ACTA FORESTALIA FENNICA

210

MATTI ROUSI

BREEDING FOREST TREES FOR RESISTANCE TO MAMMALIAN HERBIVORES — A STUDY BASED ON EUROPEAN WHITE BIRCH

METSÄPUIDEN RESISTENSSIJALOSTUS KASVEJA SYÖVIÄ NISÄKKÄITÄ VASTAAN — RAUDUSKOIVUUN PERUSTUVA TUTKIMUS

THE SOCIETY OF FORESTRY IN FINLAND
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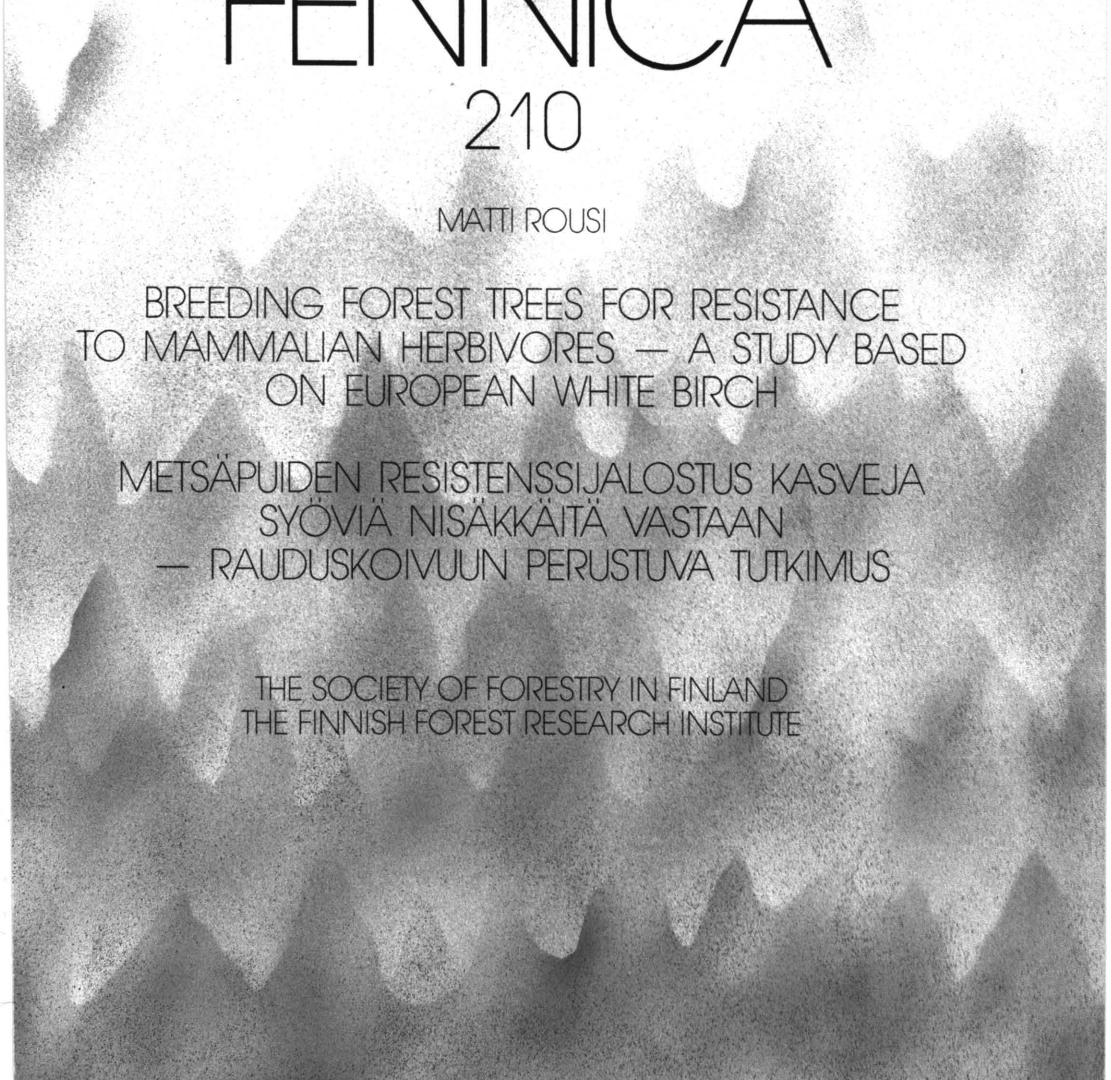

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Acta Forestalia Fennica 210

Breeding forest trees for resistance to mammalian herbivores — a study based on European white birch

Metsäpuiden resistenssijalostus kasveja syöviä nisäkkäitä vastaan — rauduskoivuun perustuva tutkimus

Matti Rousi

To be presented with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in Auditorium XII of the University Main Building, Aleksanterinkatu 5, on March 16 1990, at 12 noon

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Resistance to browsing by mammals differs among birch species, and among origins and families of European white birch. The variation in resistance is large even among individual seedlings of the same family. On the surface of the bark of European white birch seedlings there are resin droplets, and the number of droplets is strongly and positively correlated with resistance to browsing by hares. The resistance of European white birch apparently is not expensive metabolically because the rapid growth rate of seedlings was positively correlated with hare resistance, and no correlation was found between seedling size and vole resistance. In cafeteria experiments voles and hares were very discriminating in their feeding on birch seedlings. In field experiments, however, environmental heterogeneity partly masked differences in vole resistance among birch families. Fertilization of seedlings seems not to have a clear effect on resistance to hares. On the other hand, there were indications that greenhouse temperature had an effect on resistance to voles. Practical forestry applications of differences in resistance, e.g. use of species hybrids and clonal forestry, are discussed. The prospects for resistance breeding are good.

Kasveja syövät nisäkkäät ovat pahoja taimikkotuholaisia. Käytäntöön helposti sovellettavia keinoja niiden torjumiseksi ei tunneta. Mahdollisuuksia nisäkäskestävyyden eli resistenssin lisäämiseen metsänjalostuksen keinoin on tutkittu vain vähän. Nyt tehdyt tutkimukset osoittavat, että kestävyysvaihtelu eri koivulajien välillä on huomattava. Nisäkäskestävyyden vaihtelu on laajaa myös saman lajin eri alkuperien ja perheiden välillä ja jopa saman perheen sisällä.

