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**CONSENSUS DOCUMENT ON THE BIOLOGY OF EUROPEAN WHITE BIRCH (*Betula pendula* Roth)**

**JT00147638**

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OECD Environment, Health and Safety Publications

Series on Harmonisation of Regulatory Oversight in Biotechnology

**No. 28**

**Consensus Document on the Biology  
of European White Birch (*Betula pendula* Roth)**

**Environment Directorate**

**Organisation for Economic Co-operation and Development**

**Paris 2003**

## ABOUT THE OECD

The Organisation for Economic Co-operation and Development (OECD) is an intergovernmental organisation in which representatives of 30 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.

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## FOREWORD

The OECD's Working<sup>1</sup> Group on Harmonisation of Regulatory Oversight in Biotechnology decided at its first session, in June 1995, to focus its work on the development of *consensus documents* which are mutually acceptable among Member countries. These consensus documents contain information for use during the regulatory assessment of a particular product. In the area of plant biosafety, consensus documents are being published on the biology of certain plant species, on selected traits that may be introduced into plant species, and on biosafety issues arising from certain general types of modifications made to plants.

This document addresses the biology of European White Birch. It contains general information as well as more specific information on taxonomy, forestry practices, centres of origin/diversity, reproductive biology, crosses, genetic variability and ecology. 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.

Finland served as the lead country in the preparation of this document.

The Joint Meeting of the Chemicals Committee and the Working Party on Chemicals, Pesticides and Biotechnology has recommended that this document be made available to the public. It is published on the authority of the Secretary-General of the OECD.

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<sup>1</sup> In August 1998, following a decision by OECD Council to rationalise the names of Committees and Working Groups across the OECD, the name of the "Expert Group on Harmonisation of Regulatory Oversight in Biotechnology" became the "Working Group on Harmonisation of Regulatory Oversight in Biotechnology."



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## PREAMBLE

OECD Member countries are now approving the commercialisation and marketing of agricultural and industrial products of modern biotechnology. They had previously therefore identified the need for harmonisation of regulatory approaches to the biosafety assessment of these products, in order to avoid unnecessary trade barriers.

In 1993, **Commercialisation of Agricultural Products Derived through Modern Biotechnology** was instituted as a joint project of the OECD's Environmental Policy Committee and Committee on Agriculture. The objective of this project is 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 is 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 1995a).

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 harmonisation 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. *The Report of the OECD Workshop on the Commercialisation of Agricultural Products Derived through Modern Biotechnology* was also published by the OECD in 1995 (OECD 1995b).

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

Safety issues that could give rise to a safety concern are identified in the consensus documents on the biology of a specific crop and include the potential for gene transfer, weediness, trait effects, genetic and phenotypic variability, biological vector effects and genetic material from pathogens (OECD 1993a). 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 document is a "snap-shot" 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, scientists and others carrying out research.

In using this document and others related to the biology of crop plants, reference to two OECD publications which have appeared in recent years will prove particularly useful. *Traditional Crop Breeding Practices: A Historical Review to Serve as a Baseline for Assessing the Role of Modern Biotechnology* (OECD 1993b) presents information concerning 17 different crop plants. It includes sections on phytosanitary considerations in the movement of germplasm and current end uses of the crop plant. There is also a detailed section on current breeding practices. *Safety Considerations for Biotechnology: Scale Up of Crop Plants* (OECD 1993a) provides a background on plant breeding, discusses scale dependency effects, and identifies various safety issues related to the release of plants with "novel traits".<sup>2</sup>

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 relevant new scientific and technical information, and to make proposals concerning additional areas that might be considered in the future. ***A short, pre-addressed questionnaire is included at the end of this document. The information requested should be sent to the OECD at one of the addresses shown.***

<sup>2</sup>

For more information on these and other OECD publications, contact the OECD publications Service, 2 rue André-Pascal, 75775 Paris Cedex 16, France, Fax: (33) 01.49.10.42.76; E-mail: [PUBSINQ@oecd.org](mailto:PUBSINQ@oecd.org); or consult <http://www.oecd.org>

## SECTION I – GENERAL DESCRIPTION AND USE IN FORESTRY

### A. Taxonomy

#### *Taxonomy*

1. European white birch, or silver birch (*Betula pendula* Roth), belongs to the genus *Betula*. There are some 40 *Betula* species, which are distributed throughout the northern temperate region. According to the systematics created by Regel, 1876 (in Natho 1957), the *Betula* genus is divided into two main sections, *Eubetula* and *Betulaster* (Table 1). The *Betulaster* section includes just a few birch species in Japan and China, in the subsection *Acuminatae*. The *Eubetula* section is further divided into three subsections, *Costatae* (yellow birches), *Albae* (white birches) and *Nanae* (dwarf birches). *Betula pendula* belongs to the *Albae* subsection, as does the other European treelike birch, *B. pubescens*.

2. In 1753 Carl von Linné defined the European arboriform birches as one species, *B. alba*. At the end of the century the German botanist, A. W. Roth, characterised the European white birch as its own species, *B. pendula* and this is the name used today, instead of *B. verrucosa* suggested by F. Ehrhardt (Raulo 1981). An Asian birch species, *B. japonica* is very close to *B. pendula*, since the hybrids of the two species produce fertile off-spring and the species are morphologically very similar (Johnsson 1945).

3. There are many variations and forms of *B. pendula* (Fontaine 1970). Most of the special forms of *B. pendula* var. *pendula* are grown as ornamental trees in parks and homesteads. An important variation economically is var. *carelica*, curly-birch. Its wood is strong and decorative and is used for making wooden ornaments. The wood is sold according to weight, and its price makes it more valuable than ordinary birch (Ryynänen and Ryynänen 1986).

#### *Chemotaxonomy*

4. The chemicals in birch stems are useful in recognition of different birch species. Julkunen-Tiitto *et al.* (1996) compared concentrations of 12 secondary metabolites in birch seedlings and saplings. Of phenolic compounds, dehydrosalidroside was found specifically in *B. pendula*. Platyphylloside was also a typical component in *B. pendula* and was found also in *B. papyrifera* but not in *B. pubescens*. Triterpenes are found in the resin glands on the surface of young birch stems. *B. pendula* contained mainly papyriferic acid (as did *B. papyrifera* and *B. platyphylla*) accompanied with deacetylpapyriferic acid. The secondary product composition in *B. pendula* differs markedly from that of, for example, the morphologically similar *B. pubescens* by the presence of platyphylloside and terpenoids. On the other hand, *B. platyphylla* (Japanese white birch) and *B. resinifera* show a moderately close phenolic and terpenoid relationship with *B. pendula*. Besides the chemical composition of the stem, foliar chemistry is also used for recognition of birch species. The end product of the ellagitannin pathway, 2,3-(S)-HHDP-glucose accumulates in the leaves of *B. pubescens* and *B. nana*, whereas it is present only in trace amounts in the leaves of *B. pendula*.

(Salminen *et al.* 2002). These results show that, together with exomorphic and cytological features, chemotaxonomical comparison of secondary components can be used to distinguish between species or varieties (Julkunen-Tiitto *et al.* 1996).

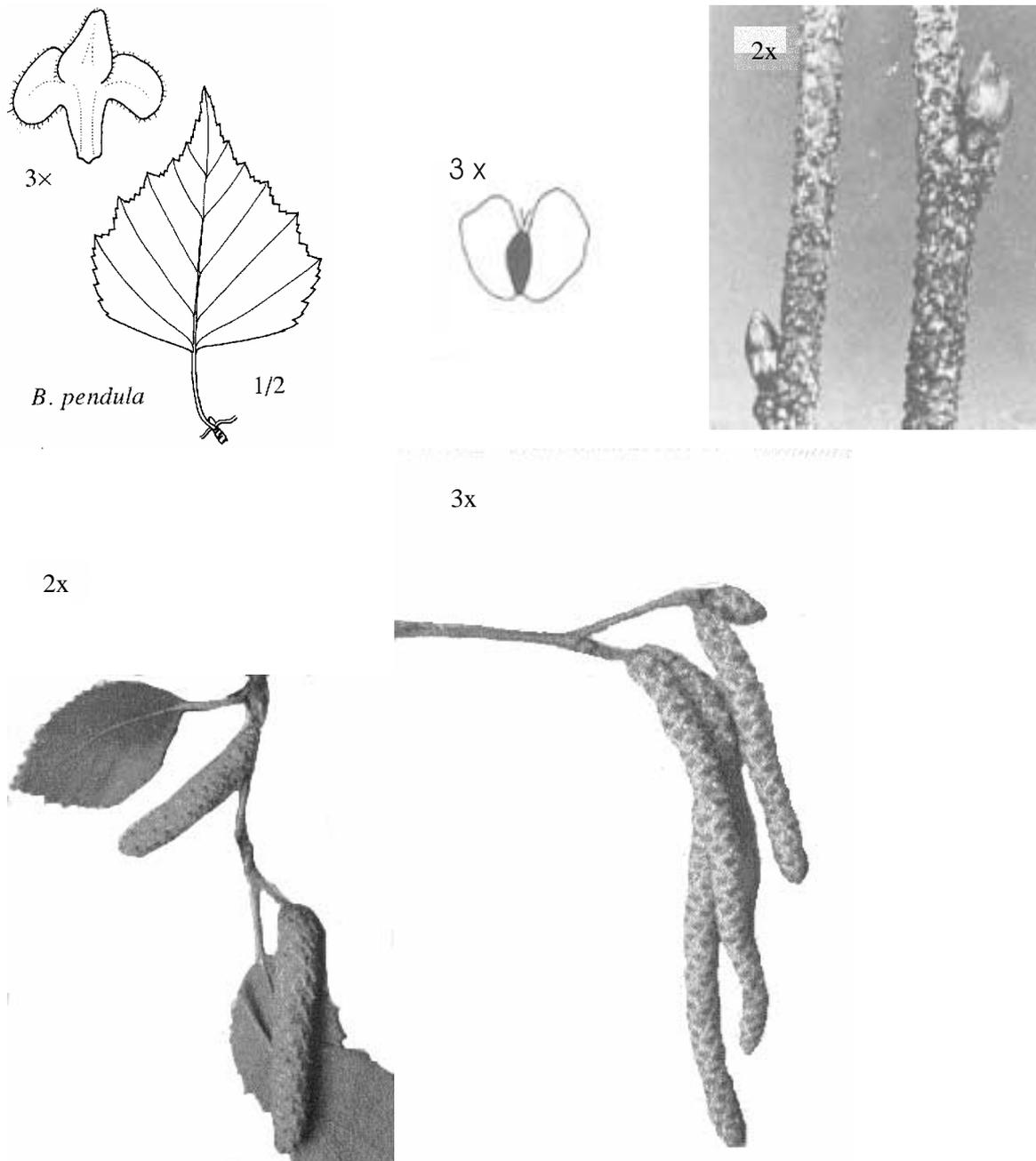
**Table 1. The taxonomy and distribution of the 44 species in the genus *Betula* (Fontaine 1970, Raulo 1981). The taxonomy of the genus *Betula* is under dispute (Flora Europaea 1993).**

