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European bird cherry (*Prunus padus* L.) – a biodiverse wild plant for horticulture

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Abstract

European bird cherry, *Prunus padus* L. (Rosaceae), was studied in 1991-1998 in Scandinavia. The studies were conducted by the Botanical Garden of University of Oulu, University of Helsinki and Nordic Gene Bank. The main objective of the study was to define and to discuss about the valuable and the varietive characteristics of the species in the perspective of horticulture. Therefore the Nordic variation and the insect resistance of the species to small ermine moths, *Yponomeuta evonymellus* L. (Lepidoptera: Yponomeutidae) were studied.

Literature illustrated a wide geographical range. The species thrives in different habitats. Literature further describes three subspecies and more than twenty varieties. The taxonomical subdivision of the species is disputed and unsolved yet. According to the research at least thirteen taxons appear in Scandinavia, including *Prunus padus* subsp. *borealis* (Schueb. ex A. Blytt). The study, however, implied that the hybrids of subspecies are common. Therefore the classification should not be made just by the visual perception of plant morphology. Many northern origins of five different varieties or formas and some crossings were planted in clonal archive in Muhos (Northern Ostrobothnia).

The observations showed that bird cherries tolerate and support rich fauna. *Tolerance* and compensatory growth are the main resistance strategies, also to small ermine moths. Their offspring cause considerable visual damages on bird cherries at regular intervals. The larvae are able to completely defoliate bird cherry stands while mass occurrence about once in ten years in southern Finland. Plant populations, however, thrive without declining in number after defoliation. The results of the chemical assays further apply to *optimal defence strategy,* which is typical for many pioneer plants. Bird cherries seem to produce very active qualitative defences against herbivores for the chemical protection of valuable immature vegetative parts and seeds. These toxic secondary metabolites are mainly cyanogenic glycosides but supposedly also certain phenols.

Some phytophagous insects have evolved with their host plants by developing detoxification mechanisms against plant metabolites. Small ermine moth as a bird cherry specialist feeder is able to detoxify cyanogenic glycosides. The production of phenols was shown to induce during the larva invasions. The phenomenon is known as *rapidly-induced resistance.* Some observations implied to *delayed-induced resistance*. It is a mechanism, where herbivory induces the annual increase in leaf phenols. The nutrient quality of leaves, the degree of defoliation and the population size of herbivores decrease as a consequence. This is, however, disputed. Production of phenols can also be induced by environmental stress or genetic mutations. Consequently, it is argued that bird cherries may have phenol-based resistance to small ermine moths.

In conclusion, European bird cherry, as a varietive, tolerant and ornamental wild species, is able to contribute to the biodiversity of rural and urban ecosystems in Nordic countries. Therefore field studies to select the best origins for landscape horticulture are recommended. The analyses of the leaf chemical profiles of different varieties would further enlighten the taxonomy and the insect resistance (parasite-assisted or stress-mediated) of this valuable woody species.

Key words: Prunus padus, genetic variation, biodiversity, Yponomeuta evonymellus, insect resistance, phytophenols

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Metsätuomi (*Prunus padus* L.) – monimuotoinen luonnonkasvi viherrakentamiseen

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Tiivistelmä

Metsätuomea, *Prunus padus* L. (Rosaceae), tutkittiin vuosina 1991-1998 Oulun yliopiston kasvitieteellisen puutarhan, Helsingin yliopiston ja Pohjoismaisen geenipankin johdolla. Tavoitteena oli arvioida tuomea viherrakentamisen kasvina. Sitä varten selvitettiin tuomen perinnöllistä muuntelua ja tuholaiskestävyyttä erityisesti tuomenkehrääjäkoille, *Yponomeuta evonymellus* L. (Lepidoptera: Yponomeutidae).

Tutkimuksen mukaan vähintään kolmeatoista metsätuomen taksonia, mukaan lukien pohjantuomi, *Prunus padus* subsp. *borealis* (Schueb. ex A. Blytt), tavataan Pohjoismaissa. Tutkimus osoitti, että pohjantuomen taksonomiaa on vaikea määrittää pelkästään kasvin morfologisten ominaisuuksien perusteella, koska alalajit risteytyvät helposti. Tuomen pohjoisia alkuperiä ja eri taksoneja istutettiin hankkeen aikana kloonikokoelmaksi Muhokselle (Pohjois-Pohjanmaa).

Vaikka tuomissa elää rikas hyönteislajisto, ne kestävät hyönteisvaurioita hyvin (*toleranssi*). Vauriot ovat poikkeuksellisen näkyviä Etelä-Suomessa noin kymmenen vuoden välein. Silloin kehrääjäkoiden toukat syövät tuomikasvustot täysin lehdettömiksi laajoilta alueilta. Tuomet kuitenkin uusivat menetetyt lehdet nopeasti (*korvaava kasvu*). Lisäksi tuomet pyrkivät optimoimaan tuholaisilta ja taudeilta suojautumiseen käytettävissä olevat voimavaransa (*optimaalinen puolustusstrategia*). Ne tuottavat myrkyllisiä yhdisteitä - pääasiassa syanogeenisia glykosideja ja mahdollisesti myös tiettyjä fenoleja - arvokkaimpien kasvinosien suojaksi.

Jotkut hyönteiset pystyvät isäntäkasveihinsa kytkeytyneen lajinkehityksen seurauksena hajottamaan tai sitomaan vaarattomaksi ravintokasviensa myrkylliset yhdisteet. Tästä syystä syanogeeniset glykosidit eivät ole vahingollisia tuomenkehrääjäkoiden toukille. Tutkimuksen mukaan solujen vaurioituminen käynnistää fenolien tuotannon toukkien syömissä tuomissa (*nopeasti indusoituva resistenssi*). Tuomen lehtien fenolipitoisuudet saattavat kasvaa myös pitkällä aikavälillä. Samalla lehtien ravinnonlaatu heikkenee. Tapahtuma voi olla kasvisyönnin laukaiseman hitaasti indusoituvan resistenssin, kasvupaikkatekijöiden aiheuttaman stressin tai mutaatioiden tulosta. Tuomi näyttäisi siis pyrkivän torjumaan kehrääjäkoita fenoleita tuottamalla.

Metsätuomi on mukautumiskykyinen, kestävä ja koristeellinen luonnonkasvi, joka lisää sekä maaseutu- että kaupunkiekosysteemien monimuotoisuutta. Tuomikantojen vertailukokeita suositellaan kestävien ja koristeellisten taksonien ja alkuperien valitsemiseksi viherrakentamisen taimituotantoon. Lehtien kemiallisten profiilien analysoiminen tuottaisi puolestaan lisätietoa lajin taksonomiasta ja tuholaiskestävyydestä. Lisäksi voitaisiin tutkija, sääteleekö lehtien kemiaan perustuva ja loisten avustama hyönteisresistenssi kehrääjäkoipopulaatioita.

Avainsanat: tuomi, Prunus padus, muuntelu, luonnon monimuotoisuus, tuomenkehrääjäkoi, Yponomeuta evonymellus, tuholaiskestävyys, resistenssi, fenolit, viherrakentaminen

Foreword

Biological diversity or biodiversity is generally defined as variation in all forms of life - from genes and species to the broad scale of ecosystems. According to Gaston and Spicer (1998) genetic diversity is one element of biodiversity. *The Nordic Gene Bank* (NGB) is a centre for the conservation and utilization of plant genetic resources in the Nordic countries (Nordic Gene Bank 2004). It aims to conserve and document the genetic variation in Nordic plant species useful for agriculture and horticulture. The actions are coordinated by six working groups.

A proposal to study the genetic variation of European bird cherry, *Prunus padus* L., was made in 1991 by the working group of Fruit, Berries, Landscape and Ornamental Plants. The task was included into NGB's *Prunus-project* investigating *Prunus*-genus. Many edible and ornamental species cultivated almost all over the world belong to this variant genus. European bird cherry has the largest geographical range and it is the most winter-hardy species in the genus. People learnt to use the different plant parts of *Prunus padus* in the preparation of food, drugs or utility articles already in ancient times. However this knowledge is disappearing in Scandinavia. This in turn seems to cause the depreciation of this multipurpose species.

Prunus padus is explored mainly in entomology, although the species is worth to be acknowledged also in horticulture. Since there are not that many Nordic or horticultural researches done, the aim of this publication is to bring together the knowledge gained during two engaged studies. The genetic variation study was performed in NGB's *Padus-subproject.* It took place at the Botanical Gardens, University of Oulu, for 15 months during 1991-1998. It was financed by Nordic Council of Ministers (NMR) and carried out by the author during several summers. The resistance mechanisms of bird cherry to insects were investigated beside the subproject. This study was conducted by University of Helsinki.

Curator Mirja Siuruainen's and Director Oiva Nissinen's comments and support are gratefully appreciated. Nordic Gene Bank, the Botanical Garden, University of Oulu and University of Helsinki are appreciated for the contributions.

Lapland Research Station, November 2004

Marja Uusitalo

Contents

1 Introduction

European bird cherry is a boreal-temperate Eurasian species, which has been known since antiquity. This deciduous tree or shrub has ornamental flowers and edible fruits. *Prunus padus* L. is a Latin name used in Europe for the species. Linné first described and gave the species its Latin name in 1743 (Scholz & Scholz 1995). Prunùs is a Roman name for plum and pàdus is derived from Theofrastos. The ancient Greek philosopher mentioned the species in his writings (Skoglund Skåtøy & Skage 1997). *Padus avium* Miller is the Latin name used in Russia (Komarov et al. 1971). The species has been named in many languages (Table 1). It shows that the species is widely distributed.

Table 1. The name of *Prunus padus* L. in the languages spoken in northern Europe.

in English:	European bird cherry	in Russian:	ceremucha obyknovennaja
in Finnish:	tuomi	in Estonian:	harilik toomingas
in Swedish:	hägg	in Lithunian:	ieva
in Norwegian:	hegg	in Latvian:	ieva
in Danish:	haeg	in Polish:	czeremcha
in Icelandic:	heggur	in German:	Gewöhnliche Trauben kirche

Formerly European bird cherries were often transplanted from natural growing-sites into home gardens especially in the North where the climate is harsh (Appendix 1). Nowadays European bird cherries are sometimes even removed from urban or rural growing-sites, because they are host plants for many herbivores and pathogens. The plant species evidently recovers from severe herbivore attacks. Therefore, for example, small ermine moth (*Yponomeuta evonymellus* L.) affects only temporarily its ornamental value. This can be considered as a sign of extraordinary viability of the plant species.

The aim of this report is to indicate the potentials of European bird cherry in landscape horticulture, and to enlighten the taxonomy of the species. A reader will find new information and minute descriptions on the variant characteristics of the species in the report. Some tools for the determination of bird cherry plants are given. The publication has been divided into two parts according to the different types of studies performed. The genetic variation of the species is discussed in the first part of the publication. It was searched in Scandinavia. The second part deals with the insect resistance strategies. The occurrence of small ermine moths and insect resistance were studied in southern Finland.

The specific research questions were:

Genetic variation:

1) *What kinds of subspecies, varieties and formas can be found in Scandinavia?*
2) *Is there a definable distribution area of Prunus padus subspecies borealis (syn. Padus avium subsp. borealis) in Scandinavia?*

Insect resistance:

3) *Are there any indivudals which avoid attacks of small ermine moth larvaes during the mass occurrence?*
4) *Is larvae resistance based on the chemistry of plants or on other strategies typical for fast growing species?*
5) *Are there any signs of growing conditions such as drought which can effect on insect resistance of bird cherries?*

2 The genetic variation of European bird cherry

2.1 Taxonomy and distribution

European bird cherry (*Prunus padus* L.) belongs to *Prunus*-genus of Rosaceae-family. The genus is further divided in six subgenera (Komarov et al. 1971, Lid 1985). Wild *Prunus*-species growing in Scandinavia belong to three subgenera. Plum-species belong to subgenus *Prunus*, cherry-species to subgenus *Cerasus*, and bird cherry -species to subgenus *Padus*.

The geographical distribution of European bird cherry is wide (Figure 1). Populations reach further north than the populations of other *Prunus*-species in Eurasia (Hegi 1995, Leather 1996). The northern border of European distribution follows 71° north parallel and the shore of Arctic Ocean. Asian distribution follows 65°-70° north parallel (personal communication with A. M. Kurdyuk, Hortus Botanicus Centralis Scientiarum, 1992). The main boundaries in the north are tundra zone in the northeast of Asia Minor and western Siberia and the timberline of coniferous forest in central and eastern Siberia and Far East (Amur and Kamtschatka) (personal communication with J. M. Nemova, Hortus Botanicus Principalis Academiae Scientiarum, 3.9.1992).

Populations are seldom found further north in Russia (personal communication with A. F. Koltsov, Hortus Botanicus Stavropol, 30.7.1992). The southern limit is more difficult to determine. The southernmost European populations have been found in Scotland, northern England, Wales, mountainous

Spain and Portugal, the island of Madeira, Morocco, the northwest of Italy, Croatia, Bulgaria and northern Balkan Peninsula in Europe (Scholz & Scholz 1995). The southernmost populations thrive in Turkish Armenia, Afghanistan, Caucasus, southern Ural, Tien-Shan, the Himalayas, northern Japan, Korea and northern China in Asia (Komarov et al. 1971).

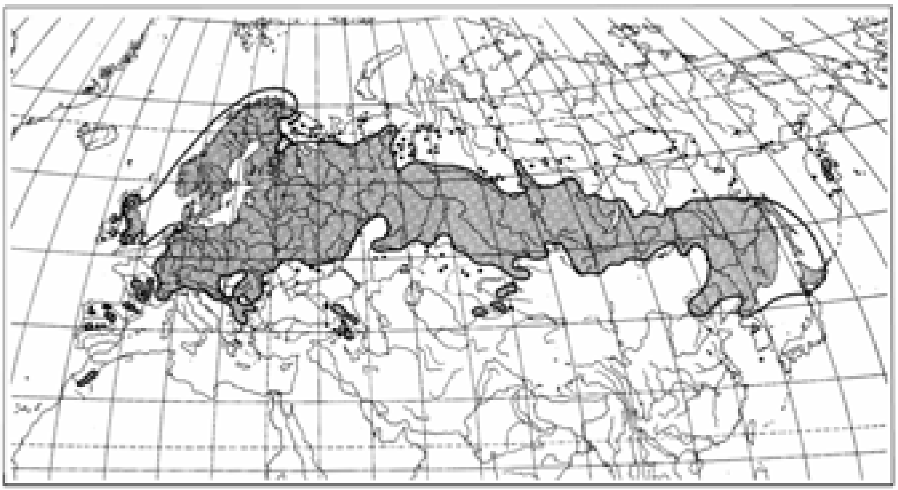

Figure 1. The geographical range of *Prunus padus* L. (Hegi 1995).

The habitus of different individuals may change a lot in the wide geographical distribution area of *Prunus padus*. The species is generally divided into tree subspecies (*padus, borealis, petraea*) on grounds of the differences in morphology and distribution area (Korovina & Belozor 1983). The populations of subsp. *borealis* occur in northern Scandinavia and Kola Peninsula, where the populations are known as *Padus schuebelerii* (personal communication with L. Kazakov, Hortus Botanicus Arcto-Alpinus Centrum Scientificum Kolaensis, 22.3.1993). The range of the subspecies is assumed to follow 70°35' of northern latitude. Populations reach up to 1200 meters a.s.l. in northern Scandinavia and 1500 meters a.s.l. in Kola Peninsula (Korovina & Belozor 1983, Lid 1985).

According to Scholz and Scholz (1995) subsp. *petraea* is native in the alpine or subalpine region which is known as 'nordherzynischen Bergland'. The habitats of subsp. *petraea* reach up to 2000 meters a.s.l. in Alps and 2200 meters a.s.l. in Atlas. Bird cherries reach higher up than any other deciduous tree in the coniferous zone of Alps (Leather 1996). The populations of subsp. *petraea* var. *discolor* are also found in the valleys of eastern and central Alps (Scholz & Scholz 1995). Tutin et al. (1978) have considered subsp. *petraea* and subsp. *borealis* synonyms.

Russian botanists believe, that there exists another pubescent taxon: *Prunus padus* var. *pubescent* (i.e. *Padus avium* var. *pubescent*). It replaces *Prunus padus* var. *padus* (i.e. *Padus avium* var. *avium*) from Yenisei to the east. Therefore it is considered an Asian variety. However, there are some evidences that Asian populations are not always pubescent (Korovina & Belozor 1983, Sokolova & Tsarenko 1989). For example, both glabrous and only somewhat pubescent bird cherries are found in central Siberia. Consequently the distribution, the taxonomy and the nomenclature of pubescent taxons are not confirmed yet.

Almost 20 different varieties or formas of subsp. *padus* have been named. They are described and discussed in the next chapters.

2.2 Habitats and growth habits

European bird cherries grow seldom solitaire, because they reproduce mainly by root suckering (Scholz & Scholz 1995, Leather 1996). The thickets of bird cherries are likely to develop (Figure 2). There are usually at least five clones, which grow within 5-20 meters from each other. Isolated stems are rare. Bird cherries usually form small groups in the undergrowth of riparian forests, groves and moist deciduous mixed forests (Komarov et al. 1971, Korovina & Belozor 1983). Shrubby thickets are common in meadows. They often create the beautifully blooming edgings of forests (enclosed spaces) which outline fields (open spaces) in landscape.

Figure 2. The thicket of *Prunus padus* subsp. *borealis* in Hetta, Finland (68º23'N) (Marja Uusitalo).