Rauduskoivujen taimien kelpaavuus jänikselle riippuu kuoressa olevien hartsinystyjen määrästä: mitä enemmän nystyjä sitä huonommin kelpaava taimi on. Rauduksen nisäkäskestävyys ei näytä olevan aineenvaihdunnallisesti kallista: 1-vuotiaiden taimien pituus näyttää korreloivan positiivisesti jäniskestävyyteen. Myyräkestävyydellä ja taimien pituudella ei ollut yhteyttä. Puiden ilmastollinen sopeutuminen vaikuttaa jossain määrin kestävyyteen. Taimien lannoituksella ei näyttänyt olevan yhteyttä jäniskestävyyteen. Artikkelissa tarkastellaan lähemmin kestävyysvaihtelun sovellutuksia, esim. lajihybridejä, kloonimetsätaloutta ja kestävyyden fenotyyppistä plastisuutta.

Keywords: resistance, breeding, pests, mammals, *Betula pendula*, *Betula platyphylla*, interspecific hybrids, clonal forestry, phenotypic plasticity, climatic adaptedness.
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Rousi, M., Tahvanainen, J. & Uotila, I. 1990a. Mechanism of resistance to hare browsing in winter-dormant European white birch *(Betula pendula)*. American Naturalist (In press).

Rousi, M., Henttonen, H. & Kaikusalo, A. 1990b. Resistance of birch (*Betula pendula* and *B. platyphylla*) seedlots to vole *(Microtus agrestis)* damage. Scandinavian Journal of Forest Research 5(3) (In press).

Preface

Many people have been involved in the project summarized in this paper. My sincere thanks to Jorma Tahvanainen for close cooperation during this study. I also thank Veikko Koski, Erkki Haukioja, Riitta Julkunen-Tiitto, P.M.A. Tigerstedt and Heikki Henttonen for stimulating discussions, Joann von Weissenberg for checking the language of the manuscript, and Ahti Anttonen, Pentti Manninen, Esko Oksa, Jouko Lehto, Hanni Sikanen, Eija Matikainen, Tiina Ylioja, Jukka Niemimaa and many others from Punkaharju Research Station for technical assistance.

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1. Introduction

Mammalian herbivores such as moose (*Alces alces*), hare (*Lepus* spp.) and vole (*Microtus* spp., *Clethrionomys* spp.) cause serious damage to forest plantations in the Holarctic zone (Kanervo & Myllymäki 1970, Hansson & Larsson 1980, Korhonen 1987 and references therein, Rousi et al. 1987, Bergeron & Tardif 1988, Kurahashi 1988, Löyttyniemi & Lääperi 1988). For example, in Finland European white birch *(Betula pendula)* is economically (Oksanen 1987) and ecologically (Sirén 1955) a very profitable species and is also used in landscaping (Mäkynen 1987). Birches are planted on a very small scale, however, and since the 1960's Finnish plywood and pulp factories have had a constant shortage of raw material. Forest owners are not willing to plant birch, basically because birches are considered to be very susceptible to damage by mammalian herbivores. This damage cannot be prevented by killing off the problematic mammals, and no feasible methods are known for preventing the damage (see Löyttyniemi & Lääperi 1988).

Resistance breeding has usually meant the same as breeding disease-resistant trees, and the genetic resistance of forest trees to mammalian herbivores has been studied on only a very limited scale. The problem with fungal diseases, microbes, nematodes and insects is that they usually are obligate monophages and produce large numbers of offspring. Thus resistance-breaking strains of fungi and even insects are likely to evolve. In theory, breeding for resistance to feeding by moose, hare and vole could be more promising because mammalian herbivores that browse on boreal forests are usually obligate polyphages (Bryant et al. 1985) and produce limited numbers of offspring. In addition, economically important tree species are not preferred browse plants, even in wintertime (Hansson & Larsson 1980, Sainio 1955). Consequently, if there is genetic variation in mammalian resistance within forest trees, it could be possible to reduce the damage permanently by means of tree breeding.

The aims of this study were to determine 1) whether tree species (especially birch), origins, families or genotypes differ with regard to their genetic resistance to feeding by vole and hare, 2) the mechanism of resistance, 3) the phenotypic plasticity in resistance, 4) the correlation between resistance and growth, and 5) whether the differences in palatability found in cafeteria experiments are so relevant in field conditions that we would be justified in defining resistance breeding as a tool for decreasing damage by mammalian herbivores to a tolerable level.

2. Differences in resistance among tree species

Browsing mammals in boreal forests clearly select among various tree species in winter (e.g. Sainio 1955, Takahashi & Nishiguchi 1966a, Klein 1977, Bryant & Kuropat 1980, Rousi 1983a, Pigott 1985, Pulliainen & Tunkkari 1987). In particular, late successional evergreens and nitrogen-fixing species tend to be avoided by mammal browsers (Bryant et al. 1985).

The variation within a genus may be very large; for example, among *Betula* species, hare and vole resistance varies significantly. Seedlings of *B. platyphylla* (Chiba & Nagata 1968, 1969, Rousi et al. 1989, 1990a, 1990b), *B. resinifera* (=*B. papyrifera* ssp. *humilis*) (Bryant et al. 1989), and *B. ermani* (Chiba & Nagata 1968, 1969) have been found to be especially resistant. The seedlings of *B. pendula* have usually been intermediate in resistance (Chiba & Nagata 1968, 1969, Bryant et al. 1989, Rousi et al. 1989). Resistance to vole and hare browsing has also been reported to differ considerably among species of *Larix* (e.g. Chiba 1963, 1977).

3. Differences in resistance within tree species

31. Differences among origins

311. Climatic adaptedness

Owing to effective pollen dispersal, there is active gene exchange between tree populations occupying the same geographical areas. Consequently, no distinct populations with differing resistance to herbivores are expected to develop. However, if a tree species, such as *B pendula*, occupies vast geographical areas with a different herbivore pressure, differences in resistance among origins are very probable. The difficulty is to assess whether such differences among origins of trees planted in the same area are really due to genetic differences in resistance or to problems in the adaptedness of the trees.

When exotic species or provenance transfers are used in forestry, great care should be taken to ensure that the material is adapted to the new growing site. 'There are not many 'absolutes' in biology, but what comes the closest to certainty is that exotic plantations will be attacked by pests of one kind or another' (Zobel 1982). Often the plant material is not adapted well enough to the climate of the new site, and poor adaptedness may decrease the resistance of plants enough for either indigenous or exotic pests to overcome the remaining resistance. These changes in resistance certainly will also have implications when global warming begins to affect the winter hardening of forest trees (Kellomäki et al. 1988).