Genus	<i>Betula</i>			
Section	<i>Eubetula</i>			<i>Betulaster</i>
Subsection	<i>Costatae</i>	<i>Albae</i>	<i>Nanae</i>	<i>Acuminatae</i>
Species	<i>B. costata</i> Trautv. <sup>1</sup> <i>B. globispica</i> Shiras <sup>1</sup> <i>B. medwediewii</i> Regel <sup>1</sup> <i>B. utilis</i> D. Don <sup>1</sup>  <i>B. ermanii</i> Cham. <sup>1</sup> <i>B. chinensis</i> Maxim. <sup>1</sup> <i>B. schmidtii</i> Regel <sup>1</sup> <i>B. potanini</i> Shirai <sup>1</sup>  <i>B. albo-sinensis</i> Burk <sup>1</sup>  <i>B. alleghaniensis</i> Britt. <sup>2</sup> <i>B. lenta</i> L. <sup>2</sup> <i>B. nigra</i> L. <sup>2</sup>  <i>B. grossa</i> Sieb. & Zucc. <sup>1</sup> <i>B. Jacquemonti</i> Spach <sup>1</sup> <i>B. coryifolia</i> Regel & Maxim. <sup>1</sup>	<i>B. japonica</i> Sieb. <sup>1</sup> <i>B. mandshurica</i> Nakai <sup>1</sup> <i>B. davurica</i> Pall. <sup>1</sup> <i>B. papyrifera</i> Marsh. <sup>2</sup>  <i>B. populifolia</i> Marsh. <sup>2</sup> <i>B. pendula</i> Roth <sup>1,3</sup> <i>B. pubescens</i> Ehrh. <sup>1,3</sup> <i>B. platyphylla</i> Sukatchev <sup>1</sup> <i>B. caerulea-grandis</i> Blanchard <sup>2</sup> <i>B. occidentalis</i> Hook. <sup>2</sup> <i>B. minor</i> Fern. <sup>2</sup> <i>B. concinna</i> Gunnarsson <sup>3</sup> <i>B. coriacea</i> Gunnarsson <sup>3</sup> <i>B. microphylla</i> Bge <sup>1</sup> <i>B. turkestanica</i> Litvinoff <sup>1</sup>	<i>B. nana</i> L. <sup>1,3</sup> <i>B. fruticosa</i> Pall. <sup>1,3</sup> <i>B. exilis</i> Sukacz. <sup>1,2</sup> <i>B. middendorffii</i> Trautv. & Mey <sup>1</sup> <i>B. pumila</i> L. <sup>2</sup> <i>B. michauxii</i> Spach <sup>2</sup> <i>B. glandulosa</i> Michx. <sup>2</sup> <i>B. humilis</i> Schrenk <sup>1,3</sup>  <i>B. glandulifera</i> Butler <sup>2</sup>  <i>B. hallii</i> Howell <sup>2</sup> <i>B. uber</i> (Ashe) Fern. <sup>2</sup>	<i>B. maximowicziana</i> Regel <sup>1</sup> <i>B. alnoides</i> Buch.-Ham. <sup>1</sup> <i>B. luminifera</i> Winkl. <sup>1</sup>
Distribution	Asia <sup>1</sup> North America <sup>2</sup>	Asia <sup>1</sup> North America <sup>2</sup> Europe <sup>3</sup>	Asia <sup>1</sup> North America <sup>2</sup> Europe <sup>3</sup>	Asia <sup>1</sup>

## B. General description

5. *Betula pendula* grows up to 30 m high, with usually one stem. It can become up to 100 years old, under favourable conditions even 150 years. The bark is smooth and silvery white and exfoliates in long, thin strands. The basal parts of the trunks of old trees are black and vertically fissured; in young trees (up to 10 years old) the bark is light brown. Older branches are often pendulous, whereas young branches are spreading or ascending. Twigs are glabrous, with peltate resin glands on the younger twigs. Buds are acute, not sticky. Leaves are 2.5 – 5 cm long, ovate-deltate, apex acuminate, base truncate or broadly cuneate. Leaf margins are double serrated with the primary teeth very prominent and curved towards the leaf apex; petioles are 10 – 18 mm long. The scales are short, with a broad cuneate base, broad lateral lobes spreading and curving towards the base, and a deltoid, obtuse middle lobe. The achene is glabrous, 1.5 – 2.4 mm long, 0.8 – 1.3 mm wide; the width of the fruit is 3 – 5 mm, the upper edge of the wings surpassing the stigmas by 0.5 – 1.5 mm (Atkinson 1992; Figure 1.).

Figure 1. The leaf, scale, seed, stem, buds and female and male catkins of *Betula pendula* (Raulo 1981, Hämet-Ahti *et al.* 1992).



### **C. Use of European white birch**

#### ***Firewood***

6. Birch has been an important source of energy, and earlier it was mostly used as firewood. The effective thermal value of birch is about 20 MJ/kg when absolutely dry, and about 15 MJ/kg with 30 % humidity. The high content of volatile oils makes the burning properties good (Salmi 1987).

#### ***Plywood production***

7. In plywood production, the value of a birch log used for planks or veneer is influenced by its diameter, stem taper, and number and size of knots and branches. Logs of required dimensions can usually be produced with proper planting densities and thinning treatments.

#### ***Pulpwood***

8. Birch fibres are relatively long and thin-walled and have a high content of hemicelluloses. As a result, birch pulp has good strength properties, low light-scattering ability and high density. The main product is bleached sulphate pulp. Coated and uncoated wood-free fine papers, which contain 50 to 90 % of bleached birch sulphate pulp, are especially important (Tammisola *et al.* 1995).

#### ***Curly-birch, Carelian birch***

9. Curly-birch (*B. pendula* var. *carelica*) is a special form of *B. pendula*, and it occurs throughout Northern Europe and parts of Central and Eastern Europe. The wood is strong and decorative and is used in wooden ornaments and furniture. The genetic background of the curly-grained trait is not known. Curly-birch is self-sterile, and in controlled crossings between two individuals a maximum of 75 % of the progeny can be curly-birch. It has been suspected that the trait is homozygotically lethal, or that it is a genetical disease caused by a micro-organism or a virus (Ryynänen and Ryynänen 1986). The establishment of a plantation is an uncertain process, because it takes 10 years to see whether an individual will become a curly-birch. Normal birches have to be removed in order to prevent the curly-birches becoming suppressed. The propagation of curly-birches from cuttings has been attempted but the results have not been promising. Micro-propagation techniques have been developed for propagating curly-birches with the optimum stem form (Ryynänen and Ryynänen 1986).

## SECTION II – FORESTRY PRACTICES

### A. Reproductive methods

#### *Flower induction*

10. In order to speed up the induction of flowering, and consequently, breeding, the Foundation for Forest Breeding in Finland built the first flower induction hall in 1976. It was equipped to provide good growing conditions for breeding material all year round. In the plastic greenhouses continuous illumination (24h day length) was kept at 10,000 – 20,000 lux by mercury and high pressure sodium lamps. Temperature was controlled by thermostats and fans. CO<sub>2</sub> concentration was increased by burning propane gas and relative humidity was kept above 60 %. Required nutrients were provided automatically via continuous drip irrigation. The best results were obtained from birch: the daily growth was 7 cm per day, male flower buds appeared in 77 days and the first seed crop was collected 8 months after sowing (Holopainen and Pirttilä 1978).

### B. Vegetative propagation

11. Birch can be propagated vegetatively, i.e. cloned, by grafting, rooting or by means of tissue culture. Production of grafts is quite expensive and grafts are used mainly for clonal collections and seed orchards (Ryynänen 1987). Also, rooting of birch cuttings is not much used in birch propagation as the percentage of rooted cuttings is low (10 – 50 %) for *B. pendula*, whereas Kling *et al.* (1985) found rooting rates of 80 % for a closely-related *B. platyphylla*.

