

Unclassified

ENV/JM/MONO(2000)10



Organisation de Coopération et de Développement Economiques
Organisation for Economic Co-operation and Development

05-Mar-2001

English - Or. English

**ENVIRONMENT DIRECTORATE
JOINT MEETING OF THE CHEMICALS COMMITTEE AND
THE WORKING PARTY ON CHEMICALS, PESTICIDES AND BIOTECHNOLOGY**

Series on Harmonization of Regulatory Oversight in Biotechnology No. 16

CONSENSUS DOCUMENT ON THE BIOLOGY OF POPULUS L. (POPLARS)

JT00103743

Document complet disponible sur OLIS dans son format d'origine
Complete document available on OLIS in its original format

**ENV/JM/MONO(2000)10
Unclassified**

English - Or. English

Also published in the Series on Harmonization of Regulatory Oversight in Biotechnology:

No. 1, *Commercialisation of Agricultural Products Derived through Modern Biotechnology: Survey Results* (1995)

No. 2, *Analysis of Information Elements Used in the Assessment of Certain Products of Modern Biotechnology* (1995)

No. 3, *Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* (1995)

No. 4, *Industrial Products of Modern Biotechnology Intended for Release to the Environment: The Proceedings of the Fribourg Workshop* (1996)

No. 5, *Consensus Document on General Information concerning the Biosafety of Crop Plants Made Virus Resistant through Coat Protein Gene-Mediated Protection* (1996)

No. 6, *Consensus Document on Information Used in the Assessment of Environmental Applications Involving Pseudomonas* (1997)

No. 7, *Consensus Document on the Biology of Brassica napus L. (Oilseed Rape)* (1997)

No. 8, *Consensus Document on the Biology of Solanum tuberosum subsp. tuberosum (Potato)* (1997)

No. 9, *Consensus Document on the Biology of Triticum aestivum (Bread Wheat)* (1999)

No. 10, *Consensus Document on General Information Concerning the Genes and Their Enzymes that Confer Tolerance to Glyphosate Herbicide* (1999)

No. 11, *Consensus Document on General Information Concerning the Genes and Their Enzymes that Confer Tolerance to Phosphinothricin Herbicide* (1999)

No. 12, *Consensus Document on the Biology of Picea abies (L.) Karst (Norway Spruce)* (1999)

No. 13, *Consensus Document on the Biology of Picea glauca (Moench) Voss (White Spruce)* (1999)

No. 14, *Consensus Document on the Biology of Oryza sativa (Rice)* (1999)

No. 15, *Consensus Document on the Biology of Glycine max (L.) Merr. (Soybean)* (2000)

Consensus Document on the Biology of Beta vulgaris L. (Sugar Beet) (in preparation)

Consensus Document on Information Used in the Assessment of Environmental Applications Involving Bacillus (in preparation)

© OECD 2000

***Applications for permission to reproduce or translate all or part of this material should be made to:
Head of Publications Service, OECD, 2 rue André-Pascal, 75775 Paris Cedex 16, France.***

OECD Environmental Health and Safety Publications

Series on Harmonization of Regulatory Oversight in Biotechnology

No. 16

**Consensus Document on the Biology of
Populus L. (Poplars)**

Environment Directorate

Organisation for Economic Co-operation and Development

Paris 2000

About the OECD

The Organisation for Economic Co-operation and Development (OECD) is an intergovernmental organisation in which representatives of 29 industrialised countries in North America, Europe and the Pacific, as well as the European Commission, meet to co-ordinate and harmonise policies, discuss issues of mutual concern, and work together to respond to international problems. Most of the OECD's work is carried out by more than 200 specialised Committees and subsidiary groups composed of Member country delegates. Observers from several countries with special status at the OECD, and from interested international organisations, attend many of the OECD's Workshops and other meetings. Committees and subsidiary groups are served by the OECD Secretariat, located in Paris, France, which is organised into Directorates and Divisions.

The Environmental Health and Safety Division publishes free-of-charge documents in six different series: **Testing and Assessment; Good Laboratory Practice and Compliance Monitoring; Pesticides; Risk Management; Harmonization of Regulatory Oversight in Biotechnology; and Chemical Accidents.** More information about the Environmental Health and Safety Programme and EHS publications is available on the OECD's World Wide Web site (see below).

This publication is available electronically, at no charge.

For the complete text of this and many other Environmental Health and Safety publications, consult the OECD's World Wide Web site (<http://www.oecd.org/ehs/>)

or contact:

**OECD Environment Directorate,
Environmental Health and Safety Division**

**2 rue André-Pascal
75775 Paris Cedex 16
France**

Fax: (33) 01 45 24 16 75

E-mail: ehscont@oecd.org

FOREWORD

The OECD's Working Group on Harmonization of Regulatory Oversight in Biotechnology focuses its work on the development of Consensus Documents that are mutually recognised among Member countries. These Consensus Documents contain information for use during the regulatory assessment of a particular product.

This consensus document addresses the biology of poplar species (*Populus* L.). Poplars are an important and prominent feature of forests throughout the Northern Hemisphere where they are also among the most frequently planted tree species. They are important raw material for wood pulp, particleboard, plywood, lumber, boxes, matchsticks, and small woodenware (Farrar 1995). The bark contains tannic acid, used in tanning of leather, and the fragrant balsam found in the buds of some species is sometimes used for medicinal purposes (Sargent 1965). While several species occur in Canada, trembling aspen (*P. tremuloides* Michx.) has the largest forest inventory of any broadleaf tree species, comprising 80% of the merchantable standing poplar timber with a volume estimated at 1,857 million m³ (Morley and Balatinecz 1993).

There are many recognised species of poplars and these hybridise extensively in nature, with many more hybrids having been produced by controlled crossing. All of the species are deciduous, fast-growing with a relatively short life span, are moisture loving, generally intolerant of shade, and are medium to large trees. Ease of propagation, speed of growth and hardiness has led to their popularity for use as ornamentals, windbreaks, large spacing and short-rotation "pulp" or "energy" plantations. In this document, poplars are discussed generally as a genus, with some emphasis on Canadian species, and are referred to as individual groups, species or hybrids only as necessary. Taxonomic and evolutionary processes are reviewed that have given rise to divergence into sections, each containing a tremendous range of genetic diversity. Reproductive biology is described with focus on aspects of the mating system, gene flow, seed production, natural stand establishment and maintenance by vegetative reproduction. The current knowledge of genetic variation within the genus is reviewed, highlighting the lack of population differentiation over large areas, except for essential adaptive traits, and the tremendous variation typically found within populations. Biological diversity and the complexity of ecological interactions with higher and lower flora and fauna are discussed. The reader is also referred to the excellent monographs on *Populus* species contained in *Silvics of North America* (Burns and Honkala 1990), and many relevant papers contained in the recently published *Biology of Populus* (Stettler et al. 1996a).

The document was prepared by the lead country, Canada, and has been revised on a number of occasions based on the input from other Member countries. It is intended for use by regulatory authorities and others who have responsibility for assessments of transgenic plants proposed for commercialisation, and by those who are actively involved with genetic improvement and intensive management of the genus.

TABLE OF CONTENTS

Preamble		9
Section I	Forestry Practices	11
	A. Deployment of reforestation materials.....	11
	B. Provenance transfer	12
	C. Breeding programs	12
	D. Conservation of genetic resources	13
Section II	Taxonomy and Natural Distribution	15
Section III	Centres of Origin/Diversity	19
	A. Natural distribution	19
	B. Evolution and migrational history	19
Section IV	Reproductive biology	21
	A. Reproductive development	21
	B. Mating system and gene flow	22
	C. Seed production	22
	D. Natural regeneration	22
	E. Vegetative reproduction in nature	23

(continued next page)

Section V	Genetics	24
	A. Cytology	24
	B. Genetic variation	24
	B.1. Population-level variability	24
	B.2. Individual-level variability	26
	B.3. Molecular genetics.....	26
	C. Inbreeding depression and genetic load	27
Section VI	Crosses	28
Section VII	Ecology and Associated Species	30
	A. Habitat	30
	B. Synecology and associated species	31
	C. Competition and stand structure	31
	D. Ecosystem dynamics	32
Section VIII	Summary	35
Section IX	References.....	36
Appendix	Genetic transformation of Poplars	52
	Questionnaire to Return to the OECD.....	55

Preamble

OECD Member countries are moving rapidly towards the commercialisation and marketing of agricultural and industrial products of modern biotechnology. They have therefore identified the need for harmonisation of regulatory approaches to the assessment of these products, to ensure safety, while avoiding unnecessary trade barriers.

In 1993, **Commercialisation of Agricultural Products Derived through Modern Biotechnology** was instituted as a joint project of the OECD's Environment Policy Committee and Committee on Agriculture. The objective of this project was to assist countries in their regulatory oversight of agricultural products derived through modern biotechnology – specifically in their efforts to ensure safety, to make oversight policies more transparent and efficient, and to facilitate trade. The project was focused on the review of national policies, with respect to regulatory oversight, that will affect the movement of these products into the marketplace.

The first step in this project was to carry out a survey concentrating on national policies with regard to regulatory oversight of these products. Data requirements for products produced through modern biotechnology, and mechanisms for data assessment, were also surveyed. The results were published in *Commercialisation of Agricultural Products Derived through Modern Biotechnology: Survey Results* (OECD 1995).

Subsequently, an OECD Workshop was held in June 1994 in Washington, D.C. with the aims of improving awareness and understanding of the various systems of regulatory oversight developed for agricultural products of biotechnology; identifying similarities and differences in various approaches; and identifying the most appropriate role for the OECD in further work towards harmonization of these approaches. Approximately 80 experts in the areas of environmental biosafety, food safety and varietal seed certification, representing 16 OECD countries, eight non-member countries, the European Commission and several international organisations, participated in the Workshop. *Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* was also published by the OECD in 1995.

As a next step towards harmonization, the Working Group on Harmonization of Regulatory Oversight in Biotechnology instituted the development of **consensus documents** which are **mutually acceptable** among Member countries. The purpose of these documents is to identify common elements in the safety assessment of a new plant variety developed through modern biotechnology, in order to encourage information sharing and prevent duplication of effort among countries. These common elements fall into two general categories: the biology of the host species or crop and the gene product.

The safety issues identified in the consensus documents on the biology of specific crop plants are intended to address the potential for gene transfer within the crop plant species, and among related species, as well as the potential for weediness. They make no attempt to be definitive in this respect, however, as the many different environments in which the crop species may be grown are not considered individually.

This consensus document is a “snapshot” of current information that may be relevant in a regulatory risk assessment. It is meant to be useful not only to regulatory officials, as a general guide and reference source, but also to industry and others carrying out research.

To ensure that scientific and technical developments are taken into account, OECD countries have agreed that consensus documents will be updated regularly. Additional areas relevant to the subject of each consensus document will be considered at the time of updating.

Users of this document are therefore invited to provide the OECD with new scientific and technical information, and to make proposals for additional areas to be considered. ***There is a short, pre-addressed questionnaire for that purpose at the end of this document. The completed questionnaire (or a photocopy) should be returned to the OECD’s Environmental Health and Safety Division at the address shown.***

Section I – Forestry Practices

It has been estimated that more than 90% of poplar cultivation throughout the world is concentrated on species and hybrids in section *Aigeiros* (Thielges 1985). This is due to the ease of intrasectional hybridisation and intersectional crosses with species in the *Tacamahaca* section, the broad adaptability of these species and hybrids in the temperate and sub-tropical zones, and the ease of vegetative propagation. Section *Turanga* has been increasing in importance, and the scale of some planting programs is enormous: the Three North Shelterbelt System is a 35.6 million hectare shelterbelt project across the desert border in northern China, where poplars make up 60% of the effort, much of it *P. euphratica* and hybrids *Populus simonii* × *P. nigra* (Weisberger et al. 1995, Wang 1996).

A. Deployment of reforestation materials

Seedling propagation of reforestation stock is most commonly used for difficult-to-root species in section *Populus*, although there are no significant reforestation efforts with species in this section in Canada (PCC 1996b). When practised, primarily for growing out controlled crosses, seed propagation is easily carried out using standard greenhouse propagation techniques (Burr 1986, Stanton and Villar 1996).

For the most part, stem cuttings from species in the *Tacamahaca* and *Aigeiros* sections root easily, while rooting is usually poor for those in sections *Populus*, *Leucoides* and *Turanga* (Zsuffa 1975). The rooting ability of *P. deltoides* varies, while that of *P. nigra* and *P. balsamifera* is very high. These latter species transmit their better rooting ability to hybrids with *P. deltoides* (Zsuffa et al. 1993). Vegetative propagation techniques for poplars in nursery culture can be divided into two groupings: autovegetative propagation, including cuttings, layering, etc., and heterovegetative propagation, including grafting, budding, etc. (Fröhlich and van der Meiden 1979).

For easy-to-root varieties, stem cuttings are normally taken from ripened one-year-old shoots during the dormant season, usually from plants in nursery stool beds, but sometimes from epicormic branches of older trees. Such varieties are often planted directly as unrooted cuttings or as pre-rooted stock on well-prepared planting sites. For harder-to-root varieties, more intensive rooting procedures must normally be used, often using greenwood material, rooting hormones and mist chamber techniques. Poplars from section *Populus*, that are notoriously difficult to propagate from stem cuttings, are more commonly propagated from root suckers, root cuttings and layers (Benson and Schwalbach 1970, Zsuffa 1971, Dirr and Heuser 1987, Hall et al. 1989).

Grafting and budding of difficult-to-root varieties is possible, and some species combinations demonstrate that intersectional compatibility is present, for example *P. tremula* on *P. trichocarpa* (Dirr and Heuser 1987), and *P. alba* or *P. × canescens* on *P. lasiocarpa* (Fröhlich and van der Meiden 1979) is possible: the most extensive application of grafting as a propagation technique has likely been in China where *P. × tomentosa* (*P. alba* × *P. adenopoda*), a variety that roots poorly from stem cuttings, is grafted onto *P. simonii* or one of its hybrids. If the grafted plant is planted with the union below the soil surface, it is felt that the scion forms its own roots over time (Zsuffa et al. 1996).

Poplars are also amenable to propagation by tissue culture and various protocols and explant materials have been used. The difficult-to-root species from section *Populus* have been propagated *in vitro* by enhanced axillary branching of shoots. Other cultivars of *P. × canadensis* (*P. deltoides* × *P. nigra*) and *P. yunnanensis* are propagated *in vitro* using dormant buds as the explant source (Dirr and Heuser 1987). *In vitro* techniques offer the most likely means for vegetative propagation of species and hybrids in section *Populus* (Fröhlich and Weisgerber 1985, Ahuja 1987). The use of somatic embryogenesis has proved successful with *P. alba* × *P. grandidentata* (Michler and Bauer 1991).

Embryo culture (also referred to as embryo rescue) techniques have been developed to improve the recovery rates of hybrid genotypes where crosses often exhibit high frequencies of aborted or immature embryos (Stanton and Villar 1996). While it has been possible to culture individual embryos or whole ovules removed several weeks after pollination (Kouider et al. 1984, Savka et al. 1987), subsequent developments have allowed the culture of half capsules or individual carpels, followed by subculture of germinated embryos (Raquin et al. 1993).

Poplars are deployed not only in production plantations, but are also important species for protection planting, especially as windbreaks on the plains for North America, and for other landscape use. Plantations may be deployed as monoclonal stands, mosaics of monoclonal blocks or clonal rows, and as intimate single-tree mixtures of various genotypes (Zsuffa 1993).