When large-scale plantations of *Pinus contorta* were started in Sweden, many researchers were doubtful as to whether that species is well enough adapted to the very severe conditions of the North (e.g. Lindgren & Lindgren 1985). When plantations were made in Sweden and Finland (c. 4—6° north of the original growing sites of *P. contorta* in Br. Columbia and the Yukon), there was a clear negative relationship between the intensity of vole damage and the latitude of the original growing site of *P. contorta* origins (Rousi 1983a, Hansson 1985). High frequency of vole damage was seen as a first warning that the winter hardening process had not taken place properly and that biotic and abiotic damages could be expected during wintertime (Rousi 1983a). The high frequency of *Gremmeniella abietina* (= *Scleroderris lagerbergii*, *Ascocalyx abietina*) damage later showed that *P. contorta* is not well enough adapted to the harsh northern climate and that restrictions on its use should be set (Karlman 1988).

In moose browsing the origin of *Pinus sylvestris* was found to be related to the degree of damage (Niemelä et al. 1989): the more southerly the origin, the more palatable it was. This same relationship seemed to hold true for moose damage on *P. contorta* (Rosvall & Friberg 1989). Although no calculations were made, there were also indications that during peak vole years *Picea abies* seedlings of Middle European origins tended to be damaged more by *Microtus agrestis* than seedlings of local southern Finnish origins were (Heikinheimo 1971, p. 23 and c.f. Kangas 1935). Voles also showed some tendency to prefer those F_1 hybrid seedlings of *Larix gmelini* and *L. leptolepis* (= *L. kaempferi*) that change needle color late in the autumn i.e. voles apparently prefer seedlings that winter-harden late in the autumn (see Table 7 in Takahashi & Nishiguchi 1966b). It is also evident that there is a strong negative correlation between dry matter content of pine needles and moose browsing (Haukioja et al. 1982, Niemelä et al. 1989). The same is true for hare browsing (Rousi 1983b).

When the southern origins of forest trees are transferred northwards, their winter-hardening process is delayed (Koski & Sievänen 1985). The dry matter content of *P. sylvestris* needles in wintertime correlates positively with the latitude of the tree's origin (Langlet 1934, 1936, 1959). Thus the reason for increased susceptibility of southern origin trees to biotic damage may be failures in the winter-hardening process. On the other hand, when the susceptibility of *P. sylvestris* origins and families to *Microtus*-damage was studied, no correlation was found between vole damage (Rousi 1989) and characters that are strongly correlated with winter hardening (according to Mikola 1980 and Thompson 1981), such as timing of bud set and proportion of seedlings in the primary needle stage. In their winter-feeding neither *Lepus timidus* nor *Microtus* voles showed any clear preference for southern *B. pendula* origins or 1-year-old seedlings with delayed winter-hardening (Rousi 1988, Rousi et al. 1989).

Although the effect of fertilization on the winter-hardening process of plants is not known with certainty, an excess of nitrogen and a severe nutrient imbalance apparently can be expected to delay the process drastically (Pellet & Carter 1981). Heavy nitrogen fertilization increased hare browsing damage in a mature Scots pine forest; but if micronutrients were applied with nitrogen, there was a tendency for the damage to be less than that found with nitrogen only (Rousi 1983b). Nitrogen fertilization also increased moose and rodent damage in saplings of Scots pines and in *Abies amabilis* (Gessel & Orians 1967, Laine & Mannerkoski 1980, Löyttyniemi 1981). In addition, snowshoe hares (*Lepus americanus*) and squirrels (*Tamiasciurus hudsonicus*) clearly preferred fertilized *P. contorta* to non-fertilized *P. contorta* (Sullivan & Sullivan 1982), although the effect of nitrogen and other fertilizers was not checked separately.

Since mammalian herbivores seem not to select browse plants according to nutrient content (Salonen 1982, Haukioja et al. 1982, Helle et al. 1986), the most readily available interpretation of the above results is that if trees do not winter-harden properly, changes may take place in their metabolites. These changes might be cold-induced because in small seedlings, which are under snowcover during wintertime, there is no correlation between characters that indicate winter-hardening and susceptibility to damage. Induction of the winter-hardening process of forest trees may vary, e.g. according to growth forms (free growth vs predetermined growth) (see Koski & Sievänen 1985). This variation may also have implications for our understanding of the discrepancy between results obtained for resistance in birch and in pine.

312. Resistance centers

Vavilov (1922) introduced the term 'gene centers' or 'centers of origin', meaning primary regions of diversity of cultivated species. A generally accepted rule today is that gene centers of cultivated plants are the best places to find genuine resistance to common diseases, insect pests and nematodes. In these centers, plants have long been exposed to selective pressure from local pathogens and insect pests and have consequently developed resistance to them (for review see Leppik 1970).

Bryant et al. (1989) indicated that duration of exposure of boreal woody plants to browsing by mammals has influenced the evolution of their defenses against browsing. Thus winter-dormant boreal *Betula* and *Salix* species from the Pleistocene refuges (Alaska and Siberia) were more resistant to browsing by snowshoe hare and mountain hare than were ecologically similar birches and willows from regions that were heavily glaciated in the Pleistocene. On the other hand, birches from Iceland, where there were no browsing mammals before Norse colonization (Darlington 1957), are more susceptible to browsing mammals than are ecologically similar plants from continental boreal regions with more browsing mammals (Alaska, Finland and Siberia) (Bryant et al. 1989).

In the present feeding experiments with hare, Alaskan birch (*B. papyrifera*) and Japanese birch (*B. platyphylla*) (Japan was not buried under ice, Darlington 1957) have been shown to be resistant to browsing (Rousi et al. 1989, 1990a, 1990b). On the other hand, Japanese larch (*L. leptolepis*), for example, is very susceptible to feeding by voles (Kurahashi 1988) and seedlings of the Siberian origin of *B. pendula* is very palatable to hare (Rousi et al. 1989). To determine the importance of 'resistance centers' as a source of mammalian resistance, more studies are clearly needed.

32. Differences among families

In order to avoid problems with climatic adaptedness, local breeding material is often used. When the basic material for tree breeding was selected in Finland, the primary criteria were growth and quality, and no attention was paid to resistance to herbivores (Oskarsson 1970, Raulo & Koski 1975). Selection according to growth apparently has not, however, decreased the resistance of F_1- and F_2-generation birches or pines, compared to seedlings from natural populations (Rousi 1988, 1989, Rousi et al. 1990a).