#### *Micro-propagation*

12. Much research on tissue culture of birches has been done and effective micro-propagation techniques have been developed. Leaf callus from young seedlings can be used (Simola 1985) but with mature trees, vegetative buds are used as tissue material (Ryynänen and Ryynänen 1986). Shoots and roots can be specifically induced on different aseptic culture media, after which the plantlets can be potted on peat and moved into the greenhouse. The development of micro-propagation methods made an effective propagation of selected adult trees possible. Micro-propagated plants have proved viable in test plantings under field conditions (Meier-Dinkel 1992; Jones *et al.* 1996). A review on micro-propagation of juvenile and mature birches including results on field trials and cold storage was compiled by Meier-Dinkel (1992). Some clonally propagated birch plants have been used for practical forest cultivation in Finland (Viherä-Aarnio 1994a). Large-scale production of micro-propagated *B. pendula* seedlings was terminated in 1994, as it was considered unprofitable (Viherä-Aarnio and Velling 2001). Today, micro-propagation is used in commercial scale for curly-birch cloning. Micro-propagated plants can also be used instead of grafts in greenhouse seed orchards, when specific genotypes are required (Viherä-Aarnio and Ryynänen 1995).

13. Viherä-Aarnio (1994a) studied the field performance of micro-propagated birch plants in a small-scale field test with three clones and three seed-born lots. The best two lots of the experiment as regards the height and diameter growth at the age of six years were clones, but the weakest lot was also a clone. This indicates that the selection for clonal propagation should be done carefully. It is also important to test the clones in field trials before wide scale propagation. In fact, further studies revealed that micro-propagated clones do not differ from seed-born seedlings in terms of growth and resistance against pests and herbivores (Viherä-Aarnio and Velling 2001).

### **C. Reproductive materials used**

#### ***Seed collection stands***

14. Seed collection stands are natural birch stands of outstanding growth and quality. The best individuals in these stands have been selected as plus trees. A part of the seed used in nurseries is collected from seed collection stands (Viherä-Aarnio and Ryyänen 1994).

#### ***Seed orchards***

15. As birch responds positively to intensive cultivation in a greenhouse, today most birch seed used for seedling production is obtained from polythene greenhouse seed orchards, a method which was developed by the Foundation for Forest Tree Breeding in Finland in 1972 (Huhtinen & Yahyaogly 1974). Most seed orchards are multi-clonal orchards with some 30 to 50 clones. Bi-clonal orchards have also been established in order to produce desired full-sib families (Viherä-Aarnio and Ryyänen 1994). Besides greenhouse orchards, open seed orchards in the field are used for seed production.

16. Seed production in greenhouse seed orchards begins three years after planting and continues for 5 to 7 years, until the trees grow too big to be kept inside. Flowering and seed ripening take place 1 to 2 weeks earlier in the greenhouse than in natural conditions. As a result, growing birches in greenhouses also prevents unwanted background pollination. A seed orchard can be established with grafts of tested plus trees, seedlings selected from the best progenies or micro-propagated clones (Viherä-Aarnio and Ryyänen 1995).

#### ***Cultivation***

17. In the Nordic countries and Europe, Finland has the longest experience in birch cultivation. The main emphasis in birch planting has been the afforestation of former agricultural land (Ferm *et al.* 1994). When a field is abandoned, it is first colonised by annual species, which then give way to perennial herbs and grasses. As field vegetation competes with tree seedlings for water and nutrients, success with field afforestation requires effective weed control during the establishment year. Soil preparation also affects the survival of trees. In 20-year-old experiments the best growth was gained when bare-rooted, large transplants of silver birch were planted on a ploughed and tilled field and weeds were properly controlled (Torpo 1991). Weed control improves the nutrient status of tree seedlings and increases growth. Birch seedlings with efficient weed control were 40 – 50 cm taller after two years than control seedlings, and they had bigger leaves (Ferm *et al.* 1994). Vegetation control reduces the risk of cicada (*Cicadella viridis*) wounding and consequently infection by pathogenic fungi, and is also effective against vole damage (Ferm *et al.* 1994).

## D. Breeding

18. In the breeding programme for birch, outstanding stands for seed collection were selected and the best individual trees in these stands were selected as plus trees. The most important selection criteria were fast growth and good stem quality. After selection of plus trees, controlled crossings have been carried out, and progeny tests with both full-sib families from controlled crosses and half-sib families from open pollinated lots have been established (Koski 1991). Plus tree selection is still being continued in order to improve the geographical coverage of the breeding material (Viherä-Aarnio 1994b).

19. Planted birch stands of improved material can reach the size of final cutting by as early as 40 years and produce over 400 m<sup>3</sup>/ha (Viherä-Aarnio 1994b). Examples of realised genetic gain cannot yet be shown, but a potential gain of 20 to 30 % in volume growth has been suggested (Koski 1991) and in first generation seed orchards, the growth rate of the best selected family is 89 % higher than the control (Wang 1996).

### *Provenance transfers*

20. Raulo and Koski (1977) reported on the first geographical transfers of silver birch. According to their study, seed transfers of 200 km northwards or southwards in central and southern Finland had no effect on the mortality or growth rate of the progenies; on the other hand they did not recommend long-distance transfers because of the risk of lower survival.

## E. Conservation of genetic resources

### *Genetic diversity of forest trees*

21. The cultivation of forest trees can be thought to endanger the genetic diversity in general. Maintaining genetic diversity in forest tree populations also means maintaining adaptability to changing environments. In naturally generated areas there is no concern about the loss of genetic diversity but large monocultures of a single clone would reduce genetic variability. However, forestry based on monoclonal blocks is not common, but cultivation of single clones is mostly applied to small plantations of special forms or variations, e.g. curly-birch (Viherä-Aarnio and Velling 2001). Moreover, real monocultures are impossible to maintain, as other trees can not be prevented from growing in the plantations.

22. Most forest trees are cross-fertilising and pollinated by wind and consequently there is crossing both between individuals in a stand and between stands. Even if small stands were to be cultivated with only one clone, effective wind-pollination will secure the mixing of genes between populations. Also, real monocultures are impossible to maintain, as other trees can not be prevented from growing in the plantations. Cultivation of single clones will probably mostly apply to small plantations of special forms or variations, e.g. curly-birch. The danger from planting large areas with a single clone arises when the adaptability of the clonal genotype is exceeded by adverse conditions. To avoid multiplication of poorly adapted or extremely susceptible genotypes, trees for micro-propagation are selected from old stands. Another option is the use of clonal mixtures which are buffering environmental risks (Kleinschmit 1998).

23. It has been estimated that a population of 500 trees is big enough to contain all possible alleles of different genes (Koski 1995), and this is the amount usually used in breeding populations. The seed from seed orchards is usually a result of cross-fertilisation of tens of plus tree clones from different localities, and it has been shown in studies with genetic markers that the genetic diversity is as large as that of natural seed collection stands (Koski 1995).

### ***Gene reserve forests***

24. Ongoing breeding activities may cause losses of genetic diversity, especially if population size is reduced from one generation to the next. Random allele loss is problematic for advanced-generation elite populations, and this has raised concerns about the maintenance of genetic diversity in forest-tree breeding programs.

25. Gene reserve forests have been established in order to conserve representative samples of the natural gene pool of forest trees. They have to be big enough (preferably tens of hectares) for the pollination to occur inside the forest and for the reserve to contain most of the local genetic diversity. Management and harvesting are allowed, but the forests are regenerated naturally or by sowing with seed from inside the forest or by planting seedlings grown from local seed. Gene reserve forests should consist of a network of forests in the area of the natural distribution of the species, in order to contain the diversity between provenances and localities. In Finland the gene reserve forests are situated in northern Finland and are part of a network of gene reserve forests covering all Europe (Parviainen *et al.* 2000).

### ***Advanced breeding strategies***

26. Two advanced models have been suggested in order to prevent random allele loss in breeding programs: HOPE (Hierarchical Open-Ended Breeding System) and MPBS (Multiple-Population Breeding Strategy) (Eriksson *et al.* 1993).

27. The HOPE system is composed of a hierarchy of breeding populations with successively higher performance levels. A large base population is maintained and is open to new material. Higher level populations are more stringently selected and from these, selections are made for commercial production. Under MPBS, a breeding population is divided into independent subpopulations which represent different sources or selection criteria. There is differentiation among subpopulations both in their source of germplasm and in their traits and environmental adaptabilities. There can be random allele loss in some subpopulations but, on average, gene frequencies remain fairly constant (Eriksson *et al.* 1993).

28. Of these, the MPBS seems to be a better choice for birch because it combines the highest possible genetic gains and the highest possible genetic diversity. It also gives the breeder more options for changing breeding goals with changing environment and markets (Eriksson *et al.* 1993).

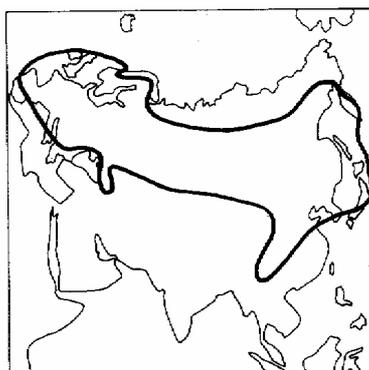
### SECTION III – CENTRES OF ORIGIN / DIVERSITY

#### A. Natural distribution and origin

##### *Natural distribution*

29. *B. pendula* is distributed throughout Eurasia (Figure 2.). It extends in Europe into the mountainous regions of Spain, Greece and Italy in the south, throughout Asia all the way to the Sea of Okhotsk and the Sea of Japan in the east and to Caucasus, Crimea and the mountains of Central Asia in the south. In the north it extends to about 65°N (Hämet-Ahti 1963; Atkinson 1992).

**Figure 2. The natural distribution of *Betula pendula* (Hämet-Ahti *et al.* 1992).**



30. The northern limit of the range of silver birch appears to be determined by protection from cold north-easterly winds. The southern limits approximate to the line of an average of 10 mm July rainfall (Atkinson 1992). There are different views of the eastern limit of the range, 60° by Jalas & Suominen (1976) and 103° by Hämet-Ahti *et al.* (1992).