While Canada presently has no regulations governing the control and certification of planting stock, a certification service has been designed and introduced by the Poplar Council of Canada. The service provides certification of: (1) varietal (clonal) identity; (2) quality and type; and (3) sanitary condition. In addition the service maintains a Canadian register of clones and varieties *not* recommended for planting (Zsuffa 1993, PCC 1996a). In Europe, the 130 cultivars registered for commercial use in any country of the European Union (EU) can be marketed within the EU since 1966, and their circulation became free in 1993 with the opening of the single market (Pinon and Valadon, 1997). In Germany, *Populus* reproductive materials are regulated by the Gesetz über forstliches Saat-und Pflanzgut (FSaatG).

B. Provenance transfer

Although large geographic variation has been observed among provenances in morphology, growth and wood properties, the results to date indicate that possibilities for gain “vary from encouraging to confusing to bleak” (Farmer 1996). Limited studies in various *Populus* species do suggest that productivity gains might be achieved through provenance transfer (e.g., Nelson and Tauer 1987), but the focus on hybrid breeding and clonal selection has precluded serious consideration of provenance transfer as an improvement strategy.

C. Breeding programs

Poplar breeding has been characterised by two main features: interspecific hybridisation and clonal selection (Bisoffi and Gullberg 1996). The spontaneous occurrence of natural hybrids among sympatric and introduced species was recognised early this century and suggested a logical starting point for breeding programs. The more often assumed rather than proven superiority of F1 hybrids has been based on performance of selected clones usually attributed to heterosis, although recent studies have confirmed the existence of hybrid vigor (Stettler et al. 1988, Bradshaw and Stettler 1995). The incorporation of clonal selection as a characteristic of poplar breeding programs is largely due to the

relative ease of vegetative propagation, compared with sexual reproduction (Mohr diek 1983, Thielges 1985).

Interest in the breeding of polyploids followed the discovery of fast-growing triploid aspens in the 1930s (Einspahr et al. 1963, Einspahr and Winton 1976) but largely declined in the 1970s, with the exception of some molecular genetics studies (Bradshaw and Stettler 1993). Renewed interest in aspen breeding in western Canada and the Lake States has focused on hybrid vigour of crosses between *P. tremuloides* and *P. tremula*, followed by clonal selection and deployment (Li and Wyckoff 1991, Li et al. 1993, Li 1995).

Important long-term breeding programmes have a long history in Europe (Italy, France, Belgium, Netherlands). More recently, co-operation between universities and pulp industries has led to a very intensive effort in the Pacific Northwest region of North America concentrating on *P. trichocarpa* × *P. deltoides* hybrids, and to a lesser extent those of *P. trichocarpa* × *P. maximowiczii*, *P. trichocarpa* × *P. nigra*, and *P. deltoides* × *P. nigra* (Stettler et al. 1996b, Zsuffa et al. 1996). In Bavaria in Germany cross breeding between *P. maximowiczii* × *P. trichocarpa* and *P. maximowiczii* × *P. nigra* has also been conducted. Intensively managed, short-rotation (5-8 years) plantations are geared toward pulp production, and over 30,000 ha are under cultivation as part of this programme between southern Oregon and British Columbia (Zsuffa et al. 1996).

Since the modern techniques of molecular biology are now being successfully applied to *Populus* it can be anticipated that novel traits, such as herbicide resistance, insect resistance and modified wood characteristics, will be introduced into these species.

D. Conservation of genetic resources

The history of poplar breeding and intensive culture spans a 70-year period. The International Poplar Commission (IPC) was established in 1947 to assist in the direction and co-ordination of this effort and to promote conservation and exchange of germplasm in 35 member nations (IPC 1996). In 1992, the IPC formally requested its member countries “to adopt appropriate measures to ensure that existing genetic resources of poplar and willow species, in natural and man-made stands, be properly preserved, stressing the role that fast-growing species may play in reducing pressure on delicate and endangered natural environments world-wide” (IPC 1992).

Some species of *Populus* are near the point of disappearing in some parts of their natural range, for example, *P. nigra* in Western Europe, while other species are still in full evolution, for example, *P. deltoides*. IPC nations have thus been encouraged to develop strategies for *in situ* conservation. Such efforts started in North China with the *ex-situ* conservation of *Populus simonii* due to three FAO co-ordinated poplar projects (Weisgerber et al. 1995), and in Europe with the conservation of *P. nigra* by the EUFORGEN network (Turok et al. 1997, Cagelli and Lefèvre, 1996). For broadly distributed species like *P. deltoides*, the recommended focus of *in situ* conservation is on small, isolated populations at the limits of the species range, as a source of adaptive variation. Once widely distributed, much of the original genetic resource for *P. nigra* was lost when natural regeneration was excluded by human activity (Steenackers 1996). The disappearance of *P. nigra* from middle Europe may also have resulted from the backcrossing of hybrids, especially of *Populus* × *canadensis* and *P. nigra*.

Other poplar species have a restricted natural range and require special protection. *P. suaveolens* (syn. *P. maximowiczii*) is well protected in natural reserves at different altitudes in the mountains of Hokkaido and can freely regenerate from seed in these areas. *P. heterophylla* is another species with

restricted distribution, growing on soils that are too wet for *P. deltoides*; a special strategy is required to protect this species *in situ* (Steenackers 1996).

Despite the long history of domestication, *ex situ* conservation efforts have been limited and rarely involve seed materials. A notable exception is the *P. trichocarpa* seed bank created by the Netherlands in the 1970s. Promotion of *ex situ* conservation efforts has been recommended as an imperative to the IPC, as has the need for guidelines for the global management and conservation of poplar genetic resources (Steenackers 1996).

Section II – Taxonomy and Natural Distribution

Poplar species (*peuplier* in French) are members of the genus *Populus* L., in the family Salicaceae (willow family) and the order Salicales. The genus is traditionally subdivided taxonomically into sections. Five of these sections are widely recognised: *Turanga*, *Leucoides*, *Aigeiros*, *Tacamahaca*, and *Populus* (known synonymously as *Leuce*) (Zsuffa 1975). Periodically, taxonomists have been inclined to add a sixth single-species section to resolve classification problems. For example, Browicz (1966) proposed section *Tsavo*, to include the east African species *P. ilicifolia*, a species not even recognised by some taxonomists and included by others in section *Turanga*. Section *Ciliata* has been proposed to include the Himalayan species *P. ciliata* Wall. Ex Royle, formerly included in *Leucoides* (Khosla and Khurana 1982), an apparent mistake that others have suggested be resolved by classifying the species under *Tacamahaca*. Still another section, *Abaso*, has been proposed to accommodate *P. mexicana* that seems weakly related to other species of section *Aigeiros*, in which it has previously been placed (Eckenwalder 1996). The dispute over the sectional classification of poplars will no doubt continue; meanwhile, it is generally accepted that three of the sections are represented in Canada: *Populus*, *Aigeiros*, and *Tacamahaca* (Krüssmann 1985, Farrar 1995).

Disagreements over the species classification of poplars show no sign of abatement. The wide distribution of many poplar species, frequent introgressive hybridisation, a long history of cultivation and ease of vegetative propagation has led to much confusion in the nomenclature of poplars. Numerous synonyms exist, and hybrids and cultivated varieties have often been named as species (Zsuffa 1975). Thus, species counts for the genus range from the low 20's to over 80, depending on the authority. The classification suggested by Eckenwalder (1996), which enjoys the transitory advantage of being the most recently published, recognises 29. This classification is presented, with synonyms recognised by Zsuffa (1975), in Table 1. Polymorphisms of DNA add new data to this “conventional” classification (Cervera *et al.*, 1997).

Section Turanga Bge

The three species in this section are native to northeast Africa and Asia. The most important is *P. euphratica* which, although not commonly cultivated in the past, can tolerate poor soils, extreme heat and soil salinity, and is now a key species for anti-desertification purposes in the large Three North Shelterbelt project in northern China (Wang 1996).

Section Leucoides Spach – Large-leaved Poplars

While no members of this section are native to Canada, swamp cottonwood (*P. heterophylla*) is a secondary species on wet sites in the central and eastern United States. Other examples of this section, *P. lasiocarpa* and *P. glauca*, are native to temperate regions of China.

Section Tacamahaca Spach – Balsam Poplars

North American members of this section, found in both Canada and the United States, are balsam poplar – *peuplier baumier* (*P. balsamifera*), black cottonwood – *peuplier de l'Ouest* (*P. trichocarpa*), and narrowleaf cottonwood – *peuplier à feuilles étroites* (*P. angustifolia*). This group includes the commonly planted Simon poplar – *peuplier de Simon* (*P. simonii*) from eastern Asia. Other important members from Asia include *P. laurifolia*, and *P. suaveolens*.

Table 1. Suggested classification, nomenclature and occurrence of *Populus* species (Eckenwalder 1996), and synonyms given by an earlier classification (Zsuffa 1975) in square brackets

Section	Scientific name & synonyms	Common names	Occurrence
<i>Abaso</i> Ecken.	<i>P. mexicana</i> Wesmael		Mexico
<i>Turanga</i> Bge.	<i>P. euphratica</i> Oliv. <i>P. ilicifolia</i> (Engler) Rouleau <i>P. pruinosa</i> Schrenk	Euphrates poplar , bahan	Spain, NE Africa, Asia E. Africa E. Eurasia
<i>Leucooides</i> Spach	<i>P. lasiocarpa</i> Oliv. <i>P. glauca</i> Haines [<i>P. wilsonii</i> Schneid.] <i>P. heterophylla</i> L.	large-leaved poplars Chinese necklace poplar	China China
<i>Tacamahaca</i> Spach	<i>P. angustifolia</i> James <i>P. balsamifera</i> L. <i>P. ciliata</i> Royle <i>P. laurifolia</i> Ledeb. <i>P. simonii</i> Carr. <i>P. suaveolens</i> Fish. [<i>P. cathayana</i> Rehd. <i>P. koreana</i> Rehd <i>P. maximowiczii</i> A. Henry] <i>P. szechuanica</i> Schneid. <i>P. trichocarpa</i> Torr. & A. Gray <i>P. yunnanensis</i> Dode	balsam poplars narrowleaf cottonwood , narrowleaf balsam poplar balsam poplar laurel poplar Simon poplar doronoki , Japanese poplar	southern Sask. And Alberta to southwestern US North America Himalayas eastern Asia eastern Asia NE China, Japan
<i>Aigeiros</i> Duby	<i>P. deltoides</i> Marsh. [<i>P. sargentii</i> Dode, <i>P. wislizenii</i> Sarg.] <i>P. fremontii</i> S. Wats. <i>P. nigra</i> L.	Cottonwoods and Black Poplars eastern cottonwood (ssp. <i>deltoides</i>), plains cottonwood (ssp. <i>monilifera</i>), Rio Grande cottonwood (ssp. <i>wislizenii</i>) Fremont cottonwood black poplar , European black poplar	Quebec, Ontario Prairie Provinces to Texas SW USA SW USA Europe, western Asia
<i>Populus</i> L. [<i>Leuce</i> Duby]	<i>P. adenopoda</i> Maxim. <i>P. alba</i> L. <i>P. gamblei</i> Haines <i>P. grandidentata</i> Michx. <i>P. guzmanantlensis</i> Vasq. & Cue. <i>P. monticola</i> Brand <i>P. sieboldii</i> Miq. <i>P. simaroa</i> Rzed. <i>P. tremula</i> L. [<i>P. davidiana</i> (Dode) Schneid.] <i>P. tremuloides</i> Michx.	aspens white poplar , silver poplar largetooth aspen , bigtooth aspen, aspen, poplar, popple Siebold aspen , Japanese aspen European aspen , tremble, Zitterpappel trembling aspen , quaking aspen	central and southern Europe to N. Africa, central Asia E. Eurasia eastern North America Mexico Mexico Japan Mexico Europe, northern Africa, north- eastern Asia North America

Section Aigeiros Duby – Cottonwoods and Black Poplars.

This section includes the “true” cottonwoods (a term also associated with *Tacamahaca*). In North America the section is represented by eastern cottonwood – *peuplier deltoïde* (*P. deltoides* ssp. *deltoides*), and plains cottonwood – *peuplier deltoïde de l’Ouest* (*P. deltoides* ssp. *monilifera*), found both in Canada and the United States, and by Fremont cottonwood (*P. fremontii*) and Rio Grande cottonwood (*P. deltoides* ssp. *wislizeni*) as secondary species in the southwestern United States. The black poplar – *peuplier noir* (*P. nigra*) is an important species native to North Africa, central and western Europe, and the cultivar known as Lombardy poplar – *peuplier noir d’Italie* (*P. nigra* cv. ‘Italica’) is commonly planted as a hardy ornamental in North America.

Section Populus L. (syn. Leuce Duby) – Aspens.

This section is further subdivided into two subsections, *Albidae* and *Trepidae*, containing the white poplars and aspens, respectively. The North American representatives of this section are both members of *Trepidae*: trembling aspen – *peuplier faux-tremble* (*P. tremuloides*), and largetooth aspen – *peuplier à grandes dents* (*P. grandidentata*). *P. tremula* is an important and highly variable aspen from Europe, while *P. sieboldii* is a recognised species from Japan. However, aspens throughout Eurasia are now thought to be races of a single, highly polymorphic species, viz. *P. tremula* (Barnes and Han 1993). While no white poplars are native to North America, the European white poplar – *peuplier blanc* (*P. alba*) was among the first species introduced from Europe.

Natural hybridisation has been reported between almost all sympatric poplar species, and between introduced and native poplars, both in North America and Europe (Schreiner 1974, Demeritt 1990). Natural hybridisation generally occurs between species in the same section to the limited extent that the parent species overlap (Brayshaw 1965, Eckenwalder 1977), although intersectional hybrids also occur. Species in different sections, though broadly sympatric, are ecologically isolated from one another, so that hybridisation occurs over large geographic areas but within a relatively narrow ecological range of overlap (Eckenwalder 1984a, c). Complicated natural hybrid populations may also form where three or more species are sympatric (Rood et al. 1986).

Eastern cottonwood was introduced into France from southeastern Canada in the late 1700’s. In southern Germany, since the early 1970’s, cross-breeding of *P. × canadensis* has been replaced by *P. trichocarpa × P. deltoides* or *P. trichocarpa × P.* Subsequent natural hybridisation with the native black poplar produced the hybrid which was named *P. × canadensis* in 1789 (Mühle Larsen 1960, Wright 1976). Clones of this hybrid are now widely planted across Europe. This hybrid was also the first poplar hybrid produced by controlled pollination, by Englishman A. Henry (Larsen 1956). Artificial hybridisation has been used in North America since the 1920s and 30s (Stout and Schreiner 1933, Heimburger 1936). Several of the more important hybrids occurring naturally in North America are listed, together with synonyms and common names, in Table 2.

Section III - Centres of Origin/Diversity

A. Natural distribution

The genus *Populus* is widely distributed throughout the Northern Hemisphere, in both the temperate and subtropical zones. Representative species are found from Alaska and Labrador south to northern Mexico, as well as Europe, North Africa, the Himalayas, mainland China and Japan (Schreiner 1974). Some species are very widely distributed. *P. tremuloides*, for example, is the most broadly distributed tree species in North America, spanning 110° of longitude and 47° of latitude, and the second most widely distributed in the world (Jones 1985, Barnes and Han 1993).