In *B. pendula* there is very large variation in resistance among F_2-generation families. This is true for 1-year-old seedlings as well as for older saplings (Rousi et al. 1989, 1990a, b). The vole resistance of Scots pine also varies strongly among families of 2-year-old seedlings as well as among families of 8-year-old saplings, and both resistant and susceptible parent trees can be identified (Rousi 1989). Consequently, the variation in resistance within well-adapted populations, which are already used in breeding programmes, might offer a safe and rapid means of increasing resistance. In its simplest form that could mean the exclusion of susceptible parent trees from later breeding work.

33. Differences among clones

Dimock et al. (1976) and Silen & Dimock (1978) have shown genetic differences in resistance to snowshoe hare and deer (*Odocoileus hemionus columbianus*) browsing among clones of Douglas fir (*Pseudotsuga mentziesii*), although there was some difference in preference between the two herbivores. Silen et al. (1986) later concluded that the family heritability of resistance to deer browsing is as high as 0.73; moreover, they could find no reciprocal, maternal or specific combining ability.

Among clones grafted from phenotypic plus trees of Scots pine, Haukioja et al. (1982) found very large variation in resistance to moose browsing. The variation in vole resistance among clones of *L. leptolepis* was also large, the most resistant clones being at the same level as a hybrid of *L. gmelini* × *L. leptolepis* (Chiba et al. 1982). These results also indicate a good potential in our breeding populations for increasing resistance to mammalian browsing by means of selection and breeding.

4. Mechanism of resistance

The digestion of Holarctic mammalian herbivores is based on microbial activity in the rumen (*Alces*), on both enzymatic and microbial processes (*Lepus*), or mainly on enzymatic activity (*Microtus* and *Clethrionomys*). The important question for resistance breeding is whether the food selection of Holarctic mammalian herbivores is made on the same basis in spite of differences in digestive processes.

It has been concluded that the food selection of herbivores is based on a search for positive factors in their browse plants. For example, in all organisms nitrogen plays a central role in metabolic processes, as well in cellular structure and genetic coding. Moreover, nitrogen is considered to be a critical element for the growth of plants. The nitrogen content of plants is thus vitally important; and because nitrogen is scarce, it may be the limiting plant nutrient for herbivores. Consequently, many herbivores are thought to select their food plants according to nitrogen content (for review see Mattson, 1980).

Clearly, however, mountain hare and moose do not select food on the basis of nitrogen or crude protein content. Nor do the contents of sugars, minerals or trace elements seem to affect the susceptibility of browse plants to mammal damage (e.g. Haukioja et al. 1982, Salonen 1982, Tahvanainen et al. 1985, Helle et al. 1986). There is more and more evidence that herbivores avoid repellent or toxic compounds in their browse plants and that their selection of woody plants as food is based mainly on avoidance (Bryant & Kuropat 1980, Bryant 1981, Bryant et al. 1983b, Reichardt et al. 1984, Bryant et al. 1985, Tahvanainen et al. 1985, Helle et al. 1986, Wink 1988, Henttonen et al. 1990, Tahvanainen et al. 1990).

The mechanism of mammalian resistance in birch is now quite well understood. The bark of some birch species, e.g. *B. pendula* and *B. resinifera*, contains many rough droplets. The number of droplets is strongly and negatively correlated with susceptibility of the seedlings to feeding by hares (Rousi et al. 1990a). These droplets contain mostly papyriferic acid and a few other triterpenes (Reichardt et al. 1984, Tahvanainen et al. 1990). Papyriferic acid is known to deter not only browsing by hares (*L. timidus* and *L. americanus*) but in very small concentrations it also prevents feeding by microtine rodents (Henttonen et al. 1990). In addition, papyriferic acid significantly decreases the rate of cellulose digestion by wapiti (*Cervus elaphus*