The phase of the intense growth of European bird cherry is scheduled in early spring, when the soils are moistest, and the microbial-mediated nutrient availability peaks (Chapin 1980, Gutschick 1981, Lorio 1986). Raulo and Leikola (1974) investigated the timing and the sequence of annual growth in height. They noticed, that the growth of bird cherries initiated when the temperature sum was +20°C, and cessated when the sum reached +250°C in Finland. Early timing is important because the temperature sum of thermal summer in southern Finland is usually slightly above +450°C (Helminen 1987). According to Leather (1996) the shoot growth and the bud set are usually completed by the end of July in Great Britain. The growth power of bird cherries depends on the latitude of growing-site, habitats and age. Growth is fastest and most variable at young age and on rich loamy soils overlying limestone. Jarvis (1960 ref. Leather 1996) measured the growth of 15-35 years old bird cherries in England. He found out that its shoots may grow 100 cm and trunk radius 4 mm annually. Mean relative growth volume appears to become constant after 15 first years. The species does not usually have a long lifespan. Urpelainen (1995) argues that wild bird cherries live seldom longer than 60 years. Owing to the rapid and dense growth, bird cherries are good competitors, and they create excellent visual and noise obstructions and windbreaks.

Growth form may vary a lot between individuals. The height of full-grown trees generally varies between 3-15 m (Scholz & Scholz 1995). The shortest bird cherry registered in Russia was 0,6 meter high (Komarov et al. 1971). According to Leather (1996), some bird cherries may grow up to 20 meters. Karhu (1991) has searched for the thickest bird cherries in Finland. He found over 15 meters high trees eith 150 centimetres (radius over 10 cm) round trunks. Subspecies *borealis* and var. *petraea* are shrubs seldom more than three meters high (Tutin et al. 1978, Scholz & Scholz 1995). The former grows sometimes five meters high (Hämet-Ahti et al. 1998). Extraordinary powerful growth is inheritable to var. *watereri* (Scholz & Scholz 1995). Pesola (1945) consider the variety a hybrid. Forma *communata* is a rather small tree, which spreads heavily (Hillier 1991).

The crown of young bird cherries are usually open and branchy (Komarov et al. 1971, Scholz & Scholz 1995, Leather 1996). The crowns look conical. The upper branches are ascending. They become lightly spreading and pendant while getting older. The forms of old crowns are round or elongate. The branches are posited asymmetrically in the lower part and symmetrically in the higher parts of canopies (Figure 3). The branches of variety *pubescent* remain ascending or parallel (Komarov et al. 1971). Forma *pendula* has very pendant branches (Hegi 1995). Such are also the slender branches of var. *laxa* (Rehder 1960). The crown form of var. *pyramidalis* is conical (Hegi 1995). Owing to the great variety of forms, European bird cherry is a suitable plant for both small and big yards.

Figure 3. The habitus of young and full-grown *Prunus padus* L. are different. Full-grown trees may have somewhat straggling look (Malmberg 1991).

2.3 Wooden parts

2.3.1 Bark

The young twigs of bird cherries turn olive in shadow and dark-purplish, cherry red or red-brown in light (Komarov et al. 1971, Godet 1984). All young twigs of f. *colorata* are red (Scholz & Scholz 1995). They are extraordinary rich in red pigments (flavonoid-anthocyanins). Therefore this taxon functions very well as an eye catcher or an accent plant in a garden. Red pigments or colourless co-pigments contribute also dark grey or brown colours in the bark of old twigs and branches (Harborne 1984, Schantz & Hiltunen 1988). Flavonoids are present in wood, leaves and flowers as well. The pigments apparently function as attractors of pollinators, as protectors from UV-light, as phytohormone regulators and even as mediators of plant relationships with symbiotic nitrogen-fixing bacteria (Rhoades 1977).

The bark of bird cherries is usually shiny (Leather 1996). Scholz and Scholz (1995) claimed that the twigs of subsp. *petraea* are shiny only in the edges. Two years old twigs of subsp. *padus* turn matte. The bark becomes thin and grooved with age. It begins to peel off lengthways, and turns whiter as a result (Godet 1984, Urpelainen 1995, Scholz & Scholz 1995). Light brown, elongate, distinct and abundant lenticels are distinguished when the bark is closely examined (Komarov et al. 1971, Godet 1984). Contrary to other taxons, the bark of var. *pubescent* contains only few visible lenticels (Komarov et al. 1971).

2.3.2 Wood

According to Urpelainen (1995) the outer wood of bird cherries is thick, and its colour varies from yellow to reddish-white. Inner wood is varicoloured. There are brown-yellow or dark brown streaks or zones. Vascular bundles are situated densely in the inner border of annual rings. They are seen as thin stripes. Pores are densely situated in crosswalls. The axial walls of bundles have thin spiral bulges here and there. Fibres are thin, and they can be 1,5 mm long. The dry-fresh density of wood reaches over 600 kg/m^3 (at 15 % of moisture). Wood shrinks and swells only little but cracks easily. It dries quickly and twists easily while drying.

Varicoloured, soft, medium heavy, firm, flexible, elastic and curly wood is decorative and rather easy to work (Helander 1922). Bird cherry wood were formerly used in many carpenters and turners manufactured utensil: handrails, the legs of chairs, the hafts of knives, knobs, the taps of barrels, chessmen, wreaths, music instruments, collar bows, fykes, fish poles or hoops, withes (ties) and heating chips (Korovina & Belozor 1983, Scholz & Scholz 1995, Skoglund Skåtøy & Skage 1997). The species is not generally considered valuable for wood industry. The small and branchy species has poor fuel value per weight of volume. But because bird cherry wood is good for glazing, it is still rarely used in furniture industry.

2.4 Vegetative parts

2.4.1 Young shoot

Fine down may cover the young twigs of subsp. *padus* at first (Scholz & Scholz 1995, Leather 1996). The young twigs of subsp. *borealis* are always pubescent (Tutin et al.1978, Hämet-Ahti et al. 1998). Also subsp. *petraea* have more or less pubescent shoots (Scholz & Scholz 1995). The young twigs of var. *pubescent* are very hairy and one-year-old twigs remain more or less velutinous (Komarov et al. 1971).

2.4.2 Bud

Tightly oppressed, narrow and sharply pointed winter-buds are enclosed by four or more bud-scales, which are light or dark brown and have ciliate edges (Komarov et al. 1971, Godet 1984, Leather 1996) (Figure 4). The scales fall off in early springtime (Urpelainen 1995). There is usually one terminal bud at the end of long shoots (Scholz & Scholz 1995). Flower buds are situated one by one in short shoots, and there are no accompanying leaf-buds (Godet 1984). Vegetative buds are more acute than flower buds. Leather (1988) has calculated that the mean interbud distance of young shoots is 20 mm. The size of buds may vary from 2-10 mm in length. Buds are usually about two millimeters wide.

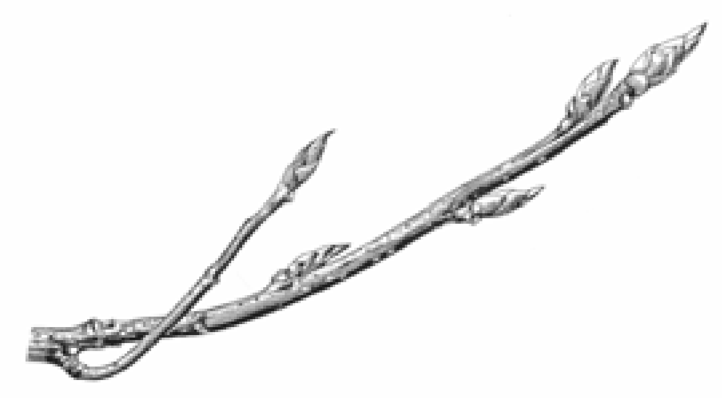

Figure 4. The twig and the winter-buds of *Prunus padus* L. (Hegi 1995).

2.4.3 Foliage

Leaves are convoluted in buds. They unfold in six stages. The duration of each stage varies from year to year at the same latitude. Bud-burst and its progress are night temperature and latitude dependent phenomenon (Table 2) (Lether 1996, Wielgolaski 2001). Forma *communata* flush very early, because its leaves unfold before winter has passed (Rehder 1960, Hillier 1991). Hegi (1995) observed that bird cherry leaves usually start shedding when the average temperature drops below 10°C. The dates of bud-burst and frost hardening may vary a lot between different origins and taxons. Therefore it is very important to favor the origins, which are acclimatized to local growing conditions.

Table 2. The bud-burst of *Prunus padus* L. depends on latitude (Leather 1996).

Location	Latitude	Mean date of bud burst
Norwich	52°30'N	25th of March
Roslin Glen	55°45'N	19th of April
Helsinki	60°10'N	1st of May

Firstly, the size of bird cherry leaves varies with age and between different taxons. Leaves are usually 5-10 cm long and 3-6 cm wide in full-size (Komarov et al. 1971, Tutin et al. 1978, Scholz & Scholz 1995, Leather 1996). Hegi (1995) have noticed that the leaves of var. *pubescent* are smaller, and the leaves of var. *watereri* on the contrary bigger than the leaves of var. *padus*. According to Pesola (1945) the average length of var. *watereri* leaves is 10,5 cm. They can sometimes reach up to 15 cm in length.

Secondly, there is variation in the shapes of bird cherry leaves (Figure 5). Elliptic, ovate or obovate bird cherry blades have obtuse or cordate base and acuminate or cuspidate tips (Tutin et al. 1978, Leather 1996). According to Scholz and Scholz (1995) oval basal leaves have acuminate tips and cordate base. The distal leaves of subsp. *padus* are usually ovate. The leaves of subsp. *petraea* on the other hand are more or less elliptic. The leaves of subsp. *borealis* have cuspidate tips (Korovina & Belozor 1993). The elliptic or short obovate leaves of var. *pubescent* have obtuse base and short mucronate tip (Komarov et al. 1971). The leaves of f. *communata* are elliptic or broad cuneate (Rehder 1960). The leaves of var. *laxa* are oblong-cuneate with acuminate tips.

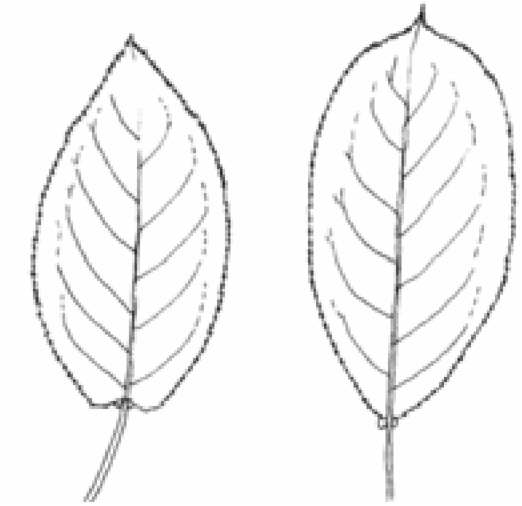

Figure 5. Two different shapes of *Prunus padus* L. leaves (Marja Uusitalo).

Thirdly, the margins of blades vary. They are generally serrate. Teeth are fine, sharp, closely spaced, even-sized and straight projecting (Leather 1996). There exist some exceptions. The leaves of flowering branches are not always serrate (Komarov et al. 1971). According to Scholz and Scholz (1995) the leaf margins of f. *communata* have coarser, more remote serration and the margins of cultivar 'Heterophylla' are lobed.

Fourthly, there is also variation in the thickness and texture of bird cherry leaves. By varying these properties, bird cherries are presumably able to adapt to humidity, quantity and quality of radiation and herbivory, which alter in the wide distribution area. According to Sokolova et al. (1989) the epidermal cells of leaves are irregular and small. Leaves are pinnately veined (Leather 1996). Usually sunken veins (vascular bundles) are scattered throughout the mesophyll. Scholz and Scholz (1995) have observed that there are no side veins on the leaves of subsp. *padus* but the side veins of subsp. *petraea* are sticking out. The leaf veins of subsp. *borealis* are also prominent (Tutin et al. 1978).

Firm, leathery and mainly matte leaves are always glabrous on the upper side, but the hairiness of leaf undersides varies. Subspecies *petraea* and subsp. *borealis* have thick and hard leaves. The leaves of subsp. *padus* are thinner (Scholz & Scholz 1995, Leather 1996, Hämet-Ahti et al. 1998). Their glabrous undersides may sometimes have white hairs along the midrib or the tufts of hairs in the axis of veins (Tutin et al. 1978, Leather 1996, Hämet-Ahti et al. 1998). Forma *spaethii* has conspicuous auxiliary tufts (Rehder 1960). Var. *rufoferruginea* has rufous-coloured barbulae in the axis, and the hairs of var. *glauca* are bluish-grey (Komarov et al. 1971, Korovina & Belozor 1983). The developing leaves of subsp. *borealis* are usually thoroughly pubescent beneath (Tutin et al. 1978). Hairs are brownish (Hämet-Ahti et al. 1998). The leaves of var. *pubescent* are very hairy (Komarov et al. 1971). Hegi (1995) has argued that the leaves of 2-3 years old twigs are permanently pubescent. According to Scholz and Scholz (1995) subsp. *petraea* has light rust-brown tufts of hairs in the axis. The full-grown leaves have shiny mosaic wax, and the leaves of subsp. *petraea* var. *discolor* are waxy only in beneath.

Fifthly, the colour of blades varies. The leaves of subsp. *padus* are dark green above and paler beneath (Komarov et al. 1971, Leather 1996). The leaves of subsp. *borealis* are greyish-green in beneath (Scholz & Scholz 1995). Their intense green pigments (chlorophylls) usually mask or hide the presence of yellow (carotenes) and red (anthocyanins) pigments protecting chloroplasts from UV-radiation (Harborne 1984, Schantz & Hiltunen 1988). Sometimes the ratio of pigments changes because of some modifications in the plant secondary metabolism where pigments are produced. The yellow pigments dominate over the others in the leaves of f. *aurea,* which are entirely yellow or golden-coloured and in the light yellow spots of the leaves of f. *aucubifolia* (Korovina & Belozor 1983, Hegi 1995). The red pigments are dominating on the other hand in the coppery-purple immature leaves of f. *colorata* (Hillier 1991, Scholz & Scholz 1995). The leaves turn sombre green in summers, but under-surfaces and veins stay purple-tinged. Taxons with exceptional leaf colours can be chosen for an accent plant of a garden. Bird cherries have usually beautiful yellow and bright red autumn colours, which are revealed and seen when chlorophyll breaks down (Komarov et al. 1971). Autumn colour lasts 2-3 weeks. According to Leather (1996) the leaf colour does not necessarily change every autumn. Leaves may instead remain green or turn partly yellow.

Bird cherries usually have red, stout, grooved and glabrous leaf stalks (petioles) (Komarov et al. 1971, Scholz & Scholz 1995, Leather 1996). Their length varies from 10 to 20 mm. There are usually two dark red or brown glands on the each side of petioles in the distal ends (Figure 5). Glands and usually subulate stipules fall early. The membranous and linear-lanceolate stipules of var. *pubescens* look somewhat different (Komarov et al. 1971).

2.5 Generative parts

2.5.1 Inflorescence

According to Hegi (1995) bird cherry flowers start flushing, when the day temperature rises above +10-12°C in shade, and the effective temperature sum of growing-site is +325°C. The onset of blooming varies from May to June (Komarov et al. 1971, Scholz & Scholz 1995, Leather 1996, Wielgolaski 2001). It depends strongly on the latitude of growing-site (Table 3). Skoglund Skåtøy and Skage (1997) have informed that farmers used to wait for bird cherry flowers to open, before they started sowing in the old days. Flowers appear after the first leaves are almost fully developed (Hämet-Ahti et al. 1998). Flowers fade in a couple of days, seldom in a week. The blooming period of f. *plena* is the longest one (Rehder 1960, Hillier 1991).

Table 3. The onset of blooming of *Prunus padus* L. in Finland (Terhivuo 1996).

Region	**Latitude**	**Onset of blooming**
Southern Finland	60-62°N	15th of May
Central Finland	62-64°N	22nd of May
Northern Ostrobothnia	64-66°N	30th of May
Lapland	66-68°N	7th of June

According to Scholz & Scholz (1995) bird cherries have the most primitive inflorescence in *Prunus*-genus (Figure 6). Racemes are solid-looking cylindrical clusters. They terminate at the ends of leafy annual shoots (Komarov et al. 1971). Racemes are also produced in the side buds of twigs, which are developed in a previous year (Urpelainen 1995). Since there is a lot of variation in the florescence, many decorative taxons can be chosen for horticultural purposes. Firstly, the length of racemes may alter from 8 to 20 cm (Scholz & Scholz 1995, Leather 1996). The racemes of var. *pubescent* are usually 10-15 cm long (Komarov et al. 1971). Var. *watereri* has exceptionally long racemes. They are 20 cm on an average, but sometimes even 25 cm long (Pesola 1945, Rehder 1960). Peduncles are hairless or sparsely hairy and leafy towards the base (Tutin et al.1978). Pedicels are usually 1-1,5 cm long and glabrous (Scholz & Scholz 1995). The pedicels of var. *parviflora* are exceptionally short. They are only 0,2-0,5 cm long (Rehder 1960). Therefore its racemes are the smallest ones among the taxons. The bracts of flowers are usually small and caduceus, except in f. *bracteosa* (Komarov et al. 1971, Scholz & Scholz 1995). According to Hegi (1995) f. *bracteosa* has exceptional big bracts.

Secondly, the position of racemes differs between the taxons. The racemes of subsp. *padus* may be ascending in the beginning, but they start drooping (strongly) at latest by the end of blooming (Komarov et al. 1971, Tutin et al.1978, Hämet-Ahti et al. 1998). The racemes of var. *laxa* are lax (Rehder 1960). The racemes of subsp. *borealis* and *petraea* are sturdy and horizontal or erect (Scholz & Scholz 1995, Hämet-Ahti et al. 1998). The racemes of var. *parviflora* are upright (Rehder 1960).

Figure 6. The inflorescence of *Prunus padus* L.

