth can be promoted in most substrate types.

The particular sensitivity of *P. nigra* seedlings to drought stress in the first 3-4 weeks following germination is accounted for by slow initial rates of root extension (approximately 4 mm day^{-1}) as seedlings invest in the growth of shoots and production of leaves. Overall progress is nevertheless slow during this period, such that by the end of the fourth week, shoots will have attained heights of no more than 3.5 cm (Barsoum 1998) and rooting depths of approximately 7-9 cm in finer sediments (Van Splunder *et al*. 1996) and 15 cm in coarser sediments (Foussadier 1998, Guilloy pers. comm.). Beyond this early establishment phase, *P. nigra* seedlings become less sensitive to alterations in soil-moisture conditions. Only prolonged waterlogging (> 11 weeks) or loss of contact with the water table will result directly in seedling death. Seedlings otherwise demonstrate very flexible root and shoot growth responses which are very much a function of rates of water table decline and the aerobic status of the substrate (Barsoum 1998, Barsoum and Hughes 1998).

To achieve well-proportioned growth, *P. nigra* seedlings require rates of water table decline which do not exceed 0.5 cm day^{-1} in faster draining sediments (coarse sands and gravel) and rates of water table decline of approximately 2.5 cm day^{-1} in slower draining sediments (silt and fine sands). Deep roots are essential for good anchorage during floods as well as resistance to drought stress. Rapidly expanding shoots are also necessary to allow seedlings to resist aggressive inter-specific competitors and to survive burial by sediment during floods. In coarse substrates, seedlings display low lateral branching of roots in response to the limited water retention capacity of these soils. As a result, seedlings tend to track the water table with one or more tap roots, leaving them vulnerable to sudden drops in water levels or to deep water tables as is common downstream of dams (Barsoum and Hughes 1998). In finer sediments, seedlings benefit from a significant time lag in the drying of soils and from a 'capillary fringe' above the water table, which is typically 30-40 cm high, but can reach 130 cm in very fine sediments. Significant lateral root branching is also observed in fine sediments, providing seedlings with a greater surface area for water absorption and the acquisition of nutrients. Critical water table depths, however, must invariably be much lower in a riparian zone with a predominantly fine substrate compared with sites with coarser substrates in order to retain the aerobic status of the substrate and encourage greater rooting depths. For similar reasons, water table fluctuations must be minimized where the water retention capacity of the substrate is high (Barsoum 1998).

By the end of the first growing season (3-4 months after germination) seedling roots are capable of reaching depths of up to 150 cm (Johnson 1994, Foussadier 1998) and seedling shoots by this stage attain heights of 10-30 cm. Growth in the second growing season and beyond is very rapid and by the end of Year 2, the seedlings become obligate phreatophytes; that is, they are almost entirely reliant on groundwater rather than superficial water sources (Busch *et al*. 1992, Barsoum 1998). Continuous contact with the water table will be required thereafter in order to meet high water demands and prevent cavitation (the highly damaging introduction of air bubbles into xylem vessels) (Tyree *et al*. 1994). The only other real threats to seedling survival, apart from drought during early establishment, include complete burial by sediments or physical displacement by scouring during 'premature' flooding events. Resistance to these threats, however, improves dramatically by the end of the first growing season with very high tolerance also observed by this stage to complete submergence (Siebel and Blom 1998, Van Splunder 1998, Barsoum 1998).

It is important to stress that patterns of recruitment will not be the same where there are significant differences in river morphology, or climate (Johnson 1994, Auble and Scott 1998). For example, a wetter growing season along a free-draining gravel-bed river will invariably improve recruitment rates at higher elevations on the floodplain than during a comparatively dry growing season (Barsoum 2001). Along single thread, meandering rivers seedling recruitment occurs on point bars in arcuate bands of successive ages, while in braided river systems seedling recruitment will have a patchy distribution across the floodplain, occurring in association with specific microsites (e.g. in patches of sand which have accumulated behind clumps of vegetation, or woody debris, in silt-filled depressions on the floodplain). Age-specific patterns of recruitment will be important to monitor as a means of regulating, where possible, the age structure of stands.

Seedlings in a natural setting.

Asexual reproduction

P. nigra is also capable of asexual, or vegetative, reproduction, as an alternative to regeneration from seed, although the generation of ramets is not spontaneous in this species. Asexual reproduction is promoted only by flood disturbances when through extended periods of submergence and/or mechanical damage to parent plants, dormant primordia in roots and shoots are stimulated to produce new shoots and roots (Barsoum 1998). Asexual reproduction in this species can therefore occur either through sprouting directly from the roots and shoots of damaged or partially buried plants (known as root suckering, coppice re-growth and flood-training, respectively), or from translocated fragments which may be transported some distance from the parent plant (Legionnet *et al.* 1997). Among these different asexual regeneration strategies, translocated fragments have been found to be the most common form of asexual recruitment in a semi-natural floodplain environment (Barsoum 2001); this implies that in addition to the localised production of clonal clusters, there may also be substantial dispersal of identical genotypes by floodwaters.

Vegetative recruits have the apparent advantage over seedlings of carbohydrate reserves, pre-formed root and shoot primordia (Schier and Campbell 1976) and possible pre-established links to water sources via the parent plant; these physiological 'advantages' are reflected in the vigorous growth and often very bushy appearance of many first year asexual recruits as well as greater tolerance to burial by sediments and water-logged conditions (Barsoum and Hughes 1998). Initiation of asexual reproduction is also much more flexible than recruitment from seed since vegetative propagules can remain dormant in damp alluvial deposits and there is less reliance on the timing of a flooding event (see Figure 3). Where water is limiting, however, asexual recruits have a distinct disadvantage over seedlings in that growth is frequently unbalanced (excessive sprouting of shoots), leaving asexually propagated recruits prone to drought-induced mortality (Barsoum and Hughes 1998).

Considering the different distinguishing characteristics of sexual and asexual reproduction in *P. nigra*, it might be expected that vegetative recruits make a substantial contribution to overall levels of recruitment, especially in the face of flooding events of increasing frequency, irregularity and/or magnitude. A number of studies attempting to determine the relative contributions of sexual and asexual recruits indicate, however, that there is little evidence of this (Legionnet *et al.* 1997, Barsoum 1998), even under frequently disturbed conditions in a channelized reach (Barsoum and Winfield, unpublished data). Among the populations studied, a very limited number of highly localized clonal patches were detected. The encounter rate of unique genotypes was, by comparison, very high and is a clear reflection of the massive propagation and release of seeds on an annual basis by large adult populations. Nevertheless, these findings do not cancel out the possibility for an imbalance in regeneration strategies to occur, where either (1) shallow water tables lead to water-logged conditions, favouring clonal over seedling survival, or (2) the timing of floods consistently disfavours seedling recruitment (e.g. unseasonal mid-summer floods have a highly negative impact on regeneration from seed, especially during the first 1-2 months following seed dispersal, but a positive influence on vegetative reproduction). Asexual reproduction otherwise acts as a 'waiting strategy', allowing for some recruitment (and dispersal) to proceed in those years when seedling recruitment is poor. Asexual recruits can also be said to play a vital role in the creation of microsites for seedling regeneration by promoting sedimentation on the floodplain, and thus stabilizing sand and gravel bars which may eventually lead to island formation.

Genetic considerations for the restoration of riparian populations

***Berthold Heinze*[1] *and François Lefèvre*[2]**

[1] *Institute of Forest Genetics, Federal Forest Research Centre, Vienna, Austria*
[2] *Unité de recherches forestières méditerranéennes, INRA, Avignon, France*

Introduction

The objective of this chapter is to provide technical recommendations for situations when new populations of European black poplar (*P. nigra* L.) are to be established, with an emphasis on the choice of genetic material for initial planting. These suggestions are based on theoretical concepts from population biology and on practical conservation and forest genetics points of view. The objective is to establish a stand that is able to produce seeds of such quantity and genetic quality that it is possible to initiate regeneration and contribute to the evolution of local genetic resources.


Old *P. nigra* surrounded by natural regeneration (Hungary).