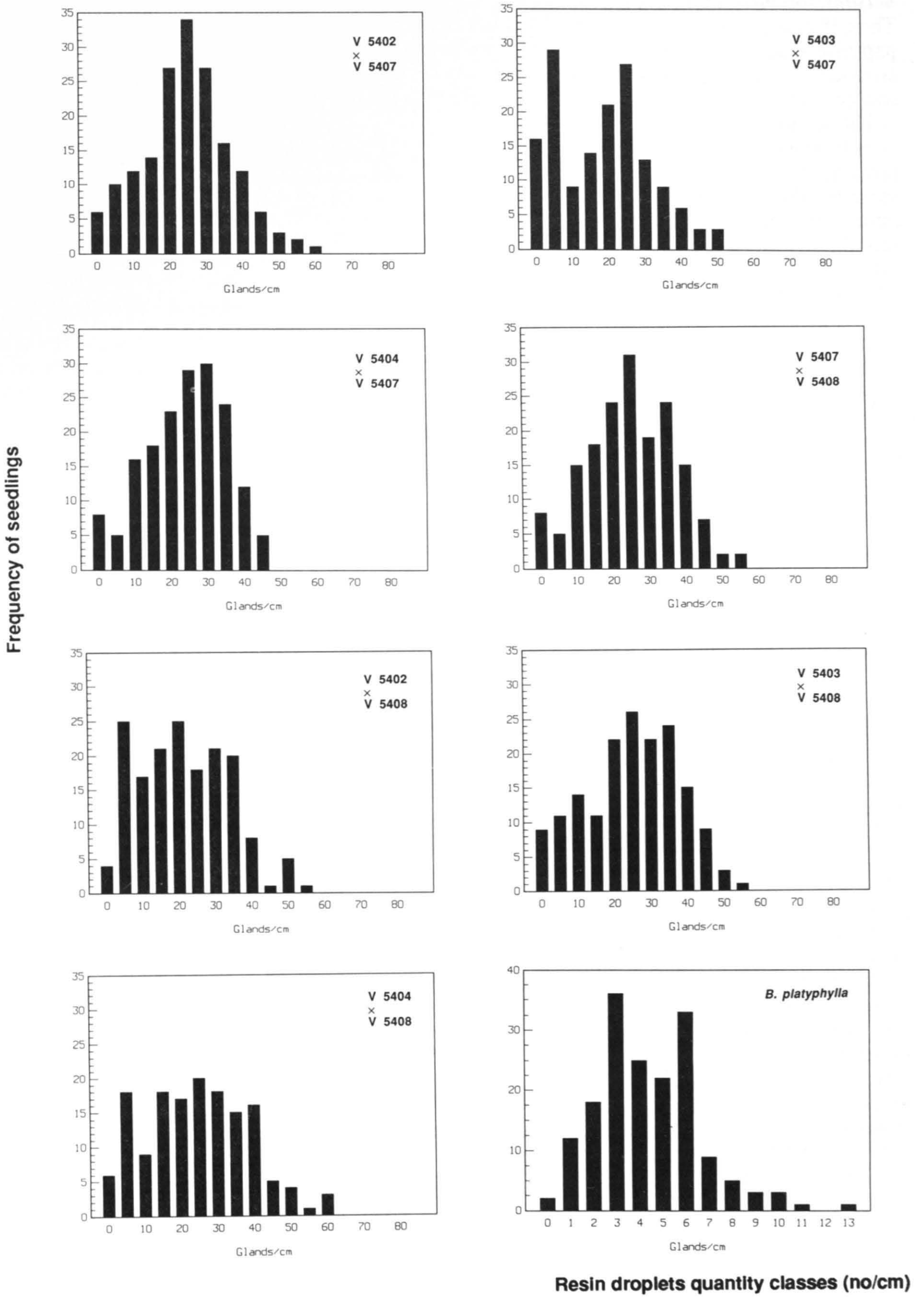

Figure 1. Frequency distributions of the quantity classes of resin droplet for birch seedlings of different families of birch.

nelsoni) rumen fluid (Risenhoover et al. 1985). Thus, if it is possible to increase the amount of papyriferic acid by means of breeding, the resistance of birches to mammalian herbivores can be improved.

The mean number of resin droplets varies greatly among F_2-families and this variation remains very large among full-siblings of the same family (Fig. 1). Preliminarily, the variation in number of resin droplets seems to be in additive genetic control (Rousi et al. 1990a). The number of resin droplets in the seedlings is easy to check (see Fig. 2), and therefore exceptionally resistant seedlings can be selected from resistant families by selecting seedlings with large numbers of droplets.

When twigs from trees of the same age are given to hares and voles, the resistance to browsing by these mammals has generally been shown to be strongly correlated among twigs of different species within the genera *Betula*, *Alnus* and *Abies*. In *Picea* and *Pinus* this correlation is considered to be quite low (r=0.44 and r=0.38, respectively) (Chiba 1977). Still, the correlations are clear enough to permit the conclusion that voles and hares select their food on the same basis.

The ecological significance of these results can be questioned, however, because hares and voles usually consume different parts of saplings. In the Holarctic zone mammalian herbivores usually destroy woody plants in wintertime when alternative food plants are under snow cover. The vole can eat the bark of birch seedlings until the basal diameter reaches 4 cm (Raulo 1981). This diameter is reached when the sapling is, on average, 5 years old, at which time the birch is so tall that hares can reach only the lowest lateral branches. The vole destroys seedlings under snowcover; hare and moose eat the uppermost branches in winter, and moose (and occasionally vole), may damage the seedlings in summertime.

In the bark of greenhouse-grown birch seedlings, resin droplets are usually located mainly in the upper parts of the seedlings, while in the lower parts there are hardly any droplets. Obviously, that is why in cafeteria or field tests with *Microtus* voles no significant correlation could be found between number of resin droplets and resistance. (Rousi et al. 1990b). The vertical distribution of secondary metabolites within plants, as well as the amount formed, may also be a phenotypically flexible trait. Thus, in addition to more studies on annual changes in the content of secondary metabolites, work on the biosynthesis and vertical distribution of these compounds within trees clearly is also needed (see Tahvanainen et al. 1990).

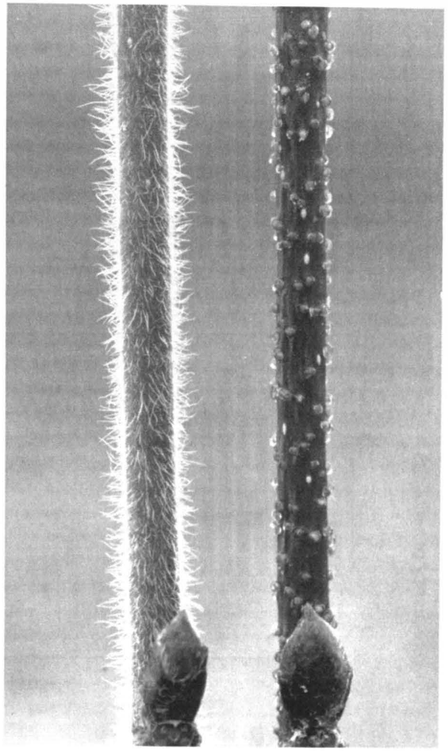

Figure 2. The variation in the amount of resin droplets within families can be considerable. The two seedlings above are selected from greenhouse grown 1-year-old seedlings of Family 1970 × 1980. (Photo Jouko Lehto).

Figure 3. Field voles cause considerable damage to birch plantations. (Photo Asko Kaikusalo).

5. Phenotypic plasticity

It has been suggested that the level of resistance of plants depends on the level of nutrients and carbon available (Bryant et al. 1983a). According to this carbon/nutrient balance hypothesis, carbon-based secondary metabolites are expected to accumulate under conditions in which, owing to a deficiency of mineral nutrients, the plant cannot divert all available carbon into growth. An application of mineral nutrients should then accelerate growth, with the consequence that less carbon should be available for secondary metabolism (Tuomi et al. 1988).

Practical experiments concerning the c/n-balance theory have produced contradictory results. Fertilization of 7-year-old *B. resinifera* saplings increased annual growth by almost 50 % and significantly decreased resistance to hare browsing (Bryant et al. 1987). On the other hand, although fertilization clearly increased the size of 1-year-old *B. pendula* seedlings of Finnish origins and families, it did not have a clear effect on palatability (Rousi et al. 1990a). The tendency in seedlings of Siberian origin toward decreasing palatability after fertilization may indicate that these seedlings are adapted to growth conditions that differ from those of seedlings of Finnish origin (Rousi et al. 1990a).

The contradictory results reported by Bryant et al. (1987) and Rousi et al. (1990a) may indicate differing responses of different species or edaphic races of birches. Consequently, there may be genetic differences among tree species, and even among origins and individual trees of the same species, that produce variable responses to fertilizer treatments.