1 = raceme
2 = cross-section of flower
3 = cross-section of pistil
4 = drupe
5 = stone

Source: www.lysator.liu.se/runeberg/nordflor/pics/312.jpg

Thirdly, the number and the size of flowers vary. There are usually 10-35 but sometimes even 40 flowers in a raceme (Komarov et al. 1971, Tutin et al.1978, Leather 1996). Corollas are usually 1-1,5 cm wide, but the corollas of varietas *pubescent* are slightly larger (Komarov et al. 1971). Kazakov (personal communication, 22.3.1993) have noticed that also subsp. *borealis* has somewhat larger flowers compared to subsp. *padus* var. *padus*. Therefore he claims that subsp. *borealis* has better ornamental value than var. *padus*. The flowers of f. *plena, spaethii* and *watereri* are impressive as well.

Their corollas may grow even two centimetres wide (Rehder 1960, Korovina & Belozor 1983). According to Pesola (1945) the corollas of var. *watereri* may sometimes grow almost three centimetres wide. Flowers per raceme are also exceptionally numerous (Scholz & Scholz 1995). The corollas of var. *parviflora* are very small. Flower diameter is less than one centimetre (Rehder 1960).

Fourthly, the number of petals varies. There are generally five petals inserted on the calyx (Komarov et al. 1971). The petals (even 14) of f. *plena* are grouped into two circles in a semi-double flower (Rehder 1960, Korovina & Belozor 1983). The inner petals are smaller. The size of petals varies from 4 to 10 mm (Komarov et al. 1971, Tutin et al.1978, Scholz & Scholz 1995, Leather 1996). According to Nemova (personal communication, 3.9.1992) the petals of var. *laxa* are smaller. According to Pesola (1945) the petals of var. *watereri* are usually over 10 mm. The shape of bird cherry petals is usually oval or obovate (Komarov et al. 1971, Scholz & Scholz 1995). Var. *pubescent* has orbicular petals, and their margins are entire or erose-denticulate (Komarov et al. 1971).

Fifthly, the colour of flowers alters. Petals are usually white (Komarov et al. 1971). The colour is caused by colourless flavonole pigments (e.g. quersetin, isoquersetin and their glycosides) (Bate-Smith 1961, Hegnauer 1973, Harborne 1984). Petals may also become temporally rose (Hämet-Ahti et al. 1998). It occurs, if leaves start producing a plenty of anthocyanins, and some of the red flavonoid pigments are translocated to petals (Harborne 1984). The permanent overproduction of anthocyanins could be the reason, why the petals of var. *roseiflora* are pale pink. The colour turns darker by the end of the blooming period (Korovina & Belozor 1983). The petals of f. *colorata* are rose as well (Scholz & Scholz 1995).

Calyx is cup-like and broadly campanulate (Komarov et al. 1971). Hypanthium has five ascending lobes, which are 2-3 mm long. Sepals are triquetrous, obtuse and pubescent inside (Bailey & Bailey 1977, Scholz & Scholz 1995, Leather 1996). Margins are gland-fringed (irregular teeth). Calyx tube is glabrous outside and villous inside. The hypanthium of var. *pubescent* has glandular-dentate lobes, and it is smooth inside (Komarov et al. 1971). Bird cherries have simple, terminal, green and glabrous pistil (Komarov et al. 1971, Bailey & Bailey 1977, Leather 1996) (Figure 6). Stigma is usually flat and covered by papilla (Scholz & Scholz 1995). The stigma of var. *pubescent* is capitate (Komarov et al. 1971). Ovary is superior with two ovules (Leather 1996). The colour of ovaries is variegated (Komarov et al. 1971).

There are 20-30 stamens inserted on a calyx tube (Komarov et al. 1971, Bailey & Bailey 1977). The stamens are about half longer than petals but shorter than sepals. They curve inwards throughout the anthesis. The anthers of the inner stamens dehisce while still curving down under the stigma. When the stigma becomes erect, the anthers brush against its edge (Leather 1996). The anthers are yellow (Scholz & Scholz 1995). The anthers of a flower can produce little less than one milligram of pollen.

Bisexual flowers are self- or cross-pollinated (Komarov et al. 1971, Hegi 1995). Insects usually pollinate the flowers, because the style develops before the stamens to prevent self-pollination (Urpelainen 1995). According to Leather (1996) automatic self-pollination occurs regularly, if insect visits fail. The pollinators of bird cherries belong to six species of Diptera-sucking flies, two species of Hymenoptera and four species of nectar-licking Coleoptera. Bird cherries are acknowledged as fine honey and pollinate plants (Belozor 1983). Nectar is secreted in receptacles to attract pollinators (Leather 1996). The daily secretion varies from 1,4 to 6,5 mg and the sugar content of nectars from 0,3 to 1,4 mg per a flower (Scholz & Scholz 1995). The flowers contain also essential oils (triterpene lupeols), ammonias, trimethylamines and gyanogenic glycosides (amygdalin) (Bate-Smith 1961, Komarov et al. 1971, Hegnauer 1973, 1990). Haahtela and Sorsa (1997) have found out that the fragrant aromatic scent of flowers may cause allergic symptoms. It seems that the scent of subsp. *padus* is heavier than the scent of subsp. *borealis* (Hämet-Ahti et al. 1998).

2.5.2 Fruit

Bird cherry fruit is a subglobose or globose-ovoid, 6-8 mm long and about 5 mm wide drupe (Komarov et al. 1971, Tutin et al. 1978) (Figure 6). A fresh drupe weighs 130-210 mg (Leather 1996). The long-ovate drupe of var. *dolichocarpa* is bigger: 12-14 mm long and 7-8 mm wide (Korovina & Belozor 1983). The drupes of var. *laxa* are exceptionally small (Rehder 1960). The relicts of sepals are usually minute. They are scarcely noticeable and fall off when drupes mature (Scholz & Scholz 1995). Var. *pubescent* has the persistent relic of calyx (Komarov et al. 1971).

Because of anthocyanins, drupes are generally black or dark purple (Komarov et al. 1971, Tutin et al. 1978, Lid 1985). The drupes of var. *leucocarpos* and *chlorocarpos* contain little or no anthocyanins. Therefore *leucocarpos*-drupes are white or light yellow and *chlorocarpos*-drupes are yellowish green (Komarov et al. 1971, Hegi 1995). The texture of skin (exocarp) is shiny and glabrous (Komarov et al. 1971, Tutin et al.1978).

The edible outer layer (mesocarp) of fruits surrounds a stone (endocarp). The hard and globose stone contains one seed (2n=32) (Komarov et al. 1971, Tutin et al.1978, Scholz & Scholz 1995). The stony endocarp protects the seed physically. The chewing and digestive fluids of animals would otherwise break the seed (Lindman 1992). The texture of seed surface varies. Most bird cherries have sulcate-noched (grooved or furrowed lengthways) and rugose stone (Komarov et al. 1971, Tutin et al. 1978, Scholz & Scholz 1995). According to Hämet-Ahti et al. (1998) the endocarp of subsp. *padus* is notched, whereas one of subsp. *borealis* is rather smooth. The stone of var. *pubescent* has flexuous ribs and furrows (Komarov et al. 1971). Var. *laxa* has smooth stones (Rehder 1960).

Fruits ripe and seeds are dispersed during July-September (Komarov et al. 1971). According to Hegi (1995) the daily average temperature has dropped below 8°C at that point. Seeds are set in most years. The interval between large seed yields is 1-3 years (Gordon & Rowe 1982). The fruit set is high when the weather is warm and dry during the blooming (Grigorev 1988). Shade has beneficial effect on the fruit production. There are 6-10 fruits per a raceme, which is grown in the shade and only three fruits per a raceme in the well-illuminated sites (Jarvis 1960 ref. Leather 1996, Leather 1988). Less than a half of flowers in a raceme will be fertilised. The seed yield is 190-220 g of seeds per kilogram of fresh fruits (Gordon & Rowe 1982).

The species has endozoic dispersal. Birds act as important disseminating agents (Jarvis 1960 ref. Leather 1996). Snow and Snow (1988) evidenced, that thrushes (*Turdidae*) and robins (*Erithacus rubecula*) ate the majority of the fruit set. Warblers (*Phylloscopus* sp.) ate about the fifth. Many fruits, which fall beneath the trees, may be subjected to dispersal and predation by small mammals (Leather 1996). The seed production is important in the dispersal and colonisation of new sites (Jarvis 1960 ref. Leather 1996). However, seedlings are not often found. They grow most commonly in the mature forest vegetation close to the parent trees (Granström 1987).

2.6 Utilisation of various compounds

Bird cherry has utility value also because of its variant chemistry. People have utilised the bark before the industrial pesticides were available (Skoglund Skåtøy & Skage 1997). Bark was spread, for example, into the potato fields and apple orchards, because the smell and bitter taste of bark. Its cyanogenic glycosides and phenols prevented cultivates from rodents and insects. People also made pharmaceutical preparations from bark or other plant parts to cure sicknesses (Belozor 1983, Korovina & Belozor 1983, Skoglund Skåtøy & Skage 1997). The drug was called Cortex Pruni padi. It was believed to cure, for example, malaria, gout, rheumatism, syphilis and stomach-aches (Scholz & Scholz 1995). Bark was mixed with cream and spread on burns, snakebites and edemas. People's fever and breathing problems and the sick feet of domestic animals were medicated with bark or leaf preparations in Finland (Skoglund Skåtøy & Skage 1997). The preparations are not recommend for pharmaceutical use any more, because they may cause allergenic symptoms on skin and mucous membrane (Haahtela & Sorsa 1997). The fruits as well as bark, powdered leaves and flowers are still used as anaesthetics and disinfectants in Russia (Belozor 1983, Korovina & Belozor 1983, Simagin 1998). Fruits are known to help problems in dysentery and digestion. They relieve stomach-ache (comparable to blueberries). Also red-brown and green paints are still made off bark and leaves in some parts of Russia and Scandinavia (Belozor 1983, Korovina & Belozor 1983, Skoglund Skåtøy & Skage 1997).

The mesocarp is fleshy and juicy (Komarov et al. 1971, Tutin et a.1978). The mesocarp contains many chemical compounds (Figure 4). The taste is bitter-sweet. The flesh is astringent because of tannins. People in Far Eastern and northern Russian hardy climates usually dry, crush and grain the fruits. Then they mix them with flours for baking or use them in tart fillings. Some Russians make bird cherry liqueur or thickened juices. The fruits added in alcoholic beverages or juices dye the liquids dark red (e.g. personal communication with T. V. Belonogova, Academy of Sciences, Karelian Research Centre, Forest Research Institute, 19.8.1992). Bird cherry sauces, jams and juices were earlier made also in Europe (Scholz & Scholz 1995).

Table 4. The chemical components of mesocarps of *Prunus padus* L. (Komarov et al. 1971, Scholz & Scholz 1995).

Group of components	**Group of compounds**	**Compounds**
main components	water	
	mono- and oligocarbohydrates	glucose fructose saccharine
	sugar alcohols	sorbit cyclite
	organic acids	malic acid citric acid
minor components	polymer carbohydrates	pectin
	amino acids	
	proteins	
	mineral salts	magnesium calcium phosphorus iron
	vitamies	
	phenols	catechines (epicatechin) leucoanthocyanes proanthocyane flavonoids flavonoid glycosides tannins

2.7 Cultivation

Bird cherries are easy to cultivate for many reasons. They grow fast and are easily reproduced by bending twigs which root easily. Bird cherries can also produce ground shoots and root suckers (Scholz & Scholz 1995). Their powerful stolons grow up almost at regular intervals from the main roots (Kiermeier 1983). In some cases there are undesirable formation of ground shoots and root suckers, which are however easily be suppressed by lawn-mowing (Skoglund Skåtøy & Skage 1997). The generative phase of transplanted bird cherries (ability to bloom and carry fruits) is remained.

Bird cherries may also be propagated by seeds. Slow germination is epigeal (Scholz & Scholz 1995, Leather 1996). According to Granstöm (1987) seeds exhibit a strong innate dormancy, which lifts gradually within few years and causes the high degree of germination. The delayed germination pattern may probably cause steadier seedlings in nature compared to the situation, where every seed set germinate annually. Seeds require 2-4 weeks of warmer weather prior to 18 weeks at temperatures less than 5°C and continually moist soil surface to germinate (Jarvis 1960 ref. Leather 1996). They are recommended to sow in autumn or stratify until spring in cultivation (Bailey & Bailey 1977). Germination rates are very variable. The average seed viability is 74 percents in cultivation (Gordon & Rowe 1982).

When choosing a growing-site for bird cherries, it is important to consider some facts. Even though the species favours shadow habitats in nature, it blooms heavily in well-illuminated places, where there is no competition (Godet 1984). Bird cherries favour humusferous, fine partite (particles Ø < 0,002 mm) and clayish peat-mull (Komarov et al. 1971, Korovina & Belozor 1983, Tilman 1990, Leather 1996). According to Godet (1984) the soil should be slightly acid (pH 6,6-6,9) and moderate nutrient rich. Chlorose is an indication of nutrient deficiency, when bird cherry grows in too acid (decomposed peat), salty, calcareous, heavily fertilised, sandy, gravel or block-stony soils. Var. *petraea* is an exception, because it thrives in stony soils (Scholz & Scholz 1995).

The moisture conditions of these impermeable soils may change a lot. When soils are wet, they become poorly aerated (Godet 1984). Because of superficial and widely spreading root system, the species tolerates standing water rather well (Komarov et al. 1971, Urpelainen 1995). The poor soil aeration may lead, however, to reduced growth (Jarvis 1960 ref. Leather 1996, Frye & Grosse 1992). Full-grown bird cherries are also drought-tolerant. They recover from water stress with little effect other than premature leaf senescence (Malygin 1980). Jarvis (1960 ref. Leather 1996) observed that young stands suffer from prolonged drought. He noticed that growth was depressed at 0,02-0,03 MPa soil moisture and stopped at 0,05-0,15 MPa.

Bird cherries sometimes suffer from herbivore attacks, which lower the ornamental value or yield (the topic is discussed more in Chapter 3). Small ermine moths (*Yponomeuta evonymellus* L.) and bird cherry-oat aphid (*Rhopalosiphon padi* L.) can cause widespread damage and severe disfigurement of trees (Dixon 1971, Leather & Lehti 1982, Leather 1986, 1993). They both are highly specific to *Prunus padus*. These common insects can be controlled mechanically in cultivation. The severe damages of sapling sands can be avoided, if the small ermine moth larvae are picked or sprayed off with pine soap water, as soon as the first damages become visible. The aphids should be sprayed with the strong water pressure. Gall mites can be controlled by destroying the leaves, which have galls. Fungal damages can be avoided only by using plants, which are resistant to fungi. According to Kazakov (personal communication, 22.3.1993) the resistant specimens to the most harmful fungi and insects are sought, for example, in Murmansk.

Tolerant and fast rooting bird cherries are highly respected as ornamental plants in urban landscaping especially in Russia (Belozor 1983, Korovina & Belozor 1983). They are, for example, used for strengthening of slopes, canals or riverbanks in European parts of Russia, South Siberia and Far East. This winter-hardy species is also used as the rootstocks of cherry grafts (Simagin 1998). People in the northern Scandinavia used to transplant wild bird cherries into home-gardens, because there were only few winter-hardy ornamental woody plants available (Raatikainen 1991, Skoglund Skåtøy & Skage 1997). Some growing-sites of the southern and the northern boundaries are protected, because the bird cherry habitats have declined. According to Kazakov (personal communication, 22.3.1993) the cutting of sprays in densely populated communities is forbidden.

Many bird cherry taxons (especially the varieties of subsp. *padus*) are already adapted into cultivation in Eurasia (Table 5). The selection of cultivars could be extended with winter-hardy origins. This task was promoted by searching for the Nordic variation of the species.

Table 5. The cultivated varieties of *Prunus padus* subsp. *padus* in the wide distribution area of the species.

Varieties	**Cultivation area**
'Albertii'	Europe[1]
'Aucubifolia' (f. *aucubifolia* Dippel)	Europe[1]
- syn. *Padus avium* var. *aucubaefolia* (Kirchner) Belozor	Russia[2]
'Chlorocarpos' (var. *chlorocarpos* Reichenb)	Europe[1]
'Colorata' (f. *colorata* Almquist)	Europe[3]
'Heterophylla'	Europe[1]
'Leucocarpos' (var. *leucocarpos* Reichenb. / f. *Salzéri* Zdarek)	Europe[1]
- syn. *Padus avium* var. *leucocarpa* (C. Koch) Belozor	Russia[2]
- native but rare in northern Ural, Belorussia and Kazahstan	
'Plena' (f. *plena* Schneid.)	Europe[1]
- syn. *Padus avium* var. *plena* Belozor	Russia[2]
- native in Murmansk region, Kirovsk	
’Watereri’ (var. *watereri* Bean / f. *grandiflora* Hort.)	Europe[1]
f. *aurea* Dippel	
- syn. *Padus avium* var. *aurea* (Dippel) Belozor	Russia[2]
f. *bracteosa* Ser.	Europe[1]
f. *communata* Dippel	Russia[2]
- native in eastern Asia	
f. *pendula* C. Koch	Russia[2]
- syn. *Padus avium* var. *pendula* Belozor	
f. *spaethii* Rehd.	Russia[2]
var. *dolichocarpa* (A. Korcz.) Belozor	Russia[2]
- native in northern European parts of Russia	
var. *glauca* Nakai	
- syn. *Padus avium* var. *glauca* (Nakai) Belozor	Russia[2]
var. *laxa* Rehder	Russia[2]
- native in Korea	
var. *parviflora* (Ser.) K. Koch	Russia[2]
var. *pyramidalis* Hort.	Europe[1]
var. *roseiflora* Sinz.	
- syn. *Padus avium* var. *roseiflora* Belozor	Russia[2]
- native in northern Ural, western Siberia, altas of Kama, Oka rivers, lower and upper courses of Volga	
- in cultivation usually grafted with var. *avium*	
var. *rufoferruginea* Nakai ex Mori	Russia[2]

[1] Hegi 1995, Scholz & Scholz 1995, Hillier 1991
[2] Korovina & Belozor 1983
[3] Hämet-Ahti et al. 1989
- some remarks

2.8 Materials and methods of variation study

2.8.1 Previous inventories on genetic variation in Scandinavia

The projects working on the species in Finland were studied. The species appeared to be a popular study object mainly in entomology. Only few inventories concerning the genetic variation of the species were found. One of them was *Pohjoiskalotti*-project, where the acclimatized hardy cultivars and ornamental wild bird cherries were searched besides other woody species. The project took place in the arctic region of Nordic countries in 1984-1986. Lapland Nature Academy in Rovaniemi conducted the inventory in Finnish Lapland under Sirkka-Liisa Peteri's leadership (personal communication, 28.6.2004). Owing to their ornamental value, thirteen origins of three taxons found in Finnish Lapland were registered.