##### *Total distribution*

31. In North America *B. pendula* is used as an ornamental and is a naturally spreading escape from cultivation for example in Ontario, Canada (Catling and Spicer 1988). The corresponding species of *B. pendula* in North America is *B. populifolia* (grey birch) which is used in re-vegetation of mine spoils, and is economically important as a source of fuel, sugar and fibre for corrugating pulp (Catling and Spicer 1988).

*Migration to Fennoscandia*

32. Birch migrated to Fennoscandia in the late glacial with pine, spruce and alder. The last remnants of the Scandinavian ice cap may have disappeared at around 8,000 years ago and the early postglacial (pre-boreal) forests in Fennoscandia were dominated by birch. In the boreal (6,800 – 5,000 BC), the climatic conditions were drier and cooler, and pine replaced birch especially in the north. At around 5,000 BC, the climate became warmer again, and birch and alder spread to new areas. At around 1,000 BC, as the climate became cooler again, spruce replaced birch and pine in many areas (Hämet-Ahti 1963).

## SECTION IV – REPRODUCTIVE BIOLOGY

### A. Sexual reproduction

33. Birches are monoecious (male and female flowers on the same tree) and diclinous (flowers unisexual). Male inflorescences are 1–2 cm long, 4 mm wide while over-wintering; 2–6 cm long, 6 mm wide at anthesis. There are 2–4 male catkins together at the ends of small shoots. Female inflorescences are erect, 1.5–3.5 cm long, 7 mm wide (Atkinson 1992). They are pale green when immature, turning brown in the late autumn.

### *Flowering*

34. Flowering usually starts when trees are between 5 and 10 years old but some single trees can be induced to flower within one year after germination (Elo *et al.* 2001). The female flowers emerge on the short-shoots at the same time as the buds open. The female flowers usually develop one day before male flowers on the same tree shed pollen. Flowers remain receptive for 4 days and after the sixth day are blackened and dead (Sarvas 1952). *B. pubescens* flowers about a week later than *B. pendula*.

35. Ripening of the flowers is closely related to the temperature conditions of the spring. The arrival of the first heat wave of daily temperatures above +10°C usually triggers flowering. Most pollen release occurs within 2 or 3 days of anthesis. Pollen shed is highest in the late afternoon and near zero from about midnight to early morning (Sarvas 1952). *B. pendula* pollen can remain viable for at least 20 days at room temperature in the dark. If the pollen is exposed to sunlight for 8 hours, however, ultraviolet rays and other factors reduce viability (Perala and Alm 1990).

36. Flowering is polygenically inherited and female and male flowers are governed by different sets of genes. Weather conditions have a strong influence on female flowering whereas they do not play a role in male flowering (Eriksson and Jonsson 1986).

37. Three cDNAs of *B. pendula* representing ADS-box genes BpMADS3, BpMADS4 and BpMADS5 are active during the development of both female and male inflorescence and the respective genes are involved in the determination of the identity of the inflorescence or flower meristem. BpMADS3 shows highest expression at late developmental stages. BpMADS4, besides regulating inflorescence, is expressed in roots and stem. Expression of BpMADS5 is inflorescence specific and continues during seed development. Ectopic expression of BpMADS3, BpMADS4 or BpMADS5 with CaMV 35S promotor in tobacco results in extremely early flowering (Elo *et al.* 2001).

## **B. Pollination**

### ***Male meiosis and pollen development***

38. The male catkins develop in the autumn but do not release pollen until spring the following year. The principal events during micro-sporogenesis are the initiation and growth of the male buds, generation and growth of the sporogenous tissue, pre-meiotic maturation of the PMCs (pollen mother cells), meiosis, the tetrad stage, androgenesis and anthesis. The species in *Betulaceae* reach the tetrad phase from late July to mid-August (Luomajoki 1986). In *Betulaceae* the heat sums seem to have less connection with the development stage of micro-sporogenesis than in conifers, as the northernmost stands of *Betula* species develop first and the southernmost last. The timing of meiosis in *Betula* is more dependent on day length, and a hypothetical critical day length of 15 hours can quite accurately predict the onset of the tetrad phase (Luomajoki 1986).

### ***Pollination***

39. Pollination is anemophilous, i.e. birch is pollinated by wind. There is an intense maximum at the immediate start of flowering lasting 2 – 3 days during which 70 – 80 % of the total pollination takes place. Prolonged cold and wet conditions are likely to reduce the total amount of pollen (Sarvas 1948).

### ***Pollen flow***

40. As an evidence of long-distance pollen transport, *Betula* pollen concentrations in Fennoscandia can be relatively high before the local flowering period. The pollen is transported by south-eastern air-masses from eastern central Europe and the Baltic countries, with travelling times for pollen grains in the range of 9 – 20 hours (Hjelmroos 1991).

41. In northern Europe, birch pollen allergy is one of the most common reason for spring-time human rhinoconjunctivitis and asthma. In Sweden, about 8 – 9 % of the population suffers from allergies related to birch pollen (Hjelmroos and van Hage-Hamsten 1993). The major birch pollen allergen Bet v I is highly homologous to pathogenesis-related plant proteins. Another well described allergen is profilin, an actin binding protein, which is predominantly expressed in the pollen of different plant species. The birch profilin is recognised by IgE antibodies in 10 % of individuals allergic to birch pollen and seems to be an intermediate or major allergen in individuals allergic to pollens of grasses and weeds (Valenta *et al.* 1991). Another birch pollen allergen, Bet v III, representing a class of Ca<sup>2+</sup> binding proteins, has also been characterised (Seiberler *et al.* 1994).

## **C. Mating system**

### ***Cross-fertilisation***

42. *B. pendula* is an outcrossing species. There is cross-fertilisation both between trees standing close in the stand and among distant individuals in the same or nearby stands. Hagman (1971) studied incompatibility in *B. pendula* and *B. pubescens* and found partial incompatibility in both cross-pollinated and self-pollinated trees. When trees from the same population were cross-pollinated some combinations were incompatible. Incompatibility occurs in the style as retarded growth of the pollen tube and is probably

based on a one-locus multiple allele system. Incompatibility reaction is also influenced by environmental conditions: compatibility is increased at low temperatures.

### *Self-fertilisation and inbreeding depression*

43. In the studies of Hagman (1971), self-incompatibility was observed after self-pollination. Self-incompatibility was not complete and the filled seed frequency was highest when the pollinations took place at low temperature.

44. Wang (1996) studied inbreeding depression in *B. pendula* and the possibility of using heterosis in breeding. He found that inbreeding depression in survival and in stem volume of progenies in three successive generations of selfing was significant. The mean survival rates were 88 %, 37 %, 28 % and 42 % for outcross controls, S1, S2 and S3 selfed progenies, respectively. Inbreeding depression for stem volume also increases with advancing generations of selfing. The mean stem volumes were 5.31, 3.15, 2.66 and 2.12 dm<sup>3</sup> for outcross controls, S1, S2 and S3 selfed progenies, respectively.

## **D. Seed crop**

### *Seed crops*

45. The percent of germinating seed is directly related to the amount of pollen shed: seed crops with the highest viability will be produced during years of abundant flowering (Sarvas 1952). Each strobile contains about 450 seeds. In the average year in ordinary regeneration areas, seed crop is some 340 filled seeds m<sup>-2</sup>, with 2 300 seeds m<sup>-2</sup> in a good seed year. In a good seed year in a pure birch stand the best annual result has been 53 200 seeds m<sup>-2</sup>, i.e. 128 kg per hectare. A crop amounting to 20 % of the best seed crop occurs only every third year, and intervening crops may be only 5 – 10 % of a good year (Sarvas 1948). Cold springs can lead to massive loss of male catkins. Birch produces empty fruits in the absence of pollination.

46. Dispersal range of birch seed is limited by the small seed size. The fall rate for silver birch seed is 0.52 m s<sup>-1</sup> (Sarvas 1948). Most seeds fall within 40 – 50 m of the source, with a maximum amount of seeds at 10 – 12 m from the tree. The amount of seeds is still 5 % of the maximum at 100 m from the source, but after 70 m most seeds are empty. In *B. pendula* seeds are also dispersed throughout the autumn and winter, so there is probably also secondary dispersal of seed over the surface of snow by wind. With *B. lenta*, seeds were distributed over an area 3.3 times greater than by initial seed fall, and further dispersal by melting water in the spring could be some 50 km (Matlack 1989).

## **E. Natural regeneration**

### *Germination and establishment in the field*

47. A non-fluorescent water-soluble substance in the seed coat has germination-inhibiting properties. This inhibitor apparently increases the oxygen and light requirement of the embryo. Un-chilled, intact seeds require light for germination, but breaking the seed coat allows rapid entry of oxygen and hastens germination in darkness (Perala and Alm 1990). A long-day photoperiod or illumination with red light induces germination, whereas blue or far-red light inhibits germination. Stratification (chilling) or temperatures above 20°C override the photoperiod requirement. Fluctuating temperatures within the range

of 20 – 30°C are more favourable for germination than steady temperatures (Perala and Alm 1990). Stratification also eliminates the effect of temperature on germination rate (Atkinson 1992). In natural conditions in the northern parts of the range of birch, the cold requirement is usually met.

48. In the autumn, after seed shed, short days and low temperatures inhibit germination and help seed survival over the winter. In the spring, after a long enough chilling period, dependence of germination on day length disappears and seeds germinate when temperature rises and there is enough moisture in the ground (Nygren 1987). Birch seeds may also germinate soon after seed deposition in the summer, if there is enough moisture in the ground. As the individual seeds are small and contain small amounts of reserve food, the radicle of the birch seedling remains short with the result that the plant frequently withers away and dies and seedlings only grow up on spots which contain enough moisture.