B. Evolution and migrational history

It was long felt that *Populus* was one of the oldest contemporary angiosperm genus, originating in China and Japan during the Triassic; however, these fossil records are now associated with other taxa. While the closest relatives in Flacourtiaceae are from tropical Asia, the fossil record now indicates that the genus *Populus* had tropical origins in North America during the late Paleocene, about 58 million years ago (Collinson 1992). These early leaf fossils are very similar to the present day *P. mexicana* in section *Abaso* (Eckenwalder 1996). In the late Eocene, the first Eurasian relatives from other sections appeared, with those of *Turanga* confined to the Old World, and an ancestor of section *Leucoides* invaded temperate habitats. During the Oligocene, precursors of *Tacamahaca* and *Aigeiros* appeared that would not become distinct sections until the Miocene, at which time members of section *Populus* also appeared (Collinson 1992, Eckenwalder 1996).

Table 2 Nomenclature of naturally occurring *Populus Hybrids*

Parentage	Hybrid designation	Common name
<i>P. alba</i> × <i>P. grandidentata</i>	<i>P.</i> × <i>roulwauiana</i> Boivin	
<i>P. alba</i> × <i>P. adenopoda</i>	<i>P.</i> × <i>tomentosa</i> Carr..	Chinese white poplar
<i>P. alba</i> × <i>P. tremula</i>	<i>P.</i> × <i>canescens</i> (Ait.) Sm.	grey poplar
<i>P. alba</i> × <i>P. tremuloides</i>	<i>P.</i> × <i>heimburgeri</i> Boivin	
<i>P. angustifolia</i> × <i>P. deltoides</i>	<i>P.</i> × <i>acuminata</i> Rydb. [syn. <i>P.</i> × <i>andrewsii</i> Sarg.]	Lanceleaf cottonwood, <i>peuplier à feuilles acuminées</i>
<i>P. angustifolia</i> × <i>P. balsamifera</i>	<i>P.</i> × <i>brayshawii</i> Boivin	Brayshaw's poplar, <i>peuplier hybride de Brayshaw</i>
<i>P. angustifolia</i> × <i>P. tremuloides</i>	<i>P.</i> × <i>sennii</i> Boivin	
<i>P. balsamifera</i> × <i>P. deltoides</i>	<i>P.</i> × <i>jackii</i> Sarg.	Jack's poplar, <i>peuplier hybride de Jack</i>
<i>P. balsamifera</i> × <i>P. tremuloides</i>	<i>P.</i> × <i>dutillyi</i> Lepage	
<i>P. deltoides</i> × <i>P. nigra</i>	<i>P.</i> × <i>canadensis</i> Moench cv. Eugenei [syn. <i>P.</i> × <i>euramericana</i> (Dode) Guinier]	Carolina poplar, <i>peuplier de Caroline</i> [syn. Canada poplar, Euramerican poplars]
<i>P. deltoides</i> × <i>P. tremuloides</i>	<i>P.</i> × <i>bernardii</i> Boivin	Bernard poplars
<i>P. deltoides</i> × <i>P. trichocarpa</i>	<i>P.</i> × <i>generosa</i> Henry [syn. <i>P.</i> × <i>interamericana</i> Brockh.]	Interamerican poplars
<i>P. fremontii</i> × <i>P. trichocarpa</i>	<i>P.</i> × <i>parryi</i> Sarg.	Parry cottonwood
<i>P. grandidentata</i> × <i>P. tremuloides</i>	<i>P.</i> × <i>smithii</i> Boivin	
<i>P. laurifolia</i> × <i>P. nigra</i>	<i>P.</i> × <i>berolinensis</i> Dippel [syn. <i>P.</i> × <i>rasumowskyana</i> Schr. and <i>P.</i> × <i>petrowskyana</i> Schr.]	Berlin poplars, Russian poplars
<i>P. deltoides</i> × <i>P. balsamifera</i> × <i>P. angustifolia</i> (natural trihybrid)	Unnamed	Unnamed

The evolution of the advanced sections of *Populus* has been characterised by rapid speciation during allopatric cycles, but influenced by widespread introgression, both within and between sections (Eckenwalder 1984b, 1996, Smith and Symata 1990, Kaul 1995). This rapid sequence of events, much conflicting evidence, and the confusion that has characterised the identification of species, has made it difficult to track the recent evolutionary history of poplars in the more advanced sections (Eckenwalder 1996). While there is evidence of evolutionary divergence among the sections, the sections themselves are very widely distributed. Species within the sections are highly related and many are among the most broadly distributed of any tree species.

It is clear that migration of genes to other section members can occur easily throughout a very large portion of the North Temperate zone. Poplars are pioneering species and migrate quickly. Pollen studies have demonstrated that *Populus* species frequently dominate the first forest communities following glaciation (Cwynar 1988, Keenan and Cwynar 1992). In Europe, *P. tremula* is the early pioneering species. *P. nigra* occurs along rivers and in pastures, together with *Salix alba*. Large stands of *P. tremuloides* in North America are thought to have originated soon after retreat of the Pleistocene ice sheet and have been since maintained asexually from root suckers, making them some of the largest and oldest organisms in the world (Barnes 1975, Kemperman and Barnes 1976, Mitton and Grant 1980, Cheliak and Dancik 1982).

Section IV – Reproductive Biology

A. Reproductive development

Poplars are normally dioecious and obligatory outcrossers; however, the occurrence of monoecious inflorescences and perfect flowers has been reported (Lester 1963a, b, Melchior 1967). Reproductive buds in *P. tremuloides* may develop into pistillate, staminate or perfect flowers, initiated at different times (Lester 1963a). *P. lasiocarpa* is a notable exception as it is normally monoecious and self-fertilising (Schreiner 1974). Overall sex ratios of 1:1 have been confirmed for *P. tremuloides* (Einspahr and Winton 1976, Grant and Mitton 1979) and for *P. deltoides* (Farmer 1964b), although an elevational gradient in sex ratio has been observed in *P. tremuloides* in the Rocky Mountains, with females more common at low elevations, while more than 90% are male above 3 200 m (Grant and Mitton 1979).

Reproductive buds are simple (Jackson and Sweet 1972). Their initiation and early development have been described in *P. tremuloides* and *P. deltoides* (Nagaraj 1952, Seitz 1958, Lester 1963a). Floral initiation takes place in buds, located in the axils of leaves on the current-year shoot. These buds are no more than small apices, each with a single bud scale when winter dormancy occurs (Owens and Blake 1985, Kaul 1995). Terminal buds burst in May, and axillary primordia initiate several bud scales during rapid shoot elongation. Reproductive apices are determined around mid-June (Lester 1963a). Pistillate primordia are first to begin development of floral parts by late June, followed by staminate primordia in early July. In *P. deltoides*, staminate flower buds can be readily distinguished from vegetative buds by midsummer, while identification of pistillate flowers requires dissection (Farmer 1976). Floral development continues within buds through September, so that anthers and ovules are well developed before winter dormancy (Owens and Blake 1985, Kaul 1995). For at least some *Populus* species, a chilling requirement must be satisfied before development will resume (Farmer 1964a). Megaspore mother cells differentiate in the spring, and microsporogenesis immediately precedes anthesis (Farmer and Pitcher 1981).

Flowers are borne in catkins (aments) early in the spring, prior to flushing of vegetative buds. When fully developed, both male and female catkins are 10 to 15 cm in length. Female flowers have from two to four, cap- or y-shaped stigmas, while the males have 30 to 80 stamens (Demeritt 1990). Each catkin bears a few dozen, one-celled capsules, each containing 10 to 30 seeds.

Male flowers ripen and shed pollen a few days before females, ensuring that pollen is in the air when the first females are receptive (Farmer and Pitcher 1981). Such pollen-pistil interactions have been largely documented in *Populus nigra* (Villar et al. 1987a, Villar et al. 1993). Variation in flowering date is due to differences among trees and in *P. deltoides* is highly heritable (Farmer 1976). This variation in flowering date extends the pollination period from 2 to 3 weeks. Another study of natural variation in *P. nigra* over 111 sites in France revealed a fair level of diversity and a low overall differentiation, with an important intraregional gene diversity (Legionnet et al. 1997).

Pollen germinates within the first few hours after pollination. Fertilisation takes place several days later and is normally complete within two weeks (Farmer and Pitcher 1981). Seed development proceeds rapidly and dispersal occurs in most species by midsummer, before the full growth of the leaves (Schreiner 1974). In North American, the period of seed maturity in sections *Populus* and *Tacamahaca* is determined by temperature sums and is quite uniform within the limits of ecotypic zones (Pauley 1950). On the other hand, seed dispersal in the *Aigeiros* poplars may continue throughout the summer and early fall (Farmer 1966).

B. Mating system and gene flow

Two factors contribute to high gene flow and genetic diversity in poplars. Firstly, most are dioecious, and thus obligatory outcrossers. And secondly, in addition to being wind-pollinated, the long white, silky hairs attached to the short stalks of the seeds promote wind dispersal over great distances (Schreiner 1974), resulting in high rates of migration.

Electrophoretic studies in *P. tremuloides* suggest that gene flow is high, leading to a lack of differentiation among populations for putative neutral allozyme loci. However, the role of non-random mating in these same studies was variable, with no deviations from Hardy-Weinberg equilibrium detected in populations sampled in Minnesota (Lund et al. 1992), while an excess of heterozygotes were found in Alberta populations (Cheliak and Dancik 1982), and a deficiency of heterozygotes observed in Ontario populations (Hyun et al. 1987).

C. Seed production

Most poplars begin flowering between age 10 and 15 years (Schreiner 1974), although flowering in *P. deltoides* may occur as early as age four (Farmer and Pitcher 1981). *Tacamahaca* and *Aigeiros* poplars produce large annual seed crops. Those in section *Populus* produce some seeds each year, but bumper crops occur at intervals of three to five years. Poplars are prolific seed producers. A typical 12 m *P. deltoides* specimen was estimated to produce almost 28 million seeds in one season, and estimates for *P. tremula* have ranged as high as 54 million seeds. Poplar seeds are very small. Species in section *Populus* can produce 6000 to 8000 seeds per gram, while North American *Leucoides* and *Aigeiros* produce from 300 to 450 seeds per gram (Schreiner 1974).

Typically, the longevity of poplar seeds under natural conditions is quite short – about two to four weeks. Under controlled low-temperature (-18 to 5° C) and stable moisture content (5 to 8%) conditions, storage time has been extended to 140 days for *P. balsamifera* (Hellum 1973), two years for *P. tremuloides* (Fechner et al. 1981), and five to six years for *Aigeiros* poplars (Tauer 1979, Muller and Tessier du Cros 1982).

D. Natural regeneration

Poplar seeds germinate or die within a few days after seedfall. Germination is epigeal. A fringe of hairs develops at the base of the hypocotyl, rendering the seedling upright and encouraging the root to grow down into the soil.

A favourable medium such as fine mineral soil is required for germination, together with light and continual moisture (McDonough 1979, Farrar 1995). Such conditions are rare, requiring fresh

exposure of mineral soils, as found on shorelines, sandbars and old gravel pits. In North America, regeneration of section *Populus* from seed is confined to newly disturbed areas, whereas the primary mode of reproduction within stands is asexual (Barnes 1966, Schier 1973, Einspahr and Winton 1976).

E. Vegetative reproduction in nature

Except for members of section *Populus*, all poplars sprout vigorously from the stump and root collar. Coppicing occurs occasionally on young aspen (Zsuffa 1975). Reproduction from adventitious shoots on roots (root suckers) is common in many species, although less frequent in those in the *Aigeiros* and *Leucooides* sections.

Clonal groups of *P. tremuloides* in eastern North America are very common, but generally less than 0.1 ha in size, while in areas of Utah, groups as large as 80 ha have been observed (Kemperman and Barnes 1976). In the semi-arid western United States, some argue that widespread seedling establishment has not occurred since the last glaciation, some 10,000 years ago (Einspahr and Winton 1976, McDonough 1985). Indeed, some biologists feel that western clones could be as old as 1 million years (Barnes 1966, 1975). It has been claimed that a single clone, nicknamed "Pando" (Latin for *I spread*), covers 43 hectares, contains more than 47,000 stems and weighs in excess of 6 million kg, making it the largest known organism (Grant et al. 1992, Mitton and Grant 1996)

Studies have also demonstrated that both natural and vegetative propagation occur in nature, for example with *P. nigra* (Legionnet et al. 1997).

Section V – Genetics

A. Cytology

Poplars are normally found in the diploid condition with $2n = 38$ chromosomes (Blackburn and Harrison 1924, Smith 1943). Polyploid individuals are rare and have only been reported in a half-dozen species (Darlington and Wylie 1956). While rare, the first discovery of a triploid forest tree was, in fact, a clone of *P. tremula* (Müntzing 1936). Several other natural triploid clones have since been found in both *P. tremula* and *P. tremuloides*, usually exhibiting larger leaves and exceptional growth (Einspahr et al. 1963, Heimburger 1968, Einspahr and Winton 1976).

Some reports suggest the sex determination in poplars is controlled by sex chromosomes (Peto 1938, Smith 1943, van Buijtenen and Einspahr 1959), however, this theory remains controversial. While published reports favour a genetic basis for gender, a linkage analysis of almost 2 500 PCR-based RAPD markers in a segregating family of F1 hybrid *P. trichocarpa* × *P. deltoides* failed to find any markers that were significantly associated with gender (McLetchie et al. 1994). The authors suggested that gender might be determined genetically by regions of the genome not sampled by the tested markers or by a complex of loci operating in an additive threshold manner or in an epistatic manner, or that gender is determined environmentally at an early zygote state.

B. Genetic variation

As already mentioned, the genus *Populus* is tremendously varied with species distributed throughout the Northern Hemisphere and the opportunities to generate novel genotypes through hybridisation are enormous. Breeding programs have not hesitated to exploit this genetic variability, although sound quantitative estimates of narrow-sense and broad-sense heritabilities, and covariances among selection criteria would undoubtedly have assisted in making breeding and selection strategies more efficient (Riemenschneider et al. 1996). Poplars are ideal species for quantitative genetics studies, as clonal replication can be readily accomplished to describe complex modes of gene action (Foster and Shaw 1988, Mullin and Park 1992, Bradshaw and Foster 1992). It is thus surprising that genetic variation has been studied in detail for only a few species and traits.

The true potential of poplar species can only be determined by genetic studies designed to resolve variation among and within stands. Unfortunately, the concentration of breeders on interspecific hybridisation has left this field largely ignored, and detailed studies of large natural populations are quite recent and only a few species are well documented (Mohrdiek 1983, Farmer 1991).

B.1 Population-level variability

Considerable clonal variation among populations may be expressed for growth traits and for *Melampsora* rust resistance, but for other characteristics there is often little geographic differentiation. Overall, data from molecular genetic studies suggest that gene flow through migration has been sufficient to prevent genetic drift, inbreeding, and other processes that might give rise to geographic variation unrelated to adaptive selection (Farmer 1996).

Significant variation over a 10° latitudinal transect was observed for phenology (Farmer et al. 1988a), shoot/root allometric coefficients (Schnekenburger and Farmer 1989), and height growth among four provenances of *P. balsamifera*, with southern sources continuing to grow later in the season (Schnekenburger and Farmer 1989, Farmer 1993). These same populations exhibited very little geographic differentiation for isozyme characters (Farmer et al. 1988a), rooting ability (Farmer et al. 1989), and date of bud break (Farmer and Reinholt 1986). Another test series including a more restricted sampling of populations over a 3.5° range found significant population differences accounting for about 12% of the variation in two-year height, leaf morphology, sylleptic branching and pest resistance (Riemenschneider et al. 1992), with populations grouped into north-western, central, and south-eastern clusters (Riemenschneider and McMahon 1993).