Greenhouse temperature affects the resistance of seedlings (Rousi 1988). Furthermore, preliminary and unpublished observations indicate that shading and fertilization may also affect the resistance of seedlings, but there may be vertical differences in the response of plants to a changing environment. All this might have practical implications when decisions are made as to what growth conditions to use in nurseries. If control of the environment is used to enhance resistance, however, it must be done in the framework of other often more important objectives in nursery practice.

6. Comparison of experimental methods

61. Plant material for experiments

The availability of homogenous plant material usually places heavy constraints on resistance experiments. One widely used method is to take branches from larger trees or from ramets (Chiba 1963, Chiba & Nagata 1968, 1969, 1976, Dimock et al. 1976, Silen & Dimock 1978, Chiba et al. 1982, Silen et al. 1986). Mammalian herbivores destroy mainly seedlings and small saplings, and it is well known that there is a sharp decrease in resistance after trees have reached certain dimensions (Bryant et al. 1985, Danell et al. 1990), although the mechanism of this loss in resistance is not understood.

Dimock et al. (1976) indicated that the palatability of small Douglas-fir seedlings to deer and hare could be predicted according to results obtained from twigs cut from grafts. But to permit predictions of juvenile differences on the basis of differences found among mature trees, correlations between juvenile and mature trees have to be studied more carefully. The same uncertainty seems to occur with rooted cuttings of older trees, although it is possible to develop or maintain the juvenility of donor trees (for review see Zobel & Talbert 1984).

To obtain truly reliable data on phenotypic plasticity, the material used should be as uniform as possible genetically. Micropropagation is a rapidly evolving method for producing true-to-type plantlets of selected clones. This method is clearly a prerequisite for studies of clonal differences in resistance. Two basic questions concerning this kind of experiment remain open, however: 1) the juvenility of micropropagated seedlings and 2) the reasons for differences in ability to micropropagate among clones of the same species.

62. Experimental herbivores

In addition to genetic differences among browse plants, among herbivores of the same species differences in ability to tolerate toxins or substances that reduce digestibility can also be expected. In natural conditions it is not possible to control and usually not even to estimate the number of animals that have caused the damage. Especially in the case of large mammalian herbivores, extensive damage may be caused by only one animal or by a very few animals. Thus, generalizations about differences in the palatability of trees based on only a few experimental plantations may be misleading. On the other hand, maintenance of large populations of moose and hare for pen trials is laborious.

It is evident that the plant consumption of experimental animals differs quantitatively, but there have been very few studies concerning qualitative differences in the food selection of herbivorous mammals. The present experiments have shown that results obtained from cafeteria and field experiments give clearly repeatable results and that the order of preference among experimental hares and voles seems to be generally the same (Rousi 1988, Rousi et al. 1989, 1990a, 1990b).

63. Field vs pen experiments

Field tests have been the conventional method used to evaluate genetic differences in tree breeding. Often, however, environmental heterogeneity masks genetic differences among experimental seedlots. Even if genetic differences in mammal resistance are studied only on sites where a particular tree species is normally planted, there still remain intrusions due to environmental heterogeneity. For example, the protein content of alternative food species is an important factor in the ability of herbivores to detoxify secondary plant metabolites (Tahvanainen & Harju 1990). Competition and shading by other plants or fertility of the site may also directly affect the resistance.

The density of pest populations may affect the interpretation of results. The obvious expectation is, other factors being the same, that if the pest population is low then there is a good possibility for selective feeding. And, on the contrary, when pest populations are high, shortage of food and competition may disturb the food selection process. In reality, the situation may not be that simple. For example, when studying the resistance of birch seedlots to vole damage, Rousi et al. (1990b) found that birches were equally resistant in the replicates where the level of vole damage was low. And contrary to predictions, when the feeding pressure was high (severe damage), voles were very selective. This was thought to be due to random environmental intrusions, probably ice formation within the snow, which affected spatial activity in *Microtus*-voles (Rousi et al. 1990b). If the same planting density were required as is found in practical plantations, the size of experimental plantations would be rather large. This would increase environmental heterogeneity, which in turn may affect not only plant characteristics but also the spatial activity of vole, hare and moose.

Plant size may also have an unwanted effect on the results of field tests. For example, when studying the influence of height of Douglas-fir seedlings on browsing damage by black-tailed deer, Dimock (1971) found a clear preference for taller seedlings. Significant differences in wintertime preferences could be detected even in seedlings that differed less than 3 cm in height, the variation in height being 13—23 cm. If in field experiments like this the aim is to study genetic differences in resistance or the trade-off between resistance and growth, it is very difficult to rule out differences in availability of different sizes of seedlings.

Vole and hare are very discriminating in their food selection, choosing even among families of *Betula pendula* and *Pinus sylvestris*. Clear selection takes place even when seedlings are growing in nursery containers in which the distance between seedlings is about 10 cm (Rousi 1988, 1989, Rousi et al. 1989). This low-cost method for studying palatability differences with hares and voles helps to minimize the environmental heterogeneity. The method does not, however, allow the control of pest populations.

In cafeteria experiments (Rousi et al. 1990a) experimental hares competently selected from tightly tied bundles those twigs that contained few resin droplets. This result shows how important food selection has been in the process of evolution and how extremely sensitive the olfactory senses of hares are to be able to detect this variation in browse plants. Good correlations between the results from field tests, pen tests and cafeteria trials (Chiba & Nagata 1968, 1969, Dimock et al. 1976, Silen & Dimock 1978, Rousi 1988, Rousi et al. 1989, 1990a, 1990b) encourage the use of controlled cafeteria trials as an economical and reliable method for detecting differences in the resistance of plants.

7. Forestry applications

71. Resistance vs growth and quality of trees

Damage by mammalian herbivores is of major importance to forest plantations in the Holarctic zone (Myllymäki 1977, Kurahashi 1988, Löyttyniemi & Lääperi 1988). Because no feasible methods of controlling this damage are known, resistance breeding might be one way to decrease the damage. In any case, resistance should not be negatively correlated with growth or other economically important characters of trees.

Plant resistance to pathogens is based on enhanced biochemical activities associated with defense reactions which are energy demanding (Hare 1966, Smedegaard-Petersen 1980, Smedegaard-Petersen & Stølen 1980). On the other hand, mammalian resistance is not based on induced resistance but rather on chemical or morphological signals received by the herbivore from the surface of potential food plants before consumption. Many observations seem to suggest that determination of the palatability of food plants by the mountain hare is based on olfactory stimuli (Tahvanainen et al. 1985, Helle et al. 1986, Rousi et al. 1990a, Tahvanainen et al. 1990) and that resistant plants are usually deterrent enough to remain intact (Rousi 1988, Rousi et al. 1989, 1990a, 1990b).

