

# **Reproductive patterns of birches (*Betula* spp.) in northern Sweden**

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som med vederbörligt tillstånd av rektorsämbetet vid Umeå universitet för erhållande av filosofie doktorsexamen i ekologisk botanik kommer att offentligen försvaras fredagen den 28 januari, kl. 10.00 i hörsal C, Naturvetarhuset.

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Reproductive patterns of birches (*Betula* spp.) in northern Sweden

**Abstract**

The aim of this thesis was to study patterns of reproduction of *Betula pendula* and *B. pubescens* coll. along an altitudinal, coastal-inland, gradient in northern Sweden. The altitudinal variation was related to the distribution of the birch taxa along the gradient.

Six years field data showed a steep decrease of seed germinability of *B. pendula* towards its altitudinal range limit in the Scandes every year. In contrast, *B. pubescens* ssp. *pubescens* showed significant positive correlations between seed germinability and altitude in three of the six years. Furthermore, there was a highly significant positive correlation between seed weight and altitude for *B. pubescens* coll., but not for *B. pendula*. Production of viable seeds fluctuated strongly between years in most populations, except in marginal *B. pendula* populations in the mountain area where it was constantly very low. On average 15 - 41 % of the seeds produced in *B. pendula* populations above 400 m altitude were attacked by gall midges (*Semudobia* spp.). Corresponding values for *B. pendula* populations below 400 m altitude were 4 - 7 %. In *B. pubescens* populations, the seeds attacked by *Semudobia* spp. never exceeded 3 %. The high frequency of *Semudobia* attacks in high altitude marginal *B. pendula* populations was suggested to be due to limited resources for defense against the seed predator.

A 3-yr study documented large variations in pollination and seed quality between taxa, high and low altitude populations, and between years. Empty seeds (without embryos) dominated among the sampled seeds in most cases. This proportion was decreased by pollen addition, in both *B. pendula* and *B. pubescens*, in mountain populations, but not in coastal populations. The high percentage of empty seeds was therefore suggested to be partly caused by pollen-limitation, but failure of pollen tube penetration - fertilisation, or maternal resource supply could also have had an influence.

A laboratory experiment showed increased pollen germination and length of the longest pollen tube per style after increased pollination. The correlations between number and length of pollen tubes per style were however mostly low in natural populations, suggesting low probability of pollen competition in the natural situation.

Sowing experiments indicated that differences in initial seedling density between *B. pendula* and *B. pubescens* was more affected by interspecific differences in seed quality than by interspecific differences in survival of seedlings after establishment.

A study of the age structure of a *B. pendula* stand, planted about 250 m above its natural altitudinal limit, indicated that this birch may reproduce above its recent range limit during temporally warmer periods.

It was concluded that the level of accumulated resources in *B. pendula* in marginal sites in the Scandes would mostly be too low for completion of the reproductive cycle. In contrast, *B. pubescens* ssp. *pubescens* is able to accumulate enough resources for reproduction also at relative high altitudes.

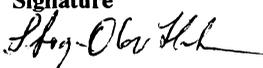
**Key words**

Reproduction, *Betula*, seed-quality, seed-set, pollination, pollen-limitation, pollen-competition, tree-line, environmental gradient, seed weight, seedling survival, *Semudobia*

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## LIST OF PAPERS

The thesis is based on the following papers which will be referred to by their Roman numerals.

- I. Holm, S.O.: Reproductive patterns of *Betula pendula* and *B. pubescens* coll. along a regional altitudinal gradient in northern Sweden. *Ecography* (in press).
- II. Holm, S.O.: Reproductive variability and pollen limitation in three *Betula* taxa in northern Sweden. Accepted by *Ecography*.
- III. Holm, S.O.: Pollination density - effects on pollen germination and pollen tube growth in *Betula pubescens* Ehrh. in northern Sweden. Accepted by *The New Phytologist*.
- IV. Holm, S.O.: Survival and growth of *Betula pendula*, *B. pubescens* ssp. *pubescens* and *B. pubescens* ssp. *tortuosa* seedlings in northern Sweden. Submitted.
- V. Holm, S.O.: Regeneration of *Betula pendula* and *B. pubescens* coll. above and below the natural altitudinal distribution limit of *B. pendula* in south-east Norway. Accepted by *Oecologia Montana*.