Similarly, in *P. tremuloides*, isozyme and RAPD variation studies have shown little differentiation among populations (e.g., Hyun et al. 1987, Lund et al. 1992, Yeh et al. 1995), whereas considerable variation among populations is well-documented for morphology, growth and wood properties (van Buijtenen et al. 1959, Barnes 1969, Einspahr and Winton 1976). Variation among populations generally follows clinal trends, with wood density declining with increasing elevation (Valentine 1962) and from south to north (Einspahr and Benson 1967). A common-garden trial showed that northern and western provenances flushed and ceased growth first, with lower survival when grown in Michigan (Brissette and Barnes 1984), and another showed that better growing clones came from lower Michigan (Reighard and Hanover 1985). There is some evidence of a north-south increase in susceptibility of *P. tremuloides* populations to *Hypoxyylon mammatum* (French and Hart 1978). Populations of *P. tremuloides* also vary with respect to ozone sensitivity, with tolerance correlated to maximum daily ozone levels, as well as annual precipitation and minimum temperature (Berrang et al. 1991).

Geographic variation is also well documented for *P. deltoides*. A wide range provenance trial established in Nebraska, included sources from Texas in the south, to Minnesota in the north and Pennsylvania in the east, and evaluated bark, stem, crown and leaf morphology, in addition to growth and survival (Ying and Bagley 1976). Clinal patterns of variation from north and west to south and east were observed for most traits. Cuttings from Nebraska, Minnesota and Wisconsin produced significantly higher numbers of roots than those from other sources (Ying and Bagley 1977). A similar clinal trend was found in a study of 40 populations in the southern Great Plains, where NW to SE patterns were observed for two-year height, diameter, branching and *Melampsora* rust resistance (Nelson and Tauer 1987). A study of nine populations in Ontario showed great variation in leaf morphology which was unrelated to latitude or longitude, and was not correlated with the moderate allozyme variation that suggested differences between eastern and western populations (Rajora et al. 1991).

A series of studies of *P. trichocarpa* populations in Washington have documented significant variation for leaf, branch and phenology characters (Weber et al. 1985), photosynthetic processes (Dunlap et al. 1993), survival height growth and biomass production (Heilman and Stettler 1985), volume production, *Melampsora* rust resistance and adaptation to arid sites (Dunlap et al. 1994), leaf and crown morphology (Dunlap et al. 1995). A sample of 10 populations over a 4.5° latitudinal range showed only

weak clinal trends for three-year height and diameter (Rogers et al. 1989). Another sample of five riparian populations in Washington showed little difference among populations with respect to flood tolerance of young seedlings and rooted cuttings (Smit 1988).

B.2 Individual-level variability

While the amount of genetic variation among populations differs greatly depending on the trait, the variation within populations is moderate to high for virtually all traits. Unfortunately, most genetic testing has focused on clonal materials without any particular family structure, and these studies have concentrated on the species and hybrids of sections *Tacamahaca* and *Aigeiros*. Generally, only estimates of broad-sense heritability (H^2) are available, and genetic structure is rarely partitioned into additive and non-additive components (Riemenschneider et al. 1996). In the limited number of studies of seedling populations, narrow-sense heritability (h^2) estimates for growth were similar to estimates of H^2 in *P. deltoides* (Farmer 1970, Ying and Bagley 1976, Nelson and Tauer 1987), and much lower in the case of *P. trichocarpa* (Rogers et al. 1989).

A large number of studies of growth and yield characters in *P. deltoides* have produced consistent estimates of H^2 between 0.20 and 0.50, with significant genotype-environment interactions, usually less than half as large as the corresponding genetic main effects (Wilcox and Farmer 1967, Farmer and Wilcox 1968, Mohn and Randall 1971, 1973, Randall and Cooper 1973, Foster 1986). A limited number of clonally replicated trials suggest that much of the genetic variance in yield is non-additive (Foster 1985, Foster and Shaw 1988). Heritability for stem growth in *P. balsamifera* was about $H^2 = 0.50$ (Farmer et al. 1988b). In both *P. deltoides* and *P. balsamifera*, C-effects (*in sensu* Lerner 1958) during the first year were often as large as that due to clones (Wilcox and Farmer 1968, Farmer et al. 1989), but appear to be less important after field planting (Farmer et al. 1988b). Detailed measurements of leaf, branch and phenological characteristics, which are known to affect tree productivity, have been employed to describe ideotypes (Dickmann and Keathley 1996) that may be useful in yield selection of *P. balsamifera* (Riemenschneider et al. 1992), *P. trichocarpa* (Riemenschneider et al. 1994), and hybrids involving *P. deltoides*, *P. nigra* and *P. simonii* (Wu 1994a, b). Indications of the utility of the ideotype concept for yield selection have been inconsistent.

Heritability of rooting and root characters is typically very high, with H^2 estimates as high as 0.85 to 0.91 in *P. deltoides* (Wilcox and Farmer 1968, Ying and Bagley 1977). Other recent studies also indicate high heritability for rooting in *P. trichocarpa* (Riemenschneider et al. 1996).

Much effort has been concentrated on the inheritance of *Melampsora* rust resistance, due to its impact on poplar culture. Early studies of rust resistance in *P. deltoides* gave estimates of h^2 between 0.38 and 0.66, and for H^2 between 0.66 and 0.88 (Jokela 1966). Similarly high estimates for rust resistance or severity have since been reported for *P. deltoides* (Farmer and Wilcox 1968, Thielges and Adams 1975), *P. tremula* and *P. tremuloides* (Gallo et al. 1985), *P. balsamifera* (Riemenschneider et al. 1992), *P. trichocarpa* and its hybrids (Hsiang et al. 1993, Riemenschneider et al. 1994), and hybrids among *P. deltoides*, *P. nigra*, and *P. maximowiczii* (Rajora et al. 1994).

B.3 Molecular genetics

In recent years a great deal of research has been directed towards associating important traits with molecular markers, and in developing corresponding genetic maps (Bradshaw et al. 1994, Cervera et al. 1997). The emphasis of this work has been directed towards adaptive traits (Bradshaw and Stettler,

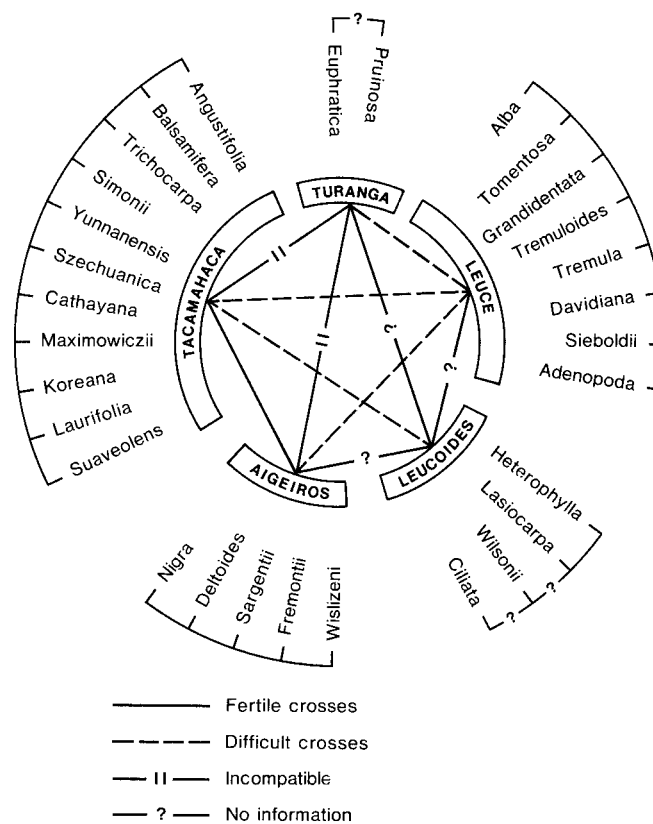
1995) and to resistance to diseases (Villar et al. 1996), and suggests the role of a few quantitative trait loci (QTL's) that have large effects on these quantitative traits.

C. Inbreeding depression and genetic load

Given the high rate of gene flow in poplars, one would expect low rates of inbreeding. A study of 200 clones of *P. tremuloides* in Ontario indicated a deficiency of heterozygotes and an average fixation index of 0.462 (Hyun et al. 1987). However, these results might well be due to a sampling phenomenon, Wahlund's effect, rather than inbreeding. In contrast to these observations, populations of *P. tremuloides* in Alberta, where clonal reproduction is more common, showed an excess of heterozygotes (Cheliak and Dancik 1982, Jelinski and Cheliak 1992). While rates of inbreeding in natural populations may be low, genetic load may be expressed as inbreeding depression in pedigrees of hybrid material, giving rise to distortion of expected Mendelian segregation ratios (Bradshaw and Stettler 1994).

Section VI - Crosses

Figure 1: Crossability of *Populus* species (from Zsuffa 1975)



Extensive crossability studies have been carried out among species in the *Populus*, *Tacamahaca* and *Aigeiros* sections, while few data are available for those in *Turanga* and *Leucoides* (Zsuffa 1975). Interspecific breeding results are summarised in Figure 1.

Hybrids between members of the same section are produced easily and are often more vigorous than their parents. Dramatic examples are the hybrids made between *P. tremuloides* and *P. tremula* (Ilstedt and Gullberg 1993). Crossing success between sections is variable. Crosses between *Aigeiros* and *Tacamahaca* are easy, while those between sections *Populus* and *Aigeiros*, and sections *Populus* and *Tacamahaca* are notoriously difficult, resulting normally in dead seed or dwarfed seedlings (Zsuffa 1975). Crosses between sections are sometimes made more easily using interspecific hybrids, rather than pure species, as parents.

The incompatibility of some species is characterised by arrested development of the pollen tube and failure to penetrate the stigma (Melchior and Seitz 1968, Guries and Stettler 1976, Stettler et al. 1980, Knox 1984, Villar et al. 1987b, Rougier et al. 1992, Villar et al. 1993). This block can be overcome in some cases by mixing the incompatible pollen with “mentor pollen”, i.e., compatible pollen that has been killed by means of gamma radiation (Stettler and Ager 1984, Knox et al. 1987, Villar and Gaget-Faurobert 1996), and by treatment of pollen and stigmas with solvents and extracts from compatible pollen (Whitecross and Willing 1975, Willing and Pryor 1976). This technique has made it possible to obtain crosses of section *Populus* with *Aigeiros* and *Tacamahaca* poplars that are otherwise difficult (Stettler 1968, Zufa 1971, Knox et al. 1972, Willing and Pryor 1976).

Section VII – Ecology and Associated Species

A. Habitat

Poplars are found in a great variety of forest ecosystems, from boreal to sub-tropical, and from mountainous to riparian. In some environments such as boreal forests and in large river valleys, they form large stands, while in other situations they are found as small stands or groups of trees. Although there is some variation among species, essentially all poplars are very intolerant of shade. They are pioneering species and among the first to invade and re-colonise areas disturbed by harvesting, land clearing and fire. The *Populus* species and their hybrids vary greatly in their adaptability to climate, although all are nutrient demanding and perform best with an abundant and continuous supply of moisture (Heilman et al. 1996).

The members of section *Populus* are very broadly distributed and thus found over a tremendous range of climates. In *P. tremuloides*, the southern limit is roughly defined by the 24° C mean July temperature isotherm, while the northern limit corresponds to a mean annual degree-day sum of 700° C, at threshold temperature of 5.6° C (Fowells 1965). Within this range the species occurs where annual precipitation exceeds evapotranspiration. While *P. tremuloides* is found on a variety of soils, ranging from shallow and rocky to deep loamy sands and heavy clays, growth is strongly influenced by drainage and fertility (Perala 1990). Throughout the more restricted range of *P. grandidentata*, moisture is adequate in all seasons, with the least precipitation occurring at the north-west limit on the prairie border in Manitoba with only 510 mm. It is far less adaptable than *P. tremuloides*, developing best on moist, fertile sandy uplands with good aeration (Laidly 1990).

The members of the *Tacamahaca* and *Aigeiros* sections are referred to collectively as the riparian cottonwoods. Species in the *Tacamahaca* section are generally found at higher elevations and latitudes (high river systems of montane and young piedmont valley floodplains) (Braatne et al. 1996). In this section, *P. balsamifera* is the most broadly distributed, withstanding climatic extremes similar to that of *P. tremuloides*. It is usually restricted to moist, low-lying ground, and is one of the few boreal species associated with poorly drained clay soils having pH greater than 7.2 (Dix and Swan 1971, Zasada and Phipps 1990). *P. trichocarpa* is most commonly found in the humid coastal forests of the Pacific Northwest, performing best on deep alluvial soils with abundant moisture, nutrients, oxygen and pH 6.0 to 7.0 (Smith 1957, DeBell 1990). *P. angustifolia* has a very limited range where it is a pioneering species on gravel and sand bars near fast-flowing rivers (Brayshaw 1965).

Members of section *Aigeiros* are limited to lower elevations and latitudes (lower river systems of mature piedmont valley flood plains) (Braatne et al. 1996). The natural range of *P. deltoides* covers a wide southern range, with frost-free days ranging from less than 100 to more than 200, and rainfall from less than 380 mm in the northwest to more than 1,400 mm in the south. This species performs best on moist, well-drained, fine sandy or silt loams, and on sites that are rarely higher than 6 m above the average level of nearby streams (Cooper and Van Haverbeke 1990).

The only North American member of section *Leucooides*, *P. heterophylla*, is found in warm, humid areas with abundant rainfall. It performs best on deep moist soils of shallow swamps and low-lying areas near tidewater, and occupies sites that are too wet for *P. deltoides* (Johnson 1990).

B. Synecology and associated species

Poplars occur in the early successional stages over a wide range of forest ecosystems, so it is no surprise that ecological associations are tremendously diverse. This is particularly true for species in section *Populus*, as they are not restricted to riparian habitats. In Europe, *P. tremula* is the early pioneer. *P. nigra* occurs along rivers and in pastures, together with *Salix alba*, *P. tremuloides* is found in pure stands across its range, but also in mixed stands where it is commonly associated with white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), *P. balsamifera*, and jack pine (*Pinus banksiana*). The associations with shrub and herbaceous species are even more numerous and varied (Perala 1990, Farrar 1995). *P. grandidentata* occurs in small pure stands, but more commonly as an associate in poplar stands with either *P. tremuloides* or *P. balsamifera*. It is a minor component of many other forest types and is thus associated with a wide range of shrubs and ground flora (Laidly 1990, Farrar 1995).

In section *Tacamahaca*, *P. balsamifera* reaches its best development on river flood plains where it occurs as pure stands and is associated with various willows and alders (Viereck et al. 1983). However, it also occurs in mixtures with boreal conifers and several hardwood species, and the associated shrub and herbaceous mixtures are numerous (Zasada and Phipps 1990). *P. trichocarpa* generally occurs in mixtures with larger willows, and to a lesser extent with several western conifers (DeBell 1990). Shrub and herbaceous associates are numerous, but better sites are characterised by beaked hazel (*Corylus cornuta*), elder (*Sambucus* spp.), salmonberry (*Rubus spectabilis*), nettles (*Stachys* spp.), swordfern (*Polystichum munitum*) and lady fern (*Athyrium filix-femina*) (Smith 1957).

On riparian sites, *P. deltoides* tends to grow as essentially pure stands or mixed in open stands with other riparian species. In the area where the species performs best, roughleaf dogwood (*Cornus drummondii*) and swamp-privet (*Forestiera acuminata*) are major shrub associates (Cooper and Van Haverbeke 1990).