The need to address ecological restoration of *P. nigra* in general and to identify potential areas for restoration projects in Europe has been emphasized in particular by the EUFORGEN *Populus nigra* Network. Three different situations can be found:

1. sites where ecosystem dynamics still produce favourable conditions for *P. nigra* regeneration, but where there is a lack of adult trees to produce seed in sufficient quantities;
2. presence of a significant adult resource, but absence of ecosystem dynamics which is needed for regeneration;
3. lack of both adult resources and ecosystem dynamics.

The first situation is mainly theoretical, and few sites probably belong to this group. The second situation is rather frequent in continental Europe, as illustrated along certain reaches of the Rhine, Danube and Loire rivers. The third situation is more frequent in northern western Europe (UK, the

Netherlands, Belgium), where river management is intensive and there has been extensive clearing of floodplain woodlands (Peterken and Hughes 1995). As the objective of any restoration project is to re-establish a dynamic evolutionary process within the gene conservation unit, attention must be paid to initial reforestation measures (which is needed in situations 1 and 3), and to the promotion of regeneration from seed (which applies to situations 2 and 3).

As *P. nigra* is a pioneer species, regeneration is dependent on both ecosystem disturbance and migration events. Restoration projects should thus aim to create the suitable ecological conditions for seedling establishment (see Barsoum, this volume) and possibilities for the interconnection of populations. Furthermore, regeneration will not occur directly under trees of reproductive age, so sites for restoration projects should be carefully evaluated, including adequate space for recruitment in the equation.

Theoretical background and approaches

For trees the concept of the minimum viable population size (MVP) considers a population relatively safe from the risks of extinction if it has a minimum size that keeps genetic, demographic and environmental risks at an acceptable level over a given period of time.

Environmental risk	Degradation of the environment by external factors where the population is situated
Demographic risk	Decline in the survival and rate of regeneration of the population due to non-genetic factors (non heritable)
Genetic risk	Reduction in the genetic resilience and, therefore, survival of the population in the long term

For example, in a population of constant size, a standard model population of 50 flowering trees of a monoecious species (under panmixia), and their direct descendants, are likely to retain 99% of their original allelic richness over the next 100 years, and are likely to survive if only the genetic risk is considered (Lawrence and Marshall 1997). General recommendations for long-term MVP in trees indicate numbers of at least 500-2000 genetically distinct trees – unique genotypes (Geburek 1992, Lynch 1996).

Genetic drift is the random loss of genetic information. It is most prominent in small populations, and it also affects quantitative genetic variation. Young *et al.* (1996) pointed out that, on the one hand, the additive component of variance decreases as the effective population size decreases; a loss of 1% of additive genetic variance, considered safe based on animal breeding experience, would make an effective population size of 50 seem suitable. On the other hand, due to fixation of alleles in small populations, genetic interactions contributing to non-additive variance will decrease, relatively, and hence additive variance may actually increase. Preventing any loss of genetic variation would require infinite population sizes. Most models in population genetics deal with constant population sizes. For tree species, however, the population size may fluctuate (expand or contract) over time, due to changes in site conditions. Seen over the course of several non-overlapping generations (which is again a non-realistic assumption for many tree species), the inbreeding effective population size is determined by the smallest generation (harmonic mean over generations). All these considerations disregard mutation as a mechanism creating new variance, the effect of which is difficult to estimate.

More specifically, in the case of *P. nigra*, these numbers are influenced by the following factors:

- the sexual system of dioecy;
- the discrepancy between genetically effective population size and census size due to unequal reproductive success of the different genotypes;
- populations have various degrees of genetic relatedness among individuals (important to minimize to avoid inbreeding);
- generation turnover is relatively short, compared to other tree species;
- there is the potential for vegetative reproduction.

While most of these factors increase estimates for MVPs, the existence of genetic back-ups (*ex situ* collections of clones and seed sources) will make the effects of the loss of trees at a restoration site less urgent.

One possible approach is to consider the Multiple Population Breeding System (MPBS, see Eriksson *et al*. 1993, 1995), in which a large population is subdivided into a minimum of 20 subpopulations with 50 genetically unrelated clones in each. This approach is recommended for most monoecious tree species. For many parts of Europe, however, the requirements are difficult to put into practice. The subpopulations are managed for rapid adaptation to different environmental conditions and/or selection regimes. This increases inter-population variation, gives more emphasis to low-frequency alleles and usually speeds up evolution. The proposed network of *in situ* conservation units throughout the distribution area of *P. nigra* (Rotach, this volume) would function similarly to a MPBS.

A more practical approach to determine the MVPs is to look for apparently isolated populations, count the number of clones, and assess the viability of their offspring e.g. through the germination ability of seeds produced in the stand (Mosseler 1998). Roberds and Bishir (1997) calculated that risk for economic failure of a clonal plantation, in the short term, i.e. for one rotation, could be minimized by introducing more than 30-40 different clones. Such a number of genetically unrelated clones safeguards against catastrophic diseases to a similar degree as in much larger populations.

Considering multiple generations, populations facing genetic risks will produce offspring of poor viability, as compared to populations safely above the threshold size. Gliddon and Goudet (1994) pointed out that actually there are a number of different "effective population sizes", those specifically affecting inbreeding, variance and extinction.

From among all of these considerations, the following points deserve attention:

- genetic variation includes additive components (gene diversity), and non-additive components (gene interactions, co-adapted gene complexes);
- variation *per se* is not the objective, but rather adaptability, i.e. the potential for adaptation, which is related to potential genetic variation (the ability to recombine the genetic information that is present in the parental population into a very large number of different genotypes in the offspring), and to phenotypic plasticity (the ability of a genotype to adapt to a wide range of environments with its phenotype);
- as a dioecious species, *P. nigra* probably has an important genetic load of deleterious alleles. In large populations and with a balanced mating system, this high level of genetic load can be sustained, especially by the immense number of offspring that is produced and offered to the action of natural selection. In small populations and populations with unbalanced mating systems, the species could be susceptible to a rapid and drastic increase in inbreeding (the so-called "vortex of extinction": reduced effective population size increases inbreeding, which reduces mean fitness of the population, which may lead to further reductions in population size, and so on). However, *P. nigra* is a prolific seed producer, and initial strong competition among seedlings at a given site may quickly eliminate maladapted genotypes.
- From the point of view of selection processes, the spatial and temporal heterogeneity of

Catkins with fruits.

environmental conditions that characterize riparian ecosystems, maintain a high level of diversity for adaptive traits (Barsoum 1998).
- non-additive components (gene interaction) may be more important for strictly allogamous species than additive components, "buffering" reduction in genetic variation following a reduction in gene diversity (see Young *et al.* 1996);
- vegetative reproduction decreases the effective population size in this respect. The ratio of vegetative to sexual reproduction depends on factors like timing, magnitude and frequency of flooding, and the effects should be judged on a case-by-case basis.

On the basis of these considerations, the following priorities are proposed:
- establish a minimum viable population or a multiple population breeding system;
- avoid the risk of catastrophic destruction;
- limit the risk of a reduction in fitness, by generally avoiding inbreeding in restored populations (therefore one should focus on the inbreeding effective population size);
- avoid any subsequent reduction in diversity.

Examples of successful breeding of captured wild animals in zoos, provide a positive outlook for guarding populations against the effects of inbreeding. Animals are also "dioecious", and breeding programmes often start with very small numbers. Designing proper mating strategies is, therefore very important. In the case of *P. nigra*, this means careful selection of clones and close attention to the planting design at restoration sites.

It should always be remembered that in *P. nigra* the numbers related to population sizes refer to clones, not the number of individual trees. Clonal duplications might be important in some stands. While some of the numbers introduced above seem very high, it should be noted that the adverse effects of small populations only strike in totally isolated populations, and only over a great number of generations. Nevertheless, once loss of genetic variation has started in the first generations, it cannot be reversed without mutation.

Genetic risks for isolated populations include inbreeding, loss of genetic variation and high inflow by hybrid poplar and var. 'Italica', pollen or seed, which could result in a reduction of the effective population size leading to the loss of genes involved in adaptive traits. Risks of non-genetic origin include catastrophes like severe flooding, drought (and other climatic abnormalities), intensive grazing, the spread of diseases against which there is no resistance, and so on. In fact, it seems much more likely that a population is lost through such events. However, it is certainly prudent to prepare with equal care for both types of risk (genetic and non-genetic ones) in any given restoration project.