The studying of previous findings continued by borrowing about 1200 herbarium samples of *Prunus padus* from Nordic botanical museums. The attention was paid to the taxonomic characteristics of the samples and their growing-sites. About 250 herbarium samples were examined more closely to find any analogy between taxons.

2.8.2 Inventories in Padus-project

The articles about the inventory in Padus-project were written in some Finnish, Swedish and Norwegian magazines to learn more from the genetic variation of European bird cherry in Scandinavia. The readers were asked to inform, if they had found any bird cherries with ornamental or extraordinary characteristics. The growing-sites and the traditional use of the species were inquired. Over 200 replies were received mainly from Finland and Sweden. Fifty growing-sites were visited in the provinces of Oulu and Lapland (Table 6). Information on the plants was collected and herbarium samples and photos were taken during the blooming period in May-July in 1993.

Table 6. The readers' findings of *Prunus padus* L. in Nordic countries.

Country	No. of findings	No. of visited sites
Finland	143	50
Sweden	87	-
Norway	4	-
Denmark	-	-
TOTAL	**234**	**50**

Botanical institutes of the former USSR exchanging seeds with the Botanical Gardens, University of Oulu, were also contacted. Any research projects dealing with the species were inquired. Over ten institutes responded the inquiry. Addition to this, Central Siberian Botanical Garden in Novosibirsk was visited. Dr Simagin's breeding work with *Prunus*-species and his clone collection of bird cherries were introduced there. The excursion was made in 1996.

2.9 Results

2.9.1 Scandinavian taxons

There were 415 northern origins or rare taxons identified in NGB's *Padus-project* (Table 7). The taxons represent a half of the known varieties of subsp. *padus*. Varietas *padus, parviflora*, *pyramidalis*, *roseiflora* and forma *spaethii* were the most common ones (Table 8). Eleven rare taxons were found all together.

Table 7. Numbers of northern origins and rare taxons of *Prunus padus* L. identified in NGB's *Padus*-project.

Region	**No. of subsp. *borealis***	**No. of *padus* x *borealis***	**No. of rare varieties**	**TOTAL**
Finland	75	27	62	164
Sweden	68	6	36	110
Norway	111	-	25	136
Denmark	-	-	5	5
TOTAL	254	33	128	415

Only eight origins of subsp. *borealis* were found among the readers' findings from northern Finland. Because there were only few "pure" populations of subsp. *borealis* in the visited sites, the distribution area of the subspecies could not be defined in this study. Few assumptios were, however, made accoding to the findings. Subspecies *padus* and subsp. *borealis* may be difficult to distinguish from each other after the certain stage of development has passed. Alternatively, their crossings are more common in northern Scandinavia than what is presumed. These characteristics may help to identify the subspecies:

(1) *Bloomig period:* Both subspecies may have pubescent young shoots and erect inflorescences in the beginning of blooming period. Therefore the pubescence of developing leaves should be observed undersurface. The immature leaves of subsp. *borealis* are very pubescent

all over, whereas the developing leaves of subsp. *padus* have hairs only along or at the edges of veins.

(2) *After blooming:* Both subspecies may have hairs only along or at the edges of the veins of mature leaves. Therefore the lignified shoots of current year should be observed. The shoots of subsp. *borealis* are pubescent, whereas subsp. *padus* has glabrous shoots.

Table 8. The varieties of *Prunus padus* subsp. *padus* found in Scandinavia.

Taxon
f. *spaethii* Rehd.
var. *parviflora* (Ser.) K. Koch
var. *pyramidalis* Hort.
var. *roseiflora* Sinz.
var. *chlorocarpos* Reichenb
f. *colorata* Almquist
f. *plena* Schneid.
var. *watereri* Bean (f. *grandiflora* Hort.)
f. *aurea* Dippel
f. *bracteosa* Ser.
f. *pendula* C. Koch

bold letters: the most common varieties according to *Padus*-project

2.9.2 Clonal archive

The preservation of fruit and berry plants is maintained on national basis in NGB. Since fruits and berries cannot usually be stored as seeds, the different cultivars and origins are kept at various clonal archives. Therefore the archive of *Prunus padus* was established at Botanical Gardens, University of Oulu, (65°04’N, 25°28’E) in 1995. The archive (ten acres) was established to conserve some northern formas, varieties and origins with promising or extraordinary ornamental values. Another objective of the archive was to compare the characteristics to learn, which one of them are caused by different growing conditions and which ones by genes. Twenty-one origins growing in northern Finland were transplanted in Muhos in 2001 (Figure 7). The new growing-site is situated in Tahvola about 50 km to south-east of Oulu. The field is situated on the northern side of Oulujoki-river. Finnish Forest Research Institute owns the site, but the botanical observations are made by University of Oulu.

The ability of *Prunus padus* to cross with other *Prunus* species are utilised in the breeding of fruit cultivars especially in Russia. Breeders try to transfer genes contributing to cold hardiness or resistances to drought, herbivores, parasites and diseases. The genes are often found in wild relatives (Scholz & Scholz 1995). One interesting breeding program are run at Central Siberian

Botanical Garden in Novosibirsk under Dr Simagin's leadership (personal communication, 24.8.1996). More productive, winter-hardy, late-blooming cultivars of European bird cherry with big and sweet fruits are obtained. Dr Simagin has aimed to postpone the blooming period of bird cherries, since local plant origins often suffer from spring frost in Siberia. Late-bloomig cultivars could avoid frost injuries and yield loss. He has crossed *Prunus virginiana* and *P. padus* with good results (Simagin 1998). Two Siberian cultivars of European bird cherry (*Prunus padus* 'Black Brilliance' and Memory of Salamatov') with sweet fruits and 17 seedlings of the cultivars or crossing of *Prunus virginiana* and *Prunus padus* were given by Dr Simagin for the comparative studies. This plant material was also planted in Muhos. Simagin's breeding material is also interesting in the perspective of climatic warming in northern Scandinavia. Heide (1993) claims, that the climatic warming will bring the bud-burst of deciduous trees forward. As a result, growing seasons will be prolonged, but the risk of frost injuries will also increase in spring.

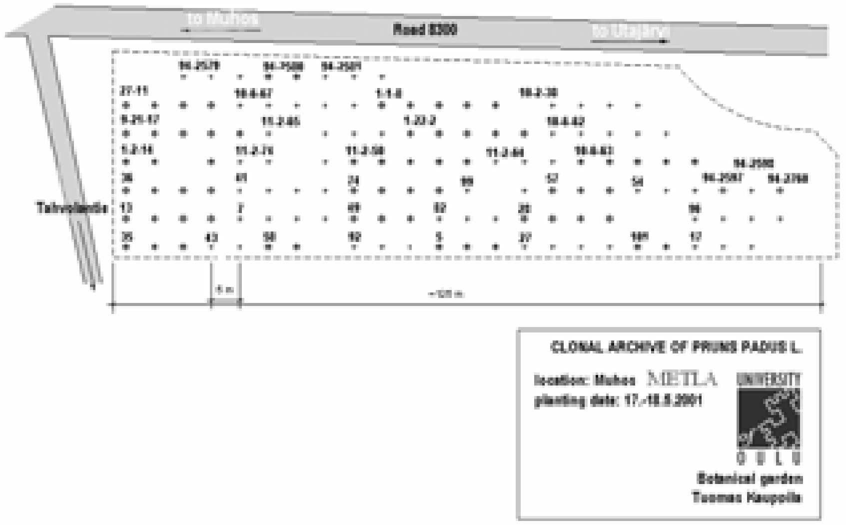

Figure 7. The clonal archive of *Prunus padus* L. in Muhos (Tuomas Kauppila).

3 The insect resistance of European bird cherry

3.1 Herbivorous insects

Bird cherries have rich and peculiar insect fauna, which causes variant damages in different plant parts (Table 9). According to Väisänen and Heliövaara (1991) species, which prefer broad-leave trees in Central Europe, feed on bird cherries in Finland.

Table 9. The insect species feeding on *Prunus padus* L.

Insect order	Insect species	Damage
Homoptera	*Alnetoidia alneti*[3]	leaf mesophyll injuries
	Brachycaudus prunicola[2]	leaf roll and curls
	Diptacus sp.[2]	leaf curls and flecks
	Eriophyes padi padi[2]	leaf and axial galls
	E. paderinus[2]	leaf and axial galls
	Myzus persicae[2]	leaf rolls
	Prunomyzus padellus[3]	phloem injuries
	Psylla pruni[2]	leaf callus
	Tetranychus urticae[2]	leaf yellowing
	Typhlocyba quercus[3]	leaf mesophyll injuries
	Vasates sp.[2]	leaf curls and flecks
Heteroptera	*Stephanitis pyri*[2]	swelling of axis
Lepidoptera	*Abraxas grossulariata*[3]	leaf injuries
	Acleris umbrana[3]	leaf injuries
	Acronicta rumicis[3]	leaf injuries
	Argyresthia ephippella[2]	flower bud injuries
	A. semifusca[2]	axial and bud galls
	Calospilos sylvatus[1]	leaf injuries
	Chloroclystis chloerata[1]	leaf injuries
	Coleophora sp.[2]	leaf mines
	Epinotia signatana[3]	leaf and shoot injuries
	Fixsenia pruni[1]	leaf injuries
	Hysteriosia schreibersiana[3]	leaf and shoot injuries
	Incurvaria sp.[2]	leaf mines
	Lomographa temerata[3]	leaf injuries
	L. bimaculata[1]	leaf injuries
	Operophtera brumata[3]	leaf injuries
	Phyllonorycter sorbi[2, 3]	leaf mines
	Stigmella sp.[2]	leaf mines
	Thecla betulae[1]	leaf injuries
	Triphosa dubitata[3]	leaf injuries
	Xestia baja[3]	leaf injuries
	Yponomeuta evonymellus[1, 3]	leaf injuries

Hymenoptera	*Caliroa cerasi* (*C. limacina*)[2,3]	leaf decay
	Hoplocampa minuta[2]	leaf decay
	H. flava[2]	leaf decay
	Neurotoma nemoralis[2]	leaf decay
	Pamphilius sylvaticus[3]	leaf injuries
	P. albopictus[1]	leaf injuries
	Pristiphora retusa[1, 3]	leaf injuries
	P. pseudogeniculata[1]	leaf injuries
	Trichiosoma aenescens[1]	leaf injuries
Coleoptera	*Anthonomus bitubercaulatis*[2, 3]	flower bud injuries, shoot gall
	A. humeralis[1, 2, 3]	shoot (adults) and bud injuries (juveniles)
	Conioctena pallida[1]	leaf injuries
	C. intermedia[1]	leaf injuries
	C. quinquepunctata[1]	leaf injuries
	Furcipus rectirostis[1, 3]	leaf (adults) and stone injuries (juveniles)
	Magdalis ruficornis[3]	leaf injuries
	Phytodecta pallida[3]	leaf injuries
	Rhamphus oxyacanthae[2]	leaf mines
	Rhynchites aequatus[3]	fruit injuries
	R. auratus[3]	leaf and fruit injuries
	R. pauxillus[3]	leaf injuries
	Saperda scalaris[3]	leaf injuries and dead wood
	Scolytus rugulosus[3]	wood injuries

1 Väisänen & Heliövaara 1991
2 Scholz & Scholz 1995
3 Leather 1996

3.1.1 Small ermine moth - a bird cherry specialist

According to Seppänen (1970) only two percent (81 species) of Finnish Lepidoptera are specialised in feeding on *Prunus*-species. The most common lepidopteron species feeding on *Prunus padus* is small ermine moth, *Yponomeuta evonymellus* L. (Yponomeutidae) (Junnikkala 1960, Leather & Lehti 1982). Small ermine moth is a small Lepidoptera with white black-spotted wings (Figure 8). Its larvae secrete webs and scatter it throughout the branches. The mass occurrence of larvae may cause total defoliation of trees (Figure 9). The defoliation happens after shoot extension is completed (Leather 1986). Plants produce new foliage after the defoliation.

Ermine moths (Yponomeutidae) mainly feed on Rosaceae-plants (Menken et al. 1992). They are able to synchronise their life cycle with the one of their host plant. According to Junnikkala (1960) the larvae of small ermine moth defoliate bird cherry populations in large areas in southern Finland in about 20 years interval. Leather (1986) assumes that dry weathers in late winter and early spring usually associate with the occurrence of large populations. It is due to the low first-instars mortality.

Female moths study the surface of potential food plants before they deposit their eggs (Chapman 1977 ref. Southwood 1986, Menken et al 1992). The eggs are laid in the clusters (up to 100 eggs) near buds or on side branches. Moths take samples to evaluate the plant nutritive value. They choose the best plant parts for their offspring (Jermy and Szentesi 1978). Sorbitol, dulcitol, sucrose and nitrogen (vital amino acids) of bird cherry leaves are important for the phytophagous insects (Dement & Mooney 1974, Van Drongelen 1979, Fung 1989). The content of soluble nitrogen is highest in spring (Dixon 1971). Its minimum is reached in late summer, but the content rises again in autumn. Herms and Mattson (1992) argue that immature leaves are usually the most nutritious to herbivorous insects, because they have high concentrations of nutrients and water and low concentrations of structural components. Small ermine moths hatch out in autumn and overwinter as larvae (Menken et al. 1992). Therefore they are able to move into buds already during the early bud-break. The earliest stages of larvae mine in developing leaves. The feeding of larvae takes almost two months all together. The length of feeding period depends mainly on the nutritive value of leaves. Many different kinds of secondary metabolites of bird cherry leaves pass into digestive organs of insects during the feeding period.

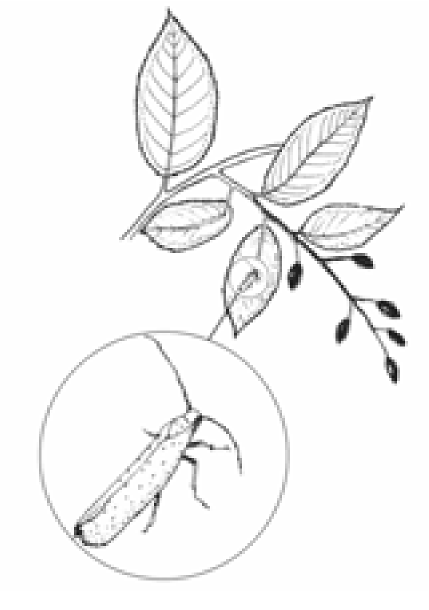

Figure 8. *Yponomeuta evonymellus* L., small ermine moth (Marja Uusitalo).

Figure 9. The loose webs of *Yponomeuta evonymellus* L. larvae in the defoliated *Prunus padus* L. (Marja Uusitalo).

There are also other insects, which may cause severe damages. The first generations of bird cherry-oat aphid (*Rhopalosiphum padi* L.) cause the curling and yellowing of leaves and even the death of terminal shoots (Leather 1996). Aphids suck the sap of immature leaves. The deposits of sooty mould build up on the honeydew. The excretion of aphids leads to reduced photosynthesis. The aphid generation, which has wings, fly to feed on grasses and cereals in the middle of June. Plum leaf gall mites (*Eriophyes padi* L.) cause reddish wart-like formations on the upper sides of leaves (Saalas 1933, Nuorteva 1957). The galls are formed by over-growing tissues. The sausage-looking mites are less than one millimetre long. Numerous mites suck plant saps in a gall.

3.2 Other injurious organisms

3.2.1 Parasites

According to Niemelä and Kotiranta (1991) European bird cherry is a host plant for only few polyphores and other fungi in Finland (Table 10). The polyphores cause trunk decay in bird cherries. Bird cherries are commonly infected by *Taphrina pruni* –fungi. The fungi cause abnormal branching. Drupes become whitish-black sporocarps of spores, and seeds do not develop. According to Kazakov (personal communication, 22.3.1993) the disease threats the generative reproduction of bird cherries.

Table 10. The parasitic and pathogenic fungi living on *Prunus padus* L.

