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

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Abstract. During the period 1877 to 1902, a number of *Betula pendula* saplings were planted in an area above the natural altitudinal distribution limit of this species in SE Norway. In 1989, I compared the regeneration of the trees in this area with regeneration in a naturally established *B. pendula* stand below its altitudinal distribution limit. The regeneration of *Betula pubescens* coll., which grows at higher altitudes than *B. pendula*, was also studied. The age structure showed that few of the trees in the *B. pendula* plantation were old enough to have been planted, instead most of the trees appear to have become established by natural recruitment of seedlings from their planted ancestors in the 1920-1930's. But no young trees or seedlings were found, and there was almost no production of viable seeds. In contrast, seedlings and saplings occurred in the *B. pendula* stand below its distribution limit, and the production of viable seeds was relatively high. *B. pubescens* coll. showed greater sexual reproduction than *B. pendula*, especially above the natural altitudinal limit of *B. pendula*. This suggests that better sexual reproduction in the mountain area may be important for the higher tree-line of *B. pubescens* coll.
Keywords: Tree-line, climatic change, age structure, seed quality, *Betula*, transplantation experiments

Introduction

Transplantation experiments are a useful way to test the influences of different factors affecting seedlings and saplings of trees above their alpine distribution limits (e. g. Kullman 1984a; Wardle 1985; Woodward 1987). However, for long-lived plants such as trees, it takes a long time until the next generation starts to reproduce. Therefore very few studies on the reproduction of trees planted above their alpine tree-lines have been made. Here I present the results of an investigation on the regeneration, growth and age structure in a *Betula pendula* Roth. stand established by planting in an area above its natural altitudinal distribution limit in SE Norway. The planting was performed during the period 1877 to 1902 (Børset 1954). I made my investigation in late August 1989. I repeated the same investigations in a naturally established *B. pendula* stand, further south, below the natural tree-line of this species. I also studied *B. pubescens* coll. Ehrh., another common Scandinavian birch. The distribution of this species continues far above the altitudinal distribution limit of *B. pendula* (e. g. Hultén 1971). I measured reproduction, growth and age structure of this species in populations close to the two investigated *B. pendula* stands. The questions addressed were: 1) Is the recent altitudinal distribution limit of *B. pendula* in equilibrium with the prevailing climate? 2) Is the higher alpine distribution limit of *B. pubescens* coll. determined by better sexual reproduction of *B. pubescens* coll. in the mountain area?

Material and methods

Study areas and studied species

I performed this study at two localities, near the city of Røros (62° 35'N, 11° 20'E) and near the city of Koppang (61° 34'N, 11° 05'E) in south- east Norway (Fig. 1). At Røros, mining activities started in 1644, when broad-scale deforestation of the area was initiated. As a consequence, soils were eroded and sand dunes were reactivated. In later years, refor-estation efforts of these areas were initiated, and during the period 1877 - 1902 an area, "Kvitsanden", about 630 m a.s.l. was afforested with different tree species, among them *B. pendula* (Børset 1954).

Røros is located in the subalpine zone, within the Scandes Mountains. The mean annual temperature (1961 - 1990) was 0.3 °C, and the mean annual precipitation 504 mm (The Norwegian Meterological Institute, Oslo). The "control area", Koppang, is situated in the boreal zone at an elevation 330 m a.s.l. Mean annual temperature is 2.0 °C and precipitation is 805 mm. The natural distribution limit of *B. pendula* is situated between Koppang and Røros.

The species studied, *B. pendula* and *B. pubescens* coll., look quite similar, but they have different levels of polyploidy. *B. pendula* is a diploid (n=14) and *B. pubescens* coll. is a tetraploid (n=28) (Johnsson 1974). They can grow in mixed stands and are often also mixed with other trees. *B. pendula* is mostly confined to dry and warm habitats, whereas *B. pubescens* coll. often grows in relatively moist sites (e. g. Arnborg 1946; Sarvas 1948;