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## INTRODUCTION

Many of the current explanations for tree-lines arise from the correlation between tree distribution and climate (Kullman 1979, Woodward 1987, Hengeveld 1990, Stevens and Fox 1991). Low temperatures decrease the photosynthetic rate of plants (Häsler 1982, Slayter and Noble 1992). As production of generative organs (flowers, seeds, fruits) requires large quantities of a tree's stored resources, this implies that it takes a relatively long time to accumulate the resources required for reproduction in cold climates (Tranquillini 1979, Crawford 1982, 1989). Thus, the frequency of years with good seed setting decreases toward higher altitudes and latitudes (e.g. Tirén 1935, Hagner 1965, Hustich 1983). Further, damage to seedlings due to, e.g., a too short growing period, frosts, drought, or wind blasting might also be critical for distribution of tree species toward high altitudes (Tranquillini 1979, Wardle 1981). Sometimes, e.g. fires, herbivory, or snow pressure modifies the shape of tree-lines (Hustich 1944, Kullman 1979, Stevens and Fox 1991, Slatyer and Noble 1992). Biotic and abiotic effects on tree-line shape may be interrelated. The degree of available resources could, for example, alter the chemical defence of plants against herbivores (Coley et al. 1985). The relative influences of different abiotic and biotic factors often vary between different parts of a tree's distribution limit (Haller 1979, Elliott 1979, Pigott 1981, Pigott and Huntley 1981). Not only recent effects of environmental factors are important as explanations for where a tree species distribution limit is situated, but also historical events such as distance to the place where its glacial refuges were situated in relation to the species dispersal capacity (Prentice 1983).

Studies on different causal connections causing alpine tree-lines have a long tradition (see e.g. Wahlenberg 1813, Smith 1920). Different ecophysiological and ecomorphological approaches have been applied (see e. g. Tranquillini 1979, Norton and Schönenberger 1984, Scott et al. 1987, Crawford 1989, Stevens and Fox 1991). In addition, temporal phenomena have been incorporated by analyses of age structures (e. g. Payette and Filion 1985, Kullman 1992), and macro and micro fossils (e.g. Jackson and Whitehead 1991). Still, relatively few comparative studies of factors affecting distribution of closely related tree taxa along arctic and alpine gradients have been published.

The aim of this thesis was to describe and quantify reproduction of three birch taxa viz. *Betula pendula*, *B. pubescens* ssp. *pubescens* and *B. pubescens* ssp. *tortuosa* and to relate this to their distribution along environmental gradients in northern Sweden. The altitudinal distribution limit of *B. pendula* is situated in the bottom of the valleys in the Scandes, while the distribution of *B. pubescens* coll. continues up to the alpine tree line. In the following, *B. pubescens* ssp. *pubescens* and *B. pubescens* ssp. *tortuosa* are named *B. pubescens* and *B. tortuosa*, respectively.

## OBJECTIVES

I have studied different stages of the reproductive process of *Betula pendula*, *B. pubescens* and *B. tortuosa* along a regional altitudinal gradient during the period 1984-1991. The aim has been to examine the recent altitudinal and annual variations in reproduction of the birches. I particularly addressed the following questions:

- 1) How does the relationship between reproductive success and altitude differ between the studied birch taxa?
- 2) How does the temperature climate affect the annual reproductive patterns of the studied birch taxa?
- 3) Is the altitudinal distribution limit of *Betula pendula* in the Scandes in equilibrium with the recent climate?
- 4) How does the degree of pollen limitation differ between birch taxa, and years, and between low altitude and marginal high altitude populations?
- 5) Does pollen competition occur in *Betula pubescens* ?
- 6) How does survival and growth of seedlings vary depending on site and sowing year?

## STUDY SPECIES

The Scandinavian tree-shaped birches *Betula pendula*, *B. pubescens* and *B. tortuosa* are distributed over wide parts of boreal Eurasia (Hultén 1970). *B. pendula* is often found in relatively dry and warm habitats and often on morainic and sandy soils. *B. pubescens* coll. is more confined to moist sites and grows often on organic soils (Arnborg 1946, Sarvas 1948, Barth 1949). In Scandinavia, *B. pendula* has its altitudinal distribution limit at the bottom of the valleys in the Scandes. *B. pubescens* continues its distribution above the limit of *B. pendula* and merges gradually into *B. tortuosa* at higher elevations. *B. tortuosa* is the dominating tree species in the Scandinavian subalpine forest. These birch taxa show the same sequential altitudinal distribution in the Scottish Highlands (Forbes and Kenworthy 1973) and in the Ural Mountains (Makhnev and Mamaev 1973).

*B. pendula* is diploid ( $2n=28$ ), while *B. pubescens* coll. is tetraploid ( $2n=56$ ) (Johnsson 1974). The shape of *B. tortuosa* varies depending on site conditions (Kallio and Mäkinen 1978). It is generally a smaller tree than *B. pendula* and *B. pubescens*, and is often polycormic. All three birch taxa may produce basal stem sprouts, and *B. tortuosa*, also root suckers (Kallio and Mäkinen 1978, Koop 1987). Ecotypic variation in morphological variables was demonstrated by Pelham et al. (1988) in a study of Scottish birches. Davy and Gill (1984) observed phenotypic plasticity in leaf shape when tetraploid trees were transplanted into heath or bog. Hagman (1971) states that the degree of self and interspecific compatibility must be considered very low in both *B. pendula* and *B. pubescens*. Johnsson (1974) reported that the germinability of seed after selfpollination is low for both *B. pendula* and *B. pubescens* (0% - 3 %). Hybrids between *B. pendula* and *B. pubescens* may rarely occur (Hagman 1971, Brown et al. 1982).