In order to be able to determine the effect of resistance on growth, at least the following information should be known: 1) what biotoxins determine the resistance, 2) what pathways lead to formation of these compounds and 3) whether these compounds are final products or can be allocated to other purposes.

Although some such compounds are already known (Bryant et al. 1983b, Reichardt et al. 1984, Tahvanainen et al. 1985, Tahvanainen et al. 1990), the biochemical pathways leading to formation of these compounds are not known. Consequently, it is not possible to estimate accurately the metabolic cost of defensive metabolites. Indirect estimations of the cost of resistance are possible, however, when the growth of young seedlings is related to resistance.

Coley et al. (1985) suggested that slow-growing plants are less preferred by herbivores than fast growing plants are. According to the hypothesis of Rhoades (1979), there is a trade-off between growth and defense i.e. available resources are allocated to growth at the expense of defense or vice versa. However, very few attempts have been made to estimate the cost of resistance with genetically known plant material grown in controlled conditions. Such experiments have shown no positive relationships between growth rate and susceptibility to damage by mammalian herbivores: voles did not select eight-year-old saplings or two-year-old seedlings of *P. sylvestris* according to growth rate. In both age classes it was possible to find parent trees whose offspring were both fast growing and resistant (Rousi 1989).

B. pendula seedlings of a seedlot with very fast growth (hybrid between a Siberian and a Finnish tree) also showed exceptional resistance to feeding by *Microtus* voles (Rousi 1988), although in later cafeteria and field experiments no relationship could be found between growth rate and resistance (Rousi et al. 1990b). The fastest growing seedlings of *B. pendula*, however, have contained the greatest number of resin droplets in their bark. This number was strongly and negatively correlated with palatability of seedlings within and among families. Consequently, growth of birch seedlots have been strongly and positively related to resistance of hare browsing (Rousi et al. 1990a).

Because the basic mechanisms behind resistance to herbivores are not known, no conclusions can be drawn from the relationship between resistance and wood quality. The wood of hardwoods is more varied and much more complicated than that of softwoods. Mammalian herbivores eat mostly juvenile wood, which (e.g. in pines) has a different cell morphology and in addition has a chemical composition that differs in such compounds as hemicelluloses, lignins and in resinous content (e.g. Zobel & Talbert 1984). In order to estimate the effects of resistance breeding on wood quality, much more information about this age-related variation, as well as predictions about future products of pulp or wood use, should be obtained. One indication that there is no relationship between wood quality and resistance is the fact that the quality differences (such as Pilodyn value, basic density, dry mass, fiber yield and fiber mass) among *P. sylvestris* origins studied by Velling & Nepveu (1986) showed no clear correlations with moose feeding in the same experiments (Niemelä et al. 1989).

72. Species hybrids

Betula pendula is excellent for use in practical forestry in Finland, and there seems to be no need to introduce exotic birch species. On the other hand, some exotic birches, e.g. *B. papyrifera* var. *neoalaskana* and *B. platyphylla*, seem to have adapted well to the Finnish climate (Heikinheimo 1956) and can be crossed with *B. pendula* to obtain new combinations of desirable characteristics (Johnsson 1945).

New studies have reduced the number of species in the genus *Betula* to about forty; and *B. platyphylla* and *B. pendula,* for example, are at present considered to be the same species (Hämet-Ahti & Alanko 1987) (To avoid confusion and because of the uncertainty of the present taxonomical status of *B. platyphylla*, the 'old' name is still used in the present text). Hybrids of *B. pendula* and these two species have been shown to thrive well in the climate of Scandinavia; and in particular the hybrid between *B. pendula* and *B. platyphylla* has shown superior juvenile growth (Johnsson 1966).

According to previous studies, hybridization is a good method for increasing the resistance of birches (Chiba & Nagata 1969). At the moment experiments are being made to determine the characteristics of hybrids resulting from a cross between good quality *B. pendula* and resistant *B. platyphylla*. Studies concerning the resistance of backcrosses between hybrids of *B. pendula* and *B. platyphylla* with *B. pendula* are also in progress.

There has been substantial difficulty with vole (*Clethrionomys rufocanus bedfordiae*) damage in Japan. Especially young plantations of native fast-growing larch (*Larix leptolepis*), one of the most important forestry species in Hokkaido, have suffered serious damage (Takahashi & Nishiguchi 1966a, Kurahashi 1988). On the other hand, Kurile and Saghalien varieties of *Larix gmelini* are slow growing but very resistant (Inukai & Haga 1953, Kurahashi 1988). After 30 years in experimental plantations, F_1-hybrids of these two species have shown nearly the same growth rate as *L. leptolepis*, in addition to excellent stem form and intermediate resistance to vole damage (Kurahashi 1988). If F_1-hybrids of larches are back-crossed with the more resistant species as the mother tree, the resistance of the resulting back-cross increases to the level of the more resistant parent tree species (Chiba & Nagata 1976, Chiba 1977). Chiba & Nagata (1976) estimated the heritability of vole resistance in hybrids of *Larix* species to be quite high: 0.527.

73. Cloned material

731. Risks of using cloned material

There has been considerable discussion about the dangers of restricting the genetic base of plantations when vegetative propagation is used. The theory that genetic uniformity causes vulnerability to disease epidemics, and likewise that genetic diversity is a major factor protecting host populations from pathogens, seems to be generally accepted. This theory, however, has only rarely been tested in field experiments on natural plant populations. When studying the mechanisms regulating the impact of disease in the clonal herb mayapple (*Podophyllum peltatum*), Parker (1988) found that in spite of the presence of a potentially damaging fungal pathogen in most mayapple colonies, the demographic impact of the disease was minimal owing to an effective morphological defense. The broad virulence of each local pathogen population implied that the impact of disease was not strongly sensitive to variation in the frequency of particular host genotypes within the colonies (Parker 1989). Thus because of the lack of experimental research on natural systems, together with examples of effective defense in clonal plants such as mayapple, the paradigm of susceptibility of genetically uniform host populations should be treated with caution (Parker 1988).