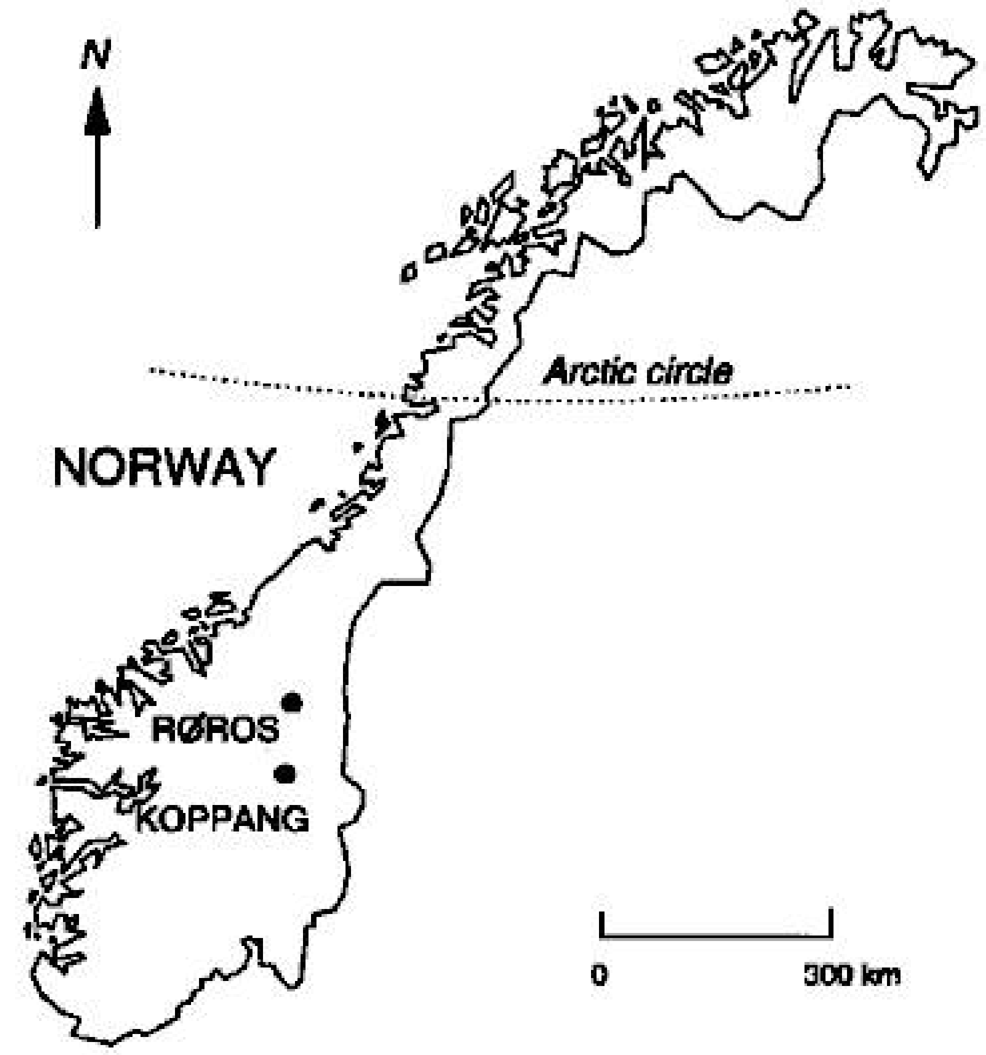

Fig. 1. Location of study sites.

Uggla 1958; Kinnaird 1968). Both species may produce large seed crops, but seed setting varies widely between years (Sarvas 1948; Koski and Tallquist 1978). In southern Norway, the alpine tree line of *B. pendula* is situated at 400 - 564 m a.s.l., while tree-shaped individuals of *B. pubescens* coll. are found up to 1,100 m, and bush-shaped *B. pubescens* coll. up to 1,250 m a.s.l. (Barth 1949). Both species are distributed over large parts of Eurasia (Hultén 1971). For detailed descriptions of the species see e. g. Johnsson (1974), Pelham *et al.* (1984), Perala and Alm (1990) and Atkinson (1992).

Methods

I performed the study in late August in 1989, when the female inflorescences (catkins) had become brown-coloured, indicating that the seeds had ripened. From an arbitary starting point in each population, I sampled the nearest 30 trees per species that carried visible female catkins. From each tree, I collected about five catkins from all aspects of the crown. The seeds were mixed in a paper bag. The seed quality was analysed in the laboratory as follows: The catkins from each tree were dried in the paper bags and stored at 2 °C for about four months, before germination was tested. Seed germinability was measured for each tree. About 200 seeds per tree were placed on wet filter paper in closed petri dishes. The temperature was 20 °C and length of the light period was about 10 houres per day. The germinated (visible radicle) seeds were counted daily and removed. I finished the test after 35 days when no germination had occurred for four to five days. Seeds which failed to germinate were examined under a stereomicroscope (X 60 magnification). The seeds were classified as follows; 1) germinable, 2) developed (filled) but not germinable 3) partly developed, not germinable (if the embryo fill less than 60 % the seeds are not germinable according to Sarvas, 1952), 4) infected by gall midges of the genus *Semudobia* Keffer, 5) other insect damage, 6) seeds with other than insect damage, e. g. fungi infections, and 7) empty seeds (no embryo). For each tree, I also scored the number of catkins on branches number 3 - 7 (counted from below), and the number of seedlings and saplings (less than 50 cm high) within a radius of 10 m from the stem. I further measured the stem diameter 1.3 m above ground, and determined the age of the trees by counting the annual rings on cores taken from the stem bases close to the ground. Relative stem diameter growth was calculated by dividing the stem diameter by age.