49. The percentage of germination of *B. pendula* seed in southern Finland (60° N) is about 61 % and it decreases towards the North, being about 53 % in central Finland (62° N). The opposite is true for *B. pubescens* with germination of 63 % and 70 %, respectively (Sarvas 1948).

50. In natural conditions the seeds are concentrated in the upper parts of the soil profile indicating a rapid turnover. Hill and Stevens (1981) showed that 80 % of the seeds were found in the litter layer and showed no long-term survival. In studies where *B. pendula* and *B. pubescens* seed were sown to two forest sites in northern Sweden, only 6 – 9 % of the seeds remained viable after one year. The depletion rate was slower in the two successive years (Granström and Fries 1985). This might be due to litter-fall and growth of mosses altering the environment, making the seeds less liable to germinate. When the seeds were buried beneath the litter layer, the viability of the seeds did not fall consistently over a five-year period even though after three years the pericarps were more or less degraded exposing naked embryos (Granström 1987).

51. 80 – 90 % of birch seedlings die within the first year, perhaps mainly as a result of drought. Establishment is best on bare mineral and humid soils and cushion Sphagnum. These surface types have the most favourable moisture conditions (Kinnaird 1974).

## **F. Vegetative reproduction in the field**

### ***Sprouting***

52. Sprouting by basal buds occurs as a response to fire as well as other damage such as felling and grazing. The sprouting ability of *B. pubescens* is stronger than that of *B. pendula*. Sprouting ability differs seasonally, and is generally higher for dormant trees. Felled *B. pendula* produces the lowest frequency of stump sprouting in summer and the highest in fall and spring. The frequency of sprouting and shoot size (but not the number of shoots) depends on light intensity and temperature. No stumps were observed to sprout at temperature lower than 10°C (Perala and Alm 1990). Sprouting depends also on the soil type: sprouting is more frequent in moist forests and on peat land than on dry heath and woodlands. Sprouting also depends on the method of regeneration. It is most frequent on clear-cut areas and least frequent on group selection cutting areas, forest fire areas and burnt-over clear-cut areas because of damage to the basal buds (Sarvas 1948).

## SECTION V - CROSSES

## A. Inter-specific crosses

53. Natho (1957) found several natural crosses between *B. pendula* and other birch species in Germany, i.e. *B. pendula* x *B. pubescens*, *B. pendula* x *B. humilis* and *B. pendula* x *B. pubescens* x *B. humilis*. Moreover, the author showed that there is a continuum from *B. pendula* via *B. pubescens* to *B. humilis* in leaf shape. This and the triple hybrid indicate that there is gene flow among the three species.

54. Johnsson (1945) found large variation among experimental crosses of *B. pendula* and five other birch species. The percentage of fruits containing seed were 53.2 %, 8.8 %, 0.9 % and 0.4 % for *B. pendula* x *B. japonica*, *B. pendula* x *B. papyrifera*, *B. pendula* x *B. ermanii* and *B. pendula* x *B. maximowicziana*, respectively. The hybrid *B. pendula* x *B. pubescens* was infertile in this experiment.

55. Clausen (1970) carried out inter-specific crosses between 12 *Betula* species (Table 2.). He observed that high-ploidy female x low-ploidy male usually gave low seed germinability. Crosses within a subsection did not give more germinable seeds than crosses between species from different subsections. Crosses with *B. ermanii* as female gave more germinable seeds than any other cross. Each species was represented by 1 – 13 individuals, so definite conclusions can not be drawn from these results. However, it is the most comprehensive study of its kind to date.

**Table 2. A summary of the results on seed germination in different crosses between *Betula* species based on data by Clausen (1970).**

		COSTATAE				ALBAE				NANAE			
		<i>len.</i>	<i>nig.</i>	<i>erm.</i>	<i>all.</i>	<i>pen.</i>	<i>pop.</i>	<i>pub.</i>	<i>pap.</i>	<i>gla.</i>	<i>hum.</i>	<i>nan.</i>	<i>pum.</i>
<i>lenta</i>	2n		0	0	***	-	*	-	0	0	0		0
<i>nigra</i>	2n	*		***	*	**	*	**	*	*	**	**	**
<i>ermanii</i>	4n	***	*		0	***	*	***	***	0	***	0	***
<i>alleghaniensis</i>	6n	*	*	*		0	*	*	***	*			*
<i>pendula</i>	2n	*	*	**	*		***	*	***	**	*	*	*
<i>populifolia</i>	2n	*	*	*	*	*		*	*	*	*		*
<i>pubescens</i>	4n	0	*	*	*	*	*		*	*	***	0	*
<i>papyrifera</i>	4-6n	**	*	**	**	***	*	***		0			***
<i>glandulosa</i>	2n		0	-	0	0	0	***	-			-	-
<i>humilis</i>	2n	0	0	***	*	*	0	***	**	0			***
<i>nana</i>	2n	-	*	0		0	*	**	0	**			0
<i>pumila</i>	4n	0	0	*	0	*	*	*	*	0	*	0	

Germinability %: <10 low (\*), 10—30 moderate (\*\*), >30 high (\*\*\*), no seed set (-)

56. Hagman (1971) studied incompatibility in *B. pendula* and *B. pubescens*. Incompatibility between *B. pendula* and *B. pubescens* is more pronounced when *B. pendula* is the male parent. Moreover, the *B. pendula* pollen tubes do not seem to be able to penetrate the style of *B. pubescens*. Low temperature gave the highest frequency of successful hybridisations. The following natural inter-specific hybrids of *Betula* species have been found in Finland (Kurtto and Lahti 1987):

*B. pendula x pubescens*; *B. nana x pendula*; *B. nana x pendula x pubescens* and  
*B. nana x pubescens*.

#### **B. Intra-specific crosses**

57. Raulo and Koski (1977) studied long-distance crosses (distances between parent trees > 100 km) in Finland in order to find out if inter-provenance crosses would result in hybrid vigour, that is, in a heterosis effect. In these experiments crosses between Finnish provenances did not result in a heterosis effect.

58. Wang (1996) studied inbreeding depression and long-distance crosses in *B. pendula* and the possibility of using heterosis in breeding. He found heterosis both in hybrids of inbreeding progenies and in provenance hybrids. The growth performance of the long-distance crosses (central Finland x Estonia, northern Finland x Latvia, Germany x southern Finland, central Finland x Austria) significantly exceeded that of controls. The southern long-distance crosses also outperformed short-distance crosses (between southern and central Finland, southern Finland and Estonia, and southern and northern Finland), but did not significantly differ from the local inbred crosses. Hybrids of selfed progeny gave a significantly better growth performance than controls of either stand origin or conventional full-sib family origin: the mean stem volume of hybrids was 52 % higher, and the volume of the best hybrid family was 112 % higher than the mean of improved full-sib family controls. These results suggest that hybrids of inbred lines or provenances could be used in breeding of silver birch for superior yield.

## SECTION VI - GENETIC VARIABILITY

### A. Genetic background

#### *Chromosome number*

59. The birches are characterised by their small chromosomes which are only a few micrometers long. A double-staining method is useful in counting the number of chromosomes in *Betula* and in other hardwood species with chromosomes of small size and large number (Hömmö and Särkilahti 1986).

60. *Betula pendula* is a diploid with 28 chromosomes; *B. pubescens* is a tetraploid with 56 chromosomes. Trees morphologically resembling tetraploid but with intermediate chromosome number ( $2n=42$ ) are sometimes found. Because the chromosomes tend to lie in groups of seven and because of small numbers of quadrivalents in meiosis in the 28 and 56 chromosome plants, the original basic chromosome number is thought to be seven rather than fourteen (Eriksson and Jonsson 1986).

61. Natural polyploidy is very frequent in the genus *Betula* and the number of ploidy levels differ between the four subsections of the genus. *Costatae* has diploid ( $2X=28$ ), tetraploid ( $4X=56$ ) and hexaploid ( $6X=84$ ) species and in addition to these, three ploidy levels. *Albae* has also a pentaploid ( $5X=70$ ) species, *Nanae* has both diploid and tetraploid species and *Acuminatae* only diploid ones. *Betula* is a young species from the evolutionary point of view which explains the polyploid nature and the occurrence of various ploidy levels (Särkilahti and Valanne 1990).

62. The possibility of using induced polyploidy to speed up the natural evolution and breeding of *Betula* arose in the 1960s (Särkilahti and Valanne 1990). The polyploidization experiments were performed by treating seeds with colchicine during germination. Of the 687 polyploid trees produced by these experiments in Turku, Finland, 287 were still alive in 1990. Moreover, a series with ploidy levels ranging from diploid to dodecaploid ( $2X - 12 X$ ) consisting of both natural and induced polyploids is available (Särkilahti and Valanne 1990).

63. Identification of polyploid trees of *B. pendula* is possible visually on the basis of leaf morphology, with polyploid trees having larger leaf blades, thicker leaf petioles and a rougher network structure on the abaxial leaf epidermis than normal trees. The mortality of colchicine polyploid trees is typically high in every growth phase, growth rate is slow and growth habit more or less abnormal. Thus, colchicine-induced autopolyploid trees are not of great value as such but they can be used for studying the effect of the ploidy level on growth, breeding, adaptability and evolution of *Betula*. In natural conditions polyploids are said to possess greater ecological and genetic amplitude and, therefore, exhibit greater variability than related diploids (Särkilahti 1990). Ploidy manipulation seems to produce mainly sterile trees but micro-propagation can be used for multiplication of polyploid material.