C. Competition and stand structure

As mentioned earlier, all poplars are shade intolerant, early successional species, and disturbance is often essential in maintaining many poplar ecosystems. The availability of sites suitable for colonisation, particularly following fires, plays a major role in determining seedling establishment (DeByle and Winokur 1985, Jelinski and Cheliak 1992, Kay 1993). Once established, fire can also remove shade-tolerant competitors, allowing vigorous *P. tremuloides* sprouts to emerge from persistent root systems (Bailey et al. 1990), with densities in excess of 1 million per hectare (Schier et al. 1985). In the absence of disturbance, aspens are regarded as transient, and successional patterns are determined by soil water regime (Roberts and Richardson 1985). Intolerant associates will often out-live aspens, while tolerant hardwoods and conifers will also dominate by virtue of their ability to regenerate under shade.

The riparian cottonwoods are all very flood-tolerant, so that establishment and growth are promoted by the disturbances characteristic of alluvial habitats. In non-alluvial habitats, they take the opportunity to establish on moist agricultural fields, forest clearings and the margins of wetlands, but are eventually dominated by secondary forest species (Braatne et al. 1996). Willows and alders may precede

the establishment of *P. balsamifera*, which is normally then replaced by white spruce (Walker and Chapin 1986, Walker et al. 1986). *P. deltoides* is a very poor competitor, as it is very intolerant of shade, and competes well only with willows, owing to its faster growth except on very wet sites (Cooper and Van Haverbeke 1990).

When established as plantations, poplars and their hybrids must generally be established in pure stands. In addition to being highly intolerant of shade, young poplars cannot tolerate competition from grass, weeds or shrubs. Control of vegetation in the first few years is essential, although poplars are highly sensitive to many herbicides used for vegetation control (Demeritt 1990).

D. Ecosystem dynamics

Poplars coexist with a wide range of insects, but most pose a more serious threat only to artificial populations of planted species and their hybrids. In North America the most serious defoliator, particularly in hybrid plantings, is the cottonwood leaf beetle (*Chrysomela scripta*). Other foliage insects include the forest tent caterpillar (*Malacosoma disstria*), the poplar tent maker (*Ichthyura inclusa*), mourning cloak butterfly larvae (*Nymphalis antiopa*), the large aspen tortrix (*Choristoneura conflictana*), a leaf beetle (*Zeugophora scutellaris*), and the aspen blotch miner (*Phyllocnistis populiella*). The cottonwood twig borer (*Gypsonoma haimbachiana*) is particularly destructive, while several other borers may also do damage. Infestations of poplar gall midge (*Prodiplosis morrisoni*) and many species aphids are also responsible for damage (Dickmann and Stuart 1983, Demeritt 1990). In China, in Ningxia Autonomous Region, it was reported that 24 million trees were destroyed due to attack by the longicorn, *Anoplophora glabripennis* (Chinese National Report, IPC 1996). Several mechanisms are thought to operate to give hybrids more or less resistance relative to their parental species, but as a rule hybrid populations are centres of insect abundance (Whitham et al. 1996).

Other insect pests include:

– Satin moth	<i>Stilpnoia salicis</i>
–	<i>Gluphisia septentrionis</i>
– Viceroy butterfly larvae	<i>Basilarchia archippus</i>
– Gypsy moth	<i>Lymantria dispar</i> [European and Asian varieties]
– Mourningcloak butterfly	<i>Nymphalis antiopa</i>
– Pandemis leafroller	<i>Pandemis pyrusana</i>
– Large aspen tortrix	<i>Christoneura conflictana</i>
– Forest tent caterpillar	<i>Malacosma disstria</i>
– Poplar/willow borer	<i>Chryptorhyuchus lapthi</i>
– Clear-winger poplar borer	<i>Panthrene robiniae</i>
– Poplar borer	<i>Saperda calcerata</i>
– Bronze poplar borer	<i>Agrilus grandulatus lirogus</i>
– Scented willow sawfly	<i>Nematus salicis odoratus</i>
– Phratora leaf Beetle	<i>Phratora californica</i>
– Flea beetle	<i>Altica</i> sp.
– Willamette balley	<i>Corythucha salicata</i>
western willow lace bug	
– Cottonwood twig borer	<i>Gypsonoma haimbachiana</i>
– Aphids	

Further information about insect pest species of poplar can be found in Peterson, et al. 1996, Hiratsuka, 1987, Furniss and Carolin, 1977, Hepting 1971 and USDA Forest Service 1979. A useful Internet website is “<http://ww.cas.psu.edu/docs/CASDEPT/PLANText/poplar.html>”.

The fungi associated with *Populus* species are tremendously diverse. More than 250 species are known to be associated with the decay of *P. tremuloides* alone (Lindsey and Gilbertson 1978). Only fungi associated with sections *Populus*, *Aigeiros*, and *Tacamahaca* have been studied to any extent, and “virtually nothing is known” of those associated with other sections (Newcombe 1996).

The five most damaging or potentially damaging diseases of *Aigeiros* and *Tacamahaca* are:

- Melampsora leaf rust (*Melampsora* spp.) which, while causing only moderate levels of mortality in plantations, can cause volume growth reduction of up to 65% (Widin and Schipper 1981). The situation is now becoming serious in Europe as variability in *Melampsora larici-populina* has been reported and interspecific hybrid trees selected for complete resistance to this fungus are now affected by new races of this pathogen (Pinon 1992a,b, Pinon, 1995, Pinon and Frey 1997);
- *Marssonina anthracnose* or leaf spot (*Marssonina* spp.), affecting *Aigeiros* species and some of their intersectional hybrids in particular, and causing an estimated 16% loss from production plantations in Italy (Thielges 1985);
- Bacterial canker (*Xanthomonas populi* Ridé), causing serious damage to non-native *Aigeiros* and *Tacamahaca* species planted in Europe (Thielges 1985);
- Dothiciza canker (*Discosporium populeum*), of minor importance in North America, but causing wide-spread, heavy losses to *P. × canadensis* clones in Europe (Waterman 1957, Thielges 1985); and
- Septoria leaf spot and canker (*Septoria musiva* Peck), which is generally limited to a leaf spot in native stands but is particularly damaging to hybrids, and has prevented the general use of most *P. × canadensis* clones in Canada, the United States and Argentina (Thielges 1985).

Members of the *Populus* section are most likely to be affected by:

- Hypoxylon stem canker [*Hypoxylon mammatum* (Whal.) Miller] is broadly distributed on host species in section *Populus*, but only becomes a disease problem in certain areas (Manion and Griffin 1986, Newcombe 1996). It sometimes causes cankers on *P. trichocarpa* in Europe (Terrasson et al. 1988) and on various hybrid clones in North America (Ostry and McNabb 1986).
- White-rotting fungus (*Phellinus tremulae* (Bond.) Bond. & Borisov.) causes serious decay in aspens (Thomas et al. 1960), although the mechanism of resistance by members of *Aigeiros* and *Tacamahaca* to decay is unknown (Newcombe 1996).

Various poplar species and hybrids display well-developed adaptations to environmental stress, but in particular to drought, flooding, salinity, cold, and atmospheric pollutants such as ozone (Blake et al. 1996, Neuman et al. 1996). It is also noted that *P. canescens* shows stability against strong winds.

Many mammals feed on the bark, leaves and roots of *Populus*, notably snowshoe hares (*Lepus americanus*), beaver (*Castor canadensis*), porcupine (*Erethizon dorsatum*), pocket gophers (*Thomomys bottae*), and opossum (*Trichosurus vulpecula*) (Edwards 1978, Bryant 1981, Cantor and Whitham 1989, Basey et al. 1990). Ungulates such as deer, moose and elk (*Cervus elaphus*) not only browse on shoots and new sprouts, but also damage bark by chewing and rubbing with their antlers (Romme et al. 1995). Cattle and sheep also browse on regeneration and cause root damage to existing trees when allowed to range through stands (Cooper and Van Haverbeke 1990, Perala 1990). While little is known about the response of mammals to patterns of hybridisation in *Populus*, there is tremendous variation in feeding preference among hybrids and individual clones. It is suspected that this is due to variation in concentrations of phenolic glycosides which are known to be defensive toward mammals (Whitham et al. 1996).

Mice and voles can cause severe damage in young plantations (DeBell 1990). Many species of birds thrive in poplar forests, and a few can cause damage through their feeding. The ruffed grouse and the sharp-tailed grouse feed on aspen buds, and the ruffed grouse also feeds on the leaves during the summer months. Red-breasted and yellow-bellied sapsuckers may scar trees with drill holes as they forage for bark insects (Fowells 1965).

The riparian cottonwoods are one of the most productive and sensitive components of riparian ecosystems in western North America. The number of vertebrate species associated with these communities is four times higher than the numbers associated with spruce-fir, lodgepole pine, or Douglas-fir communities, yet human activities result in the loss of over 100 000 ha of riparian habitat each year (Finch and Ruggiero 1993). While riparian ecosystems occur on less than 1% of the western North American landscape, they provide habitat for more bird species than all other vegetation types combined (Knopf et al. 1988). Zones of hybridisation are thought to be centres of biodiversity (Whitham et al. 1996), representing a refugium for insect species (Whitham 1989), and thus a superior habitat for insectivorous birds (Martinsen and Whitham 1994, Dickson and Whitham 1996).

Section VIII – Summary

The wide distribution of *Populus* throughout the Northern Hemisphere represents an important and valuable component of many forest ecosystems and great potential for domestication. Evolution of the genus has been characterised by divergence into various sections, which offer even more opportunities for novel genetic combinations through hybridisation. Gene flow within the range of the individual species is usually very high, with populations distinguished only by their adaptive response to environmental selection pressures.

While initial establishment is by seeds, which may travel long distances to invade newly disturbed areas, the maintenance of populations often relies on poplar's ability to reproduce vegetatively. Plantation culture of poplars has exploited this trait, and most breeding programs are characterised by deployment of selected clones. Clonal variation is high for yield traits, as well as disease resistance and wood quality.

In North America, *P. tremuloides* is the most widely distributed tree species and an important component of many forest types. The riparian cottonwoods, from sections *Aigeiros* and *Tacamahaca*, play an important role in the maintenance of complex riparian communities, in addition to their importance in plantation culture. Although North American poplar communities are still largely intact, small populations on the edge of species' ranges are in need of conservation. Of even greater concern is the erosion of genetic resources, particularly for *P. nigra*, that has resulted from human activity in Europe.

Poplar is ideally suited as a model organism for understanding growth processes in forest trees. It has and will undoubtedly continue to be a target for domestication and forest management in many parts of the world.

Section IX – References

- Ahuja, M.R. 1987. *In vitro* propagation of poplar and aspen. *In* Cell and tissue culture in forestry. Vol. 3. Edited by J.M. Bonga and D.J. Durzan. Nijhoff, The Hague. pp. 207-223.
- Bailey, A.W., Irving, B.D., and Fitzgerald, R.D. 1990. Regeneration of woody species following burning and grazing in Aspen Parkland. *Journal of Range Management* 43: 212-215.
- Barnes, B.V. 1966. The clonal growth habit of American aspens. *Ecology*, 47: 439-447.
- Barnes, B.V. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern Lower Michigan. *Silvae Genet.* 18: 130-142.
- Barnes, B.V. 1975. Phenotypic variation of trembling aspen in western North America. *For. Sci.* 21: 319-328.
- Barnes, B.V., and Han, F.Q. 1993. Phenotypic variation of Chinese aspens and their relationship to similar taxa in Europe and North America. *Can. J. Bot.* 71: 799-815.
- Basey, J.M., Jenkins, S.H., and Miller, G.C. 1990. Food selection by beavers in relation to inducible defenses of *Populus tremuloides*. *Oikos* 59: 57-62.
- Benson, M.K., and Schwalbach, D.E. 1970. Techniques for rooting aspen root sprouts. *Tree Plant. Notes*, 21: 12-14.
- Berrang, P., Karnosky, D.F., and Bennett, J.P. 1991. Natural selection for ozone tolerance in *Populus tremuloides*: an evaluation of nationwide trends. *Can. J. For. Res.* 21: 1091-1097.
- Bisoffi, S., and Gullberg, U. 1996. Poplar breeding and selection strategies. *In* *Biology of Populus and its implications for management and conservation*. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 139-158.
- Blackburn, K.B., and Harrison, J.W.H. 1924. A preliminary account of the chromosomes and chromosome behaviour in the Salicaceae. *Ann. Bot.* 38: 361-378.
- Blake, T.J., Sperry, J.S., Tschaplinski, T.J., and Wang, S.S. 1996. Water relations. *In* *Biology of Populus and its implications for management and conservation*. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 401-422.
- Braatne, J.H., Rood, S.B., and Heilman, P.E. 1996. Life history, ecology and conservation of riparian cottonwoods in North America. *In* *Biology of Populus and its implications for management and conservation*. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 57-85.

- Bradshaw, H.D. and Foster, G.S. 1992. Marker-aided selection and propagation systems in trees: advantages of cloning for studying quantitative inheritance. *Can. J. For. Res.* 22: 1044-1049.
- Bradshaw, H.D., Jr., and Stettler, R.F. 1993. Molecular genetics of growth and development in *Populus*. I. Triploidy in hybrid poplars. *Theor. Appl. Genet.* 86: 301-307.
- Bradshaw, H.D., Jr., and Stettler, R.F. 1994. Molecular genetics of growth and development in *Populus*. II. Segregation distortion due to genetic load. *Theor. Appl. Genet.* 89: 551-558.
- Bradshaw, H.D., Villar, M., Watson, B., Otto, K., Stewart, S., and Stettler, R. F. 1994. Molecular genetics of growth and development in *Populus*. III. A genetic linkage map of a hybrid poplar composed of RFLP, STS and RAPD markers. *Theor. Appl. genet.* 89: 167-178.
- Bradshaw, H.D., Jr., and Stettler, R.F. 1995. Molecular genetics of growth and development in *Populus*. IV. Mapping QTLs with large effects on growth, form, and phenology traits in a forest tree. *Genetics* 139: 963-973.
- Brayshaw, T.C. 1965. Native poplars of southern Alberta and their hybrids. Publ. No. 1109, Department of Forestry, Ottawa. 40 pp.
- Brissette, J.C., and Barnes, B.V. 1984. Comparisons of phenology and growth of Michigan and western North American sources of *Populus tremuloides*. *Can. J. For. Res.* 14: 789-793.
- Browicz, K. 1966. *Populus ilicifolia* (Engler) Rouleau and its taxonomic position. *Acta Soc. Bot. Poloniae*, 35: 325-335.
- Bryant, J.P. 1981. Phytochemical deterrence of snowshoe hare browsing by adventitious shoots of four Alaskan trees. *Science*, 313: 889-890.
- Burns, R.M., and Honkala, B.H. 1990. *Silvics of North America*. Agriculture Handbook 654, Forest Service, USDA, Washington, DC. 877 pp.
- Burr, K.E. 1986. Greenhouse production of quaking aspen seedlings. *In* Gen. Tech. Rep. RM-125. Rocky Mtn. For. Range Exp. Sta., USDA For. Serv. pp. 31-37.
- Cagelli, L., and Lefèvre, F. 1996. The conservation of *Populus nigra* L. and gene flow with cultivated poplars in Europe. *Forest Genetics*, 2:135-144
- Cantor, L.F., and Whitham, T.G. 1989. Importance of belowground herbivory: pocket gophers may limit aspen to rock outcrop refugia. *Ecology*, 70: 962-970.
- Cervera, M. T., Villar, M. Faivre-Rampant, P., Goué, M. C., Van Montagu, M. and Boerjan, W. 1997. Applications of molecular marker technologies in *Populus* breeding. *In* Micropropagation, Genetic Engineering, and Molecular Biology of *Populus*. Gen. tech. Rep. RM-GTR-297, Fort Collins, CO:USDA, Forest Service, : Klopfenstein, N. B. Chun, Y. W., Kim, M. S. and Ahuja, M. R. *Edited by*, Dillon, M. C., Carman, R. C. and Eskew, L. G.(tech. eds.) pp 101-116.