30 of the nearest *B. pendula* trees from an arbitary starting point in the plantation at Røros, irrespectivly of size, were age-determined by boring close to ground level, or in one case, by taking a stem disc. The age structure of these trees was compared with yearly mean values for the warmest months, June, July and August. Mean monthly temperatures since 1871 from a climate station in Røros were used (source: The Norwegian Meterological Institute, Oslo).

Results

Only two of the 30 *B. pendula* trees in the Røros area were old enough to represent the initial cohort, planted before 1902. The majority had become established during the period 1920 - 1930. Seedling recruitment coincided with a slight increase of mean temperatures during the growing periods in the early 1930's. The youngest tree had been established in 1955 (Fig. 2). No seedlings or saplings of *B. pendula* were found in the area of the Røros plantation. At Koppang, *B. pendula* showed a more complete age distribution, with occurrence of seedlings and saplings. This was also the case for *B. pubescens* coll., both at Koppang and at Røros. The seedling density was generally larger for *B. pubescens* than for *B. pendula* (Fig. 3 A). The seed germinability of *B. pendula* was very low in the Røros stand - significantly lower than the seed germinability of *B. pendula* in the Koppang stand. Further, seed germinability was generally higher for *B. pubescens* coll. than for *B. pendula*. *B. pubescens* coll. showed even higher seed germinability at Røros than at Koppang (Fig. 3 B). The number of catkins was also generally higher for *B. pubescens* than for *B. pendula*, and slightly higher for *B. pendula* at Koppang than at Røros (Fig. 3 C). Growth rate of the trees was about the same for the two species. However, the growth was about twice as large at Koppang than at Røros (Fig. 3 D). The proportions of germinable, developed but not germinable, and partly developed (not germinable) seeds were larger in *B. pendula* from Koppang than in *B. pendula* from Røros (Table 1). For *B. pubescens* coll., the result was the opposite, the same seed classes showed higher proportions at Røros than at Koppang. Empty seeds (without embryo) was the dominat seed class in the seeds that failed to germinate, except for *B. pubescens* seeds from Røros, in which the proportion of partly filled seeds was most common among the ungerminated seeds. The proportions of different insect damage, and other damage to seeds, were relatively low (Table 1).

Discussion

The occurrence of *B. pendula* trees established from seed in the plantation at Røros, indicates that natural regeneration of *B. pendula* is possible above the present altitudinal distribution limit of the species. Peak regen-