Johnsson (1974) reported that four of seven artificial crosses between *B. pendula* and *B. pubescens* gave a small proportion of filled seeds (0.2% - 1.5 %; a total of more than 20 000 seeds were examined). *B. tortuosa* ( $2n=56$ ) is suggested to have developed through introgressive hybridisation between *B. pubescens*, *B. pendula*, and *B. nana* (dwarf birch) in northern Scandinavia (Kallio et al. 1983). Its low, vertically spread growth form, and high capacity of stump and root sprouting, may be an effect of *Betula nana* genes (Vaarma and Valanne 1973).

The studied birches are monoecious, anemophilous, dichogamous trees, with male and female flowers in separate inflorescences (catkins). Each female catkin contains about 200 flowers. The flowers lack perianth and have two free styles. The ovary is two-celled with one anatropous ovule in each cell (Sedgley and Griffin 1989, Atkinson 1992). The catkins are formed the year before flowering. Female catkins are first enclosed by scale leaves (winter buds) while male catkins are visible already at the end of the summer the year before flowering. *B. pendula* starts flowering about one week before *B. pubescens*, but towards higher altitudes and latitudes this time difference fades out. The pollen grains are small; *B. pendula*  $22.1 \pm 1.9$   $\mu\text{m}$ , *B. pubescens*;  $25.0 \pm 2.2$   $\mu\text{m}$  and *B. tortuosa*;  $26.2 \pm 2.2$   $\mu\text{m}$  (Means  $\pm$  SD, according to Prentice 1981). Most of the pollen is deposited within a distance of a few tree crown diameters (Andersen 1970), but long distance dispersal of 600 km has been reported (Wallin et al. 1991). The small winged seeds ripen in August - September, later towards the north and higher altitudes. Most seeds are dispersed in the autumn, but seed fall may continue throughout the winter. Sarvas (1948) observed that in *B. pendula* seed dispersal declined exponentially with distance from seed source, and very few seeds travelled more than 50 m. Occasionally, long seed transports, especially on wind-blasted snow surfaces may occur (Helms and Jørgensen 1925, Matlack 1989). Birches have an enormous seed production capacity. Sarvas (1948) estimated the seed fall in a birch stand to be 53 200 filled seeds per  $\text{m}^2$ . But the size of birch-seed crops varies greatly from year to year. A *B. pendula* crop amounting to 20 % of the best seed crop occurs only every third year, and intervening crops may be only 5-10 % of a good seed year (Sarvas 1948). The small birch seedlings are very sensitive to drought and competition from surrounding vegetation (Hough 1937, Perala and Alm 1990). Therefore, scarified ground cover highly improves successful seedling recruitment (Kinnaird 1974, Miles and Kinnaird 1979). *Betula pendula* may become 300 years old, while *B. pubescens* ages faster (Barth 1949). An age of 240 years for a *B. pubescens* tree has been noted (P-A. Esseen, pers. comm.). Because of their stump sprouting capacity it is, however, difficult to obtain exact information on the lifespan of a birch genet.

## SUMMARY OF PAPERS I - V

### **(I) Reproductive patterns of *Betula pendula* and *B. pubescens* coll. along a regional altitudinal gradient in northern Sweden**

One purpose of this study was to investigate if the range limit of *B. pendula* in the study area is in equilibrium with the present climate. Another purpose was to investigate if the higher situated distribution limit of *B. pubescens* coll. compared with *B. pendula* is largely conditioned by some mechanism affecting reproductive success.

The reproduction of *B. pendula* and *B. pubescens* coll. was measured in a number of populations along an altitudinal gradient across northern Sweden during the period 1984-1989. Almost no viable seeds were produced in altitudinally marginal *B. pendula* sites, suggesting that the altitudinal distribution of this species is in equilibrium with the present climate. Further, the viability of seeds showed a much steeper altitudinal decrease for *B. pendula* than for *B. pubescens* coll.. The production of viable seeds and the seedling density were much lower in marginal high altitude populations of *B. pendula* than in *B. pubescens* coll. populations in the same area. The main reason for failure of seed germination was that the seed was empty (due to no pollination, failure of fertilisation, or abortion of the embryo). Attacks by gall midges (*Semudobia* spp.) strongly decreased the quality of the seed crop in high altitude, marginal *B. pendula* populations. These populations were heavily attacked every year, while the percentage of *Semudobia* attacked seeds was much lower for *B. pendula* populations in the lowlands, and for *B. pubescens* in both lowland and mountain populations. The relatively large attacks on *B. pendula* in the mountains is suggested to be an effect of a low defence capacity due to resource limitation of these trees. The weight of *B. pubescens* coll. seeds was strongly positively correlated with altitude, which not was the case for *B. pendula*. The number of stump sprouts was about three times higher in *B. tortuosa* than in *B. pendula* and *B. pubescens*. This result supports the hypothesis that vegetative reproduction would become more important than generative reproduction toward colder high altitude areas (e. g. Crawford 1982, 1989). The percent germinable seeds showed a stronger positive correlation with the temperature sum of the growth period of the year preceding the summer of seed maturation than with the temperature sum of the growth period when seeds matured. This indicates that negative effects of low temperatures on initiation of flower primordia may be more important than negative temperature effects on seed maturation for production of germinable seeds.