Species	**Habitus / Symptoms**
Antrodiella americana[1] - rare polyphore	yellowish-white layer on dead twigs or fallen trunks
Botrytis cinerea[2]	dead of seedlings
Capnodiaceae (Pseudosphaeriales) sp.[2]	heavy leaf fall
Cytospora leucostoma[3]	
Gnomonia padicola (*Asteroma padi*)[3]	
Granulocystis flabelliradiata[1] - rare, threatened, corticoid fungi	on dead twigs or fallen trunks
Datronia mollis[1]	small, dark brown cap
Heterobasidion annosum[3] - pathogen	
Hymenochaete tabacina[1] - common polyphore	brown, thin layer on sprouts pressed by snow
Hypocreopsis lichenoides[1] - threatened, vulnerable ascomycete	ribbon lobes in whorls on dead twigs and fallen trunks
Leucotelium cerasi[2]	leaf injuries
Microgloeum pruni[3]	
Micropera padina[3]	
Monilia cinerea (*M. fructigena*)[2]	shoot wilting

M. linhartiana[2]	shoot wilting
Nectria galligena[2]	bark tumours after rost injuries
Phellinus punctatus[1] - common perennial polyphore	dark brown lumps with grey edges on annual rings on living twigs and trunks, aggressive (quick dead)
Phloeosporella padi[3]	
Phomopsis padina[3]	
P. stipata[3]	
Podosphaera tridactyla[3]	
Polysitgma fulvum[3]	
P. rubrum[3]	
Pucciniastrum padi[1, 3] - pathogen	
Pycnoporus cinnabarinus[1] - thermophile polyphore	small bright red cap on dead twigs or fallen trunks
Sclerotinia laxa[3] - pathogen	leaf flecks which dry and fall off
Stigmina carpophila[2]	abnormal branching of twigs, deformated fruits, folded and thick leaves
Taphrina padi[2, 3]	same
T. pruni[2, 3]	leaf flecks which dry and fall off
Trametes hirsuta[1]	pubescent, light green, half-round, thin, shelf-like sporangium-cap on living twigs and trunks under snow press
T. pubescent[1] - rare polyphore	fine down, yellowish white sporangium-cap on dead twigs or fallen trunks
Tranzschelia discolor[2]	leaf injuries
T. pruni-spinosae[2]	leaf injuries

1 Niemelä & Kotiranta 1991
2 Scolz & Scholz 1995
3 Leather 1996
- some remarks

3.2.2 Bacterial and viral pathogens

According to Scholz and Scholz (1995) bird cherries may be infected also by different micro-organisms via crafting, root contacts, mechanical damages or the invasion of plant lice (seldom nematodes) (Table 11).

Table 11. The bacterial and viral pathogens infecting *Prunus padus* L. (Scholz & Scholz 1995).

Pathogen	Species	Symptoms
bacteria	*Pseudomonas mors-prunorum*	leaf yellowing or folding
	P. syringae	leaf and seedling injuries
	other bacteria-species	shoot wilt, leaf and fruit spots, cracker
viruses	ring fleck virus	flecks, yellowing, necroses, enation of leaves, stunted buds, other deforms, bark necroses, gum flow
	plum band mosaic virus	leaf flecks
	cherry albino virus	lack of colour
	fruit diminish virus	reduce of fruit size
	cherry leaf roll virus	leaf roll

3.3 Hairs as physical and mechanical barriers

Plant hairs can function as mechanical and physical barriers against herbivorous insects. Hairs absorb effectively the long rad wave thermal radiation (Burrage 1971). As a result, the temperature of leaf arises. Respiration trough stomatas develops favourable humid layers on the leaf surfaces. When temperature arises, the protective layer becomes thinner and water starts evaporating from the tissues of insects (Willmer 1986). Long hairs can also prevent the mouthparts or ovipositors to reach the surface layer of leaves (Smith 1989). Wellso (1979) claims that if eggs cannot reach the evaporating layer, they dry out. It is possible that the relative humidity on the pubsecent undersurfaces of subsp. *borealis* leaves affects on the survival of larvae and small insects by regulating their water balance.

3.4 Natural insecticides

According to Dement and Mooney (1974) many deciduous species are able to protect themselves against the larvae attack by phytochemicals (Lorio 1986, Rosenthal and Kotanen 1994). Polyphenols are complex secondary compounds with long carbon-chains. These polymeric phenols are abundant in Rosaceae-plants (Harborne 1982). They are also known as quantitative metabolites (Feeny 1976). They make vascular bundles and stereome of bark and other lignified long-living plant parts hard and inflexible (Shen et al. 1986). Therefore herbivores cannot tear or penetrate the tissues. Low-molecular-weight (simple) phenols and gyanogenic glycosides are qualitative metabolites. They cause direct physiological damages to majority of herbivorous insects, parasitic and pathogenic fungi or micro-organisms at small concentrations (Rhoades and Cates 1976). The compounds are mutagenic, nerve toxins, or they depress the vesicular breathing or change the hormone balance of insects (Luckner 1990).

3.4.1 Phenols

Since the winter-buds are exposed to herbivores for a long time, woody plants produce phenol polymers to protect themselves (Wilde 1988). The winter-buds of bird cherries contain considerable amount of tannins, which dilute in flushing. According to Hegnauer (1973, 1990) the concentrations of tannins are also high in the old bird cherry leaves (Table 12). These physical barriers protect woody plants from herbivorous insects, which damage meristem and vascular bundles (Rhoades and Cates 1976, Lapinjoki et al. 1991). Polyphenols work also as a chemical control of herbivores. Tannins are chronically toxic. As large quantities they may weaken the digestion of herbivores by forming hydrogen or covalent bonds with proteins, polysaccharides or other macromolecules (Feeny 1969, 1970, Ryan 1973, Keen 1981). The development of herbivorous insects slows down, and the insects expose themselves longer to parasites and predators (Faeth and Bultman 1986). Tannins function also in the drought resistance and the protection of roots from acidic and reducing environments (Rhoades 1977, Pizzi and Cameron 1986, Meinzer et al. 1990).

According to Rao (1988) the inactive cells of adventory buds may contain also other toxic metabolites in small vesicles. The vesicles of a growing cell fuse into the vacuoles. Since the compounds are toxic to all living cells, they are usually isolated in the vacuoles and bound into sugars to form water-soluble glycosides. The simple phenols are usually located in the outermost layer, which is developed first (Neumann et al. 1991). When the simple phenols of immature leaves (hydroxycinnamic acids, the glycosides of phenolic acids) react with enzymes and oxidative molecules, they usually polymerise or oxidise to quinones very easily (Harborne 1980). The oxidised phenolic compounds can further oxidise new phenols or release the chain reaction of polymerisation (Appel 1993).

The toxicity of phenols bases on the reactive oxygen or free organic radicals, which are produced in oxidation. The radicals are dangerous to living cells and have many implications. They break DNA-chains and suppress the vesicular breathing by preventing the ATP-synthesis of mitochondrion. They are able to break membranes by dissolving lipids (Stenlid 1970, Larsson 1988). They can also change metabolism on the gut epithelium by inactivating enzymes (Lindroth and Peterson 1988, Raubenheimer 1992). Quinones can bind food proteins by covalent bonds (Barrbeau and Kinsella 1983, Felton et al. 1989, Felton and Duffey 1991). According to Duffey (1986) they can also bind the peritrofic membrane, which is made off proteins and chitin. The membrane protects the gut epithelium cells from concentrated intestine fluid (Wigglesworth 1984). When the flavonol glycosides (rutins) of leaves oxidise to quinines, they can dissolve or bind thiamine (Jones 1983, Duffey 1986). Thiamine is B_1-vitamin, which is involved in the binding of carbon dioxide in carboxylation and decarboxylation reactions in the intestine fluid of insects (Wigglesforth 1984).

Table 12. The leaves of *Prunus padus* L. contain numerous phenols (Bate-Smith 1961, Hegnauer 1973, 1990, Scholz & Scholz 1995).

Type	Group of compounds	Compound
simple phenols	hydroxycinnamic acids	p-coumaric acid caffeic acid ferulic acid sinapic acid
	glycosides of phenolic acids	p-hydroxybenzoic acid vanillic acid
polyphenols	flavonoid glycosides	dihydrowogonin eriodictyol hesperetin isosakuranetin naringenin pinostrobin sakuranetin rutin
	flavanoles	aromadendrin dihydrokaempferid padmatin taxifolin
	flavones	chrysin genkwanin luteolin tectochrysin skutellarin apigenin pinocembrin
	flavonoles	kaempferol prudomestin quercetin

3.4.2 Gyanogenic glycosides

The immature leaves of bird cherries contain prunasin (Bate-Smith 1961, Hegnauer 1973, 1990). These gyanogenic glycosides are produced from the surplus of nitrogen. The bark, fruit bases and unripe fruits also contain cyanogenic glycosides: prunasin and prulaurasin (Van Drongelen 1979, Scholz & Scholz 1995). Their concentration varies between plant parts from 0,1 to 2 % of dry tissue weight. When epidermal cells get broken, the glycosides isolated in vacuoles and the enzymes of stereome (ß-glycosidase and lyase) set free and react (Wilde 1988). Mandelonitriles are produced from the glycosides (Harborne 1984). These alkalines further dissolve without any reagent in the gut of an animal, and hydrocyanic (prussic) acid (HCN) is released. The CN^- -radical of hydrocyanic acid is hazardous. It blocks the electron transport chain in mitochondrion (Conn 1980). Cyanogenic glycosides have been shown to function also as a temporary nutrient storage (Selmar et al. 1988).

Bird cherry seeds are also chemically protected. About five percent of the seed weight consist cyanogene glycosides (amygdalin) and at least 10-40 % are seed oils (palmatic and stearin acids and glycerine) (Hegnauer 1973, 1990, Scholz & Scholz 1995). The compounds protect the seeds chemically from the most of herbivores and parasites. The dozens of digested seeds could be dangerous to a human. A toxic dose depends on the time passed from last meal, the pH level of stomach and the chewing intensity. According to Scholz & Scholz (1995) the risk disappears if seed is roasted or boiled.

3.4.3 Other compounds

Addition to polyphenols, all *Prunus*-species produce a hemicellulose derivate for protection (Scholz & Scholz 1995). The gum starts flowing, if bark is mechanically damaged. The gum is composed of arabinose, xylose, galaktose, mannose, rhamnose, glucorone acid and prunin-isoflavone. Wax covers the surface of old leaves and fruits (Harborne 1984). It is composed of paraffin, sitosterin, and aliphatic alcohol and oleanolic and ursolic acids. These acids are common triterpens in the plant kingdom. They protect leaves from evaporation, herbivores, parasitic or pathogenic micro-organisms.

3.4.4 Detoxification

The toxic secondary metabolites function usually best against so called generalist insects, which feed on many plant species. Edwards and Wratten (1980) argue that all herbivorous insects have originally been generalist feeders. Plants become resistant to generalist herbivores by evolving the chemistry and morphology of plant parts. After a lag, changes may occur in the food intake and metabolism of some insect, which become adapted to the plants.

These specialist feeders are usually able to overcome the new chemical barriers of their host plants via coevolution. Because bird cherries contain many toxic compounds, the majority of insects feeding on bird cherries are specialists (Leather 1985).

It has been shown that some specialist feeders, which have coevoluted with their food plants, have developed the ability to detoxify phenolic compounds by raising the gut pH or by reducing the gut redox-potential (Feeny 1970, Berenbaum 1980, Appel and Martin 1990). Insects may be able to produce the surfactants, which bind toxins (Martin and Martin 1984, Martin and Bernays 1987). Insects may also have peritrofic membranes, which absorb toxins (Bernays 1981). The digestion of animals may be promoted by glycosidase (Bernays and Woodhead 1982). Rhoades and Cates (1976) argue that specialists are usually able to break through the phytobarrier of secondary metabolites. They do not, however, feed on plants, which contain tannins. Zucker (1983) disagrees by claiming, that specialists seek for the plants, which contain toxic tannins, because they try to avoid the competition for food. It seems that Zucker’s theory is not the feeding strategy of small larvae moths, because they prefer the bursting leaves as their food sources. Therefore the larvae may be found to be sensitive and susceptible to the polyphenol content of bird cherry leaves. It is unknown or disputed, how these compounds react in small ermine moth larvae.

3.5 Materials and methods of resistance study

There are many factors related to the temporal variation of the herbivore populations of different insect species. The major factors are natural enemies, plant quality, weather conditions and intra- and inter-specific competition (Barbosa & Schultz 1987). The focus of this resistance study is on the leaf chemistry and drought stress of bird cherries during the outbreak of small ermine moths in southern Finland.

3.5.1 Chemical analysis of bird cherry leaves

There are different kinds of plant secondary metabolites, which can act as repellents or chemical barriers. If a potential food plant contains any toxic compounds or its nutritive value is poor, herbivores will reject the plant and start searching a new host (Fritzsche et al. 1988). Therefore the chemical content of different plant parts may indicate the chemical resistance of plant species to herbivores. Because small ermine moth larvae are evidently able to produce enzymes, which detoxify prussic acid, prunasin of immature leaves is not harmful to insects (Van Drongelen 1979). But the effects of phenolic compounds on larvae are disputed or unknown.

To perform the research, leaf samples were collected from bird cherries in southern Finland, where the outbreak of small ermine moth mostly occurs (Figure 10). The leaf samples were collected from six bird cherry plants in three habitats (a shore, a meadow and a forest edge). Trees were about the same age and size. A half of the trees were almost fully defoliated (at least 80 % of the canopy) in June 1992, when the first research observations were made and the first samples were collected. Two individuals were uninjured, and one was only partly defoliated (less than 40 %). Chlorophyll fluorescence of the injured and the uninjured leaves were measured in situ (see stress-analysis). After the measurements the leaves were collected for chemical analyses, which were carried in laboratory. The measurements were repeated again in July and August 1992. Leaves were collected from the distal and the basal ends of long shoots. The distal leaves are the youngest (immature) and the basal leaves the oldest (mature) leaves of shoots.

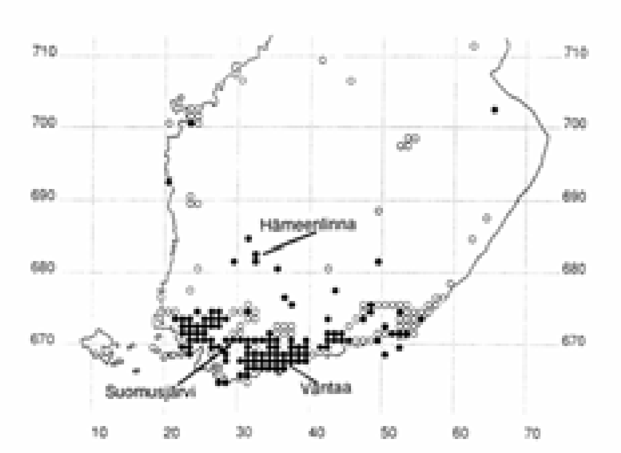

Figure 10. Three research sites in southern Finland in 1992 and the occurrence of ermine moths, *Yponomeuta evonymellus,* in previous year 1991 (Hyönteiskartoitus 81 1995).

black dots (•) = defoliated trees

Total phenol content

The quantitative estimation of total phenols in biological extracts can be accomplished in different ways. Most phenolic compounds are readily attacked by various oxidising agents to form coloured compounds. Folin-Denis-analysis is an old method which is often used as an indicator analysis of phenolic metabolites (Swain and Hills 1959).

Plant tissues (in this study air dried and grinned bird cherry leaves) were extracted by 50 % methanol and diluted with water. Folin-Dennis reagent (a complex of sodium wolframate, phosphomolybdate and orthophosphate acids) was added into the solution. The reagent formed a complex (pigment) when reacting with OH-groups of phenols. Extra-saturated sodium carbonate was added to the solution to increase the precipitation. After being stabled for an hour the solutions showed definite absorption peaks in the ultra-violet of spectrophotometer. The height of the peaks depended on the depth of blue colour. There were almost a linear relationship between absorptivity and the concentration of phenols. All the extracted leaf samples were compared with a control. The standard was made out of different volumes of tannic acid in distilled water. The total phenol content was read on the tannic acid standard line (Appendix 2). Leaf phenol contents were expressed as tannic acid equivalent (TAE) percent of dry weight. The content was counted as follows:

$$\frac{\text{content of tannic acid equivalent (mg/ml)} \times \text{extraction volume (ml)} \times \text{dilution volume (ml)}}{\text{final volume of sample solution (ml)} \times \text{dry weight of leaf sample (mg)}} \times 100\ \%$$

Polyphenol content

The total phenol content of leaves includes, for example, anthocyanins which act as pigments but not as behavioural antifeedants (Goodwind and Mercer 1983). Therefore specific methods are needed, when polyphenols are measured. Chronically toxic polyphenols are able to reduce the digestibility of plant tissues by complexing with the digestive enzymes of insect saliva or intestine fluids. One simple tannin assay is haemanalysis or Heme-test (Bate-Smith 1973, Schultz et al. 1981). It measures the content of leaf tannins precipitating proteins. Haemoglobin (derived from fresh calf blood in the study) acted as a binding substrate of long-chain polyphenols.

Blood cells were lysed by the addition of cold water (5ºC) immediately after incubation (haemolyse). The mixture was returned to laboratory on ice, where it was centrifuged, diluted with more water and stored at 5ºC for maximum of 3-4 days. The leaf extractions (for preparation see Folin-Denis-analysis) were mixed with the diluted blood. After that the solution was centrifuged for 30 minutes in 20ºC. Tannin-haemoglobin-complex precipitated on the bottom of tubes. The absorption peaks of remaining haemoglobin in the supernatant solutions of different leaf samples were measured in spectrophotometer. They were compared to the tannic acid standard curve approximated by Mathematica-software (Appendix 2). The peak showed the concentration of the chromoprotein. The total phenol contents of the leaf samples were counted by using the function of tannic acid standard curve and the previous formula.

Total nitrogen content

The most of the nitrogen compounds in plants appears as free amino acids or proteins (McClure 1983). Therefore Kjeldahl´s total nitrogen content is often used as indicator analysis of nitrogen bound in plant proteins. It is a method, where the organic matters of leaves (for preparation see Folin-Denis-analysis) were burnt with sulphuric acid (Feeny 1970, Lillevik 1970). Nitrogen was reduced into ammonium sulphate. This salt was then converted into ammonia and the content of ammonia was measured by acid titrating in Kjelltec Auto –analysator. The total nitrogen content was counted as a percent of dry weight:

$$\frac{[\text{ volume of HCl in sample titrating (ml)} - \text{volume of HCl in water titrating (ml) }] \times 0{,}05\ (\text{CHCl mol/l}) \times 14{,}01\ (\text{g/mol}) \times 1\ (\text{Kjeldahl standard})}{\text{dry weight of sample (mg)}} \times 100\ \%$$

3.5.2 Stress-analysis of bird cherry leaves

Mattson and Haack (1987) argue that different plant species have different stress symptoms, which are caused by environmental factors. When hazard conditions are only temporal, stress often reduces only assimilation but does not have effects on growth. For instance, drought can accelerate the dissolving of leaf proteins and starch to nitrogen and sugar compounds (Kennedy and Booth 1959, Mattson and Addy 1975). Therefore their contents in sap increase. In this way stress may improve the nutritive value of plants and increase insect damages. Prolonged stress has opposite effects. It can increase the production of secondary metabolites (Edwards & Wratten 1980).