The most effective way to counter genetic risks is to allow for migration, i.e. the exchange of pollen and seed with neighbouring *P. nigra* populations. In a less obvious sense, migration also takes place if additional clones are planted at the site, or if younger stands nearby come into their flowering age. It follows that given a certain number of plants available for a restoration project, it may be wise to scatter planting across a wide area, e.g. along the same river, so that they are:

- still in 'genetic contact' via pollen and seed transport, but
- less vulnerable to catastrophic events.

This is mimicking to some extent the innate strategy of poplars to fight off such adverse stochastic effects: i.e. the production of very large seed crops and wide dispersal.

To assess risks to a restored population of *P. nigra*, we therefore also need to consider:

- the degree of isolation of a given population (pollen and seed export and import from other true *P. nigra*),
- the likelihood of losing a whole population through a single catastrophic event, and
- the degree of genetically effective isolation from hybrid poplar and var. 'Italica' introgression.

Practical implications: what material is available and how is it best employed?

It is clear that minimum viable population size is probably higher than we can at present put into practice for *P. nigra*. Therefore, it is not very sensible to restore riverside populations where they will no longer have contact with neighbouring stands, where they cannot spread or increase their numbers through successful recruitment of seed, and where there is no possibility of stand management. For the restoration of populations it is important to consider (see also Table 2):

- the origin of the material, particularly because of its adaptation to local climate;
- the genetic variation in the material (full-sib family, number of open-pollinated families, number of potential pollen donors, proportion of unrelated clones);
- the degree of monitoring and management measures in the planting;
- over- and under-representation of individual genotypes in partially clonal stands.

Considering relatedness among clones, it is important to have variation at different levels. Diversity is needed in cytoplasmic as well as nuclear genes, and in gene combinations (genotypes within and among families).

Table 2. Overview of sources of reproductive material for the restoration of *P. nigra* populations.

Source	**Local adaptation***	**Unrelatedness (absence of parents and offspring or siblings)**	**Number of genotypes available**
National collection	+/-	++	++
Local collections	++	-*	+/-*
Seed collections	+	-	+
Controlled crossings of *P. nigra*	+	- -	-
Clones from neighbouring regions	+/-	+	+
Distribution area-wide collections	-	++	++

"+" and "-" correspond to advantageous and disadvantageous factors, respectively.
* Research needs were identified in these areas by the EUFORGEN *Populus nigra* Network.

- Cytoplasm: cell organelles and their genetic information are only passed on through seed, not through pollen. Certain genetic factors, as yet unknown, may be transmitted by cytoplasm only (in mitochondrial and chloroplast DNA). Disease resistance factors in maize are an example from plants. In this example, all clones that are descendants of a susceptible maternal line will also be susceptible. Therefore, diversity in maternal lines is desirable.
- Nuclear genes: interrelated families harbour less diversity in nuclear genes than families obtained by breeding independent parents. An extreme example of a related family is a topcross (pollination of many females with pollen from the same male). The inbreeding effective population size in a topcross equals 4, approximately. Different clones contain a more or less unique combination of nuclear genes each, even if they are related and contain similar sets of nuclear genes.

National collections, which typically consist of 100-500 clones, are mostly "unrelated" and "diverse", but not always suitable for all sites in a country. Clones from a neighbouring region of another country might be more suitable (quite often, rivers form borders between European countries, and clones from each side of a given river are certainly suitable for restoration on either side). Introduction of clones from further away might cause the breakdown of co-adapted traits encoded by more than several genes working together, in later generations (Lynch 1996). This would be especially true for species with outbreeding depression. There is currently insufficient data to assess if there is outbreeding depression in *P. nigra* (this kind of data may however be present in the files of national breeding programmes, see e.g. Pichot and Teissier du Cros 1988).

Higher numbers of distinct genotypes provide a better safeguard against unwanted effects; therefore, for a given planting area, the highest reasonable number of clones should be used. On the other hand, if the number of clones is limited, but plenty of space available, planting many trees from each clone will minimize the risk of losing a clone altogether.

The pattern of planting is also important. Dense mixtures of different genotypes will give competitive clones an advantage, while mosaics of monoclonal plots will give slower growing clones greater chances of survival and increase the likelihood of effective reproduction.

Single clones should not be used for too long in an increasing number of restoration projects and it is advisable to turn over clones in the collection from which plants for restoration projects are produced quickly. If several sites are to be planted with material from the same source material, then the use of different proportions of plants from individual clones should be considered. This gives clones with poor juvenile growth rates and later onset of flowering a greater chance of passing on their genes. One might argue that such clones, being less fit, would perish anyway, because in the case of *in situ* conservation, natural evolution is more important than the conservation of favourable forestry-related traits. However, by slowing down the impact of natural selection, the potential to form a great diversity of new genotypes is retained, and tolerant genotypes might evolve over time, especially in very small populations where late-flowering genotypes might harbour unlinked genes important for other traits (e.g. very rare pests or diseases). The number of new genotypes that can be formed depends on the effective number of gametes. A genetically sound restoration strategy is to gradually substitute the original clones with seedlings from established restoration sites.

The sex-ratio of the clonal mixtures planted at a restoration site should be fairly equal, mimicking the natural situation. In special situations, e.g. when supplementing existing populations with an unbalanced sex-ratio, or when trying to maximize seed flow from a restored population that has pollen inflow from existing sites, unequal numbers of male and female trees might be necessary.

Mixing different sources of reproductive material for restoration projects will sometimes be necessary, for instance because there are not enough local clones available. The only real risk of mixing provenances is the unwanted breakdown of adaptive traits (see above section). The general recommendation, therefore, is not to transfer reproductive material over steep climatic gradients or boundaries (e.g. across major watersheds, over a great latitudinal range), and not to transfer over too great distances in a given climate. Depending on local geographic and climatic conditions, an estimate for this distance is up to 500 km (on the basis of general findings of Farmer

1996 and Pichot and Teissier du Cros 1988). If seed zones exist, then these should provide an indication. A low percentage of clones could also be added from appropriate non-local sources. Such a strategy would mimic clinal variation, which is typical for many long-lived, widely occurring tree species. The results of research, including the on-going EU-funded EUROPOP project <www.cordis.lu>, will provide better estimates for *P. nigra.*

For completely isolated restoration projects, the use of at least 100 unrelated clones (no full sibs or half-sibs), with both sexes (if known) in equal proportions are recommended (Lefèvre *et al*. 1998). If full sib or half-sib progenies are used as reproductive material rather than genetically unrelated genotypes, then a higher number of trees is needed to obtain the same limited level of inbreeding in the next generations. In theory we can estimate the level of inbreeding in the seeds produced by a population of N_e unrelated genotypes. We can also estimate this inbreeding coefficient when the population is made up of related individuals of different progenies, and therefore estimate the equivalent number of unrelated genotypes that would lead to the same level of inbreeding. These numbers (Table 3) can be used as "rules of thumb" to adjust the number of trees when progenies are used as reproductive material.

Table 3. Rules of thumb for assessing the number of unrelated equivalents in a population of 100 trees derived from different types of reproductive material: unrelated genotypes or limited numbers of female parent trees, and either half sibs or full sibs.

Total number of trees	Number of families	Number of trees/progeny	N_e equivalents
100	100	1	100 (reference)
100	50 true HS	2	66
100	25 true HS	4	40
100	10 true HS	10	18
100	1 true HS	100	2
100	25 HS (4 males)	4	35
100	10 HS (4 males)	10	15
100	1 HS (4 males)	100	1.6
100	50 FS	2	50
100	25 FS	4	25
100	10 FS	10	10
100	1 FS	100	1

HS, half sib progenies (such material is usually derived from seeds collected on mother trees; we consider two cases: when each mother tree was effectively pollinated by a large number of different pollinators – true half sibs, and when each mother tree was only pollinated by a limited number of 4 pollinators). **FS, full sibs** (such material is usually derived from controlled crosses with one male per female tree). Details on the derivation of these numbers are available from F.L.