### **(II) Reproductive variability and pollen limitation in three *Betula* taxa in northern Sweden.**

This study examined the effect of pollen supply on the production of viable seeds. The pollination varied considerably between birch taxa, years, and altitude. In mountain populations, usually only a few percent of the flowers contained pollen tubes at all, and if so - often only one pollen tube, indicating high degree of pollen limitation. Pollen supplementation, however, only slightly increased the percent germinable seeds. In some cases, a slightly increased seed germination rate was also noted after supplemental pollination. The natural pollination in coastal populations was mostly larger than in mountain populations, and supplemental pollination had no significant effect on seed quality in coastal populations. An examination of seeds deriving from supplementally pollinated flowers, showed that apart from pollen limitation, also other factors such as

insect predation and limitations of maternal resources for seed maturation, may largely alter the quality of the seed crop.

### **(III) Pollination density - effects on pollen germination and pollen tube growth in *Betula pubescens* Ehrh. in northern Sweden.**

Study II showed a slight positive effect of pollen addition both on seed germinability and seed germination rate. As competition between male gametes may improve the quality of plant offspring (see e. g. Mulchay and Mulchay 1987), I hypothesised that these signs of increased seed quality might have been due to increased pollen competition in enlarged pollen populations.

An *in vitro* test showed highly significant correlations between the germinability of *B. pubescens* pollen grains and the number of pollen grains per volume of growth medium. A controlled pollination experiment indicated that both maternal and paternal identity may affect the growth rate of pollen tubes through the styles. Increased pollination tended to increase the length of the longest pollen tube per style, but not the mean length of the pollen tubes. If flowers collected from natural *B. pubescens* populations were examined, the level of significance for the correlation between number and lengths of pollen tubes per style was very low - lower than the same correlations of the experimental data. This suggests that pollen competition would be rare in *B. pubescens* in natural situations.

### **(IV) Survival and growth of *Betula pendula*, *B. pubescens* ssp. *pubescens* and *B. pubescens* ssp. *tortuosa* seedlings in northern Sweden.**

The performance of birch seedlings was studied through sowing experiments in 12 sites along an altitudinal gradient across northern Sweden during the period 1984-1991. At each site, seeds were sampled from local birches and sown both on prepared sowing plots and on intact ground vegetation. The pattern of germination, emergence, and survival of seedlings differed considerably between different birch taxa, as well as between sites and sowing years.

Differences between *B. pendula* and *B. pubescens* in initial density of seedlings per sowing plot was more affected by differences in the viability of the seeds than by survival of the established seedlings. This indicates that environmental influences that affects seed viability may have a relatively larger impact on interspecific differences in seedling abundance than influences affecting the performance of the seedlings.

Seedling survival decreased along a gradient towards the tree-line. The seedling density at high altitude marginal sites was, however, larger for *B. pubescens* than for *B. pendula*, due to better seed quality in *B. pubescens* in the mountain area.

Light penetration had a relatively large effect on growth of birch seedlings. In shady conditions, the seedlings never exceeded 2-3 cm in height.

Scarified ground was necessary for establishment of birch seedlings.

### **(V) Regeneration of *Betula pendula* and *B. pubescens* coll. above and below the natural altitudinal distribution limit of *B. pendula* in south east Norway.**

Transplantation experiments of plant species outside their recent range is a useful method to get knowledge of whether the species is in equilibrium with the present climate, or not (Woodward 1987). As trees have long pre-reproductive stages, often many decades, such experiments usually examine the performance of seedlings and saplings, but not later stages of their life cycles. In this study, I have used a *B. pendula* stand, planted

about 250 m above the natural altitudinal range of the species in the area. The initial cohort was planted during the period 1877-1902 (Børset 1954). This gave the opportunity to get a measure also on the performance of later stages in the life cycle of this tree, outside its natural range. The reproduction in the *B. pendula* plantation was compared with the reproduction in a control population of naturally established *B. pendula*, situated below the altitudinal *B. pendula* limit, and also with the reproduction of *B. pubescens* coll. above and below the *B. pendula* limit.