Relative water content

Living cells should be saturated with water to function normally. Drought changes the water balance of plants. Relative water content (RWC) is one simple way to describe the plant water deficit (Turner 1981). Fresh leaf samples were weighed first for the roughly estimation of RWC of the bird cherry leaves. After fresh weights (FW) were measured, the leaves were chopped and water-soaked (in light). Then the water contents of leaf samples were measured again and expressed as fully turgid weight (TW). Finally the chopped leaves were oven-dried (12 h, 85ºC) and measured to estimate the dry weight (DW). The relative water contents were counted:

$$\text{RWC} = \frac{\text{FW-DW}}{\text{TW-DW}} \times 100\ \%$$

Chlorophyll fluorescence

Photosynthesis and assimilation may be blocked, for example, during the stress caused by drought (Farquhar and Starkey 1982, Hanson and Hitz 1982). Drought has effects on chlorophylls, which suffer from water deficit. As a consequence, the primary light receptors shrink. The shrinking in turn causes the decrease in photosynthesis (Berkowitz and Gibbs 1983, Gupta and Berkowitx 1988, Blanco et al 1992).

There exists an inverse relationship between fluorescence emission and the activity of photosynthesis II. The photosynthetic apparatus absorbs radiation. Only five percent of this light energy discharges as fluorescence in healthy plants. If chlorophylls are damaged, the photosynthetic apparatus are losing more energy as fluorescence. Therefore the red chlorophyll fluorescence of green leaves is a simple and sensitive tool to detect damage of the photosynthetic apparatus and stress in situ without damaging living tissues (Tyystjärvi 1988, Somersalo 1994).

The chlorophyll fluorescence induction of bird cherry leaves were measured with a plant stress meter (BioMonitor's) in the growing-sites. The instrument counted automatically a decrease in the ratio of the variable (Fv) and the maximal (Fm) chlorophyll fluorescence, which reflects the photoinhibition (Figure 11). The minimum of the ratio is about 0,80 in well-functioning chlorophylls (Tyystjärvi 1988, Björkman & Demming 1987).

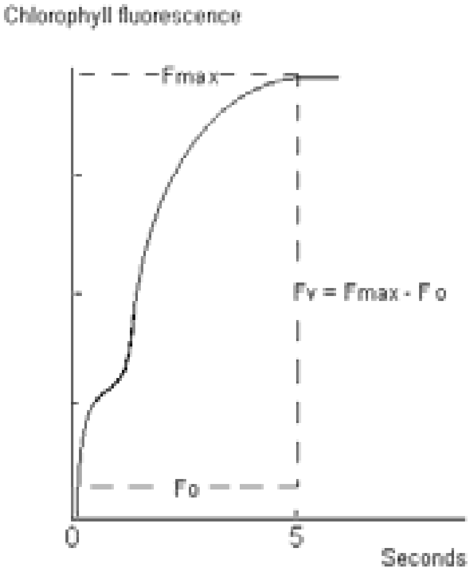

Figure 11. The induction curve of chlorophyll fluorescence of pine (*Pinus sylvestris* L.) needles (Öqvist & Ögren 1985).

F_0 = min fluorescence
F_{max} = max fluorescence
Fv = variable fluorescence

3.5.3 Statistical analysis

Three-way ANOVA-test was computed to compare the group means of the leaf samples, which were grouped according to the following variables:

growing- site:	shore – meadow – edge of the woods (three levels)
time of season:	June – July – August (three levels)
defoliation experience in June:	uninjured – partly defoliated – almost fully defoliat. (three levels)
leaf age:	distal (immature) – basal (mature) (two levels)
leaf injures in June:	uninjured – injured (two levels in defoliated trees)

Student-Neuman-Keuls- a posterior test (SNK) was used to find any differences between the levels of variables.

Linear regression analysis was run to find, if there were any linear correlations between the chemical (i.e. nutrient value) and physical (i.e. stress status) leaf parameters. Logistic regression analysis was computed to test: (1) if the ratio of nitrogen and tannin contents of leaves could explain the defoliation, (2) if the total phenol content could explain the leaf value better than other parameters.

3.6 Results

3.6.1 Occurrence of small ermine moths

In spring 1991 there were 18 growing-sites in southern Finland, where some bird cherries did not experience defoliation when others did. This information was received from Finnish entomologist through the inquiry. Next year the population size of small ermine moths exceeded the level of the last mass occurrence, which took place about ten years ago in 1981 (Figure 12). Therefore uninjured trees were reported in only two of 18 sites in 1992. The sites were in Hämeenlinna and Vantaa.

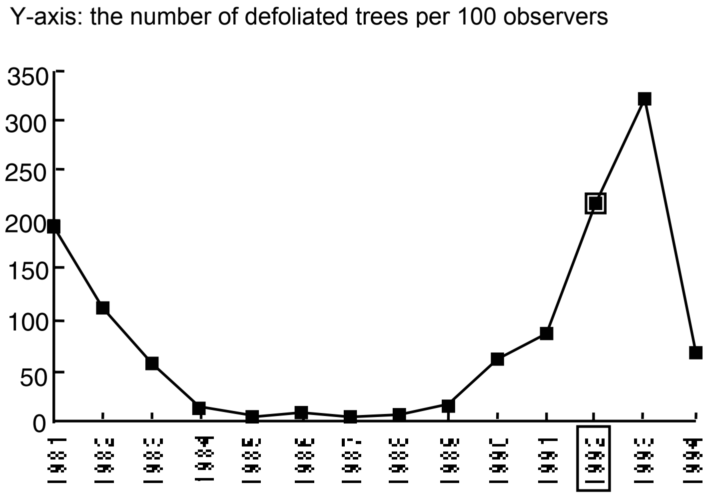

Figure 12. The annual fluctuations of *Yponomeuta evonymellus* L. populations in southern Finland (Hyönteiskartoitus 81 1995).

3.6.2 Nutrient quality of leaves

The phenol and nitrogen content of leaves were related. When the nitrogen contents increased, the phenol contents decreased. The total phenol contents (r = -0,47***) had somewhat stronger relation to the total nitrogen contents compared to the polyphenol contents of leaves (r = -0,34***). The nutrient quality of leaves in different origins was analysed as a ratio of nitrogen and polyphenol (tannin) contents, because the ratio reflected best the defoliation (Table 13). These results supported the hypothesis made according to the literature.

Table 13. The nutrient quality of leaves of *Prunus padus* L. was the best indicator of defoliation (logistic regression) in 1992.

Equation variable	**B**	**S.E.**	**df**	**Wald**	**R**	**Exp (B)**	**Other variables**	**df**	**Test value**	**R**
Quality	-0,23	0,70	1	10,75***	-0,38	0,80	Phenols	1	1,72	0,00
Constant	12,47	3,71	1	11,33***			Polyphenols	1	2,36	0,08
							Nitrogen	1	2,55	0,10
							RWC	1	3,32	0,15

N = 144; Khi square = 34,6; df = 1; p < 0,000***

Khi square of residual = 5,8; df = 5; p < 0,326
*** p < 0,001

There were variations in the nutrient quality of leaves between different trees (defoliation experience), growing-sites and time of season. The nutrient quality (i.e. the ratio of nitrogen and tannin contents) of the uninjured trees was generally better than the quality of the defoliated trees (Table 14).

Table 14. The changes in the leaf nutrient quality of *Prunus padus* L. in 1992 (three-way ANOVA).

	Time of growing season		
Defoliation in June	June %	July %	August %
Partly defoliated	32 **d**	48 b	38 c d
Almost fully defoliated	44 b	45 b	39 c
Uninjured	63 **a**	45 b	47 b

Means marked with the same letter do not differ significantly ($p_{SNK} > 0,05$)
% = ratio of nitrogen and polyphenol contents

However, there were not any differences between the leaves of the defoliated and the uninjured bird cherries in July, when the nutrient quality of leaves was measured the second time. The defoliated trees rebursted leaves after defoliation. The nutrient quality of the uninjured bird cherries weakened after the first observations and measurements, whereas the nutrient quality of the almost fully defoliated trees did not weaken until August. The biggest differences between the nutrient qualities of the trees were in June: the leaves of the uninjured bird cherries had the best quality and the partly defoliated tree had the worst one. There seems to be correlation between nutrient quality and defoliation (Table 15).

Table 15. The leaf nutrient quality of *Prunus padus* L. in June 1992 (ANOVA).

Origin	**Quality of leaves** %
Partly defolitated in Suomusjärvi (shore)	32 **e**
Almost fully defoliated in Suomusjärvi (shore)	38 d
Almost fully defoliated in Hämeenlinna (forest edge)	39 d
Almost fully defoliated in Vantaa (meadow)	54 c
Uninjured in Hämeenlinna (forest edge)	59 b
Uninjured in Vantaa (meadow)	67 **a**

Means marked with the same letter do not differ significantly ($p_{SNK} > 0,05$)
% = ratio of nitrogen and polyphenol contents

3.6.3 Total phenol content of leaves

Nitrogen and polyphenol contents were expected to correlate with the leaf age. It was the assumption made according to the literature. The total phenol content of leaves (i.e. a sum of both simple phenols and polyphenols) reflected, however, better the different types and values of leaves than polyphenol or nitrogen levels (Table 16).

Table 16. The total phenol contents of *Prunus padus* L leaves were the best indicators of leaf value in 1992 (logistic regression).

Equation variable	**B**	**S.E.**	**df**	**Wald**	**R**	**Exp (B)**	**Other variables**	**df**	**Test value**	**R**
Phenols	1,27	0,24	1	26,90***	0,35	3,55	Tannins	1	0,23	0,00
Quality	0,08	0,03	1	6,53**	0,15	1,09	Nitrogen	1	0,00	0,00
Constant	-11,65	2,77	1	17,64***			RWC	1	3,81	0,10

N = 144; Khi square = 51,2; df = 2; p < 0,000***
Khi square of residual = 5,9; df = 3; p < 0,118
** p < 0,01
*** p < 0,001

The phenol content of the uninjured trees increased during the growing season (Figure 13). The distal (immature) leaves of the long shoots generally contained more phenols than the basal (mature) leaves. The first leaves (June) of the almost fully defoliated trees had the highest phenol contents. The lowest amounts were in contrary measured in the basal leaves of the uninjured trees. There were equal amount of phenols in the distal and the basal leaves of the almost fully defoliated bird cherry in Suomusjärvi in June, whereas the distal leaves of the other trees had more phenols than the basal leaves (Table 17).

Table 17. The total phenol contents of basal and distal leaves of *Prunus padus* L. in June 1992 (ANOVA).

	Leaves	
Origin	Basal TAE %	Distal TAE %
Uninjured in Vantaa (meadow)	2,5 **d**	5,6 b c
Uninjured in Hämeenlinna (forest edge)	3,4 **d**	5,7 b c
Almost fully defoliated in Vantaa (meadow)	4,6 c	6,2 b
Almost fully defoliated in Suomusjärvi (shore)	6,1 b	6,6 b
Partly defoliated in Suomusjärvi (shore)	6,5 b	8,1 **a**
Almost fully defoliated in Hämeenlinna (forest edge)	6,7 b	8,7 **a**

Means marked with the same letter do not differ significantly ($p_{SNK} > 0,05$)
TAE % = Total phenol content (of d. w.)

There was inexplicable variation in the total phenol contents between the injured and uninjured leaves in the defoliated trees (Table 18). Some uninjured leaves had low phenol contents.

Table 18. The phenol contents of injured and uninjured leaves of *Prunus padus* L. in June 1992.

	Leaf type			
Origin	Uninjured basal leaves TAE %	Injured basal leaves TAE %	Uninjured distal leaves TAE %	Injured distal leaves TAE %
Almost fully defoliated in Vantaa (meadow)	3,8 ± 0,1	5,3 ± 0,7	7,0 ± 0,3	5,3 ± 0,2
Almost fully defoliated in Hämeenlinna (forest edge)	6,4 ± 0,5	7,0 ± 0,1	7,9 ± 0,1	9,6 ± 0,4
Partly defoliated in Suomusjärvi (shore)	6,5 ± 0,2	6,6 ± 0,2	8,2 ± 0,2	8,1 ± 0,1
Almost fully defoliated in Suomusjärvi (shore)	6,8 ± 0,2	5,5 ± 0,1	6,7 ± 0,1	6,4 ± 0,1

TAE % = Total phenol content (of d. w.)

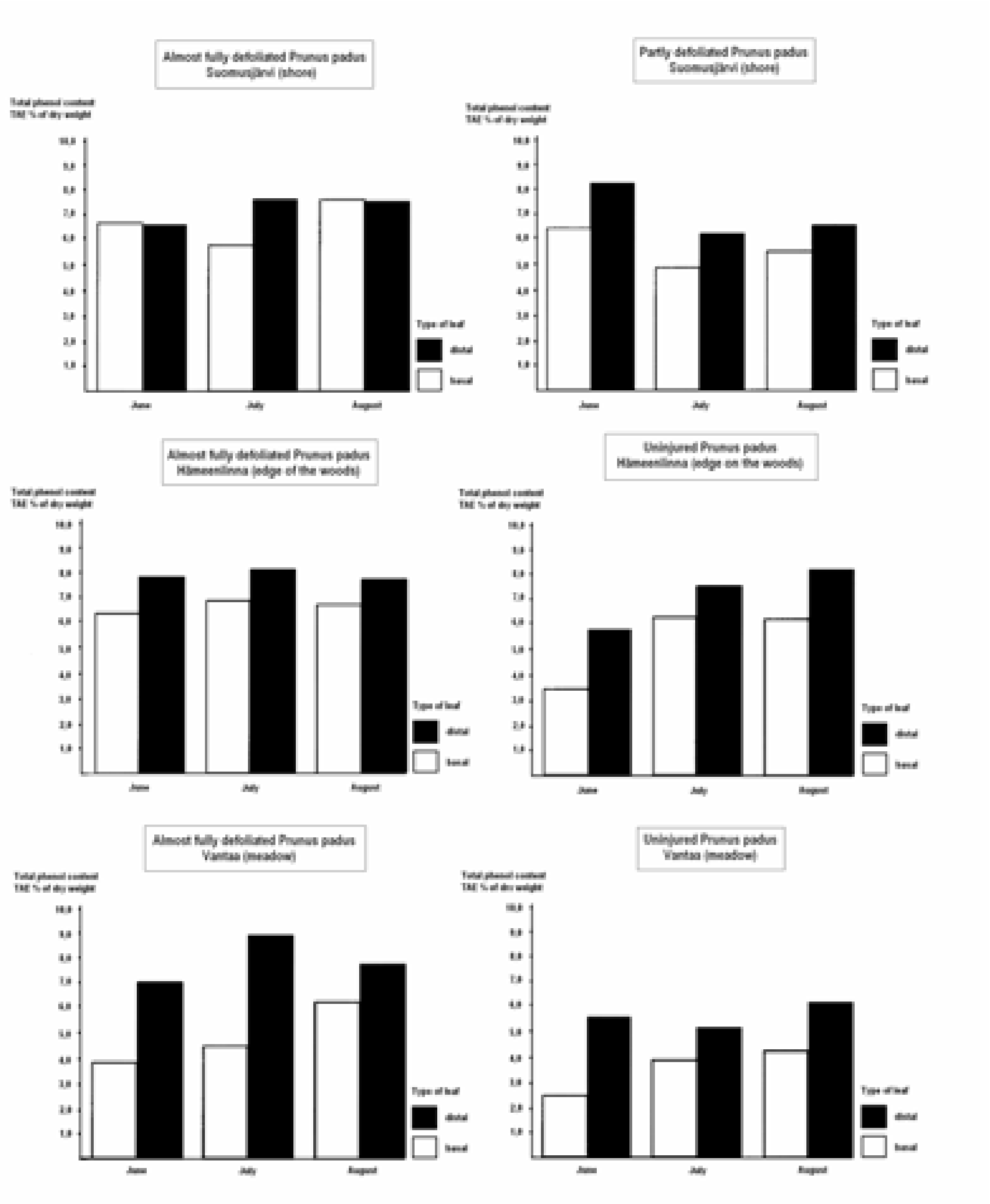

Figure 13. The changes of total phenol contents of distal and basal leaves in *Prunus padus* L. in 1992.

3.6.4 Efficiency of assimilation

The total phenol (r = -0,20**) and polyphenol (r = -0,27**) contents were related to chlorophyll fluorescence. There were variations in the fluorescence of leaves between different trees (defoliation experience), growing-sites and the time of season. Assimilation was most ineffective (the smallest ratio) in the almost fully defoliated trees in June (Table 19). Their Fv/Fm –ratio, however, increased in the progression of growing season.

Table 19. The changes in the chlorophyll fluorescence of *Prunus padus* L. leaves in 1992 (ANOVA).

	Time of growing season		
Defoliation experience in June	June Fv/Fm	July Fv/Fm	August Fv/Fm
Uninjured	0,798 b c	0,779 b c	0,834 **a**
Partly defoliated	0,795 b c	0,797 b c	0,819 a b
Almost fully defoliated	0,722 **d**	0,767 c	0,820 **a**

Means marked with the same letter do not differ significantly ($p_{SNK} > 0,05$)
Fv/Fm = chlorophyll fluorescence

The efficiency of assimilation differed between basal (mature) and distal (immature) leaves only in June, when leaves were bursted (Table 20). It was slightly more efficient in the basal leaves. Basal and distal leaves are basicly of same age during the leaf bust.

Table 20. The changes in the chlorophyll fluorescence of basal and distal leaves of *Prunus padus* L. in 1992 (ANOVA).