A range of clones, cytoplasm, and families should be present at any restoration site. If there is a fair chance for the restored population to be in genetic contact with other populations of *P. nigra*, then the overall minimum number of clones could be reduced to 50. If the chances for genetic contact are considered to be low to moderate, around 75 clones will probably be sufficient.

In a situation of high genetic contact among previously established and newly planted trees, a breeding unit (i.e. population) is formed. In this way, it may be possible to create a network of 'minipopulations' from remaining stands and new plantings, which could act as a large metapopulation. It follows that restoration plantings can be successful if they 'top up' the number of existing trees to a higher level than recommended above. In other situations, it may be possible to link existing trees genetically by planting new clones in between, for instance in linear bands along roads or rivers.

The shape of the newly planted stands may be important. Linear stands along the river may be more successful in capturing pollen inflow, and in releasing larger quantities of seed more efficiently. Planting large blocks of trees; on the other hand, may result in less efficient exchange of genes (lower dispersal rates).

The situation is more difficult where not enough local clones are available. Here, the existing *ex situ* collections become even more important and should be closely linked with previously restored populations. The populations to be planted could be composed of:

- available local/national clones in varying proportions at different sites;
- mixtures of local/national clones and introduced clones from neighbouring regions with comparable climatic conditions.

Vegetative reproduction as a natural process.

Further management

Genetic exchange among newly established populations and *ex situ* collections could be achieved by adding seedlings raised from seed collected from individuals at the restored site, to *ex situ* clone collections. Poorly flowering clones could be re-planted to give them a fair chance of passing their genes on to a new generation. By constantly monitoring, increasing and supplementing the genetic make-up of such impoverished populations, it may be possible to counteract the effects of gene loss. It may also be possible to neutralise founder effects of existing populations that descend from a limited number of genotypes. Genetic analyses may be necessary in such cases to determine the exact relationship between trees to be introduced and trees already present at a particular restoration site, and among trees at different restoration sites. Repeated planting at 10-year intervals would mimic natural processes in that a patchy network of even-aged cohorts would result. Once the oldest generation starts flowering, their sexual reproduction should be favoured. No additional planting will be desirable at a site if space is limited and especially where planting will decrease natural regeneration potential.

However, a ‘plant and walk away’ strategy is inappropriate where we are already below the levels of population sizes considered safe for a tree species. Management measures should include re-planting of poorly flowering clones, corrective thinning, new additions to and from the genebanks, and removal of unsuitable clones due to the threat of introgression or poor adaptation. Active management could be carried out with decreasing intensity and eventually stop when monitoring indicates that survival and reproduction, and especially the quality of the offspring, are acceptable. Hopefully, over the years, our knowledge of the parameters and processes that influence the long-term survival of *P. nigra* will increase and enable us to make even better informed decisions.

Indicators for monitoring genetic diversity

François Lefèvre[1] ***and Davorin Kajba***[2]

[1] *Unité de recherches forestières méditerranéennes, INRA, Avignon, France*
[2] *Faculty of Forestry, Zagreb, Croatia*

Introduction

The definition of indicators for monitoring *in situ* conservation of genetic diversity is becoming a critical question in research. Obviously, *in situ* conservation of the target species is primarily governed by its biological features, and general concepts need to be implemented on a species-specific basis. In this chapter, we suggest ways to implement the general concepts developed for forest gene conservation (Savolainen and Kärkkäinen 1992, Namkoong *et al.* 1996, Brown *et al.* 1997, Palmberg-Lerche (1998) and Thomson *et al.* in preparation) for the particular case of *P. nigra*.

The dynamics of European black poplar (*P. nigra* L.) is tightly linked to the dynamics of the riparian ecosystem, which in fact means the dynamics of the river itself: many indicators of the genetic evolution of the species are thus expected to result from ecological observations. It is possible to identify two different scales for *in situ* management: the conservation unit, a local site often structured into different forest associations where *P. nigra* is represented, and the network of *in situ* conservation units within the species' distribution area. The overall objective of maintaining genetic diversity refers to the whole network of *in situ* conservation units, whereas monitoring is mainly, but not only, required at the level of each conservation unit.

While the various types of conservation units suitable for black poplar have been described in previous chapters of this volume, this chapter refers more specifically to natural *in situ* conservation units and managed *in situ* conservation units. A set of indicators to monitor and to evaluate gene conservation within each conservation unit is proposed. Dealing with a pioneer species that can only be maintained through disturbance of the ecosystem and colonization of open areas, the processes need to be followed on a broad scale, rather than observing the sites where poplar trees currently grow. Furthermore, the dynamics of riparian ecosystems are subject to temporal changes, from stochastic environmental factors (e.g. decennial flooding events) to more permanent changes (e.g. impact of global climate change on the hydroperiod).

General concepts and their application to *P. nigra*

The general approach in three steps proposed by Namkoong *et al.* (1996) to monitor *in situ* conservation applies to *P. nigra* in the following way:

1. identify the processes that govern the evolution of genetic diversity:
   - **population turnover rate** through extinction and colonisation processes which are needed for regeneration;
   - the genetic processes which modify the genetic information transmitted across generations: **drift** (random effect on gene frequencies and differentiation in finite populations, related to population size, it affects the genetic diversity and its structure and increases inbreeding), **mating system** (system whereby individuals of opposite sexual type are paired to produce progeny, it may increase inbreeding), **migration** (exchange of seed and pollen among genepools, it affects the structure of genetic diversity; the diversity is locally increased but in some cases local adaptation can be affected), **selection** (directional change of gene or genotype frequencies due to environmental factors or human activities, it affects the genetic diversity)[1].

2. identify management practices that can affect these processes:
   - water management;
   - forestry and landscape management;
   - others.

3. determine criteria that should be achieved for long-term *in situ* conservation of genetic diversity, determine indicators to follow these criteria, and verifiers of these indicators:
   - ecological indicators;
   - demographic indicators;
   - genetic indicators.

Land managers typically deal with multiple objectives, and this is particularly true for riparian forests. At the European level, riparian habitats are preserved for their biological diversity (which includes riparian tree species such as poplar, but also insects, mammals, birds, or other plants) (Sedgwick and Knopf 1990, Naiman and Décamps 1997), for their ecological role in water regulation, and their influence on water quality (Gilliam 1994, Haycock *et al*. 1993). It becomes evident that management practices cannot be governed by the single objective of conservation of *P. nigra* diversity. This can be illustrated as follows: to implement a policy, several management practices are carried out, each of these having several impacts on the global environment, including multiple consequences for *P. nigra* diversity (Figure 4 and Table 4).

Indicators should support decisions in the entire process of evaluation of the impact of practices on *P. nigra* diversity. Because we can only reach the point of identification of indicator variables, further research is needed to determine the threshold values.

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[1] mutation is considered here to be beyond the scope of monitoring

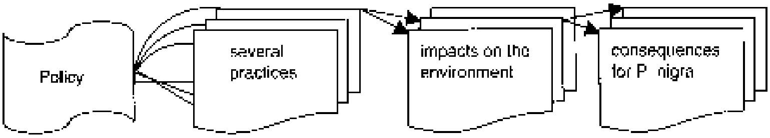

Figure 4. Management of *P. nigra* conservation units: from the decisions to their consequences.

Choice of indicators

A set of ecological, demographic, and genetic indicators relevant for monitoring *in situ* conservation of *P. nigra* genetic resources is proposed (Table 5). These indicators are related to the processes shaping the evolution of genetic diversity. As stated by Brown *et al.* (1997), a single indicator is generally related to several processes, and the study of individual processes requires the use of a set of indicators. All indicators listed here are considered to be realistic although they might require different levels of technical and financial investment. Indicators are relevant at a specific point in time, but most of them may also change over time and such changes may be even more informative: a 5-year period of re-evaluation can be recommended in order to adjust management practices when needed.

These indicators concern the monitoring of each *in situ* conservation unit; other specific indicators for the monitoring of the network of conservation units as a whole (structure of diversity among conservation units) would also be required in the future.

Ecological indicators

Ecological indicators are obtained by observing the ecosystem. They provide information about long-term perspectives on a large scale (e.g. evolutionary tendencies of the whole riparian ecosystem), and on current demographic and genetic processes (e.g. suitability of a site for sexual regeneration of poplar – see Barsoum and Hughes 1998).