- Cheliak, W.M., and Dancik, B.P. 1982. Genic diversity of natural populations of a clone-forming tree *Populus tremuloides*. *Can. J. Genet. Cytol.* 24: 611-616.
- Collinson, M.E. 1992. The early fossil history of the Salicaceae. *Proc. Roy. Soc. Edinburgh Sect. B (Biol. Sci.)*, 98: 155-177.
- Cooper, D.T., and Van Haverbeke, D.F. 1990. *Populus deltoides* Bartr. ex Marsh. Eastern cottonwood. *In* *Silvics of North America. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala. Agriculture Handbook 654, Forest Service, USDA, Washington, DC.* pp. 530-543.
- Cwynar, L.C. 1988. Late Quaternary vegetation history of Kettlehole Pond, southwestern Yukon. *Can. J. For. Res.* 18: 1270-1279.
- Darlington, C.D., and Wylie, A.P. 1956. *Chromosome atlas of flowering plants.* MacMillan Co., New York.
- DeBell, D.S. 1990. *Populus trichocarpa* Torr. & Gray. Black cottonwood. *In* *Silvics of North America. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala. Agriculture Handbook 654, Forest Service, USDA, Washington, DC.* pp. 570-576.
- DeByle, N.V., and Winokur, R.P. 1985. *Aspen: ecology and management in the western United States.* Gen. Tech. Rep. RM-119, USDA Forest Service, Fort Collins, CO. 283 pp.
- Demeritt, M.E., Jr. 1990. *Populus* L. Poplar hybrids. *In* *Silvics of North America. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala. Agriculture Handbook 654, Forest Service, USDA, Washington, DC.* pp. 577-582.
- Dickmann, D.I., and Keathley, D.E. 1996. Linking physiology, molecular genetics, and the *Populus* ideotype. *In* *Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council of Canada, Ottawa, ON.* pp. 491-514.
- Dickmann, D.I., and Stuart, K.W. 1983. *Culture of hybrid poplars in northeastern North America.* Michigan State University, Department of Forestry, East Lansing, MI. 168 pp.
- Dickson, L.L., and Whitham, T.G. 1996. Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia*, 106: 400-406.
- Dirr, M.A., and Heuser, C.W., Jr. 1987. *The reference manual of woody plant propagation: from seed to tissue culture.* Varsity Press, Athens, GA. 239 pp.
- Dix, R.L., and Swan, H.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. *Can. J. Bot.* 49: 657-676.
- Dunlap, J.M., Braatne, J.H., Hinkley, T.M., and Stettler, R.F. 1993. Intraspecific variation in photosynthetic traits of *Populus trichocarpa*. *Can. J. Bot.* 71: 1304-1311.
- Dunlap, J.M., Heilman, P.E., and Stettler, R.F. 1994. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. VII. Two-year survival and growth of native black cottonwood clones from four river valleys in Washington. *Can. J. For. Res.* 24: 1539-1549.

- Dunlap, J.M., Heilman, P.E., and Stettler, R.F. 1995. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. VIII. Leaf and crown morphology of native *P. trichocarpa* clones from four river valleys in Washington. *Can. J. For. Res.* 25: 1710-1724.
- Eckenwalder, J.E. 1977. North American cottonwoods (*Populus*, Salicaceae) of sections *Abaso* and *Aigeriros*. *J. Arnold Arboretum* 58: 193-208.
- Eckenwalder, J.E. 1984a. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. I. Population studies of *P. X parryi*. *Can. J. Bot.* 62: 317-324.
- Eckenwalder, J.E. 1984b. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigeiros* and *Tacamahaca*. III. Paleobotany and evolution. *Can. J. Bot.* 62: 336-342.
- Eckenwalder, J.E. 1984c. Natural intersectional hybridization between North American species of *Populus* (Salicaceae) in sections *Aigerios* and *Tacamahaca*. II. Taxonomy. *Can. J. Bot.* 62: 325-335.
- Eckenwalder, J.E. 1996. Systematics and evolution of *Populus*. In *Biology of Populus and its implications for management and conservation*. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 7-32.
- Edwards, W.R.N. 1978. Effect of salicin content on palatability of *Populus* foliage to opossum (*Trichosurus vulpecula*). *N. Z. J. Sci.* 21: 103-106.
- Einspahr, D.W., and Benson, M.K. 1967. Geographic variation of quaking aspen in Wisconsin and Upper Michigan. *Silvae Genet.* 16: 106-112.
- Einspahr, D.W., and Winton, L.L. 1976. Genetics of quaking aspen. Res. Pap. WO-25, USDA For. Serv. 23 pp.
- Einspahr, D.W., van Buijtenen, J.P., and Peckham, J.R. 1963. Natural variation and heritability in triploid aspen. *Silvae Genet.* 12: 51-58.
- Farmer, R.E., Jr. 1964a. Cottonwood flowering as related to cold requirements of flower buds. *For. Sci.* 10: 296-299.
- Farmer, R.E., Jr. 1964b. Sex ratio and sex-related characteristics in eastern cottonwood. *Silvae Genet.* 13: 116-118.
- Farmer, R.E., Jr. 1966. Variation in time of flowering and seed dispersal of eastern cottonwood in the lower Mississippi Valley. *For. Sci.* 12: 343-347.
- Farmer, R.E., Jr. 1970. Genetic variation among open-pollinated progeny of eastern cottonwood. *Silvae Genet.* 19: 149-151.
- Farmer, R.E., Jr. 1976. Sexual reproduction of eastern cottonwood. In *Proceedings of Symposium on Eastern Cottonwood and Related Species*, Greenville, Mississippi. Louisiana State Univ., Baton Rouge, LA. pp. 89-98.

- Farmer, R.E., Jr. 1991. Genetic improvement of poplar in western Canada: alternatives, opportunities, and pitfalls. *In Aspen management for the 21st century. Edited by S. Navratil and P.B. Chapman.* pp. 129-134.
- Farmer, R.E., Jr. 1993. Latitudinal variation in height and phenology of balsam poplar. *Silvae Genet.* 42: 148-153.
- Farmer, R.E., Jr. 1996. Geneecology of *Populus*. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley.* NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 33-55.
- Farmer, R.E., Jr., and Pitcher, J.A. 1981. Pollen handling for Southern hardwoods. *In Pollen management handbook. Edited by E.C. Franklin.* Agriculture Handbook 587, USDA For. Serv., Washington, DC. pp. 77-83.
- Farmer, R.E., Jr., and Reinholt, R.W. 1986. Genetic variation in dormancy relations of balsam poplar along a latitudinal transect in northwestern Ontario. *Silvae Genet.* 35: 38-42.
- Farmer, R.E., Jr., and Wilcox, J.R. 1968. Preliminary testing of eastern cottonwood clones. *Theor. Appl. Genet.* 38: 197-201.
- Farmer, R.E., Jr., Cheliak, W.M., Perry, D.J., Knowles, P., Barrett, J., and Pitel, J.A. 1988a. Isozyme variation in balsam poplar along a latitudinal transect in northwestern Ontario. *Can. J. For. Res.* 18: 1078-1081.
- Farmer, R.E., Jr., Garlick, K., and Watson, S. 1988b. Heritability and C effects in a 3-year-old balsam poplar clonal test. *Can. J. For. Res.* 18: 1059-1062.
- Farmer, R.E., Jr., Freitag, M., and Garlick, K. 1989. Genetic variance and 'C' effects in balsam poplar rooting. *Silvae Genet.* 38: 62-65.
- Farrar, J.L. 1995. Trees in Canada. Fitzhenry & Whiteside/Canadian Forest Service, Markham and Ottawa.
- Fechner, G.H., Burr, K.E., and Myers, J.F. 1981. Effects of storage, temperature, and moisture stress on seed germination and early seedlings development of trembling aspen. *Can. J. For. Res.* 11: 718-722.
- Finch, D.M., and Ruggiero, L.F. 1993. Wildlife habitats and biological diversity in the Rocky Mountains and the northern Great Plains. *Natural Areas Journal* 13: 191-203.
- Foster, G.S. 1985. Genetic parameters for two eastern cottonwood populations in the lower Mississippi Valley. *In Proceedings of the 18th Southern Forest Tree Improvement Conference, 21-23 May 1985, Long Beach, MS. Edited by R.C. Schmidting and M.M. Griggs.* pp. 258-266.
- Foster, G.S. 1986. Provenance variation of eastern cottonwood in the lower Mississippi Valley. *Silvae Genet.* 35: 32-38.
- Foster, G.S., and Shaw, D.V. 1988. Using clonal replicates to explore genetic variation in a perennial plant species. *Theor. Appl. Genet.* 76: 788-794.

- Fowells, H.A. 1965. Silvics of forest trees of the United States. Agricultural Handbook No. 271, Forest Service, USDA, Washington, DC. 762 pp.
- French, J.R., and Hart, J.H. 1978. Variation in resistance of trembling aspen to *Hypoxyylon mammatum* identified by inoculating naturally occurring clones. *Phytopathology*, 68: 485-489.
- Fröhlich, H., and van der Meiden, H.A. 1979. Propagation of poplars: nursery techniques. *In* Poplars and willows in wood production and land use. Food and Agriculture Organization of the United Nations, Rome. pp. 88-106.
- Fröhlich, H.J., and Weisgerber, H. 1985. Research on *in vitro* techniques within the framework of poplar breeding - results and future trends. *Silvae Genet.* 34: 132-137.
- Furniss, R. L. and Carolin, V. M. 1977. Western Forest Insects. USDA Forest Service Miscellaneous Publication No. 1339.
- Gallo, L.A., Stephan, B.R., and Krusche, D. 1985. Genetic variation of *Melampsora* leaf rust resistance in progenies of crossings between and within *Populus tremula* and *P. tremuloides* clones. *Silvae Genet.* 34: 208-214.
- Grant, M.C., and Mitton, J.B. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolution*, 33: 914-918.
- Grant, M.C., Mitton, J.B., and Linhart, Y.B. 1992. Even larger organisms. *Nature*, 360: 216.
- Guries, R.P., and Stettler, R.F. 1976. Prefertilization barriers to hybridization in the poplars. *Silvae Genet.* 25: 37-43.
- Hall, R.B., Colletti, J.P., Schultz, R.C., Faltonson, R.R., Kolison, S.H., Jr., Hanna, R.D., Hillson, T.D., and Morrison, J.W. 1989. Commercial-scale vegetative propagation of aspens. *In* Proceedings of Aspen Symposium, 25-27 July 1989, Duluth, MN. Gen. Tech. Rep. NC-140, USDA Forest Service, Duluth, MN. pp. 211-219.
- Heilman, P.E., and Stettler, R.F. 1985. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. II. Biomass production in a 4-year plantation. *Can. J. For. Res.* 15: 384-388.
- Heilman, P.E., Hinckley, T.M., Roberts, D.A., and Ceulemans, R. 1996. Production physiology. *In* Biology of *Populus* and its implications for management and conservation. *Edited by* R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 459-489.
- Heimbürger, C. 1936. Report on poplar hybridization. *For. Chron.* 12: 285-290.
- Heimbürger, C. 1968. Poplar breeding in Canada. *In* Growth and utilization of poplars in Canada. Publ. No. 1205, Can. For. Bra. pp. 88-100.
- Hellum, A.K. 1973. Seed storage and germination of balsam poplar. *Can. J. Plant Sci.* 53: 227-228.

Hepting, G. H. 1971. Diseases of Forest Shade Trees of the United States. USDA Forest Service Agricultural Handbook No. 386.

Hiratsuka, Y. 1987. Forest Tree Diseases of the Prairie Provinces. Can. For. Serv., North For. Cent., Edmonton, Alberta. Inf. Rep. NOR-X-286. ISBN 0-662-15281-6, ISSN 0704-7673.

Hsiang, T., Chastagner, G.A., Dunlap, J.M., and Stettler, R.F. 1993. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. VI. Field susceptibility of seedlings to *Melampsora occidentalis* leaf rust. Can. J. For. Res. 23: 436-441.

Hyun, J.O., Rajora, O.P., and Zsuffa, L. 1987. Genetic variation in trembling aspen in Ontario based on isozyme studies. Can. J. For. Res. 17: 1134-1138.

Ilstedt, B., and Gullberg, U. 1993. Genetic variation in a 26-year-old hybrid aspen trial in southern Sweden. Scand. J. For. Res. 8: 185-192.

[IPC] International Poplar Commission. 1992. Proceedings Working Party on Breeding and Selection of Poplars and Willows, 19th Session IPC, Zaragoza, Spain, 22-25 September 1992. International Poplar Commission.

[IPC] International Poplar Commission. 1996. Synthesis of national reports on activities related to poplar and willow areas, production, consumption and the functioning of the National Poplar Commissions. Secretariat Note, 20th Session, Budapest, Hungary, 2-4 October 1996, International Poplar Commission. 10 pp.

Jackson, D.I., and Sweet, G.B. 1972. Flower initiation in temperate wood plants: a review based largely on the literature of conifers and deciduous fruit trees. Horticult. Abstr. 42: 9-24.

Jelinski, D.E., and Cheliak, W.M. 1992. Genetic diversity and spatial subdivision of *Populus tremuloides* (Salicaceae) in a heterogeneous landscape. Amer. J. Bot. 79: 728-736.

Johnson, R.L. 1990. *Populus heterophylla* L. Swamp cottonwood. In *Silvics of North America*. Vol. 2, Hardwoods. Edited by R.M. Burns and B. H. Honkala. Agriculture Handbook 654, Forest Service, USDA, Washington, DC. pp. 551-554.

Jokela, J.J. 1966. Incidence and heritability of *Melampsora* rust in a seedling plantation of hybrid poplar. In *Breeding pest resistant trees*. Edited by H.D. Gerhold, E.J. Schriener, R.E. McDermott and J.A. Winieski. Pergamon Press, Oxford, UK. pp. 111-117.

Jones, J.R. 1985. Distribution. In *Aspen: ecology and management in the western United States*. Edited by N.V. DeByle and R.P. Winokur. Gen. Tech. Rep. RM-119, USDA Forest Service, Fort Collins, CO. pp. 9-10.

Kaul, R.B. 1995. Reproductive structure and organogenesis in a cottonwood, *Populus deltoides* (Salicaceae). Int. J. Plant Sci. 156: 172-180.

Kay, C.E. 1993. Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. Northwest Sci. 67: 94-104.

Keenan, T.J., and Cwynar, L.C. 1992. Late Quaternary history of black spruce and grasslands in southwest Yukon Territory. Can. J. Bot. 70: 1336-1345.