## B. Variability within and between populations

64. Long-lived species such as forest trees are subject to conditions varying greatly from year to year. Thus, they have a large within population variation so that there are always genotypes well adapted to the varying conditions at regeneration. For example, in studies of five year heights of *B. pendula* progenies Velling (1985) stated that the within-population variation was as large as that between populations originating from latitudes 60 – 63° N. Raulo and Koski (1977) found that intra-group variation within provenances and between individuals was large compared to variation between stands or localities. Birch stands are not closed populations and gene exchange between stands is successful as a result of pollen dispersal by wind. A large within-population variation was also reported, for example, in two separate studies (Johnsson 1951 and Langhammer 1982, cited by Eriksson and Jonsson 1986).

### *Differences in qualitative traits; marker techniques*

65. Raulo and Koski (1977) reported a large variation in growth and stem quality between progenies from different plus trees. Many progenies attained a stem volume that exceeded the mean value of the test by more than 40 %, and good progenies could be found among both open-pollinated and cross-pollinated families. Variation in wood density is generally smaller than that in growth and stem quality characteristics, but significant differences can be found between progenies (Velling 1979a). Nepveu and Velling (1983) studied the inheritance in wood quality characteristics. The inheritance in basic density and shrinkage was fairly strong, but volume growth and pulp yield showed low heritability.

66. As attention has focused on the external quality of the stem for plywood production, no active breeding or selection of wood quality has so far been applied. The properties of birch pulpwood could be improved if the bark content could be reduced, the size and/or number of branches reduced and the carbohydrate content of the wood increased. Increasing the number of fibres without affecting the fibre length would improve the optical properties and bulk of the pulp. Tammissola *et al.* (1995) studied tree-to-tree variation to determine if there is variation in the pulpwood properties of *B. pendula* that can be used in breeding. They found that significant variation occurred between individual trees in the properties studied, and high significance levels give support for underlying genetic differences.

67. If DNA markers closely associated with pulping and papermaking properties were found, it would be possible to select the most desirable trees within a progeny more quickly and cheaply compared to the more or less destructive analyses of mature trees (Tammissola *et al.* 1995). Altogether 157 nucleotide sequences and 177 proteins of *B. pendula* are listed in the database of NCBI. Molecular biology is the most active research area within biology and the number of known nucleotide sequences and proteins is increasing rapidly. The databases at <http://www.ncbi.nlm.nih.gov/> have the most updated information about genetic markers. For an old review on genetic markers in *Betula*, see (Hattermer *et al.* 1990).

## C. Adaptivity to climatic conditions

### *Growth cessation and winter hardening*

68. In cool and temperate regions the annual temperature rhythm is the main regulating factor of the environment. Forest trees are adapted to the variation of the growing season between years as well as to the long-term average.

69. The timing of growth cessation and the subsequent process of winter hardening is determined by a joint effect of heat sum and night length (Koski and Sievänen 1985). In Punkaharju, Finland (61°48' N),

growth ceased at the cumulative temperature sum of 800 degree-days and night length of 7.5h. Koski and Sievänen (1985) predicted that an adapted provenance of *B. pendula* will cease growth by the accumulation of about two-thirds of the total heat sum for a normal growing season. If northern provenances were moved southwards, growth would cease with two thirds of the original local heat sum, but due to longer nights, growth would cease a few days earlier, that is, with a smaller heat sum than at the original locality. A northern provenance from Punkaharju (Finland) moved to Suwalki (Poland) would cease growth three weeks earlier than the local one. The opposite transfer northwards of southern provenances would lead to growth cessation three weeks later than the local ones. The heat sum characteristic of southern provenances would not be reached until the beginning of September, but long nights would induce growth cessation 10 days earlier, thus adapting the trees for the local growing season (Koski and Sievänen 1985).

70. Breaking the dormant state is affected by chilling temperatures during winter. The effect of chilling is cumulative increasing up to a threshold when the buds are released from dormancy. Bud burst and growth start in spring occur after the accumulation of a certain heat sum above a specific base temperature (Myking and Heide 1995).

### ***Growth start***

71. As *B. pendula* is geographically widely distributed, it has by latitude and altitude determined ecotypes with different optimum and critical chilling temperatures and durations. The ecotypes of northern origin have the earliest bud burst with variation in the requirement for duration of chilling but not for chilling temperature. A longer chilling requirement is found in southern ecotypes. A clinal difference in the base temperature for growth among the ecotypes is also found. In the studies of Myking and Heide (1995) the north Norwegian ecotypes flushed 2.5 months earlier and developed faster and had a lower base temperature for growth than ecotypes from southern Scandinavia. The Danish birches have adapted to a milder and more variable winter climate by developing greater dormancy stability involving both a longer chilling requirement and a higher base temperature. Night length had no effect on bud burst after the chilling requirement was fully met. After full dormancy release, time of bud burst in birch depends solely on the temperature regime in late winter and spring (Myking and Heide 1995).

72. The upper temperature limit for normal dormancy release in birch is probably slightly above 12°C. Chilling deficit is thus unlikely to occur in Scandinavia and in other areas where the chilling requirement is far exceeded, even with a climatic warming of 7 – 8°C above the current normal winter temperature. The likely effects of a climatic warming include earlier bud burst, a longer growing season and increased risk of spring frost injury, especially in northern ecotypes (Myking and Heide 1995).

### ***Growth capacity of different provenances***

73. In provenance trials with *B. pendula* at four sites within the latitudinal range of 56 – 64°, Johnsson, 1977 (cited by Eriksson and Jonsson 1986) reported that long-distance transfers both southwards and northwards tend to result in growth reduction. The longer the transfer northwards, the more is the growth period prolonged for the material from the south and the higher is the risk for dieback of the leaders. Short-distance transfers (< 250 km) do not influence the height growth considerably. Kleinschmit and Svolba (1982) reported on three-year heights of populations from central Europe to Finland. The Finnish and Swedish populations moved to Germany performed poorly as a consequence of the long-distance transfer southwards. In a study of growth of seedlings (Velling 1979b) a dependence between height and latitude of the origins was found. Seedlings of different provenances (from Latvia, 56°31'N, to central Finland, 61°48'N) were grown in central Finland and the more southern the origin, the greater the

height of seedlings. A correlation was also found between the degree of leaf yellowing and the origin of seedlings. While the Finnish origins had turned completely yellow in the autumn, the Latvian origins still retained their green colour. The colouring was connected with survival, with poor winter resistance causing increased mortality in the southern origins.

## SECTION VII – ECOLOGY AND PHYSIOLOGY

### A. Dynamics of regeneration

74. Birch is a pioneer species, and it quickly colonises bare areas and does not tolerate shading. Young birches can not survive fire because of their thin bark, but some mature trees may, because the thin forest floor under birches can not support intense and persistent surface fires. Post-fire pioneer successions are often dominated by birch. Abundant seed production enhances the pioneering character of birch. Without fire or human intervention birches would be replaced in succession by more shade-tolerant and longer-lived species (Perala and Alm 1990).

#### *Light*

75. Seedling density is independent of canopy cover, i.e. germination is unaffected by light, but the ability of birch seedlings to penetrate the canopy is low and they cannot establish in even the lowest vegetation. Most birch seedlings are only about 5 – 12 cm tall after the first year, and competing vegetation on fertile sites can easily overgrow and subdue them. The birches are also sensitive to chemical interference (allelopathy) by other plants (Perala and Alm 1990). Moreover, shaded birches are a preferred host by insect herbivores (see e.g. Ruohomäki *et al.* 1996).

76. Shading by neighbouring trees has a profound effect on shoot growth. In a short-term experiment shaded seedlings were higher than those reared in the simulated sun-light (Aphalo and Lehto 1997). Fewer buds are initiated and a higher proportion die in zones of heaviest shading (Atkinson 1992). Optimum sunlight for silver birch height growth was found to be 43 % of full sunlight for weeded seedlings, but 24 % for seedlings competing with weeds. Silver birch has also been found to grow less when sunlight decreases from 56 to 16 %. In greenhouse experiments with conifers, birch was more sensitive to both its own canopy and root competition than to competition by conifers (Perala and Alm 1990).

77. The Eurasian birches can endure as much as 90 % shade by adapting leaf structure. As sunlight diminishes, the light intensity for photosynthetic saturation, maximum photosynthetic rate, leaf mesophyll thickness, and chlorophyll concentration all diminish. The maximum photosynthetic efficiency for silver birch is at 10 – 50 % full sunlight, much higher than for shade-tolerant plants (Perala and Alm 1990).

#### *Temperature*

78. The birches are adapted to cool climate and grow best at about room temperature. Once the soil temperature reaches 2 – 3°C, the growth of silver birch depends more on air temperature than on soil temperature. Seedling shoots grow in direct proportion to heat sums, gradually diminishing as photoperiod shortens. New shoots can tolerate growing season temperatures of -3 to -5°C (Perala and Alm 1990).

### *Water requirements*

79. Assimilation of silver birch is fastest at about  $-5 \times 10^2$  kPa and water use diminishes in wet conditions. The birches are sensitive to both drought and flooding. Seedling mortality increases at water potentials below  $-1.6 \times 10^2$  kPa. However, adaptability of birches to anaerobic conditions by oxygen transfer from the shoots to the roots, reduces the effects of flooding. Fertilisation improves water uptake and drought resistance (Perala and Alm 1990).

80. The birches use water inefficiently. Silver birch seedlings maintain turgor at high soil water potential only by closing stomata, which partially close at about  $-15 \times 10^2$  kPa. In large trees daily transpiration per unit of foliage mass is about 514 kg water/kg foliage. Extreme transpiration demand reduces growth even on moist soil because transpiration and photosynthesis have partly separate control systems. Drought depresses photosynthesis more than it does transpiration (Perala and Alm 1990).