Data were collected in the autumn of 1989. No younger trees or seedlings were found, in the plantation and almost no viable seeds were produced in 1989. The age structure of 30 sampled trees indicated that most of the trees present today were established by natural regeneration of the planted trees in the 1920's - 1930's. Climatic data (The Norwegian Meteorological Institute) suggests slightly warmer summers during this period. These results indicate that *B. pendula* may regenerate successfully above its altitudinal range limit, but only occasionally during climatically favourable periods. In contrast, seedlings and saplings occurred, and the seed germinability was relatively high in 1989 in the lower situated naturally established *B. pendula* stand.

*B. pubescens* coll. showed higher seedling density and higher density of catkins per tree than *B. pendula*, both below and above the *B. pendula* limit. Seed germinability was also much higher for *B. pubescens* above, but not below, the *B. pendula* limit.

## CONCLUSIONS AND FUTURE STUDIES

Differences in seed set, establishment and survival of seedlings, and in the capacity of stump and root sprouting affects the spatial separation of the Scandinavian birch taxa along the altitudinal gradient. The importance of climatically determined differences in production of viable seeds, and in sprouting capacity, increases towards marginal populations at high altitudes.

The production of viable birch seeds as well as the success of seedling establishment vary strongly between years. For *B. pendula*, the production of viable seeds decreases, with increasing altitude every year, but this general pattern is not found in *B. pubescens*. An explanation of this difference could be that *B. pendula* is badly adapted to the relatively low amount of resources that is available in the marginal mountain area in the Scandes, and that these trees therefore seldom reaches the level of accumulated resources that are necessary for successful completion of the whole reproductive cycle from pollination to mature seeds. In contrast, *B. pubescens* seems to be able to accumulate enough resources for successful seed set also at relatively high altitudes. The altitudinal pattern revealed by this study is similar to that found in a study of the latitudinal variation in seed set of *B. pendula* and *B. pubescens* coll. over many years in Finland (Koski and Tallquist 1979). The frequency of good seed years decreased toward higher latitudes and this decrease was slightly more apparent for *B. pendula* than for *B. pubescens* coll. (Fig. 1).

To get a closer understanding of the interactions between climatic variations and the reproduction of forest trees, long term data on forest tree reproduction, e.g. the above mentioned publication by Koski and Tallquist (1979), should be correlated with climatic records from weather stations nearby. Such an approach could be used to construct a model to predict the effects of an increased "greenhouse effect" (see e.g. Roberts 1989) on boreal forests.