- Kemperman, J.A., and Barnes, B.V. 1976. Clone size in American aspens. *Can. J. Bot.* 54: 2603-2607.
- Khosla, P.K., and Khurana, K.D. 1982. Evolution of genus *Populus* L. and systematic placement of *P. ciliata* Wall. ex Royle. *J. Tree Sci.* 1: 81-87.
- Knopf, F.L., Johnson, R.R., Rich, T., Samson, F.B., and Szaro, R.C. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bull.* 100: 272-284.
- Knox, R.B. 1984. Pollen-pistil interactions. *In Cellular interactions. Edited by H.F. Linskens and J. Heslop-Harrison.* Springer Verlag, Berlin. pp. 508-608.
- Knox, R.B., Willing, R.R., and Pryor, L.D. 1972. Interspecific hybridization in poplars using recognition pollen. *Silvae Genet.* 21: 65-69.
- Knox, R.B., Gaget, M., and Dumas, C. 1987. Mentor pollen techniques. *Int. Rev. Cytol.* 107: 315-332.
- Kouider, M., Skirvin, R.M., Saladin, K.P., Dawson, J.O., and Jokela, J.J. 1984. A method to culture immature embryos of *Populus deltoides* *in vitro*. *Can. J. For. Res.* 14: 956-958.
- Krüssmann, G. 1985. Manual of cultivated broad-leaved trees and shrubs. Vol. II, E-PRO. Timber Press, Portland, OR. 445 pp. [Translated by M.E. Epp from the 1977 German edition]
- Laidly, P.R. 1990. *Populus grandidentata* Michx. Bigtooth aspen. *In Silvics of North America. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala.* Agriculture Handbook 654, Forest Service, USDA, Washington, DC. pp. 544-550.
- Legionnet, A., Faivre-Rampant, P. Villar, M. and Lefèvre, F. 1997. Sexual and asexual reproduction in natural stands of *Populus nigra*. *Bot. Acta* 110: 257-263.
- Larsen, C.S. 1956. Genetics in silviculture. Oliver and Boyd, Edinburgh. [Translated by M.L. Anderson]
- Lerner, I.M. 1958. The genetic basis of selection. John Wiley & Sons, New York. 298 pp.
- Lester, D.T. 1963a. Floral initiation and development in quaking aspen. *For. Sci.* 9: 323-329.
- Lester, D.T. 1963b. Variation in sex expression in *Populus tremuloides* Michx. *Silvae Genet.* 12: 141-151.
- Li, B. 1995. Aspen improvement strategies for western Canada - Alberta and Saskatchewan. *For. Chron.* 71: 720-724.
- Li, B., and Wyckoff, G.W. 1991. A breeding strategy to improve aspen hybrids for the University of Minnesota Aspen/Larch Genetics Cooperative. *In Proceedings of the International Energy Agency 1991 Joint Meeting of the Task V Activity Groups on Exchange of Genetic Material, Disease/Management, and Joint Trials of *Alnus*, *Populus*, and *Salix*, 22-27 August, 1991.* Iowa State University, Ames, Iowa. pp. 33-41.
- Li, B., Wyckoff, G.W., and Einspahr, D.W. 1993. Hybrid aspen performance and genetic gains. *North. J. Appl. For.* 10: 117-122.

- Lindsey, J.P., and Gilbertson, R.L. 1978. Basidiomycetes that decay aspen in North America. *Bibl. Mycol.* 63: 1-406.
- Lund, S.T., Furnier, G.R., and Mohn, C.A. 1992. Isozyme variation in quaking aspen in Minnesota. *Can. J. For. Res.* 22: 521-524.
- Manion, P.D., and Griffin, D.H. 1986. Sixty-five years of research on *Hypoxylon canker* of aspen. *Plant Disease*, 70: 803-808.
- Martinsen, G.D., and Whitham, T.G. 1994. More birds nest in hybrid cottonwoods. *Wilson Bull.* 106: 474-481.
- McDonough, W.T. 1979. Quaking aspen - seed germination and early seedling growth. Res. Pap. INT-234, USDA For. Serv., Ogden, UT. 13 pp.
- McDonough, W.T. 1985. Sexual reproduction, seeds and seedlings. *In Aspen: ecology and management in the western United States. Edited by N.V. DeByle and R.P. Winokur. Gen. Tech. Rep. RM-119, USDA Forest Service, Fort Collins, CO.*
- McLetchie, D.N., Tuskan, G.A., and Dietrichson, J. 1994. Gender determination in *Populus*. *Norweigan J. Agric. Sci.* 18: 57-66.
- Melchior, G.H. 1967. Zwei Funde von Zwitterigkeit an Pappeln der Sektion *Aigeiros*. *Silvae Genet.* 16: 77-80.
- Melchior, G.H., and Seitz, F.W. 1968. Interspezifische Kreuzungssterilität innerhalb der Pappelsektion *Aigeiros*. *Silvae Genet.* 17: 88-93.
- Michler, C. H. and Bauer, E.O. 1991. High frequency somatic embryogenesis from leaf tissue of *Populus* spp. *Plant Science* 77: 111-118.
- Mitton, J.B., and Grant, M.C. 1980. Observations on the ecology and evolution of quaking aspen *Populus tremuloides*, in the Colorado front range. *Amer. J. Bot.* 67: 202-209.
- Mitton, J.B., and Grant, M.C. 1996. Genetic variation and the natural history of quaking aspen. *BioScience*, 46: 25-31.
- Mohn, C.A., and Randall, W.K. 1971. Inheritance and correlation of growth characters in *Populus deltoides*. *Silvae Genet.* 20: 182-184.
- Mohn, C.A., and Randall, W.K. 1973. Interaction of cottonwood clones with site and planting year. *Can. J. For. Res.* 3: 329-332.
- Mohrdiek, O. 1983. Discussion: future possibilities for poplar breeding. *Can. J. For. Res.* 13: 465-471.
- Morley, P.M., and Balatinecz, J.J. 1993. Poplar utilization in Canada: past, present and future. *For. Chron.* 69: 46-52.
- Mühle Larsen, C. 1960. L'Amélioration du peuplier par voie génétique. Extrait de bulletin de la Société Royale Forestière de Belgique, Mars-Avril: 48 pp.

- Müntzing, A. 1936. The chromosomes of a giant *Populus tremula*. *Hereditas*, 21: 383-393.
- Muller, C., and Tessier du Cros, E. 1982. Storage of *Populus nigra* seed for five years. *Ann. Sci. For.* 39: 179-185.
- Mullin, T.J., and Park, Y.S. 1992. Estimating genetic gains from alternative breeding strategies for clonal forestry. *Can. J. For. Res.* 22: 14-23.
- Nagaraj, M. 1952. Floral morphology of *Populus deltoides* and *P. tremuloides*. *Bot. Gaz.* 114: 222-243.
- Nelson, C.D., and Tauer, C.G. 1987. Genetic variation in juvenile characters of *Populus deltoides* Bartr. from the southern Great Plains. *Silvae Genet.* 36: 216-221.
- Neuman, D.S., Wagner, M., Braatne, J.H., and Howe, J. 1996. Stress physiology -- abiotic. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley.* NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 423-458.
- Newcombe, G. 1996. The specificity of fungal pathogens of *Populus*. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley.* NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 223-246.
- Ostry, M.E., and McNabb, H.S., Jr. 1986. *Populus* species and hybrid clones resistant to *Melampsora*, *Marssonina*, and *Septoria*. Res. Pap. NC-272, North Central Forest Experiment Station, USDA Forest Service. 6 pp.
- Owens, J.N., and Blake, M.D. 1985. Forest tree seed production. Inform. Rep. PI-X-53, Petawawa National Forestry Institute, Can. For. Serv., Chalk River, ON. 161 pp.
- Pauley, S.S. 1950. Flowering habits in *Populus*. *Genetics*, 35: 684. [abstract]
- Perala, D.A. 1990. *Populus tremuloides* Michx. Quaking aspen. *In Silvics of North America. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala.* Agriculture Handbook 654, Forest Service, USDA, Washington, DC. pp. 555-569.
- Peterson, E.B., Peterson, N. M., and McLennan, D. S. 1996 (March). Black Cottonwood and Balsam Poplar Manger's Handbook for British Columbia. FRDA Report #250. ISSN 0-7726-2952-8.
- Peto, F.H. 1938. Cytology of poplar species and natural hybrids. *Can. J. Res. (Sec. C)* 16: 445-455.
- [PCC] Poplar Council of Canada. 1996a. Activities related to poplar and willow cultivation, exploitation and utilization. Canadian report to the 20th session of the International Poplar Commission, Canadian Forest Service, Poplar Council of Canada, Ottawa, ON. 12 pp.
- [PCC] Poplar Council of Canada. 1996b. Environmental and social issues in poplar and willow growing and utilization. Canadian report on the theme of the 20th session of the International Poplar Commission, Canadian Forest Service, Poplar Council of Canada, Ottawa, ON. 12 pp.

- Pinon, J. 1992a. Variability in the genus *Populus* in sensitivity to rusts. *Silvae Genet.* 41: 25-34.
- Pinon, J. 1992b. Frequency and evolution of *Melampsora larici-populina* Klebahn races in North-Western France. *Ann. Sci. For.* 49: 1-15.
- Pinon, J. 1995. Présence en France d'une nouvelle race de *Melampsora larici-populina*, agent de la rouille foliaire des peupliers cultivés. *Rev. For. Fr.* 47: 230-234.
- Pinon, J. and Frey, P. 1997. Structure of *Melampsora larici-populina* populations on wild and cultivated poplar. *Eur. J. Plant. Pathol.* 103: 159-173.
- Pinon, J. and Valadon, A. 1997. Comportement des cultivars de peupliers commercialisables dans l'Union Européenne vis-à-vis de quelques parasites majeurs. *Ann. Sci. For.* 54: 19-38.
- Rajora, O.P., Zsuffa, L., and Dancik, B.P. 1991. Allozyme and leaf morphological variation of eastern cottonwood at the northern limits of its range in Ontario. *For. Sci.* 37: 688-702.
- Rajora, O.P., Zsuffa, L., and Yeh, F.C. 1994. Variation, inheritance and correlations of growth characters and *Melampsora* leaf rust resistance in full-sib families of *Populus*. *Silvae Genet.* 43: 219-226.
- Randall, W.K., and Cooper, D.T. 1973. Predicted genotypic gain from cottonwood clonal tests. *Silvae Genet.* 22: 165-167.
- Raquin, C., Troussard, L., and Villar, M. 1993. In-ovary embryo culture as a tool for poplar hybridization. *Can. J. Bot.* 71: 1271-1275.
- Reighard, G.W., and Hanover, W. 1985. Progeny testing of native aspens and their hybrids for biomass production in Michigan. *In Proceedings 29th Northeastern Forest Tree Improvement Conference, Morgantown, WV, 1984.* pp. 5-22.
- Riemenschneider, D.E., and McMahon, B.G. 1993. Genetic variation among Lake States balsam poplar populations is associated with geographic origin. *For. Sci.* 39: 130-136.
- Riemenschneider, D.E., McMahon, B.G., and Ostry, M.E. 1992. Use of selection indices to increase tree height and to control damaging agents in 2-year-old balsam poplar. *Can. J. For. Res.* 22: 561-567.
- Riemenschneider, D.E., McMahon, B.G., and Ostry, M.E. 1994. Population-dependent selection strategies needed for 2-year-old black cottonwood clones. *Can. J. For. Res.* 24: 1704-1710.
- Riemenschneider, D.E., Stelzer, H.E., and Foster, G.S. 1996. Quantitative genetics of poplars and poplar hybrids. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley.* NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 159-181.
- Roberts, M.R., and Richardson, C.J. 1985. Forty-one years of population change and community succession in aspen forests on four soil types, northern lower Michigan, USA. *Can. J. Bot.* 63: 1641-1651.

- Rogers, D.L., Stettler, R.F., and Heilmann, P.E. 1989. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. III. Structure and pattern of variation in a 3-year field test. *Can. J. For. Res.* 19: 372-377.
- Romme, W.H., Turner, M.G., Wallace, L.L., and Walker, J.S. 1995. Aspen, elk, and fire in northern Yellowstone National Park. *Ecology*, 76: 2097-2106.
- Rood, S.B., Campbell, J.S., and Despins, T. 1986. Natural poplar hybrids from southern Alberta. I. Continuous variation for foliar characteristics. *Can. J. Bot.* 64: 1382-1388.
- Rougier, M., Jnoud, N., Said, C., Russell, S., and Dumas, C. 1992. Interspecific incompatibility in *Populus*: inhibition of tube growth and behaviour of the male germ unit in *P. deltoides* X *P. alba*. *Protoplasma*, 168: 107-112.
- Sargent, C.S. 1965. *Manual of the trees of North America (exclusive of Mexico)*. Dover, New York. 934 pp.
- Savka, M.A., Dawson, J.O., Jokela, J.J., and Skirvin, R.M. 1987. A liquid culture method for rescuing immature embryos of eastern cottonwood. *Plant Cell Tissue Org. Cult.* 10: 221-226.
- Schier, G.A. 1973. Origin and development of aspen root suckers. *Can. J. For. Res.* 3: 45-53.
- Schier, G.A., Jones, J.R., and Winokur, R.P. 1985. Vegetative regeneration. *In Aspen: ecology and management in the western United States. Edited by N.V. DeByle and R.P. Winokur. Gen. Tech. Rep. RM-119, USDA Forest Service, Fort Collins, CO.*
- Schnekenburger, F., and Farmer, R.E., Jr. 1989. Genetic variance in growth of balsam poplar under 16- and 8-hour photosynthetic periods. *For. Sci.* 35: 903-919.
- Schreiner, E.J. 1974. *Populus* L. -- Poplar. *In Seeds of woody plants in the United States. Edited by C.S. Schopmeyer. Agricultural Handbook No. 450, Forest Service, USDA, Washington, DC. pp. 645-655.*
- Seitz, F.W. 1958. Frühtreibversuche mit Blühreisern der Aspe. *Silvae Genet.* 7: 102-105.
- Smit, B.A. 1988. Selection of flood-resistant and susceptible seedlings of *Populus trichocarpa* Torr. & Gray. *Can. J. For. Res.* 18: 271-275.
- Smith, E.C. 1943. A study of the cytology and speciation in the genus *Populus*. *J. Arnold Arboretum* 24: 275-304.
- Smith, J.H.G. 1957. Some factors indicative of site quality for black cottonwood (*Populus trichocarpa* Torr. and Gray). *J. For.* 55: 578-580.
- Smith, R.L., and Symata, K.J. 1990. Evolution of *Populus nigra* (sect. *Aigeiros*): introgressive hybridization and the chloroplast contribution of *Populus alba* (sect. *Populus*). *Amer. J. Bot.* 77: 1176-1187.
- Stanton, B.J., and Villar, M. 1996. Controlled reproduction of *Populus*. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 113-138.*

- Steenackers, V. 1996. Towards a global management of poplar genetic resources. Presentation at 20th Session of the International Poplar Commission, Budapest, Hungary, 1-4 October 1996, International Poplar Commission. 11 pp.
- Stettler, R.F. 1968. Irradiated mentor pollen: its use in remote hybridization of black cottonwood. *Nature*, 219: 746-747.
- Stettler, R.F., and Ager, A.A. 1984. Mentor effects in pollen interactions. *In Cellular interactions. Edited by H.F. Linskens and J. Heslop-Harrison.* Springer Verlag, Berlin. pp. 609-623.
- Stettler, R.F., Koster, R., and Steenackers, V. 1980. Interspecific crossability studies in poplars. *Theor. Appl. Genet.* 58: 273-282.
- Stettler, R.F., Fenn, R.C., Heilman, P.E., and Stanton, B.J. 1988. *Populus trichocarpa* X *Populus deltoides* hybrids for short rotation culture: variation patterns and 4-year field performance. *Can. J. For. Res.* 18: 745-753.
- Stettler, R.F., Bradshaw, H.D., Jr., Heilman, P.E., and Hinkley, T.M. 1996a. *Biology of Populus and its implications for management and conservation.* NRC Research Press, National Research Council Canada, Ottawa, ON. 539 pp.
- Stettler, R.F., Zuffa, L., and Wu, R.L. 1996b. The role of hybridization in the genetic manipulation of *Populus*. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley.* NRC Research Press, National Research Council Canada, Ottawa, ON. pp. 87-112.
- Stout, A.B., and Schreiner, E.J. 1933. Results of a project in hybridizing poplars. *J. Hered.* 24: 217-227.
- Tauer, C.G. 1979. Seed tree, vacuum, and temperature effects on eastern cottonwood seed viability during extended storage. *For. Sci.* 25: 112-114.
- Terrasson, D., Pinon, J., and Ridé, M. 1988. L'infection naturelle de *Populus trichocarpa* par *Hypoxyylon mammatum*. *Rev. For. Fr.* 40: 126-130.
- Thielges, B.A. 1985. Breeding poplars for disease resistance. Forestry Paper 56, FAO, Rome. 66 pp.
- Thielges, B.A., and Adams, J.C. 1975. Genetic variation and heritability of *Melampsora* leaf rust resistance in eastern cottonwood. *For. Sci.* 21: 278-282.
- Thomas, G.P., Etheridge, D.E., and Paul, G. 1960. Fungi and decay in aspen and balsam poplar in the boreal forest region, Alberta. *Can. J. Bot.* 38: 459-466.
- Turok, J., Lefèvre, F., de Vries, S. and Toth, B. 1997 *Populus nigra* network. Report of the third meeting, 5-7 October 1996, Saver, Hungary, IPGRI, Rome, Italy. 27p.
- USDA Forest Service, 1979. A Guide to Common Insects and Diseases of Forest Trees in the Northeastern United States. USDA Forest Service, Northeast. Area State Priv. For. Publ. NA-FR-4 (Address: Northeastern Area, State and Private Forestry, 370 Reed Road, Broomal, PA 19008).