- The hydroperiod is informative with regard to potential local extinction, seed dispersal by the river, the potential for and the balance between seedling and vegetative recruitment, and the possibility for young cohorts to reach the adult flowering stage; e.g. in contrast with exceptional flooding events, annual floods release only minimal resources (space and fresh alluvial sediments) and thus limit recruitment potential. This indicator only varies across a long time scale and does not require regular re-evaluation.
- Predominant sediment type (fine *versus* coarse textured sediments) will indicate how suitable a site is for *P. nigra*. Fine sediments (clays,

fine sand and silt) are generally not favoured, especially where the water table is high. Also, rate of sediment deposition. This can affect the balance of regeneration strategies. There is no need for re-evaluation of this indicator in the short-term.

- The area of floodplain in pioneer *versus* adult stages provides information on the current demographic structure, potential seed production and seedling recruitment. This indicator can easily be evaluated on the basis of aerial photographs and may have huge temporal variations: these fluctuations and trends are also informative (e.g. when a river system becomes less dynamic, the demographic structure of *P. nigra* may be directly affected).
- The area of floodplain free of post-pioneer species or indicator species of such a stage is an analogue to the previous indicator. Its estimation requires field observations. Temporal variations should be considered.
- The occurrence and abundance of aggressive inter-specific competitors (e.g. *Robinia pseudoacacia, Polygonum persicaria, Buddleja davidii, Impatiens glandulifera, Ambrosia artemisifolia, Urtica*) provide information on colonisation pressures in open areas. This indicator can even be estimated on a broad scale. It may change over a short period of time.
- The surface area occupied by cultivated varieties in the neighbourhood (hybrids and pure *P. nigra*) provides information about potential gene flow with the cultivated genepool and possible impacts on the effective population size (mating system).
- The occurrence of pests and diseases may have a significant impact on natural selection and seedling recruitment potential, eventually leading to local extinction. As changes over time depend on the pathogen in question, trends in this indicator should be continuously monitored.

Very old isolated tree: river Loire (central France).

Demographic indicators

Demographic indicators are obtained after specific observation of the *P. nigra* population. They describe current demography and future trends. They are related to genetic processes.

- The abundance and spatial distribution of seedlings provide direct information on the possibilities for effective recruitment, and describe whether seedling recruitment is uniform or scattered across the conservation area; observations must be made at a very early stage, soon after seed germination when seedlings still have their cotyledons, in order to distinguish vegetative recruits from recruits of seed origin. Change over time will also be informative.
- The frequency of occurrence and spatial distribution of vegetative reproduction provide information on the suitability of ecological conditions for efficient recruitment from seed (e.g. high numbers of vegetative recruits suggest high frequency of flood disturbance). Also if vegetative recruits are suspected of reaching the adult stage (through genetic analysis, see below) this can affect the mating system and effective population size; however, in the field, vegetative reproduction is only observed with full confidence at the juvenile stage. Change over time in this indicator will be informative.
- The number of flowering trees determines the population size and directly relates to potential drift effects. This indicator can be more easily scored on a log-scale basis; it is not expected to change frequently.
- The sex-ratio may significantly deviate from 1:1 in some places, which directly affects the mating system and effective population size, potentially leading to drift. This indicator also shows only long-term variations.
- The spatial distribution and surface area occupied by young saplings (individuals < 2 m in height) provide information on survival rates during the first few seasons following recruitment (most of the seedlings in a given year occur in the most disturbed places where they have very little chance of survival). Changes over time are informative.
- The spatial distribution and surface area occupied by older saplings (> 2 m in height and not flowering) represent the potential for the next generation. Changes over time are informative.

Genetic indicators

Genetic indicators require consideration of the *P. nigra* genome. They can be compared to their expected value in a reference population in order to infer genetic processes of evolution. They require specific technical tools for laboratory analyses, which are now available for *P. nigra*. These indicators should be evaluated in conjunction with demographic structure (i.e. within the different cohorts), and then re-evaluated only when the demographic structure has changed significantly.

- Genetic diversity can be assessed through genetic markers (allelic richness, gene diversity) and adaptive traits (additive variance); it provides information on the effect of genetic drift, on the mating system (including the potential impact of vegetative reproduction on the effective population size), and on selection.
- Differentiation among age classes is influenced by drift and possible recent bottleneck effects, selection and migration processes.
- Differentiation among stands provides information on drift, gene flow, and selection at another spatial scale; it includes differentiation between a given conservation unit and other populations in the neighbourhood, as well as differentiation among the different conservation units within the whole network; this is also an indicator for management at the network level within the species' distribution area.
- Introgression, which could be defined for this purpose as gene exchanges with the cultivated genepool (either *P. nigra* cultivated clones, or interspecific hybrids), is related to gene flow, and also to the effective population size.

Needs for the further development of indicators

Concerning the monitoring of a future network of *in situ* conservation units, at present we can only give some recommendations. Any such network should attempt to sample the genetic diversity of the species within its distribution area. Individual states are responsible for the conservation and sustainable use of their own genetic resources. International coordination can assist them in developing and implementing the national gene conservation strategies, in addition to providing an effective link between them.

Natural and managed *in situ* conservation units should be self-sustaining in the long term. We could theoretically allow some sites to disappear given that the diversity is maintained at the level of the network, but this would not be realistic because land managers cannot change their objectives easily, and once a site is dedicated to *P. nigra* conservation, it is opportune to maintain the conservation objective. For selecting such sites, even a rough evaluation of **ecological and demographic indicators** on a large scale can easily provide valuable information on the potential processes shaping the species' evolution. Preliminary information can also be derived from the minimum standard information (stand descriptors) recommended for inventories (Alba 2000). Concerning the size of a natural or managed conservation unit (see Rotach, this volume, for definition), the unit should be large enough to include all demographic stages (adult trees and recruits from seed), and large enough to be able to absorb gene flow from outside without major damage to local adaptation. Owing to the particular nature of the riparian ecosystem, conservation units will never be completely isolated. The question of "what is large enough?" is still subject to research. Moreover, one should keep in mind the pioneer status of the species and the characteristics of the ecosystem which is widely open to gene flow: attention should also be paid to the area of the river adjacent to a conservation unit, as a buffer zone that may also require monitoring.

Spatial structure of different age classes.

In a further step, the monitoring of *in situ* conservation units, using a typically multiple-objective policy, will rely on an accurate evaluation of the possible impact of the management practices that are planned, on the monitoring of existing genetic diversity and possible changes to genetic diversity. This requires a more intensive use of indicators: i.e. evaluation of **ecological and demographic indicators** on a small spatial scale and the use of genetic indicators. Defining scales of measurement and threshold values for each indicator then becomes crucial in order to optimize their efficiency and minimize management costs. As stated earlier, research is still needed to determine these threshold values, although some key features of black poplar population biology, and its relation to the riparian ecosystem have already been established (cf. list of references from the EUFORGEN *P. nigra* Network: <www.ipgri.cgiar.org/networks/euforgen/euf_home.htm>.

Different national and international research programmes are currently dealing with *P. nigra*. Among these, the EU-funded EUROPOP project (Van Dam and de Vries 1999) addresses questions from the genetic point of view such as: what is the structure of genetic diversity in the species distribution area?; what is the scale of gene flow along a river system?; what is the effective population size of a *P. nigra* stand?

From another point of view, the EU-funded EESD-FLOBAR2 project combines ecological and socio-economic approaches to develop guidelines for river basin flow management. Information on these research projects can be found on the Web site of the European Community Research and Development Information Service <www.cordis.lu>.

Table 4. Some examples of management practices in the riparian ecosystem that can affect *P. nigra* population dynamics through their impact on the environment.