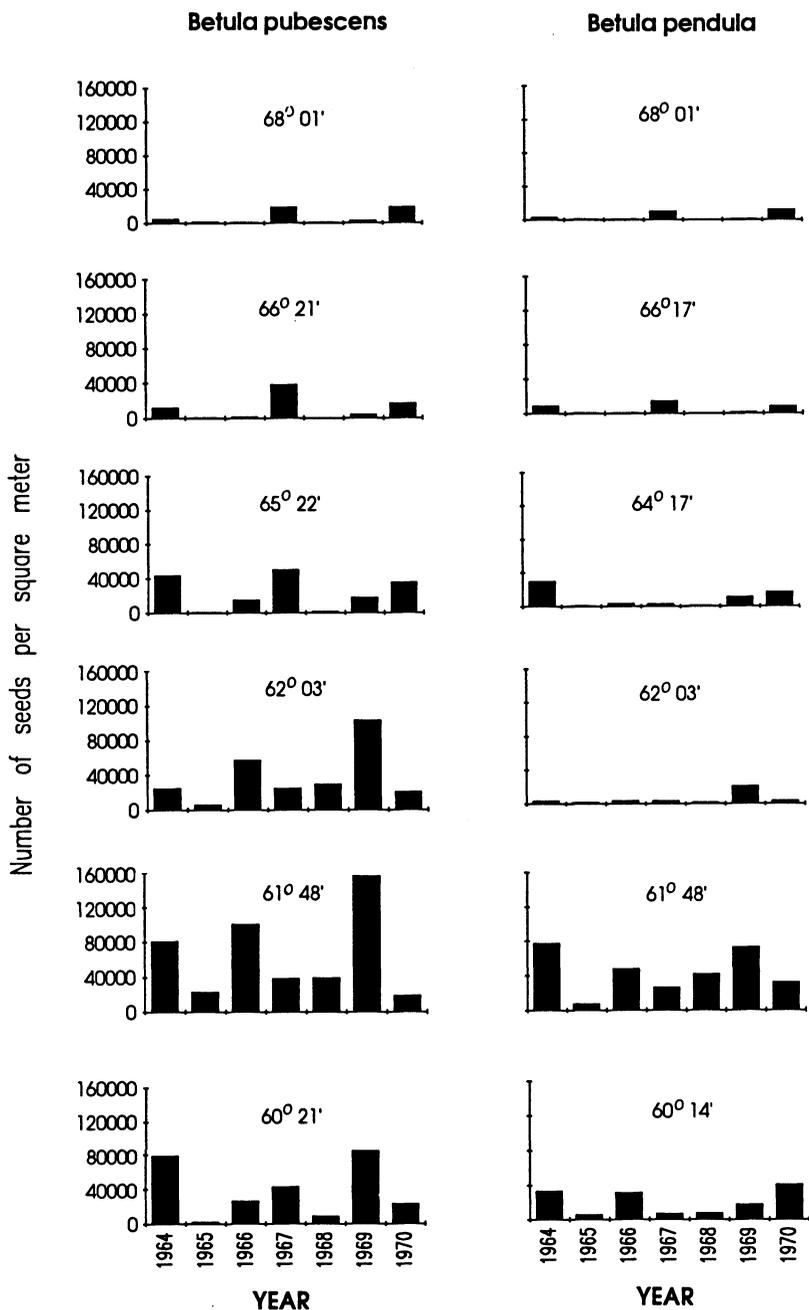


Fig. 1. Number of *Betula pubescens* and *B. pendula* seeds trapped per square meter in *B. pubescens* and *B. pendula* stands, respectively at different latitudes in Finland, 1964 - 1970 (Drawn from data in Koski and Tallquist 1978).

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## REFERENCES

- Andersen, S.T. 1970. The relative pollen productivity and pollen representation of north Europas trees, and correlation factors for tree pollen spectra. Geological survey of Denmark. II Series, Copenhagen.
- Arnborg, T. 1946. Om vårtbjörkens och glasbjörkens ståndortskrav. *Skogen* **33**: 163-165.
- Atkinson, M.D. 1992. Biological flora of the British Isles: *Betula pendula* Roth. (*B. verrucosa* Ehrh.) and *B. pubescens* Ehrh. *Journal of Ecology* **80**: 837-880.
- Barth, A. 1949. Björka. Det Norske Skogsselskap, Oslo.
- Brown, R.K., Kennedy, D. and Williams, D.A. 1982. The occurrence of natural hybrids between *Betula pendula* Roth. and *B. pubescens* Ehrh. *Watsonia* **14**: 133-145.
- Børset, O. 1954. Skogreisning på Røros. *Tidsskrift for skogbruk* **62**: 413-420.
- Coley, P.D., Bryant, J.P. and Stuart, C. 1985. Resource availability and plant antiherbivore defense. *Science* **230**: 895-899.
- Crawford, R.M.M. 1982. Habitat specialisation in plants of cold climates. *Transactions of the Botanical Society of Edinburgh* **44**: 1-12.
- Crawford, R.M.M. 1989. Studies in plant survival. Ecological case histories of plant adaptation to adversity. Blackwell Scientific Publications, London.
- Davy, A.J. and Gill, J.A. 1984. Variation due to environment and heredity in birch transplanted between heath and bog. *New Phytologist* **97**: 489-505.
- Elliott, D.L. 1979. The stability of the northern Canadian tree limit: Current regenerative capacity. Thesis, Department of Geography. B.A., Californian State University, Fullerton.
- Forbes, J.C. and Kenworthy, J.B. 1973. Distribution of two species of birch forming stands on Deeside, Aberdeenshire. *Transactions of the Botanical Society of Edinburgh* **42**: 101-110.
- Hagman, M. 1971. On self and cross incompatibility shown by *Betula verrucosa* Ehrh. and *Betula pubescens* Ehrh. *Communicationes Instituti Forestalis Fenniae* **73**: 1-125.