### *Nutrients*

81. To achieve maximum productivity, white birch requires all necessary nutrients, an optimum ratio of nitrogen sources  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in a rhizosphere and an optimal total nutrient solution (Ingestad 1971). In general, *B. pendula* is a nitrogen-limited species. Low-nitrogen conditions reduce growth and increase amount of condensed tannins, whereas in high nitrogen conditions *B. pendula* grows faster and the content of flavonoids in foliage is higher (Keinänen *et al.* 1999). The effects of nitrogen fertilisation on herbivore resistance are not clear. Nitrogen fertilisation did not affect preference of mammalian herbivores on *B. pendula* seedlings. On the other hand, the autumnal moth grew larger on fertilised seedlings (Mutikainen *et al.* 2000). The limiting effects of other nutrients on the birches are not as well defined. At optimum levels, both zinc and manganese stimulate seedling growth, but toxicity problems have also been reported. There is a wide genetic variation in zinc tolerance and uptake. *B. pendula* has a high requirement for sulphur and it readily takes up boron. It sometimes suffers from manganese toxicity on poorly drained peat. The pH optimum for *B. pendula* and *B. pubescens* is between 4 and 5. *B. pendula* can tolerate some soil salinity (Perala and Alm 1990).

### *Effects on soil*

82. *B. pendula* grows on fertile mineral soils and on drier and lighter soils than *B. pubescens*, which grows commonly on both peat and mineral soils (Gimingham 1984). The birches usually improve soils by efficiently cycling nutrients. First generation birch stands on former *Calluna vulgaris* (heather) heathland have increased earthworm activity, higher soil pH, greater total P, higher base status, faster rates of N mineralisation and cellulose decomposition and more diverse ground flora. Surface soil N, P, K, Ca, Mg and Mn is increased. Silver birch on Sphagnum peat soils accelerates microbial decomposition, accumulates dead woody roots and increases soil bulk density (Perala and Alm 1990).

### *Photosynthesis*

83.  $\text{CO}_2$  exchange variables showed considerable genetical variance in *B. pendula*. 54 % of variation in net photosynthesis, 36 % of variation in stomatal conductance and 45 % of variance in intercellular  $\text{CO}_2$  were assigned to family (Wang *et al.* 1995). Photosynthesis related traits are modified by environmental factors as well. Defoliation reduces leaf area and biomass, but not photosynthesis, since *B. pendula* is able to compensate the damage by increasing photosynthetic activity. In fact, in nitrogen-rich environments damaged leaves have higher photosynthetic activity than the undamaged controls (Ovaska *et al.* 1993). The degree of compensation is dependent on the source of damage. The compensative response of *B. pendula*

after artificial damage does not differ from that of the autumnal moth (Ovaska 1993), whereas the response was relatively weak after the damage by the alder beetle *Agelastica alni* (Oleksyn *et al.* 1998).

### ***Root development***

84. Birch trees exploit soils efficiently by developing both an extensive and dense surface root system to intercept precipitation and sinker roots to penetrate dense ‘pans’ and exploit deep water. The tap-root becomes horizontal after about 30 cm or is overtaken by side roots. Narrower roots may penetrate to a considerable depth. The extreme length of horizontal roots can be 25 m on sandy soils. In anaerobic conditions, *B. pendula* and *B. pubescens* roots elongate more than in aerobic conditions. Birch roots penetrate deep into poorly drained soils such as peats, and benefit inter-grown conifers by oxygenating the soil. On the other hand, birch small-root biomass may be twice that of the conifers offering intense root competition (Perala and Alm 1990).

### **B. Mycorrhizae**

85. Early mycorrhizal infection is an important factor in the successful establishment of birch seedlings especially on nutrient-poor soils. The rates of nitrogen mineralisation of many forest litters are so slow that nitrogen can become the key growth limiting element. Some ectomycorrhizal fungi (e.g. *Amanita*, *Boletus*, *Paxillus*, *Suillus* and *Thelephora*) have proteolytic activity and thus the potential to mobilise nitrogen from proteins, peptides and amino acids and make it available to the plant. Some fungi, like *Laccaria laccata*, lack this activity and are dependent upon mineralisation processes initiated by other organisms (Read 1991). The assimilation of mycorrhizal amino compounds also provides supplementary carbon as well as nitrogen to the host plant. Abuzinadah and Read (1989) showed that up to 9 % of the carbon assimilated by the host plant (*B. pendula*) over a period of 55 days was derived heterotrophically from the protein by mycorrhizal fungi. This is thought to be an adaptation to shade stress in young trees which spend the early part of their lives under the canopy of mature trees and which need to supplement their carbon budgets by heterotrophic assimilation. Grellier *et al.* (1984) showed that association with a mycorrhizal fungus (*Paxillus involutus*) practically doubled the growth of *in vitro* grown birch seedlings compared to non-mycorrhizal seedlings. Soil fauna have also been found to positively influence nutrient uptake and net production of birch seedlings (Setälä and Huhta 1991). Mycorrhizae can be inhibited by acute phosphorous deficiency, but can be encouraged even by a light application of phosphorous. Mycorrhizae like *Paxillus involutus* increase zinc tolerance by adsorbing zinc to the hyphae and slowing its transport to the shoots (Perala and Alm 1990).

86. Because little growth is possible on the nutrient reserves available in the seed, the seedlings are dependent on an external nutrient supply by the production of the first pair of leaves. Newton and Pigott (1991) report that ectomycorrhizal infection was indeed recorded by the time the first pair of leaves had expanded. Two groups of mycorrhizal fungi have been recognised: “early-stage“ fungi (*Inocybe* spp., *Hebeloma* spp. and *Laccaria* spp.) can inoculate roots of seedlings from basidiospores or from added inoculum whereas “late-stage“ fungi (e.g. *Lactarius pubescens* and *Leccinum roseofractum*) infect by hyphal connection. In natural circumstances the “late-stage“ fungi are the most vigorous colonists of birch seedlings (Read 1991).

## C. Diseases

### *Firm Rot*

87. Black coloured firm rot around the pith is a serious cause of concern in young cultivated birch stands. Several different pathogens (fungi and bacteria) are responsible for the defect. Their entrance is, obviously, facilitated by frost cracks, insect exit holes (possibly the exit holes of *P. betulae*) and especially vole or moose browsing. The defect is especially harmful in plywood industry if the black colouring spreads outside the peeler core (Uotila 1987).

### *Birch rust*

88. Birch rust (*Melampsorium betulinum*) is the most common leaf disease of *B. pendula*. The rust causes yellowing and premature falling of the leaves, but it does not affect buds or the wood. If epidemics appear in several consecutive years, the growth of young seedlings can be decreased because of the shortened assimilation period (Uotila 1987; Vuorinen 1992). There are clear genetic differences in susceptibility to rust among birch clones, and screening clones for resistance could be used in breeding. A leaf-disc bioassay was used for determining the field rust resistance of birch clones in the study of Poteri and Rousi (1996).

### *Stem spotting*

89. Stem spot disease caused by a group of fungi (*Godronia multispora*, *Botrytis cinerea*, *Fusarium avenaceum*, *Cylindrocarpon* sp., *Alternaria* sp.) is common in nurseries and can be very detrimental to young birch seedlings. The small necrotic lesions in the bark produced in the autumn enlarge during winter, and seedlings may die before spring. These fungi infect trees through mechanical wounding sites, frost cracks or insect (especially cicada, *Cicadella viridis*) wounding sites (Juutinen *et al.* 1976). Stem spotting is common in birch trees grown in unsuitable sites, e.g. in waterlogged soils (Uotila 1987).

### *Rot fungi*

90. *B. pendula* is mainly rotted by *Polyporaceae* fungi, which start the rotting in the heartwood in the inner part of the trunk, and then proceed to the living sapwood. Especially timber is susceptible to decay. *Fomes fomentarius* and *Inonotus obliquus* are the most common rot fungi and they attack living trees through wounds. *Ochroporus igniarius* also infects living trees.

91. *Piptoporus betulinus* is less common and attacks old or dead trees, destroying both heartwood and sapwood at the same time. The best way to prevent rot damage of living trees is good forestry practice: thinning should be done in time and only dead branches pruned, since branch scars act as a route for rotting fungi (Uotila 1987). Other fungi that rot dead trees and timber are *Stereum sanguinolentum*, *S. purpureum*, *Pycnoporus cinnabarinus*, *Cerrena unicolor*, *Trametes multicolor* and *T. hirsuta* (Uotila 1987).

## D. Insect herbivory

92. Insect herbivory affects birch growth. For instance, in 1965 – 1967 the autumnal moth (*Epirrita autumnata*) defoliated over 5000 km<sup>2</sup> of birch forest in Finnish Lapland (Lehtonen and Heikkinen 1995). On the other hand, birches have a large community of invertebrate herbivores (Annala 1987), which may

damage seedlings and trees locally, but at the stand scale birch is able to compensate the damage. Of geometrid defoliators living on *B. pendula*, *Opheroptera brumata* is among the most voracious species (Tikkanen *et al.* 1998, 1999, 2000). The species is common in Baltic countries, southern Scandinavia and central Europe. The damage may be severe after the insect outbreak but usually climatic conditions enable birch to compensate the damage by re-growth. Beetles may damage trunks of mature trees, and thereby reduce the economical value of the timber. For instance, *Hylecoetus dermestoides* and *Trypodendron signatum* bore tunnels in logs and timber. *H. dermestoides* can attack also living trees and a simultaneous infection by rot fungi can be fatal to the tree (Raulo 1981). Larvae of the birch cambium fly, *Phytobia betulae*, mine in the birch wood near the cambium layer and cause 1 – 4 mm wide brown streaks in the wood. The streaks decrease the value of birch wood used in plywood and furniture industry. The damage is aesthetic; the mechanical strength of the wood is not affected. The resistance mechanisms of birch and the biology of *Phytobia betulae* are not known. Ylioja *et al.* (1995) studied the susceptibility of European (*B. pendula*) and Japanese white birch (*B. platyphylla*) to *Phytobia* damage. Birch progenies which had *B. platyphylla* in their ancestry included more pith flecks than pure *B. pendula* progenies. Fast growing birches were also more susceptible to *Phytobia* attack. Differences in susceptibility to *Phytobia* attack between birch clones and progenies of plus trees could be used in resistance breeding.