Practices	Impact on environment/ecosystem	Impact on *P. nigra* populations
Water management		
- Control of water flow in rivers and prevention of flooding (channelization, regulation using weirs and dams)	- exceptional floods removed, hydroperiod altered, general decline in water table levels and rates of water table decline - stabilized riverbanks - incision of riverbed, with lowering of water table - altered sediment texture and rates of sediment deposition - altered species composition - encroachment of dense vegetation stands onto floodplain, to river edge - appearance of aggressive competitors	- colonization - health conditions - age structure - competition
Extraction		
- extraction of sediment from the riverbed	- incision of the riverbed, with lowering of the water table - stabilized riverbank	- colonization - health conditions - competition
- extraction of sediment outside riverbed	- bare soil exposed	- colonization
- extraction of groundwater	- rate of water table decline and fluctuation	- colonization - health conditions - age structure - competition
Ecological engineering		
- removal of vegetation and organic top layer	- bare soil exposed - increased availability of resources supports nature development	- colonization - competition

Forestry and landscape management		
- logging *P. nigra*		- age structure - selection - introgression
- logging cultivated poplars (*P. nigra*, hybrids)		- introgression
- planting wild *P. nigra* (restoration)		- population size - gene flow
- planting cultivated poplars		- introgression
- coppicing *P. nigra*		- flowering - health conditions
- thinning stands in riparian forests	- stand density reduced	- flowering - selection
Other uses		
- grazing	- herbaceous layer affected	- colonization - competition - health conditions - age structure
- game management	- herbaceous layer affected	- colonization - competition - health conditions - age structure
- recreation	- anthropic damage	- colonization - health conditions

Table 5. Indicators and their information on processes of evolution of *P. nigra* diversity.

Indicator	Related processes of evolution				
	population turnover	**drift**	**mating system**	**migration**	**selection**
Ecological indicators					
- hydroperiod and water levels	X		?	X	X
- predominant sediment types	X		?	X	X
- surface area of floodplain available for colonization *versus* mature stages and persistence of both through time (aerial photographs)	X			X	
- surface area of floodplain free of post-pioneer species or indicator species of this stage	X			X	
- surface area where aggressive inter-specific competitors are significantly detected	X			X	X
- surface area occupied by cultivated varieties in the neighbourhood			X		
- incidence of pests and diseases	X			X	X
Demographic indicators					
- abundance and spatial distribution of seedlings				X	
- abundance and spatial distribution of vegetative recruits			X	X	
- number of adult trees		X	X		
- sex-ratio		X	X		
- distribution and surface area occupied by young saplings (< 2 m in height)				X	
- distribution and surface area occupied by older saplings (pre-adults and > 2 m in height)			X		
Genetic indicators					
- genetic diversity		X	X		X
- differentiation among age classes			X	X	
- differentiation among stands		X			X
- introgression			X		

References and further reading

Alba, N. 2000. Standardized minimum list of descriptors for inventories of *P. nigra* stands. Pp. 15-25 *in Populus nigra* Network. Report of the sixth meeting, 6-9 February 2000, Isle sur La Sorgue, France (Borelli, S., S.M.G. de Vries, F. Lefèvre and J. Turok, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Auble, G.T. and M.L. Scott. 1998. Fluvial disturbance patches and cottonwood recruitment along the upper Missouri River, Montana. Wetlands 18(4):546-556.

Barsoum, N. 1998. A comparison of vegetative and non-vegetative regeneration strategies in *Populus nigra* L. and *Salix alba* L. PhD Thesis, University of Cambridge, England, UK.

Barsoum, N. and F.M.R. Hughes. 1998. Regeneration response of black poplar to changing river levels. Pp. 397-412 *in* Hydrology in a changing environment, Vol. 1 (Wheater, H. and C. Kirby, editors). Wiley.

Barsoum, N. 2001. Relative contributions of sexual and asexual regeneration strategies in *Populus nigra* and *Salix alba* during the first years of establishment on a braided gravel bed river. Evolutionary Ecology (*in press*).

Bessey, C.E. 1904. The number and weight of cottonwood seeds. Science 20:118.

Braatne, J.H., S.B. Rood and P.E. Heilman. 1996. Life history, ecology and conservation of riparian cottonwoods in North America. Pp. 57-85 *in* Biology of *Populus* and its implications for management and conservation (Stettler, R.F., H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinckley editors). NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada.

Busch, D.E., N.L. Ingraham and S.D. Smith. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: A stable isotope study. Ecological Applic. 2(4):450-459.

Brown, A., A. Young, J. Burdon, L. Christidis, G. Clarke, D. Coates and W. Sherwin. 1997. Genetic indicators for state of the environment reporting, Australia: State of the Environment Technical Paper Series (Environmental indicators). Department of the Environment, Sport and Territories, Canberra, Australia.

Cadbury, J. 1998. The flora of grazing marsh ditches: status, habitat requirements and management. Pp. 197-215 *in* United Kingdom Floodplains. (Bailey, R.G., P.V. José and B.R. Sherwood, editors). Westbury Academic & Scientific Publishing, West Yorkshire, England, UK.

Cagelli, L. 1997. Guidelines for seed and pollen storage. Pp. 12-13 *in Populus nigra* Network. Report of the third meeting, 5-7 October 1996, Sárvár, Hungary (Turok, J., F. Lefèvre, S.M.G. de Vries and B. Tóth, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Cagelli, L. and F. Lefèvre. 1995. The conservation of *Populus nigra* and gene flow with cultivated poplars in Europe. Forest Genetics 2:135-144.

Cagelli, L., S. Bisoffi and L. Vietto. 1999. *Ex situ* conservation: update on the EUFORGEN core collection and the database of clones. Pp. 70-72 *in Populus nigra* Network. Report of the fifth meeting, 5-8 May 1998, Kyiv, Ukraine (Turok, J., F. Lefèvre, S.M.G. de Vries, B. Heinze, R. Volosyanchuk and E. Lipman, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Cooper, D.J. and B.P. Van Haveren. 1994. Establishing felt-leaf willow from seed to restore Alaskan floodplains. Arctic & Alpine Research 26(1):42-45.

Cordes, L.D., F.M.R. Hughes and M. Getty. 1997. Factors affecting the regeneration and distribution of riparian woodlands along a northern prairie river: the Red Deer River, Alberta, Canada. Journal of Biogeography 24:675-695.

Décamps, H. and E. Tabacchi. 1994. Species richness in vegetation along river margins. Pp. 1-20 *in* Aquatic Ecology: Scale Pattern and Process (Giller, P.S., A.G. Hildrew and D.G. Rafaelli, editors). Blackwell.

Eriksson, G., G. Namkoong and J.H. Roberds. 1993. Dynamic gene conservation for uncertain futures. Forest Ecol. Manage. 62:15-37.

Farmer, R.E. and F.T. Bonner. 1967. Germination and initial growth of eastern cottonwood as influenced by moisture stress, temperature and storage. Bot. Gaz. 128(3/4):211-215.

Farmer, R.E. 1996. The genecology of *Populus*. Pp. 33-55 *in* Biology of *Populus* and its implications for management and conservation (Stettler, R.F., H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinckley, editors). NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada.

Foussadier, R. 1998. Initiation des successions vegetals dans les lits endigues des cours d'eau Alpins. PhD Thesis, University Joseph Fourier, Grenoble, France.

Friedman, J.M., M.L. Scott and W.M. Lewis. 1995. Restoration of riparian forest using irrigation, artificial disturbance and natural seedfall. Environ. Management 19(4):547-557.

Geburek, T. 1992. Wie groß sollten Populationen sein, um bedrohte Tier- und Pflanzenarten zu erhalten? [How big should be the population size to conserve endangered animal or plant species?] Allg. Forst- und Jagd-Zeitung 163:129-133.

Gilliam, J.W. 1994 Riparian wetlands and water quality. Journal of Environmental Quality 23:370-376.

Gliddon, C. and J. Goudet. 1994. The genetic structure of metapopulations and conservation biology. Pp. 107-114 *in* Conservation Genetics (Loeschke, V., J. Tomiuk and S.K. Jain, editors). Birkhäuser Verlag.

Guilloy, H., E. Muller, N. Barsoum and F.M.R. Hughes. 2001. Regeneration of *Populus nigra* L. (Salicaceae): dispersal, germination and survival in changing hydrological conditions. Wetlands (*in press*).

Haycock, N.E., G. Pinay and C. Walker. 1993. Nitrogen retention in river corridors: European perspective. Ambio 22:370-376.

Heinze, B. 1998. Erhaltung der Schwarzpappel in Österreich – forstwirtschaftliche, genetische und ökologische Aspekte [Conservation of black poplar in Austria – forestry, genetic and ecological aspects]. FBVA Berichte 106. Forstliche Bundesversuchsanstalt Waldforschungszentrum, Vienna, Austria.