- Valentine, F.A. 1962. Natural variation in specific gravity in *Populus tremuloides* in northern New York. In Proceedings 9th Northeastern Forest Tree Improvement Conference, 1961. pp. 17-24.
- van Buijtenen, J.P., and Einspahr, D.W. 1959. Note on the presence of sex chromosomes in *Populus tremuloides*. Bot. Gaz. 121: 60-61.
- van Buijtenen, J.P., Einspahr, D.W., and Joranson, P.N. 1959. Natural variation in *Populus tremuloides* Michx. Tappi 42: 819-823.
- Viereck, L.A., Dyrness, C.T., van Cleve, K., and Foote, M.J. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13: 703-720.
- Villar, M., Gaget, M. and Dumas, C. 1987a The route of pollent tube from stigma to ovule in *Populus nigra*: a new look. Ann. Sci For. 44:259-264.
- Villar, M. Gaget, M. Said, C., Knox, R. B., and Dumas, C. 1987b Incompatibility in *Populus* : structura and cytochemical characteristics of the receptive stigmas of *Populus alba* and *Populus nigra*. J. Cell. Sci. 87:483-490.
- Villar, M., Gaget, M., Rougier, M., and Dumas, C. 1993. Pollen-pistil interactions in *Populus* : beta galactosidase activity associated with pollen tube growth in the crosses *P. nigra* x *P. nigra* and *P. nigra* .x *P.alba*. Sex. Plant Reprod. 65:249-256.
- Villar, M., Lefèvre, F., Bradshaw, H. D., Teissier du Cros, E. 1996. Molecular genetics of rust resistance in poplars (*Melaampsora larici-populina* Kleb/*Populus* sp.) by bulked segregant analysis in a 2 x 2 factorial mating design. Genetics 143: 531-536.
- Villar, M., Gaget-Faurobert, M. 1996. Mentor Effects in pistil-mediated pollen-pollen interactions. In "Pollen biotechnology for Crop Production and Improvement." K. R. Shivanna and W. K. Sawhney Edited by Cambridge University Press, new York, pp. 315-322.
- Walker, L.R., and Chapin, F.S., III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology, 67: 1508-1523.
- Walker, L.R., Zasada, J.C., and Chapin, F.S., III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology, 67: 1243-1253.
- Wang, S. 1996. Approaching poplar's functions in the improvement of environment in China's Tree North Shelterbelt System. In Environmental and social issues in poplar and willow cultivation and utilization. Proceedings 20th Session of the International Poplar Commission, Budapest, 1-4 October 1996. Vol. 1. Edited by I. Bach. International Poplar Commission, FAO, Budapest. pp. 500-503.
- Waterman, A.M. 1957. Canker and dieback of poplars caused by *Dothichiza populea*. For. Sci. 3: 175-183.
- Weber, J.C., Stettler, R.F., and Heilman, P.E. 1985. Genetic variation and productivity of *Populus trichocarpa* and its hybrids. I. Morphology and phenology of 50 native clones. Can. J. For. Res. 15: 376-383.
- Weisgerber, H., Kowanatzki, D., and Mussong, M. 1995. Natural poplar resources in China and their significance for breeding and afforestation. Silvae Genetica, 44:298-303.

- Whitecross, M.I., and Willing, R.R. 1975. Hybridization of incompatible poplars following solvent treatment of stigmas. *Experientia*, 31: 651-653.
- Whitham, T.G. 1989. Plant hybrid zones as sinks for pests. *Science*, 244: 1490-1493.
- Whitham, T.G., Floate, K.D., Martinsen, G.D., Driebe, E.M., and Keim, P. 1996. Ecological and evolutionary implications of hybridization: *Populus*-herbivore interactions. In *Biology of Populus and its implications for management and conservation*. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 247-275.
- Widin, K.D., and Schipper, A.L., Jr. 1981. Epidemiology and impact of *Melampsora medusae* leaf rust infection on yield of hybrid poplars in the north-central United States. *Eur. J. For. Path.* 11: 438-448.
- Wilcox, J.R., and Farmer, R.E., Jr. 1967. Variation and inheritance of juvenile characters of eastern cottonwood. *Silvae Genet.* 16: 162-165.
- Wilcox, J.R., and Farmer, R.E., Jr. 1968. Heritability and C effects in early root growth of eastern cottonwood cuttings. *Heredity*, 23: 239-245.
- Willing, R.R., and Pryor, L.D. 1976. Interspecific hybridization in poplar. *Theor. Appl. Genet.* 47: 141-151.
- Wright, J.W. 1976. Introduction to forest genetics. Academic Press, New York. 463 pp.
- Wu, R.-L. 1994a. Quantitative genetics of yield breeding for *Populus* short-rotation culture. II. Genetic determination and expected selection response of tree geometry. *Can. J. For. Res.* 24: 155-165.
- Wu, R.-L. 1994b. Quantitative genetics of yield breeding for *Populus* short rotation culture. III. Efficiency of indirect selection on tree geometry. *Theor. Appl. Genet.* 88: 803-811.
- Yeh, F.C., Chong, D.K.X., and Yang, R.C. 1995. RAPD variation within and among natural populations of trembling aspen (*Populus tremuloides* Michx.) from Alberta. *J. Hered.* 86: 454-460.
- Ying, C.C., and Bagley, W.T. 1976. Genetic variation in eastern cottonwood in an eastern Nebraska provenance study. *Silvae Genet.* 25: 67-73.
- Ying, C.C., and Bagley, W.T. 1977. Variation in rooting capacity of *Populus deltooides*. *Silvae Genet.* 26: 204-207.
- Zasada, J.C., and Phipps, H.M. 1990. *Populus balsamifera* L. Balsam poplar. In *Silvics of North America*. Vol. 2, Hardwoods. Edited by R.M. Burns and B.H. Honkala. Agriculture Handbook 654, Forest Service, USDA, Washington, DC. pp. 518-529.
- Zsuffa, L. 1971. A rapid method for vegetative propagation of aspens and their hybrids. *For. Chron.* 47: 36-39.
- Zsuffa, L. 1975. A summary review of interspecific breeding in the genus *Populus* L. In *Proceedings 14th meeting of the Canadian Tree Improvement Association, part 2*. Dept. Environment, Canadian Forestry Service, Ottawa. pp. 107-123.

Zsuffa, L. 1993. Proposal for establishment and implementation of a certification service for poplar and willow planting stool. *Poplar Council of Canada Newsletter* 4: 4-6.

Zsuffa, L., Sennerby-Forsse, L., Weisgerber, H., and Hall, R.B. 1993. Strategies for clonal forestry with poplars, aspens and willows. *In Clonal forestry II: Conservation and application. Edited by M.R. Ahuja and W.J. Libby. Springer-Verlag, Berlin. pp. 91-119.*

Zsuffa, L., Giordano, E., Pryor, L.D., and Stettler, R.F. 1996. Trends in poplar culture: some global and regional perspectives. *In Biology of Populus and its implications for management and conservation. Edited by R.F. Stettler, H.D. Bradshaw Jr., P.E. Heilman and T.M. Hinkley. NRC Research Press, National Research Council of Canada, Ottawa, ON. pp. 515-539.*

Zsuffa, L. 1971. Summary report on poplar and pine breeding in 1968 and 1969. *In Proc. 12th Meet. Comm. Forest Tree Breed. Can., Part 2. pp. 53-63.*

Appendix

Genetic Transformation of Poplars

Poplar is the first forest tree species to have been transformed (Fillatti et al. 1987). Since that time, a number of different transformation procedures have been optimized on poplar species in many laboratories. These allow for the easy recovery of transgenic poplar plants (Jouanin et al. 1993). *Agrobacterium*-mediated transformation appears to be the most widely used vector for DNA transfer in poplar (Leplé et al. 1992). The first reports on poplar transformation deal primarily with the introduction of marker genes: the GUS gene or genes conferring selectable traits such as resistance to antibiotics or to herbicides (Brasiliero et al. 1992). Since 1990, an increasing number of studies have focused on the expression of genes potentially able to modify agronomic traits, for example: tolerance to insect attack (Robinson et al. 1994, Leplé et al. 1995, 1998), control of flowering (Weigel and Nilsson, 1995), modification of wood quality through altered lignin content and composition (Baucher et al. 1996, Van Doorselaere et al. 1995), improvement to oxidative stress tolerance (Strohm et al. 1995). Until recently, most of the results have been obtained using juvenile material grown under controlled conditions, however, an increasing number of field trials are now being set up with transgenic poplars in order to validate results obtained in the greenhouse. Moreover, these field evaluations will answer a number of questions concerning the spatial and temporal stability of transgene expression in mature trees that are subject to a natural changing environment (Pilate et al. 1997).

References

- Baucher, M., Chabbert, B., Pilate, G., Van Doorselaere, J., Trollier, M-T., Petit-Conil, M. Cornu, D., Monties, B., Van Montagu, M., Inzé, D., Jouanin, L., and Boerjan, W. 1996. Red xylem and higher lignin extractability by down-regulating a cinnamyl alcohol dehydrogenase in poplar. *Plant Physiol.* 112: 1479-1490
- Brasiliero, A. C. M., Tourneur, C., Leplé, J. C. Combes, V. and Jouanin, L. 1992. Expression of the mutant *Arabidopsis thaliana* acetolactate synthase gene confers chlorsulfuron resistance to transgenic poplar plants. *Transgenic Res.* 1: 133-141.
- Fillatti, J. J., Sellmer, J., McCown, B., Haissig, B. and Comai, L. 1987 *Agrobacterium*-mediated transformation and regeneration of *Populus*. *Mol. Gen. genet.* 206:192-199.
- Jouanin, L., Brasiliero, A. C. M., Leplé, J. C., Pilate, G. and Cornu, D. 1993. Genetic transformation. A short review of methods and their applications, results and perspectives for forest trees. *Ann. Sci. For.* 50: 325-336.
- Leplé, J. C., Brasiliero, A. C. M., Michel, M. F., Delmotte, F. and Jouanin, L. 1992. Transgenic poplars: expression of chimeric genes using four different constructs. *Plant Cell Rep.* 11: 137-141.

- Leplé, J. C., Bonade-Bottino, M., Augustin, S., Pilate, G., Letan, V. D., Delplanque, A., Cornu, D. and Jouanin, L. 1995. Toxicity to *Chrysomela tremulae* (coleoptera: *chrsomelidae*) of transgenic poplars expressing a cysteine proteinase inhibitor. *Mol. Breeding* 1: 319-328.
- Leplé, J. C., Pilate, G. and Jouanin, L. 1998. Genetic transformation of poplar. *In* *Biotechnology in Agriculture and Forestry*, vol. 44, *Edited by* Bajaj, Springer Verlag, Berlin, New-York (in press).
- Pilate, G., Ellis, D. and Hawkins, S. 1997. Transgene expression in field-grown poplar. *In* Klopfenstein, N. B. Chun, Y. W., Kim, M. S. and Ahuja, M. R. *Edited by* Microporopatation, Genetic Engineering, and Molecular Biology of Populus. USDA Forest Service - in press.
- Robinson, D. J., McCown, B. H. and Raffa, K. F. 1994. responses of gypsy moth (*Lepidoptera Lymantriidae*) and forest tent caterpillar (*Lepidoptera: Lasiocampidae*) to transgenic poplar, *Populus* spp., containing a *Bacillus thuringiensis* delta-endotoxin gene. *Env. Entomol.* 23: 1030-1041
- Strohm, M., Jouanin, L., Kunert, K. J., Pruvost, C., Polle, A., Foyer, C. H. and Rennenberg, H. 1995. Regulation of glutathione sythesis in leaves of transgenic poplar (*Populus tremula* x *P. alba*) overexpressing glutathione synthetase. *Plan J.* 7: 141-145
- Van Doorselaere, J., Baucher, M., Chognot, E., Chabbert, B., Tollier, M. T., Petitconil, M., Leplé, J. C., Pilate, G., Cornu, D., Monties, B., Vanmontagu, M., Inze, D., Boerjan, W. and Jouanin, L. 1995. A novle lignin in poplar trees with a reduced caffeic acid 5-hydroxyferulic acid *O*-methyltransferase activity. *Plant J.* 8: 855-864.
- Weigel, D. and Nilsson, O. 1995. a developmental switch sufficient for flower initiation in diverse plants. *Nature* 377: 495-500.

QUESTIONNAIRE TO RETURN TO THE OECD

This is one of a series of OECD Consensus Documents that provide information for use during regulatory assessment of particular micro-organisms, or plants, developed through modern biotechnology. The Consensus Documents have been produced with the intention that they will be updated regularly to reflect scientific and technical developments.

Users of Consensus Documents are invited to submit relevant new scientific and technical information, and to suggest additional related areas that might be considered in the future.

The questionnaire is already addressed (see reverse). **Please mail or fax this page (or a copy) to the OECD, or send the requested information by E-mail:**

**OECD Environment Directorate
Environmental Health and Safety Division
2, rue André-Pascal
75775 Paris Cedex 16, France**

**Fax: (33) 01 45 24 16 75
E-mail: ehscont@oecd.org**

For more information about the Environmental Health and Safety Division and its publications (most of which are available electronically at no charge), consult <http://www.oecd.org/ehs/>

- =====
1. Did you find the information in this document useful to your work?
 Yes No

 2. What type of work do you do?
 Regulatory Academic Industry Other (please specify)

 3. Should changes or additions be considered when this document is updated?

 4. Should other areas related to this subject be considered when the document is updated?

Name:..... Institution or company:..... Address:..... City: Postal code:..... Country: Telephone:..... Fax:..... E-mail: Which Consensus Document are you commenting on?

FOLD ALONG DOTTED LINES AND SEAL

PLACE
STAMP
HERE

**OECD Environment Directorate
Environmental Health and Safety Division
2, rue André Pascal
75775 Paris Cedex 16
France**