When micropropagation of many tree species becomes standard procedure and methods of using somatic embryogenesis are developed, a cautious attitude towards the possibility of increased risks will be needed. Usually, the danger from planting large areas with a single clone arises when the adaptability of the clonal genotype is exceeded by adverse conditions (Zobel & Talbert 1984). There are examples of disasters in which certain *Cryptomeria* or *Populus* clones were used. The difficult job is usually to assess accurately whether death or decline is simply the result of offsite planting or whether it has been caused by a narrowed genetic base (Zobel & Talbert 1984). When determining the safe number of clones, one must take into consideration rotation age, intensity of forest management, genetic variability of the clones used, likely risks and acceptable levels of loss (Libby 1982).

To avoid multiplication of poorly adapted or extremely susceptible genotypes, trees for micropropagation are selected from old stands. Due to the fact that testing is still short term, we do not know whether there are cyclophysical effects because some genes are already blocked. If some are blocked, this could mean shorter rotation period, poor stem form and restricted growth of micropropagated seedlings. It is evident that top branches of birches lose their resistance to mammalian feeding at about 8 — 10 years of age. Thus micropropagated seedlings may also be very susceptible to mammalian herbivores. On the other hand, tests of palatability with mammalian herbivores provide the possibility to study the maturation of micropropagated seedlings.

Multiplication of birch by means of micropropagation has been successful for only a limited number of birch genotypes. The amount of secondary metabolites in the plants might negatively affect their ability to regenerate. Preliminary and unpublished results from experiments in progress do not, however, give any indication that resistant seedlings are more difficult to micropropagate than susceptible seedlings are.

732. Birch in Finnish forestry — a case study

When the tree species that can be used in Finnish forestry are considered, at the moment only birch can be multiplied by micropropagation on a practical scale; in addition, the possibilities for using somatic embryogenesis in birch must be considered good (Kurtén et al. 1990). Among individual trees of *B. pendula* there seems to be a very large quantitative variation in the amounts of toxic or repellent secondary metabolites (Tahvanainen et al. 1990). Because birches are a very variable species genetically (Hämet-Ahti 1987), qualitative variation can also be expected. It is evident that browsing mammals must feed upon several plant species in order to avoid ingestion or overdose of toxic secondary metabolites (Bryant et al. 1985). Consequently, if the amount of secondary metabolites can be increased by selection and breeding and qualitative variation can be kept to a minimum by using only a very few birch genotypes in our plantations, browsing damage by mammalian herbivores could be kept at a low level. The larger the quantitative and qualitative variation in the amount of secondary metabolites in our plantations, the more damage by mammalian herbivores can be expected. Fast-growing 1-year-old seedlings have usually been resistant to such damage (Rousi et al. 1990a). By using vegetative propagation, most resistant individuals could be multiplied and used in practical forestry.

Other than mammalian herbivores, no real pests or economically important fungal diseases of birches are known in Finland (Annila 1987, Uotila 1987). Moreover, there is no reason why mammalian resistance should be negatively correlated with resistance to insects or fungi. Annual birch plantations cover about 0.05% of the total forest area in Finland. Individual birch plantations usually cover very small acreages (1—2 ha) and only 1600—2000 seedlings are planted per hectare. On fertile sites, which is where birches are planted in Finland, it is impossible to keep other tree species from growing in the plantations. Consequently, although only one single genotype is planted, real monocultures are impossible to maintain. In clonal forestry, for various reasons monoclonal blocks are recommended. In order to be cautious with pests the size of each monoclonal block should be limited to 20 ha (Zobel & Talbert 1984). By Finnish standards that means that even though only one single genotype is used in all plantations, no real problem should be expected. In practice, however, it is quite likely that various clones are used; in addition, as breeding programs advance and the needs of industry change, the genotypes planted also change very rapidly.

8. Summary: possibilities to use resistance breeding as a method of decreasing mammalian damage in birch

Many economically important tree species in the Holarctic zone are low preference food for mammalian herbivores, and birch is an especially low quality browse species (e.g. Salonen 1982). For example, when a previously multispecies habitat became birch-dominated (*B. papyrifera*) after a forest fire, the moose population starved (Oldemeyer et al. 1977). If birch bark is added to laboratory food given to voles, the toxification effects in *Microtus* voles are clear, even with small amounts of bark (Tahvanainen & Harju 1990).

The first of the present experiments showing genetic differences in the resistance of European white birch breeding population was designed to study the climatic adaptedness of seedlings. Voles clearly selected according to seedlot, but in 1-year-old experimental seedlings damage was not related to sowing time. (Rousi 1988). Further experiments were carried out to determine the extent of variation in the resistance of birch to hare (Rousi et al. 1989, 1990a) and vole (Rousi et al. 1990b). Although there were differences among birch origins, there were no clear latitudinal trends (Rousi et al. 1989). The F_2-families of *B. pendula* used in our cafeteria experiments were randomly selected from the breeding pools of the Finnish Forest Research Institute. F_2-families did not generally differ from forest origins, and both very resistant families and susceptible families were found (Rousi et al. 1989, 1990a). In addition, the variation among full siblings within F_2-families was extremely large (Rousi et al. 1990a).

When seedlings of birch families were planted on high-risk vole areas, the voles showed clear selection in areas where vole damage was severe. In those areas, voles severely damaged c. 25 % of the seedlings of the most resistant European white birch family, and damage to *B. platyphylla* seedlings was at the same level. Probably owing to difficult snow conditions, vole feeding was not clearly selective in all experimental areas, even tough it was in the cafeteria trials with the same birch material (Rousi et al. 1990b).

In our breeding pool of European white birch the genetic variation in resistance is large. In addition, it seems possible to increase the resistance of European white birch by making species hybrids with *B. platyphylla*. The resistance of birch seedlings is usually positively correlated with growth; and the resistance to feeding by moose, hare and vole is probably based on the same chemical compounds found in the plant. Consequently, there should be no obstacles to adding the increasing of resistance to the breeding objectives for birch.

The aim of resistance breeding is, by means of plant breeding, to make our tree species such poor food that mammalian herbivores will turn mostly to other browse plants. It is clear, however, that trees cannot be made completely immune to browsing by herbivores, but the damage could be decreased to a tolerable level. By making use of other methods, e.g. repellents and silvicultural methods, in high risk areas, mammal damage could be decreased to low levels. The mechanism of resistance is known (Rousi et al. 1990a); therefore by breeding certain species as better browse plants, the browsing of herbivores could be directed to designated areas.

Our material gave no indication that breeding for growth and quality will decrease the level of resistance or that resistance and growth are negatively correlated (Rousi et al. 1990a, 1990b). Thus, as it is evident that we will not lose in yield, the prospects for breeding for mammalian resistance should be considered to be good.

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