Herpka, I. 1986. A survey of development and possibilities of growing: natural forests of poplars and willows. Pp. 21-36 *in* Poplars and Willows in Yugoslavia. Poplar Research Institute, Novi Sad, Yugoslavia.

Johnson, C.A. 1994. Woodland expansion in the Platte River, Nebraska: Patterns and causes. Ecol. Monogr. 64:45-84.

Koski, V., T. Skrøppa, L. Paule, H. Wolf and J. Turok. 1997. Technical guidelines for genetic conservation of Norway spruce (*Picea abies* (L.) Karst.). International Plant Genetic Resources Institute, Rome, Italy.

Larsson, H.C. 1976. Technique of mass-producing jackii poplar seed under greenhouse conditions. Proceedings of Northeast.For.Tree Improve. Conf. 23:158-165.

Lawrence, M.J. and D.F. Marshall. 1997. Plant population genetics. Pp. 99-113 *in* Plant Genetic Conservation – the *In Situ* Approach (Maxted, N., B.V. Ford-Lloyd and J.G. Hawkes, editors). Chapman and Hall.

Lefèvre, F. and S.M.G. de Vries. 1997. Third meeting of the EUFORGEN *Populus nigra* Network, a pioneer network for a pioneer tree species: growing up. Pp. 1-3 *in Populus nigra* Network. Report of the third meeting, 5-7 October 1996, Sárvár, Hungary (Turok, J., F. Lefèvre, S.M.G. de Vries and B. Tóth, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Lefèvre, F., A. Legionnet, S.M.G. de Vries and J. Turok. 1998. Strategies for the conservation of a pioneer tree species, *Populus nigra* L., in Europe. Genetics Selection Evolution 30:181-196.

Lefèvre, F., D. Kajba, B. Heinze, P. Rotach, S.M.G. de Vries and J. Turok. 2001. Black poplar: a model species for gene conservation in forest ecosystems. Forestry Chronicle 77(2):239-244.

Legionnet, A., P. Faivre-Rampant, M. Villar and F. Lefèvre. 1997. Sexual and asexual reproduction in natural stands of *Populus nigra*. Bot. Act. 110:257-263.

Lynch, M. 1996. A quantitative-genetic perspective on conservation issues. Pp. 471-501 *in* Conservation Genetics – Case Studies from Nature (Avise, J.C. and J.L. Hamrick, editors). Chapman and Hall.

Maestro, C. 1995. Poplar germplasm conservation: *ex situ* conservation methods under controlled conditions. Pp. 11-14 *in Populus nigra* Network. Report of the first meeting, 3-5 October 1994, Izmit, Turkey (Frison, E., F. Lefèvre, S.M.G. de Vries and J. Turok, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Mahoney, J.M. and S.B. Rood. 1998. Stream-flow requirements for cottonwood seedling recruitment – an integrative model. Wetlands 18(4):634-645.

Maxted, N., B.V. Ford-Lloyd and J.G. Hawkes, editors. 1997. Plant Genetic Conservation – the *In Situ* Approach. Chapman and Hall.

Moss, E.H. 1938. Longevity of seed and establishment of seedlings in species of *Populus*. Bot. Gaz. 99:529-542.

Mosseler, A. 1998. Minimum viable population size and the conservation of forest genetic resources. Pp. 191-205 *in* Tree improvement – applied research and technology transfer (Puri, S., editor). Science Publ., Inc., Enfield, NH, USA.

Muller, C. and E. Teissier du Cros. 1982. Conservation pendant 5 ans de graines de peupliers noirs *Populus nigra* L. Ann. Sci. Forest. 39(2):179-185.

Naiman, R.J., H. Décamps and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3(2):209-212.

Naiman, R. J. and H. Décamps. 1997. The ecology of interfaces: Riparian zones. Ann. Rev. Ecol. Syst. 28:621-658.

Namkoong, G., T. Boyle, H.-R. Gregorius, H. Joly, O. Savolainen, W. Ratnam and A. Young. 1996. Testing criteria and indicators for assessing the sustainability of forest management: genetic criteria and indicators. CIFOR Working Paper No. 10.

Palmberg-Lerche, C. 1998. Management of forest genetic resources: some thoughts on options and opportunities. FAO Forest Genetic Resources 26:43-44.

Pardé, M. 1933. Fleuves et Rivieres. Collection Armand Colin. Section de geographie No. 155. Colin, Paris.

Peterken, G.F. and F.M.R. Hughes. 1995. Restoration of flooodplain forests in Britain. Forestry 68(3):187-202.

Pichot, Ch. and E. Teissier du Cros. 1988. Estimation of genetic parameters in the European black poplar (*Populus nigra* L.): consequence on the breeding strategy. Ann. Sci. For. 45:223-238.

Roberds, J.H. and J.W. Bishir. 1997. Risk analyses in clonal forestry. Canadian Journal of For. Res. 27:425-432.

Savolainen, O. and K. Kärkkäinen. 1992. Effect of forest management on gene pool. New Forests 6:329-345.

Schier, G.A. and R.B. Campbell. 1976. Differences among *Populus* species in ability to form adventitious shoots and roots. Can. J. For. Res. 6:253-261.

Schreiner, E.J. 1974. *Populus* L. Pp. *in* Seeds of woody plants in the United States: U.S. Dept. Agric. Handbook No. 450. (Schopmeyer, C.S., editor). U.S. Dept. Agri., Washington, D.C.

Sedgwick, J.A. and F.L. Knopf. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. J. Wildl. Manag. 54:112-124.

Siebel, H.N. and C.W.P.M. Blom. 1998. Effects of irregular flooding on the establishment of tree species. Acta Bot. Neerl. 47(2): 231-240.

Stanton, B.J. and M. Villar. 1996. Controlled reproduction of *Populus*. Pp. 113-138 *in* Biology of *Populus* and its implications for management and conservation (Stettler, R.F., H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinckley, editors). NRC Research Press, National Research Council of Canada, Ottawa, ON, Canada.

Steenackers, V. 1996. Towards a global management of Poplar genetic resources. Proc. XIXth Session of the International Poplar Commission (FAO), Budapest, Hungary.

Teissier du Cros, E. and I. Bilger. 1995. Conservation of beech genetic resources in France. Pp. 196-209 *in* Genetics and Silviculture of Beech, Proc. IUFRO Project Group P1.10-00, Mogenstrup, Denmark.

Tucker, T.L. and W.C. Leininger. 1990. Difference in riparian vegetation structure between grazed areas and exclosures. Journal of Range Management 43:295-299.

Tyree, M.T., K.J. Kolb, S.B. Rood and S. Patino. 1994. Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta – a possible factor in the decline of the ecosystem? Tree Physiology 14:455-466.

Van Andel, J. 1998. Intraspecific variability in the context of ecological restoration projects. Perspectives in Plant Ecology, Evolution and Systematics 1/2:221-237.

Van Dam, B.C. and S.M.G. de Vries. 1999. EUROPOP: European cooperation in research on black poplar. IPGRI Newsletter for Europe 15:7.

Van Splunder, I., H. Coops, L.A.C.J. Voesenek and C.W.P.M Blom. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuations. Acta Bot. Neerl. 44(3): 269-278.

Van Splunder, I., L.A.C.J. Voesnek, H. Coops, X.J.A. De Vries and C.W.P.M. Blom. 1996. Morphological responses of seedlings of four species of Salicaceae to drought. Can. J. Bot. 74:1988-1995.

Van Splunder, I. 1997. Floodplain forest, willows and poplar along rivers. RIZA report 97.030.

Van Splunder, I. 1998. Floodplain forest recovery: Softwood forest development in relation to hydrology, riverbank morphology and management. PhD Thesis, Nijmegen Katholieke University, The Netherlands.

Vietto, L. 2000. Update on the EUFORGEN core collection and the database of clones. Pp. 26-28 *in Populus nigra* Network. Report of the sixth meeting, 6-9 February 2000, Isle sur La Sorgue, France (Borelli, S., S.M.G. de Vries, F. Lefèvre and J. Turok, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Vries, S.M.G. de. 1996. Guidelines for maintenance and duplication of *ex situ* field collections of *Populus nigra*. Pp. 11-12 *in Populus nigra* Network.