93. Besides the genuine seasonal change in foliar phenolics (Salminen *et al.* 2002), insect grazing or artificial damage increases the level of phenolics in the leaves of *B. pendula*. In the study of Hartley (1988), increases in phenolic compounds did not affect further feeding, either by a natural birch-feeding herbivore (*Apocheima pilosaria*) or a polyphagous non-birch feeding insect (*Spodoptera littoralis*). Hence, there is no evidence that the tree's responses were specific defences against further attack by insect herbivores.

#### E. Mammalian herbivores

94. In Scandinavia, trees of the genus *Betula* are important winter food for herbivorous animals, especially voles (*Microtus*, *Clethrionomys*), hares (*Lepus*) and moose (*Alces alces*) (Rousi *et al.* 1989, 1990; Jia *et al.* 1997). They usually destroy woody plants in wintertime when alternative food plants are under snow cover. The variation of resistance among origins and families and even among individual seedlings within a genus can be very large. The centres of origin of cultivated plants are thought to be the best places to find resistances to diseases and herbivores. In these centres, plants have been exposed to selective pressure from local pathogens and herbivores for a long time, and have consequently developed resistance to them. Bryant *et al.* (1989) indicated that *Betula* and *Salix* species from Pleistocene refuges (Alaska and Siberia) were more resistant to mountain hare than species from regions that were glaciated during the Pleistocene. Likewise, birches from Iceland, where there were no browsing mammals before the Norse colonisation, were more susceptible than birches from regions with more browsing mammals, that is, Alaska, Siberia and Finland (Bryant *et al.* 1989).

95. The bark of seedlings, young shoots and twigs of *B. pendula* contain resin droplets that consist of papyriferic acid and other triterpenoids. The juvenile resistance is accounted for by the resin, which is synthesised in and excreted by glands that are active only during the season when the primary apical growth of the shoot takes place (Taipale *et al.* 1993). On the other hand, phenolic substances are present in winter-dormant birches of all growth stages, but are rapidly metabolised by the plant in the spring when leaves emerge. Of these, platyphylloside is shown to exhibit repellent and anti-nutritional effects in mountain hares (Palo *et al.* 1992).

96. In *B. pendula* there is a sharp decrease of resistance after the tree has reached certain dimensions and the tree is no longer within reach of the herbivores. In the feeding trials with hare, Rousi *et al.* (1989)

found that 1-year-old seedlings were less palatable than twigs taken from 7-year-old saplings of the same origin.

### *Vole*

97. Voles cause considerable damage to forest plantations, especially during the peak years of density fluctuations. Birch plantations are especially vulnerable, since they are often afforestations of old fields, which are habitats favoured by *Microtus* voles (Rousi *et al.* 1990). The vole destroys birch seedlings under snow cover and it can eat the bark of the seedlings until the basal diameter reaches 4 cm (when the seedling is about 5 years old). Triterpenes in young birch seedlings seem to be deterrents of vole feeding. However, as the resin droplets are mainly situated in the top parts of the seedlings, and voles usually feed at the base of the seedling, they avoid the deterrent substances of the resin droplets. In field tests of Rousi *et al.* (1990), there were no clear differences in resistance between European white birch families in field tests with voles, but the Japanese white birch (*B. platyphylla*) turned out to be especially resistant to vole feeding. Rousi *et al.* (1990) suggest that hybrids between *B. pendula* and *B. platyphylla*, or Finnish-Siberian crosses of *B. pendula*, could be used to increase vole resistance.

### *Hare*

98. Hares feed on the upper branches of young birch seedlings (of 40 – 70 cm) and especially in winter the damage can be fatal for the seedlings. Hares are discriminating feeders and determination of palatability is guided to a large extent by olfactory stimuli, and the resistance of young birch seedlings is tied to the production of papyriferic acid. For example, in the feeding experiments of Rousi *et al.* (1991), for the mountain hare (*Lepus timidus*) the palatability of birch seedlings and saplings was strongly and negatively correlated with the number of resin droplets on the bark. The Japanese white birch (*B. platyphylla*) turned out to be the most resistant of different birch species.

99. Rousi *et al.* (1991, 1996) also tested how the growth of birch correlates with resistance and whether fertilisation lowers the resistance of seedlings to browsing. Contrary to predictions of growth-defence trade-off theories, no trade-offs were found in the resistance and growth rate. Fertilisation stimulated growth but did not affect the palatability of the seedlings. Consequently, fast growing birch species and families should not be more susceptible to damage by herbivores, and fast growth can be promoted parallel with herbivore resistance by means of breeding.

### *Moose*

100. Moose browsing on young birch seedlings occurs throughout the year. During winter only twigs are browsed, but during summer both leaves and young twigs are browsed. In order to feed on the young twigs of the crown, moose often break the main stem of the saplings. Moose can cause serious damage to birch plantations. In Finland, plantations established in 1976 – 1977 were studied in 1985 (Heikkilä and Raulo 1987). Only one third of the plantations were found to be undamaged. Half of the total area had been damaged slightly and 15 % seriously. At the time of the establishment, though, the moose density was very high, 3 – 8 animals/1 000 ha. With a density of 2 – 3 animals/1,000 ha moose are not a serious threat to growing birch. Also, establishing plantations close to built-up areas or main roads can considerably prevent the risk of moose damage.

101. Heikkilä *et al.* (1993) showed that after stem breakage, the recovery during the first two years was fairly good. If the stems were at the leader shoot of the previous year, re-growth was weaker than in unbroken trees, the angle of crookedness was stronger and wound healing weaker. Injuries to the wood

commonly become discoloured, and there was discoloration in 80 % of the sample trees. The significance of discoloration and decay depends on their distance from the wood surface, and the effect of discoloration on the quality of logs, when used for saw timber or veneer, can only be determined after a longer growth period. Bergström and Danell (1987, 1995) simulated winter browsing and summer browsing of moose, and studied the effects on the morphology and biomass of *B. pendula*. The birches responded to simulated winter browsing by growing fewer but larger and more branched shoots. There was also a slight decrease in viable seed production (Bergström and Danell 1987). In the experiments of Danell and Huss-Danell (1985) birches browsed by moose had more ants, psyllids, leaf-galls, leaf-miners and other leaf-eating insects. The leaves of browsed trees were larger and heavier, appeared greener and contained more nitrogen and chlorophyll. A decrease in resin content was observed. The trees seemed to allocate most of the nutrients and energy to growth in order to grow above the browsing line (Danell and Huss-Danell 1985). No induced defence in juvenile trees has been found; those trees that had been browsed during the previous winter were more palatable than previously un-browsed trees (Danell *et al.* 1985). Defoliation (simulated summer browsing) resulted in an overall decline in biomass and reduction in height and diameter growth. The long-shoots produced on defoliated trees were smaller and suffered more from tip-drying than shoots on control trees (Bergström and Danell 1995).

#### F. Abiotic damage

102. Abiotic damages are caused by too high ground water, drought, frosts and frost cracks (Uotila 1987). Snow load can cause stem breakage or permanent bending in young trees (Hannellius *et al.* 1989). Mechanical wounding increases fungal infections. UV-radiation does not seem to affect the growth, morphology or specific leaf area of *B. pendula* seedlings. The absorption by the secondary metabolites (phenolic glucoside, phenolic acids and flavonoids) provides the main part of the total UV absorbance of birch leaves. Plant secondary metabolism responds to enhanced UV-radiation by increasing synthesis of the above mentioned compounds that are the most effective UV-protectors (Lavola *et al.* 1997). The growth of *B. pendula* does not seem to be adversely affected by acid rain (Ashenden and Bell 1988). Instead, there was a stimulation in the height of birch seedlings with increasing acidity. A slight chlorosis of leaf margins after exposure to 2.5 pH rainfall was observed. Soil characteristics might have an influence on the sensitivity to acid rainfall.

103. Ozone causes physical damage on leaf surface, i.e. chlorosis, decoloration, black spots and necrotic areas and finally, leaf shedding (Maurer *et al.* 1997). Moreover, it changes the balance between CO<sub>2</sub> assimilation and stomatal conductance, which may severely limit plant's ability to repair ozone damage at the cellular level (Zhang *et al.* 2001). Ozone activates biosynthetic pathway, and thus the production of phytohormone ethylene (Kangasjärvi *et al.* 1997). Sequences of the cDNA of 1-aminocyclopropane-1-carboxylate oxidase (ACO), the enzyme catalysing the last step in ethylene biosynthetic pathway, as well other possible ACO-homologue fragments have been submitted to the Plant Gene Register (EMBL accession numbers X97993, X97992, X97994 and Y10749). Interestingly, *B. pendula* is among the most ozone-resistant woody plants in central Europe. The gas exchange traits differ by factor or two when compared to more vulnerable woody plants (Zhang *et al.* 2001).

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