	Leaf type	
Time of growing season	Basal Fv/Fm	Distal Fv/Fm
June	0,783 b	0,735 **c**
July	0,782 b	0,773 b
August	0,826 **a**	0,820 **a**

Means marked with the same letter do not differ significantly ($p_{SNK} > 0,05$)
Fv/Fm = chlorophyll fluorescence

3.6.5 Water deficit

The relative water content was related to the polyphenol (r = -0,27***) and nitrogen (r = -0,27***) contents. However, there was a lot of inexplicable variation in RWC between different time of season and origins. June and July of year 1992 were exceptionally dry months. The monthly precipitations were only 65 % of the average of 30 years. The weather was driest in June in Hämeenlinna and Vantaa (Appendix 3). At that time the bird cherries in Hämeenlinna had the lowest relative water content (Table 21). Respectively the highest RWCs were measured from the bird cherries in August in Vantaa, where it rained most.

Table 21. The changes of the relative water contents of *Prunus padus* L. leaves in 1992 (ANOVA).

	Time of growing season		
Origin	June %	July %	August %
Almost fully defoliated in Hämeenlinna (forest edge)	79 **d**	83 c	80 **d**
Uninjured in Hämeenlinna (forest edge)	81 **d**	85 b c	85 b c
Partly defoliated in Suomusjärvi (shore)	85 b c	81 **d**	85 b c
Almost fully defoliated in Suomusjärvi (shore)	86 b	80 **d**	84 b c
Uninjured in Vantaa (meadow)	86 b	84 b c	90 **a**
Almost fully defoliated in Vantaa (meadow)	86 b	80 **d**	85 b c

Means marked with the same letter do not differ significantly ($p_{SNK} > 0{,}05$)

4 Discussion

4.1 Taxonomy

The variations in the habitus and the phenology of native European bird cherries (*Prunus padus* L.) in Scandinavia are caused either by genes or different growing conditions. The variation in habitus is determined by the differences in growth power and form, the colour, texture, thickness, serration and pubescence of leaves, the position and the length of racemes, the lengths of petioles, petals and pedicles, the number and colour of flowers and petals, the size and colour of corollas and fruits. Addition to these variables, the length of blooming and other phenology related characteristics vary between individuals, which grow in different latitudes. These characteristics along with the distribution area define the taxon and the ornamental value of different origins or phenotypes. Korovina and Belozor (1983) studied the inner variation of subsp. *padus*. They divided the natural variation of *Prunus padus* subsp. *padus* into 11 taxons, which share certain inheritable characteristics. They developed a synoptic key to determine theses varieties on the grounds of their studies (Table 22).

Pubescence is used as the most important distinctive mark to divide bird cherry populations with distinct geographical range into subspecies. The taxonomy of the species is not, however, indisputable. Scholz and Scholz (1995) have, for instance, claimed that the division of *Prunus padus* into different subspecies should not only be based on the hairiness of foliage and shoots. Botanists should instead search for additional distinctive marks and study the distribution of the subspecies. Inter-specific crossings, which are common in *Prunus*-genus, demonstrate how closely the species relate. Since the genes are exchanged easily between individuals, it was found challenging to distinguish the subsp. *borealis* from subsp. *padus* especially in the southern limits of the hypothetical distribution area of subsp. *borealis* in Scandinavia.

Table 22. The synoptic key to the varieties of *Prunus padus* subsp. *padus* (Korovina and Belozor 1983).

1.	white flowers	2
-	pale pink flowers	var. *roseiflora*
2.	single flowers	3
-	double flowers	var. *plena*
3.	ascending branches	4
-	pendulous lower branches	var. *pendula*
4.	ovate fruits	5
-	long-ovate fruits, 12-14 mm x 7-8 mm	var. *dolichocarpa*
5.	black fruits	6
-	light yellow fruits	var. *leucocarpa*
6.	young twigs and petioles light pubescent or glabrous, leaves beneath light pubescent with whitish or reddish hairs	7
-	young twigs, petioles and leaves beneath very pubescent, reddish hairs	var. *pubescent*
7.	young leaves beneath and veins with red-brownish hair, old leaves almost glabrous	var. *rufoferruginea*
-	young leaves beneath and veins with whitish hairs, old leaves with reddish hairs, sometimes almost ovate	8
8.	thick and blunt-ended leaves	var. *petraea*
-	thin and pointed leaves	9
9.	bluish-grey upper face of the blade	var. *glauca*
-	not bluish-grey upper face of the blade	10
10.	golden or yellow-coloured leaves	11
-	dark green leaves beneath slightly bluish-grey, veins with whitish hairs, young twigs glabrous	var. *padus*
11.	yellow-coloured oval leaves 8-10 x 4-5 cm	var. *aucubaefolia*
-	golden-coloured pointed leaves over 10 x 4 cm	var. *aurea*

The previous studies have also paid attention to the determination of other pubescent taxons. Many botanists regard the taxon *pubescent* as *Prunus padus* subsp. *pubescent* Browicz. Some Russian authors have considered both *pubescent* and *borealis* as a different species: *Padus schuebeleri* Orlova (Komarov et al. 1971, Belozor 1983, Korovina & Belozor 1983). Sokolova et al. (1989) evidenced that the leaf and shoot anatomies of *padus* and *pubescent* are very similar. Therefore they refused to consider *pubescent*-taxon a subspecies. They instead named it *Padus avium* var. *pubescent* Polozh. (syn. *Prunus padus* var. *pubescent* Regel et Tilling). It is possible that the pubescent bird cherries in northern Scandinavia should not either be considered as subsp. *borealis* but instead as a var. *pubescent*, since they share the same characteristics (see Table 22). This hypothesis would be disproved, if any inheritable variations were found among the northern pubescent populations. Such findings are, however, missing so far (Scholz and Scholz 1995). On the grounds of the variation some taxonomists consider *petraea*-taxon as *Punus padus* subsp. *petraea* (Tausch) Domin (syn. *Padus avium* subsp. *petraea* (Tausch) Holub or *Padus avium* var. *petraea* (Tausch) Belozor). There are two different varieties of subsp. *petraea* found and named: var. *petraea* Passarge and var. *discolor* (Braun-Blanquet) Passarge.

4.2 Viability

There is a wide range of plant suitabilities as host plants to insects. The patterns of defensive investment and the development of resistance mechanisms appear to reflect the frequency and severity of herbivory experienced by populations over time (Feeney 1976, Rhoades and Cates 1976, Horber 1980). Plants show exceptional abilities to avoid, repel, retard, restrict and localise the insect infestations. Or they tolerate the herbivory by fast regrowth and recover by other ways from the attacks.

4.2.1 Compensate growth

This study implied that bird cherries have many survival strategies, which is typical to competitors. The trees tolerated the defoliation by small ermine moth larvae well. The defoliated bird cherries produced new leaves after the defoliation. The compensate growth is an indicator of tolerance. It appeared to be the most important resistance mechanism of bird cherries to small ermine moths. Leather (1986, 1993) has argued that bird cherries indeed have the remarkable power of recovering from early and repeated defoliation. The young saplings of bird cherry are even favoured for grazing by rabbits and small mammals (Leather 1996). However, tolerance depends on growing conditions. Competitors withstand herbivory well only, if light conditions and other growth factors are optimal (Velusamy & Heinrichs 1986, Berryman 1988).

If herbivory reduces the number of leaves, light will penetrate better through the vegetation (Welter 1989). Plant nutrients and stored energy will be released to cycle (Mattson & Addy 1975, Watson & Casper 1984, Chapin et al. 1986). Additionally, the water balance of plants will improve (Turner and Heichel 1977, Heichel and Turner 1983). Consequently, the plants will start producing photosynthetic enzymes from nitrogen (Wareing et al. 1968). The primary metabolism and assimilation of remained leaves will become more effective and new leaves will grow soon to replace the lost ones as a consequence (Brown and Ewel 1988, Welter 1989). Eventhough the assimilation of the defoliated bird cherries increased later in the season, it was low during the herbivory compared to the assimilation of the uninjured trees. The stress was evidently due to the damages of photosynthesis appartus by herbivory and water deficit, which was caused by the exceptionally dry season.

4.2.2 The optimal defence

Herms and Mattson (1992) have argued that defences are costly. Their optimal defence theory predicts that the resources are allocated to defence in ways, which optimise the investment. Tolerance has obvious benefits. A tolerant competitor does not have to maintain the defensive secondary metabolism. It can direct its energy to growth, which in turn improves the competitiveness. During the periods of intense growth, the secondary metabolism may be substrate and energy limited. That is because the primary and secondary metabolic pathways share the common precursors and intermediates. There are evidences that the phenol synthesis competes with the protein synthesis. Therefore a choice has to be made between defence and growth. The ratio of nitrogen and phenol contents of bird cherry leaves also reflects the metabolism path of plants. The ratio indicates how plants allocate resources during herbivory.

Rapidly-induced resistance and sink/source -interaction

The first observations, which were made in the study, implied that the uninjured bird cherries in Hämeenlinna and Vantaa were better-protected chemically against small ermine moths. This was expected to be the reason, why these two trees did not have any feeding larvae, when almost all bird cherries in southern Finland were defoliated in 1992. The uninjured bird cherries were assumed to have higher polyphenol level compared to the defoliated ones. On the contrary, the trees where larvae were feeding had worse nutrient quality compared to the uninjured ones. This finding referred to the induction of chemical resistance. Genetic mutations, infections (by parasites and microorganisms) and repeating defoliation (by herbivores) can trigger insect resistance in plants (Edward and Wratten 1980, Haukioja 1980, Rhoades 1983, Zucker 1983, Jones and Firn 1991). The defoliated trees allocated their resources to defence during the most intensive growth.

Firstly, a plant defending itself by the induced resistance does not have to maintain the secondary metabolism constantly at the cost of growth. Especially the competitors benefit from induced resistance. The damage of tissues induces the production of secondary compounds via secondary metabolism (Ryan 1983). Small pectin pieces and other dissoluble compounds are released, when the enzymes of herbivores or a plant decompose cell walls. They become chemical signals, which are carried through the cytoplasm and the xylem of the plant. Untouched cells which have active metabolism will start producing phytoalexins (e.g. phenols, terpenoids or proteinase-inhibitors) after a couple of hours. They are shown to be the key compounds of rapidly-induced resistance. Enzymes which activate phytoalexins are located in cytoplasm, cell organs and walls. If cell structure is damaged, the enzymes and the glycosides get free and react. Mobile toxic compounds will be released, as well as complex polyphenols from sugar parts. These toxic aglycones will accumulate in the damaged tissues. Plants can also start producing more small-molecular-weight phenols (Haslam 1985, Sutic & Sinclair 1991, Appel 1993). The compounds may be converted into more toxic forms or polymerised. Chemical barriers which were produced in secondary metabolism usually return to primary metabolism afterwards. Therefore resources (nutrients and assimilates) are only temporarily taken from growth (Coley et al. 1985, Herms and Mattson 1992).

Secondly, plants defend their tissues in direct proportion to the cost of their loss. Plants produce toxic metabolites for the protection of indispensable tissues and plant parts (Sylvertsen & Cunningham 1977, Mooney and Gulmon 1982, Haukioja et al. 1990). Easily replaced and less critical ones can be sacrifised. Immature leaves frequently experience the higher levels of herbivory compared to mature ones. Full-grown leaves are less valuable to a plant compared to immature ones, since the production of photoassimilates decline as the leaves mature. The adventory buds are the most valuable parts, because they have future value in the competition of light and in the production of assimilates. They also direct growth hormonally. Consequently, the prestages of new growth, which are located in adventory buds, and young leaves are worthwhile to defend.

Hermas and Mattsson (1992) are talking about bimodality in the phenological patterns of leaf defence. Loomis et al. (1990) have stated that there is modular construction in plants. Resources and defences are distributed according to the cellular system of specialized morphological subunits (modules). The distribution is regulated through the complex source/sink relationship. The patterns of resource usage within plants are determined by the within-module as well as the between-module (whole plant) allocation. At the level of the whole plant, resource distribution reflects the power of modules to draw assimilates. Consequently, secondary metabolism or metabolites in mature modules will be limited if they export much of their photoassimilates or metabolites to strong vegetative or reproductive “sinks”.

The results of the study indeed refer to the modular construction and hierarchy between bird cherry modules. The immature (distal) leaves had presumably more induced simple phenols than the mature (basal) leaves throughout the season. The immature leaves had also better nutrient quality measured as a ratio of nitrogen and polyphenol content. Theses measurements imply to source/sink interaction, i.e. the transportation of photoassimilates and phenols from mature to immature leaves. The secondary metabolites of “sinks” are usually highly potent low-molecular-weight toxins and deterrents, such as alkaloids and cyanogenic glycosides (nitrogen-based), glucosinolates (sulphur-based), simple phenols or terpenoids (McKey 1974, Feeny 1976). These toxins are especially prevalent in the plants growing in fertile environments, where nutrients are unlikely to limit growth (Levin 1976, Matsson 1980, Bryant et al. 1983). According to Herms and Mattson (1992) qualitative defences are cost-effective, since they function in low concentrations and are easily returned to primary metabolism. As tissues mature, the low-molecular-weight secondary metabolites may be converted to quantitative defences and structural compounds, i.e. to tannin or lignin polymers (Feeny 1976, Harborne 1984).

Damages which occur frequently in certain plant parts, especially in developing leaves can be fatal. By increasing the chemical variation between plant parts and using quickly-spreading toxic compounds, plants can disperse insects all around the canopy while insects are attacting (Janzen 1979, Watson & Casper 1984, Edwards & Wratten 1987, Honkanen & Haukioja 1994, Rosenthal & Kotanen 1994). Any changes which increase the chemical mosaics are advantageous to a competitor, because the balance of resource division between plant primary and secondary metabolism is unchanged (Whitham et al. 1984). This might have been one strategy of the bird cherries during herbivory, because the phenol contents between the leaves within the defoliated trees varied regardless of the occurrence of leaf damages.

Consequently, the rapid induction of qualitative defences into the most valuable plant parts seems to be the main optimal defence strategy of bird cherries. According to Edwards and Wratten (1983) induced resistance can last for many days. The compensated leaves of the completely defoliated bird cherries contained as much or more phenols than the early-bursted leaves. Edwards and Wratten (1980) argue that with induced resistance plants can also repel the feeders, which arrive later in season. This way new and remained foliage will produce enough assimilates for storage, which are further used for growth or defend next year.

Delayed-induced or mutation-regulated resistance

The main part of the nutrients of perennial deciduous species is located in canopies during growth. Secondary metabolites are biosynthesized after the periods of intensive growth or in late season and used for the defence of overwintering buds and expanding tissues in many plant species (Bryant et al. 1983, Lapinjoki et al. 1991). However, if nutrients are lost during the intensive growth due to herbivory, the growth of roots may slow down and some capillary roots may even die (Mihaliak & Lincoln 1989). Therefore the nutrient intake of plants decreases. Phenylammoniumlyase is an enzyme in secondary metabolism. It is activated by cytocin-hormone. The deficiency of nutrients and increased light level may stimulate the production of hormone and enzyme (Waterman & Mole 1989). As a consequence, carbon compounds may be assimilated and stored into roots and wooden parts. The compounds will be further used in phenol synthesis next year. The activation of phenol synthesis and the slow increase of leaf phenols might have collapsed the ermine moth populations in southern Finland after a lag in 1994 (Figure 12). The gradual reduce of food quality might have slown down the development of larvae. They have become weaker and susceptible to predators, parasites and pathogens. The delayed-resistance may effect on herbivory even for three years (Haukioja 1980, Rhoades 1983, Bryant et al. 1988).

The resistance to herbivores may be induced both quickly and slowly. For example, Clausen et al. (1989) have found out that the delayed resistance mechanism of aspen (*Populus tremuloides* L.) increases the concentration of secondary compounds, whereas the rapidly-induced resistance mechanism transfers secondary compounds into more toxic forms. This could basically happen also in bird cherries. The other bird cherry in Suomujärvi was defoliated two weeks later. This implies to the worse nutrient qualityof leaves, the higher levels of toxic polyphenols and the rejection behaviour of egg-laying moths (Kooi 1990). Small ermine moths might have avoided this tree, when they were choosing food plants for their larvae in previous fall. Furthermore the observations support Van Drongelen's (1980) findings. According to his explanations the larvae had to move to the less nutrient or more toxic host, because they run out of food in the defoliated tree. Alonso's et al. (2000) findings support Van Drongelen's argument for shortage of food. They monitored the defoliations of bird cherries in two areas in southern Finland for 15 years to explain the insect outbreaks and collapses. They observed that high defoliation in one year did not necessarily predict the degree of defoliation in the following year. On the grounds of these findings they concluded, that quantity (shortage) rather than quality (defences) of food and drastic variation in insect densities between areas regulate insect populations.

It is possible that the observations of this study do not have any correlation to delayed-induced resistance. Instead, the uninjured or the partly defoliated bird cherries might have expressed extraordinary genetic profiles. The rare mutations could have caused the changes in phytochemistry. Mutations sometimes occur in the genes, which regulate cell metabolism. New structures of phytochemicals, which change and confuse the detoxification mechanisms of herbivores, may be produced (Bowers & Puttick 1988, Berenbaum et al. 1991, Jones & Firn 1991). Mutations are beneficial for a plant because they are easily copied by vegetative clones.

4.2.3 Stress-induced resistance

Such climatic or environmental stress factors as drought may depress the growth of sink modules. Carbon compounds will start accumulating and photosynthesis will slow down (Chapin et al 1990, Luxmore 1991). If accumulated compounds are toxic organic secondary metabolites, herbivore resistance may be improved (Del Moral 1972, Mattson and Haack 1987).