Report of the second meeting, 10-12 September 1995, Casale Monferrato, Italy (Turok, J., F. Lefèvre, L. Cagelli and S.M.G. de Vries, compilers). International Plant Genetic Resources Institute, Rome, Italy.

Young, A., T. Boyle and T. Brown. 1996. The population genetic consequences of habitat fragmentation for plants. Trends in Ecology and Evolution 11:413-417.

Zsuffa, L. 1974. The genetics of *Populus nigra* L. Anales Forestales (Zagreb) 6/2:29-53.

Glossary of terms

adaptation	The process of change in structure and/or function that makes an organism or a population better suited to survive in an environment. Adaptation may be achieved by phenotypic tuning to prevailing environmental conditions, or through evolutionary changes of genetic structure at the population level.
adaptedness	The state of being adapted that allows a population to survive, reproduce and permanently exist in certain conditions of the environment.
allele	An alternative form of a gene. Alleles are located on corresponding loci of homologous chromosomes.
anemogamous	Wind pollinated.
autochthonous (population)	A population which has been continuously regenerated by natural regeneration.
clone	Group of individuals (ramets) derived originally from a single ancestor individual (ortet) by vegetative propagation (e.g. cuttings, grafts, layers) and thus having an identical genetic constitution.
conservation stand	Gene conservation stand or population.
dioecious	Describes a species in which the male and female gametes are formed on different trees. It results in obligatory outcrossing in these species.
distribution area	The geographical occurrence and arrangement of a species, or a population; usually refers to the natural extension of the area occupied by a species.
drift (genetic d.)	Random loss of genetic variants due to stochastic processes.
ecosystem	The ecological complex of, e.g. a forest community, including the non-living components of the environment and functioning together as a stable system in which exchange of nutrients follows a circular path.

effective population size	In a broad sense, the number of individuals in a population successfully involved in reproduction in a given generation.
evolutionary adaptability	The potential or ability of a population to adapt to changes in environmental conditions through changes in its genetic structure.
genebank	Facility where genetic resources are stored in the form of seeds, pollen or tissue culture, as well as collection of living trees as stoolbeds or adult trees (in the case of poplar).
gene conservation stand or population *in situ*	Forest stand in which appropriate management is carried out to ensure the conservation of genetic resources of target species.
gene conservation stand or population *ex situ*	Population established with the specific objective of genetic conservation using basic material collected by random sampling in the target gene conservation unit.
gene conservation unit	A common term for all units in which genetic resources are maintained, including gene reserves, *in situ* and *ex situ* gene conservation stands or populations, seed lots stored in genebanks, clone collections, seed orchards and arboreta.
geneflow	The exchange of genetic material between populations due to the dispersal of gametes (through pollen) and zygotes (through seeds).
gene frequency	The frequency of the occurrence of alternative forms of genes (alleles) in relation to the frequency of all the alleles at a particular locus in a given population.
genepool	The sum of all genetic information encoded in genes and their alternative forms (alleles) present in a population at a given time.
gene reserve	=> (*in situ*) gene conservation stand or population

gene (genetic) conservation	All activities including, e.g. collecting, maintenance, storage, management, protection and regeneration, aimed at ensuring the continued existence, evolution and availability of genetic resources; *in situ* and *ex situ*:
***in situ* c.**	Conservation of genetic resources 'on site', in the natural and original population, on the site formerly occupied by that population, or on the site where genetic resources of a particular population developed their distinctive properties. Although usually applied to stands regenerated naturally, *in situ* conservation may include artificial regeneration whenever planting or sowing is done without conscious selection and in the same area where the reproductive material was collected.
***ex situ* c.**	Conservation of genetic resources that entails removal of individuals or reproductive material from its site of natural (original) occurrence, i.e. conservation 'off site'.
genetic diversity	A measure of genetic variation present in a population as a consequence of its evolution.
genetic resources	The biological material containing useful genetic information of actual or potential value.
genetic variability	The ability of a population to produce individuals carrying different genetic variants (alleles, genes or genotypes); the capability of a population to generate genetic variation.
genetic variance	A statistical measure of genetic variation.
genetic variation	The occurrence of genetic variants (alleles, genes or genotypes). Genetic variation is brought about by a change in genes, as distinct from differences due to environmental factors.
genotype	Genetic constitution of an individual tree possessing a particular set of alleles (i.e. different forms of genes which may occupy the same position on a chromosome).
heliophilous	Adapted to life in full sunlight.

hybridization	The formation of a diploid organism, mostly by sexual reproduction between individuals of dissimilar genetic constitution.
inbreeding	A mating system in which mating events occur between individuals that are more closely related than average pairs chosen from the population at random.
inheritance	The transmission of genetic information from parents to progeny.
mating system	System whereby individuals of opposite sexual type are paired to produce progeny.
metapopulation	Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible.
multiple population (system)	The arrangement when two or more populations of sufficient size, originating from a single large resource population, are established over a broad array of environmental conditions, managed or unmanaged, with the purpose of integrating tree breeding and gene conservation.
open pollination	Natural, or random pollination, i.e. when the transfer of pollen from an anther to a stigma is freely exposed to geneflow.
origin	For an autochthonous stand of trees the place in which the trees are growing; for a non-autochthonous stand the place from which the seeds or plants were originally introduced.
outbreeding	The mating system in which mating events occur successfully between individuals that are less closely related than average pairs chosen from the population at random. It is the most common mode of sexual reproduction in forest trees.
outcrossing	Mating among unrelated individuals.
panmixia	Random mating without the restrictive influence of natural or other selection.

phenotype	The observable (structural and functional) characters of an individual resulting from interaction of the genotype with the environment.
population	A (Mendelian) population is defined as a unit present under certain (environmental) conditions, composed of biological organisms, which are able to reproduce sexually and where every pair of individuals is allowed to have common ancestry over generations. A population that has been continuously regenerated by natural regeneration is an autochthonous population. The population may be regenerated artificially from reproductive material collected in the same population or autochthonous populations within close proximity.
progeny	Offspring; descendants of a particular mating event or of a particular mate.
provenance	The place in which any stand of trees is growing. The stand may be autochthonous or non-autochthonous (see => origin).
regeneration	The process of rejuvenation of a collection, stand or population. In the case of a population, regeneration can be natural (regeneration stock originates from matings in the respective population) or artificial.
reproduction	The process of forming new individuals of a species by sexual or asexual means. Sexual reproduction involves the union of gametes that are typically haploid and of two kinds (male and female). The production of new individuals by detachment of some part of the current individual is called vegetative reproduction. Sometimes this term is used synonymously with asexual reproduction, in which case it includes all forms of reproduction in which daughter individuals are produced without the sexual process of gamete and zygote formation.
reproductive age	The age at which the tree produces its first flowers and seed crop.
reproductive material (forest r. m.)	Seeds (cones, fruits and seeds) and vegetative parts of trees intended for the production of plants as well as plants raised by means of seeds or vegetative fragments; also includes natural regeneration.

restoration (ecological r.)	The process of renewing and maintaining ecosystem health. The Society for Ecological Restoration (1995) includes in this definition the enhancement of existing populations and translocation of populations.
sampling	The selection of populations and trees within populations from which seeds or other material is collected.
seed source	Trees within an area (stand or seed orchard) from which seed is collected.
seed (collection) stand	A stand of trees superior to the accepted mean for the prevailing ecological conditions when judged by a standard set of phenotypic criteria and which may be treated for the production of seeds.
seed (collection) zone	Zone defined for seed collection purposes, occupied by trees with relatively uniform genetic composition as determined by progeny testing various seed sources. The area encompassed is based on geographic boundaries, climate and growing conditions (e.g. elevation range) and usually refers to a definite administrative unit.
selection	Any non-stochastic process, natural or artificial, which permits a change in the genetic structure of populations in succeeding generations.
stand (forest s.)	A population (natural or planted) of trees possessing sufficient uniformity in composition, constitution and arrangement to be distinguishable from adjacent populations. 'Stand' is the conventional unit for forestry management and is used interchangeably with the term 'population' (see ⇒population).

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