- Hagner, S. 1965. Cone crop fluctuations in Scots Pine and Norway Spruce. *Studia Forestalia Suecica* 33: 1-21.
- Haller, J.R. 1959. Factors affecting the distribution of Ponderosa and Jeffery Pines in California. *Madrono* 15: 65-71.
- Helms, A. and Jørgensen, C.A. 1925. Birkene paa Maglemose. *Botanisk Tidsskrift* 39: 57-134.
- Hengeveld, R. 1990. Dynamic Biogeography. Cambridge University Press, Cambridge.
- Hough, R.F. 1937. A study of natural tree production in the Birch- Maple - Hemlock type. *Journal of Forestry* 35: 376-378.
- Hultén, E. 1970. The Circumpolar Plants. II Dicotelydons. *Kungliga Svenska Vetenskapsakademiens Handlingar*. 13: 1.
- Hustich, I. 1944. Skogsgränsproblemet. *Svensk Botanisk Tidsskrift* 38: 131-132.
- Hustich, I. 1983. Tree-line and tree-growth studies during 50 years: some subjective observations. *Collection Nordicana* 47: 181-188.
- Häsler, R. 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia* 54: 14-22.
- Jackson, S.T. and Whitehead, D.R. 1991. Holocene vegetation patterns in the Adirondack Mountains. *Ecology* 72: 641-653.
- Johnsson, H. 1974. Genetic characteristics of *Betula verrucosa* Ehrh. and *B. pubescens* Ehrh. *Annales Forestales, Zagreb* 6: 91-130.
- Kallio, P. and Mäkinen, Y. 1978. Vascular flora of Inari Lapland. 4. Betulaceae. *Reports from Kevo Subarctic Research Station* 14: 38-63.
- Kallio, P., Niemi, S., and Sulkinoja, M. 1983. The Fennoscandian birch and its evolution in the marginal forest zone. *Collection Nordicana* 47: 101-110.
- Kinnaird, J.W. 1974. Effect of site conditions on regeneration of birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.). *Journal of Ecology* 62: 467-472.
- Koop, H. 1987. Vegetative reproduction of trees in some European forests. *Vegetatio* 72: 103-110.
- Roberts, L. 1989. How fast can trees migrate? *Science* 243: 735-737.
- Koski, V. and Tallquist, R. 1978. Results from long-time measurements of the quality of flowering and seed crop of forest trees. *Folia Forestalia* 364: 1-60.
- Kullman, L. 1979. Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915-1975. *Acta Phytogeographica Suecica* 65: 121 pp.
- Kullman, L. 1992. Climatically induced regeneration patterns of marginal populations of *Pinus sylvestris* in northern Sweden. *Oecologia Montana* 1: 5-10.
- Matlack, G.R. 1989. Secondary dispersal of seeds across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology* 77: 853-869.
- Makhnev, A.K. and Mamaev, S.A. 1973. Intraspecific variation and structure of birch populations in the mountains of the southern Urals in relation to altitude zones. *Soviet Journal of Ecology* 3: 16-25.
- Miles, J. and Kinnaird, J.W. 1979. Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-shire. *Journal of Ecology* 61: 93-98.
- Mulchay, D.L. and Mulchay, G.B. 1987. The effect of pollen competition. *American Scientist* 75: 44-50.
- Norton, D.A. and Schönenberger, W. 1984. The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. *Arctic and Alpine Research* 16: 361-370.
- The Norwegian meteorological Institute, Oslo.
- Payette, S. and Fillion, L. 1985. White spruce expansion at the tree line and recent climatic change. *Canadian Journal of Forest Research* 15: 241-251.
- Pelham, J., Gardiner, A.S., Smith, R.I. and Last, F.T. 1988. Variation in *Betula pubescens* Ehrh. (Betulaceae) in Scotland: its nature and association with environmental factors. *Botanical Journal of the Linnean Society* 96: 217-234.
- Perala, D. A. and Alm, A.A. 1990. Reproductive ecology of birch: A review. *Forest Ecology and Management* 32: 1-38.
- Pigott, C.D. 1981. Nature of seed sterility and natural regeneration of *Tilia cordata* near its northern limit in Finland. *Annales Botanici Fennici* 18: 255-263.
- Pigott, C.D. and Huntley, J. 1981. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range III. Nature and causes of seed sterility. *New Phytologist* 87: 817-839.

- Prentice, I.C. 1981. Quantitative birch (*Betula* L.) pollen separation by analysis of size frequency data. *New Phytologist* **89**: 145-157.
- Prentice, I.C. 1983. Postglacial climatic change: Vegetation dynamics and the pollen record. *Progress in Physical Geography* **7**: 273-286.
- Sarvas, R. 1948. A research on the regeneration of birch in south Finland. *Communicationes Instituti Forestalis Fenniae* **35**: 1- 41.
- Scott, P.A., Bentley, C.V., Fayle, D.C.F. and Hansell, R.I.C. 1987. Crown forms and shoot elongation of White Spruce at the treeline, Churchill, Manitoba, Canada. *Arctic and Alpine Research* **19**: 175-186.
- Sedgley, M. and Griffin, A.R. 1989. Sexual reproduction of tree crops. Academic Press, London.
- Slatyer, R.O. and Noble, J.R. 1992. Dynamics of montane tree lines. In: Landscape Boundaries. Consequences for biotic diversity and ecological flows. Edited by Hansen, A.J. and di Castri, F. *Ecological Studies* **92**, pp 346-359. Springer-Verlag, New York.
- Smith, H. 1920. Vegetationen och dess utvecklingshistoria i det centralsvenska högfjällsområdet. Norrländskt handbibliotek 8, Uppsala.
- Stevens, G.C. and Fox, J.F. 1991. The cause of treeline. *Annual Review of Ecology and Systematics* **22**: 177-191.
- Tirén, L. 1935. Om granens kottsättning, dess periodicitet och samband med temperatur och nederbörd. *Meddelanden från statens skogsförsöksanstalt* **4**: 413-525 (English summary).
- Tranquillini, W. 1979. Physiological Ecology of the Alpine Timberline. *Ecological Studies* **31**. Springer-Verlag, Berlin.
- Vaarma, A. and Valanne, T. 1973. On the taxonomy, biology and origin of *Betula tortuosa* Ledeb. *Reports from the Kevo Subarctic Research Station* **10**: 70-84.
- Wahlenberg, G. 1813. De vegetatione et climate in Helvetia septentrionale. Zurich.
- Wallin, J-E., Segerström, U., Rosenhall, L., Bergmann, E., and Hjelmros, M. 1991. Allergic symptoms caused by long-distance transported birch pollen. *Grana* **30**: 265-268.
- Wardle, P. 1981. Is the alpine timberline set by physiological tolerance, reproductive capacity, or biological interactions? *Proceedings of the Ecological Society of Australia* **11**: 53-66.
- Woodward, F.I. 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge.