Unordinary dry soil conditions in June and July might have influenced in the relative water content of leaves (Appendix 3). RWC of leaves explained the low efficiency of assimilation in the defoliated bird cherries during June-July period. Their photosynthetic apparatus was probably damaged because of drought and defoliation. These effects were seen especially in the immature leaves. Consequently, the drought may have either caused or just accelerated the production of phenols. Improved chemical resistance due to drought could have mediated the collapse of population size of small ermine moths in southern Finland after one year lag in 1994. Since the assay was inaccurate, this is only an assumption. Some plants species have adapted to prolonged or continuous environmental stress. They are called stress-tolerators (Haukioja et al 1990, Hermms and Matsson 1992).

5 Summary and conclusions

European bird cherry (*Prunus padus* L.) is very potential plant for landscape horticulture and natural landscaping. Since the species is remarkably varietive, it holds many advantages. Owing to adaptability and winter-hardiness, bird cherries thrive in different growing conditions. Therefore the species has colonized the wide range of habitats. It blooms very early in spring and has edible fruits. That is why it is important honey plant in northern Scandinavia for rare insect species, which generally live in valuable broad-leaved trees in southern Scandinavia. There are about 60 different herbivorous insects feeding on the species. Most of them consume bird cherry leaves.

European bird cherries are unfortunately often avoided in cultivation because of their abundant fauna. The wild stands are sometimes even destroyed by farmers, because bird cherry-oat aphid (*Rhopalosiphon padi* L.) may transmit Barley Yellow Dwarf Virus (BYDV) while removing the sap from cereals. Owing to *Yponomeuta evonymellus* L (another abundant bird cherry specialist) landscape designers and horticulturists have often undervalued the plant species. Defoliation by small ermine moth larvae and their loose webs lower the ornamental value of bird cherries substantially for some weeks in spring especially during the outbreaks. Defoliation is not lethal to bird cherry stands. The pest-host relationship is dynamic, because these species are co-evolving.

Overwintering first-instar larvae do not supposedly survive in severe winter conditions (Appendix 4). Therefore the insect outbreaks are evidently rare in northern Scandinavia (Appendix 1).

Since the morphological characteristics of bird cherries vary between and within populations, it was presumed that there also exist diverse tactics against herbivorous insects. A set of variable resistance mechanisms is an indicator of optimal defence strategy, which is typical of competitors. The observations of the study support the hypothesis of tolerance as a main strategy of bird cherries against small ermine moths. It is likely that cyanogenic glycosides are the most common qualitative phytotoxins of immature bird cherry leaves. The compounds are obviously effective in generalist feeders but ineffective in the larvae of small ermine moths. Low-molecular-weight phenols may function better against these specialists. There were also evidences of increased production of leaf phenols in the defoliated trees. This further implied to rapidly-induced resistance to small ermine moths. Other defence tactics are just hypothetical and need thorough investigations. The existence of delayed-resistance in bird cherries is disputable as well as the occurance of mutations and drought-related resistances. However, these factors could mediate some changes in the chemical composition of leaves and improve the insect resistance of bird cherries as consequence.

Different compounds function differently in the guts of larvae. The capability of Lepidoptera species to detoxify different phenols varies a lot. Detoxification is dependent for example on the chemical structures of different phenols, which effects on the stability of chemical bonds. For example different polyphenols function differently. Zucker (1983) argue that hydrolytic tannins are more poisonous to insects compared to condensed tannins. The latter strengthen cell walls. There are some evidences that highly specified insect species react only to certain phenols (Sunnerheim et al 1988). Addition to chemical composition, the efficiency of chemical resistance depends on concentrations, which may alter a lot within and between growing seasons (Figure 14). Host plants can allocate most of their energy to primary metabolism and growth by timing the production of a specific qualitative defence (e.g. a low-molecular phenol) at the vulnerable stage or the food uptake of insects (via induced resistance).

Advanced chromatography (GLC, HPLC) and mass-spectrometry could be used in phenolic fingerprinting studies (Raymond et al. 1995). These kinds of studies reveal, if the quality of food or the exisistence of defences have any influence on the larvae of small ermine moths. The phenol profiles of leaves could be analysed to study also the taxonomy of the species. The collection of bird cherry leaves should be timed at late August, when moths deposit their eggs, and at late May, when first-instar larvae mine inside the leaf tissues. The protective shields (the hibernaculum), where the larvae overwinter and where their development begins, should be counted. The amount of hibernaculums should then be compared with the degree of defoliation and the phenol content of leaves. The sugar compounds (feeding stimulators) and terpens (growth inhibitors bonding with proteins) of leaves could also be detected. Different compounds should be identified from fresh leaf samples, which are frozen into liquid nitrogen. Entomologists could simultaneously execute antibiotic and antixenotic feeding trials to study the effects of identified phenolic compounds on the feeding behaviour, the digestion and the survival of small ermine moth larvae.

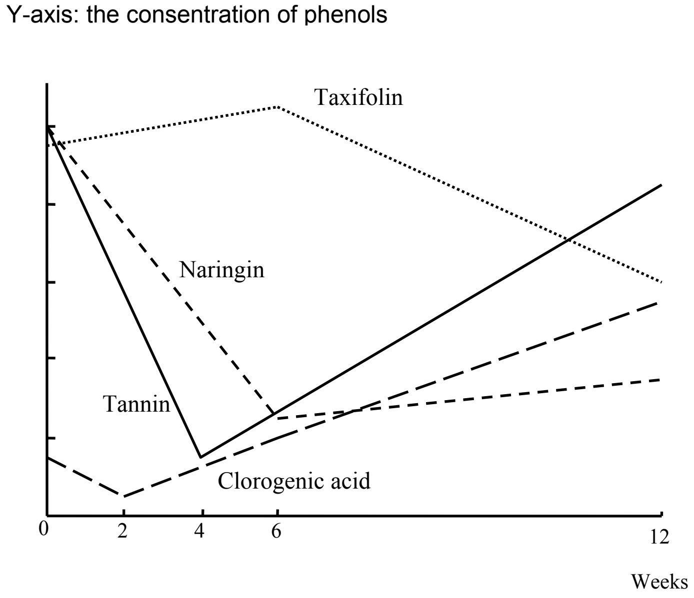

Figure 14. The variation in the phenol profile of *Pseudotsuga menziesii* (Mirbel) Franco), douglas spruce (Horner 1984 ref. Cates 1987).

Stress caused by unfavourable growing conditions could have effects on carbon/nutrient balance, on the production of secondary metabolites and hence on larvae feeding behaviour. The study showed that drought effected on the efficiency of assimilation of bird cherry leaves. Stress effects on the herbivore resistance of bird cherries should be studied more. That could be done by measuring chemically the water deficit of different bird cherry origins, which grow in same conditions (a field trial). The analysis of proline and abscissine acids or advanced physiological (based on respiration) analysis are potential methods. This knowledge could also be compared with the occurrence of drought and damages by small ermine moth larvae. The statistics would show if there are any correlations. The clonal archive of *Prunus padus* in Muhos offers interesting material for further studies.

Genetic variation is an important element of biodiversity. Many genotypes of *Prunus padus* are already taxonomically determined as subspecies, varieties or formas. Many taxons and origins are adapted as cultivars in horticulture or used as gene resources in fruit breeding programmes especially in the fringe of distribution area. Many wild origins with promising utility values were found in Scandinavia in the study. There are more potential origins to be discovered for field trials. When taxons are searched for cultivation, attention should also be paid to local origins and phenology. Morphological observations and DNA-analysis (or chemotaxonomic bioassays) should be conducted to confirm the taxons of origins. Especially the taxonomy of *Prunus padus* subspecies *borealis* needs to be clarified.

Finally, *Prunus padus* L. should not be seen just as an interesting research subject in entomology or as a promising source for breeding programmes, but as a valuable ornamental species with many potential varieties and formas. Nielsen (1989) has expressed that increasing diversity would improve the natural resistance of urban plantings to urban stress (e.g. air pollution, wind, radiant heat, soil compaction, salts). European bird cherry as a varietive and adaptable species is able to promote the biodiversity of local ecosystems especially in northern Scandinavia. Consequently, *Prunus padus* L. will be hopefully favoured by landscape designers and horticulturist in Scandinavia in future.

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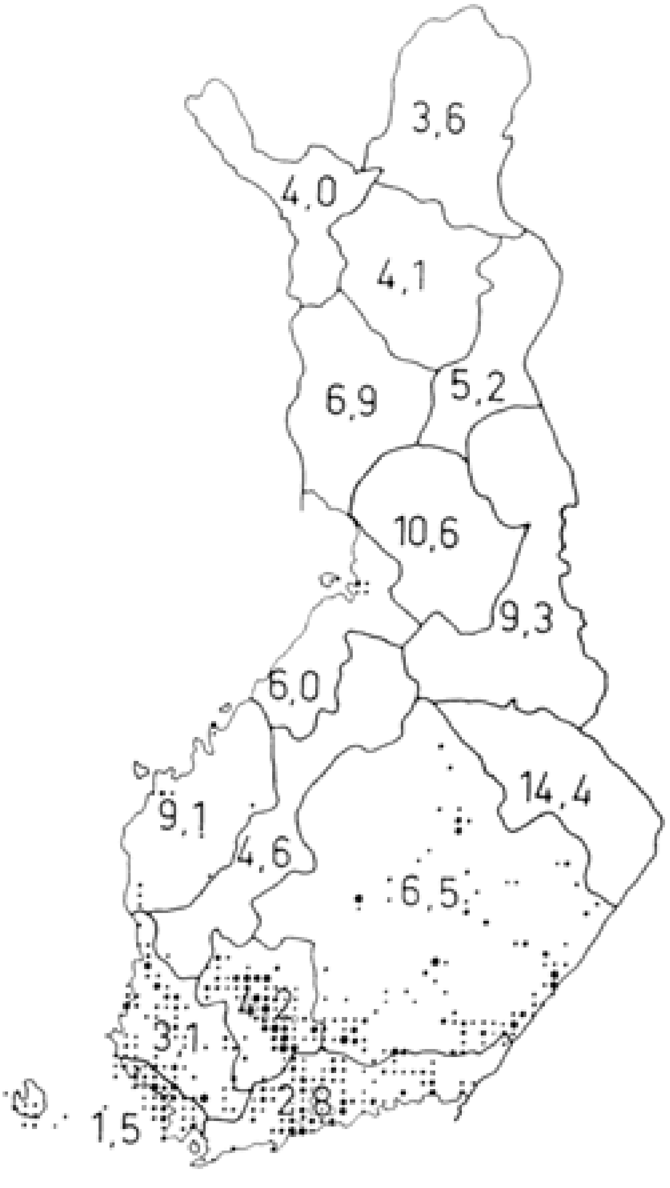
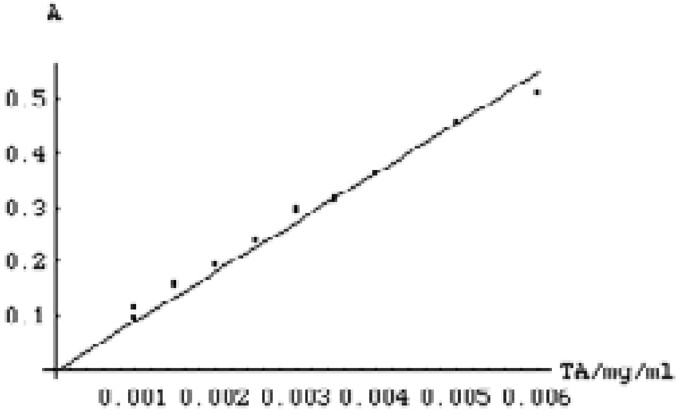
7 Appendices

Appendix 1. *Occurrence of small ermine moths (damages as dots) and transplanted (% observed yards) European bird cherries in Finland (Hyönteiskartoitus 81 1985, Raatikainen 1991).*



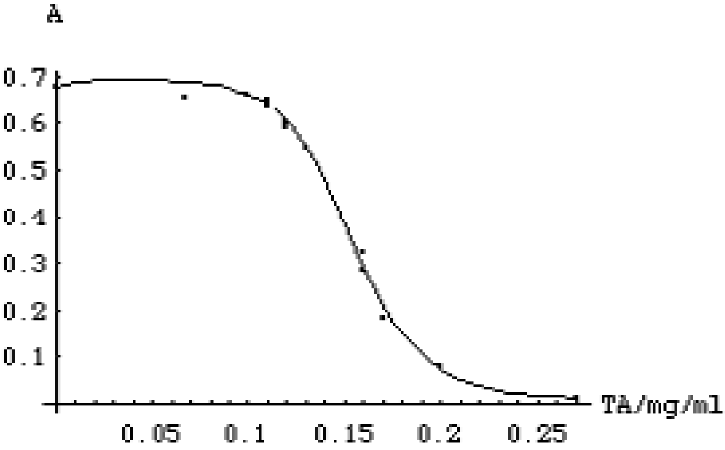
Appendix 2. *TAE - standard curves of phenol analysis*

a) Folin-Dennis -analysis

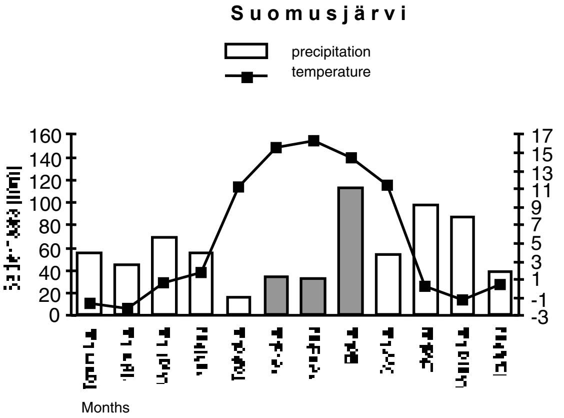


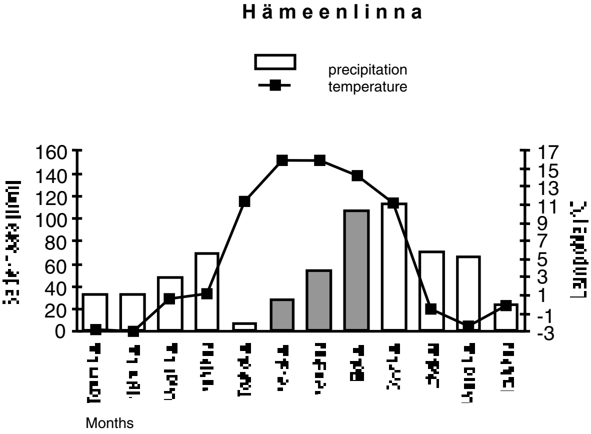
A = absorbance of coloured sample liquid
TA = consentration of tannic acid

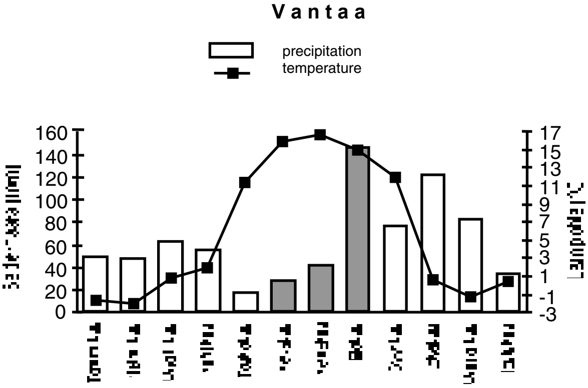
b) Haemanalysis



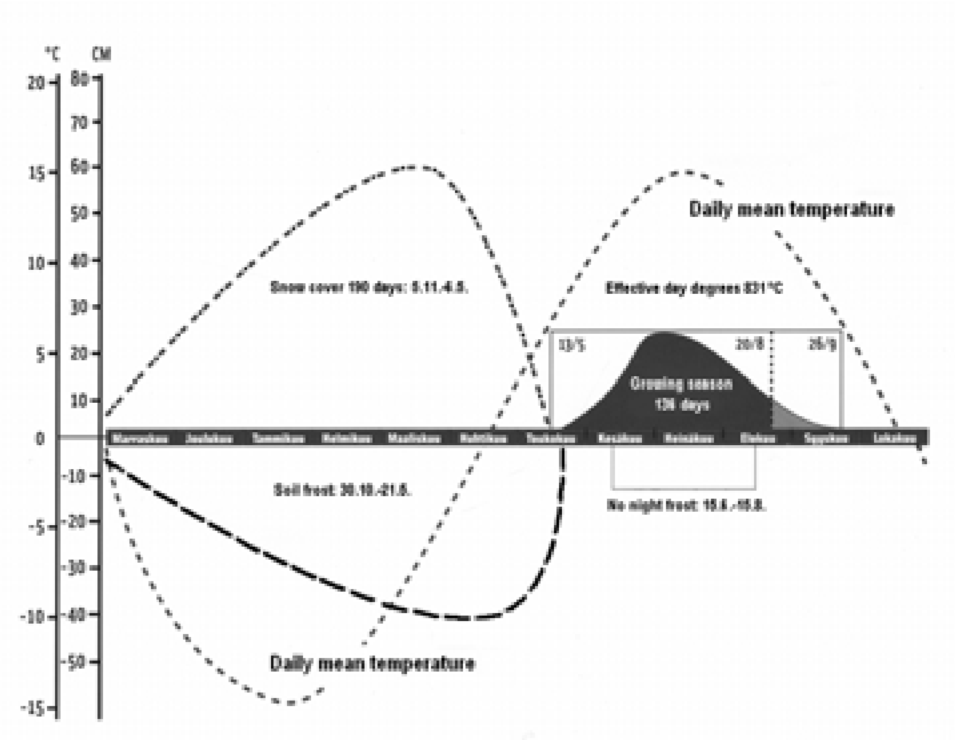
Appendix 3. *Precipitation and temperatures in 1992 in the study sites: (a) Suomusjärvi, (b) Hämeenlinna and (c) Vantaa (Ilmatieteen laitos 1994).*







Appendix 4. *Average climatic condition at Lapland Research Station in Rovaniemi (66°35´ N, 26°01’ E, 103 m a.s.l) as an example of severe climates in the Northern Scandinavia (Nissinen 1996, 31).*



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