- Kullman, L. 1979: Change and stability in the altitude of the birch tree-limit in the southern Swedish Scandes 1915-1975. *Acta Phytogeographica Suecica* **65**.
- Kullman, L. 1984a. Transplantation experiments with saplings of *Betula pubescens* ssp. *tortuosa* near the tree-limit in central Sweden. *Holarctic Ecology* **7**:289-293.
- Kullman, L. 1984b. Germinability of mountain birch (*Betula pubescens* ssp. *tortuosa*) along two altitudinal transects downslope from the tree-limit, in Sweden. *Reports from Kevo Subarctic Research Station* **19**:11-18.
- Kullman, L. 1991: Structural change in a subalpine birch woodland in Northern Sweden during the past century. *Journal of Biogeography* **18**:53-62.
- Kullman, L. 1992: Climatically induced regeneration patterns of marginal populations of *Pinus sylvestris* in northern Sweden. *Oecologia Montana* **1**: 5-10.
- Langehammer, A. 1982: Vekststudier på hengbjørk (*Betula verrucosa* Ehrh.) i Norge. *Meldinger fra Norges lanbrukshøgskole* **61**:1-43 (English summary).
- Løken, A. 1957: Lavlandsbjørkas (*Betula verrucosa* Ehrh.) utbredelse i Pasviksdal. *Meddelelser fra det Norske skogførsøksvesen* **48**:319-338.
- Miles, J. 1973: Early mortality and survival of self-sown seedlings in Glenfeshire, Inverness-Shire. *Journal of Ecology* **61**:93-98.
- Miles, J. and Kinnaird, J.W. 1979: The establishment and regeneration of birch, juniper and Scottish pine in the Scottish highlands. *Scottish Forestry* **33**:102-119.
- Pelham, J., Kinnaird, J.W., Gardiner, A.S. and Last, F.T. 1984: Variation in, and reproductive capacity of, *Betula pendula* and *B. pubescens*. *Proceedings of the Royal Society of Edinburgh* **85B**:27-41.
- Perala, D.A. and Alm, A.A. 1990: Reproductive ecology of birch: a review. *Forest Ecology and Management* **32**:1-38.
- Pigott, C.D. 1981: Nature of seed sterility and natural regeneration of *Tilia cordata* near its northern limit in Finland. *Annales Botanici Fennici* **18**:255-263.
- Pigott, C.D and Huntley, J. 1981: Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range III. Nature and causes of seed sterility. *New Phytologist* **87**:817-839.
- Raulo, Y. 1976: Development of *Betula pendula* Roth. progenies in northern Lapland. *Communicationes Instituti Forestalis Fenniae* **88**:1-18.
- Roskham, J.C. and Van Uffelen, G.A. 1981: Biosystematics of insects living in female birch catkins III. Plant - insect relation between white birches, *Betula* L., Section *Excelseae* (Koch) and gall midges of the genus *Semudobia* Keffer (Diptera, *Cecidomyiidae*). *Netherland Journal of Zoology* **31**:533-553.
- Sarvas, R. 1948: A research on the regeneration of birch in south Finland. *Communicationes Instituti Forestalis Fenniae* **35**:1-41.
- Sarvas, R. 1952: On the flowering of birch and the quality of seed crop. *Communicationes Instituti Forestalis Fenniae* **40**:1-35.
- Slatyer, R.O. and Noble, J.R. 1992: Dynamics of montane tree lines. In *Landscape boundaries, Consequences for biotic diversity and ecological flows* (eds. A.J. Hansen and F. di Castri) pp. 346-359. Ecological studies 92. Springer Verlag, New York.
- Stevens, G.C. and Fox, J.F. 1991: The causes of tree-lines. *Annual Review of Ecology and Systematics* **22**:177-191.
- Uggla, E. 1958: Skogsbrandfält i Muddus nationalpark. *Acta Phytogeographica Suecica* **41**.
- Wardle, P. 1985: New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craighburn Range, Canterbury. *New Zealand Journal of Botany* **23**:219-234.
- Woodward, F.I. 1987: Climate and plant distribution. Cambridge university press, Cambridge.
- Örtenblad, T. 1902. Om masurbjörkens (*Betula verrucosa* Ehrh.) utbredning i Scandinavien. *Botaniska notiser*: 229-234.