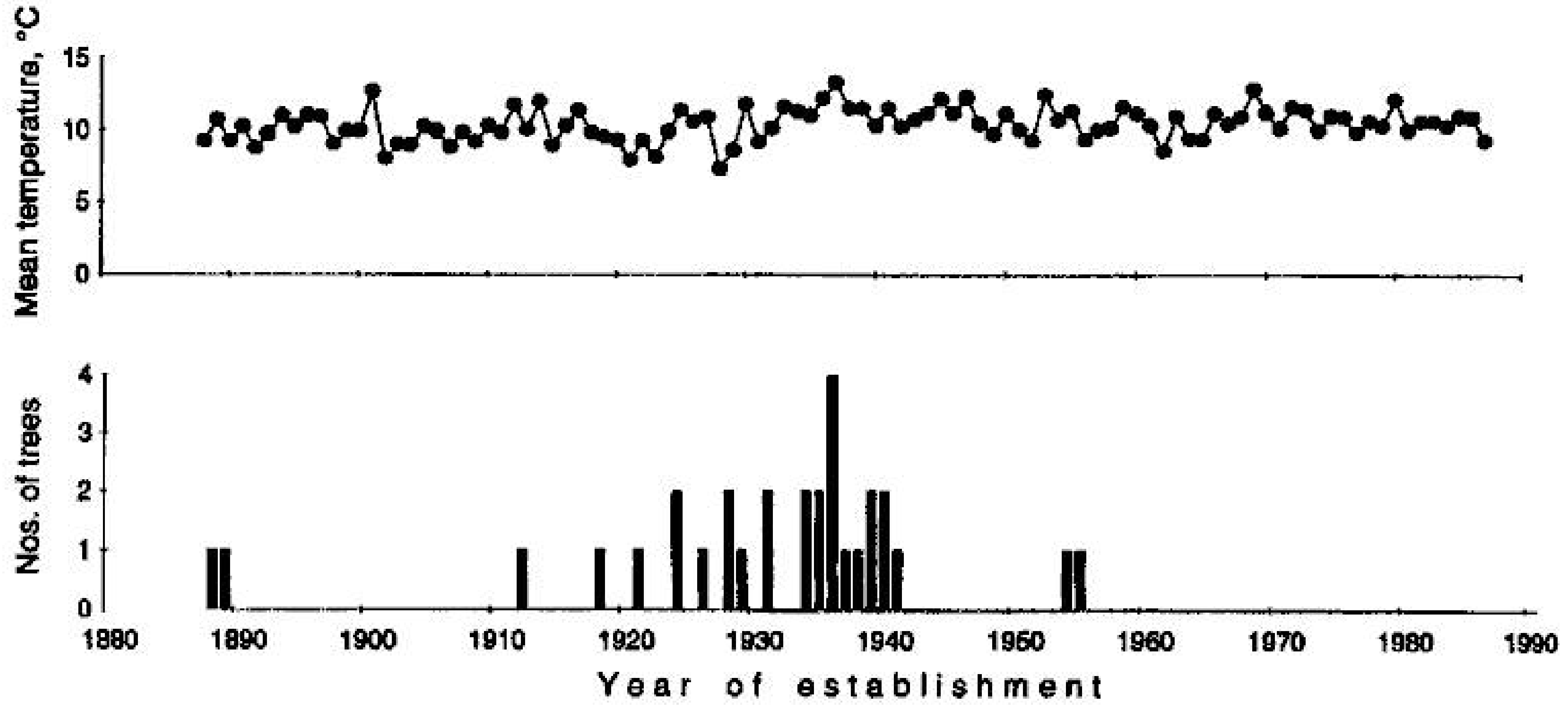

Fig. 2. Top, annual mean temperatures of the warmest months, June, July, and August during the period 1888 to 1986 at Røros. Bottom, years of establishment of the 30 studies *B. pendula* trees in the plantation at Røros.

eration coincided with a slight increase of summer temperatures in the 1930's. Other studies have also shown fairly successful regeneration of forest trees in northern Scandinavia during the 1930's (Hustich 1983; Ågren, Isaksson and Zackrisson 1983; Kullman 1991). The fact that the spontaneous regeneration was mainly confined to this slightly warmer period fits a more general pattern, showing the importance of occasional favourable events for maintaining or enlarging the distribution areas of tree species (Woodward 1987; Kullman 1979; Slatyer and Noble 1992, Kullman 1992). This result also suggests that the distribution of *B. pendula* is in equilibrium with the prevailing climate. No regeneration had taken place before 1912 since until then the planted trees would not have been old enough for setting seeds (Örtenblad 1902). Alternatively, the younger *B. pendula* trees might have grown from buds of the trunks rather than from seeds. However, this seems less likely as no remnants of "parent trees" were found.

The production of viable seed in *B. pendula* was much lower at Røros than at Koppang, suggesting that seed production is critical for determing the altitudinal distribution limit of *B. pendula*. Empty seeds constituted the major proportion of the seeds that failed to germinate. Since birches may produce empty seeds even without fertilisation or because of abortion of the embryo (Frolova 1956; Johnsson 1974), the high proportion of empty seeds, especially in *B. pendula* at Røros, may be due to failure of fertilisation. Such a limitation could depend on a number of factors, including pollen limitation (Sarvas 1952; Kullman 1984 b), pollen damage (Løken 1957), low penetration capacity of pollen tubes (Sarvas 1952), or damage on the styles (Hagman 1971). In *Tilia cordata*, the northern distribution limit in Great Britain is suggested to be mainly caused by inhibited pollen tube growth at low temperatures (Pigott and Huntley 1981). The relatively low proportion of partly filled seeds (fully developed) suggests a weak effect of the prevention of seed maturation on actual seed quality. But since empty seeds may develop even after the embryo has aborted (Johnson 1974), it is difficult to distinguish between the effects of fertilisation failure and limitation of resources (sufficiently high temperature sum) for seed maturation. In *Tilia cordata*, the northern distribution limit in southern Finland is suggested to be set mainly by limitations of resources for seed maturation (Pigott 1981).

The proportion of seeds infected by *Semudobia* spp. was low compared with other observations. In a study in northern Sweden, on average 17.9 % of *B. pendula* seeds and 1.4 % of *B. pubescens* seeds were infected during a six-year period (Holm, in press). Miles and Kinnaird (1979) reported *Semudobia* infections of 0.05 to 10.7 percent in *B. pubescens* in the Scottish Highlands. Roskham and van Uffelen (1981) reported commonly less than 5 % infections, but occasionally more, for both birch species in the Netherlands. Temporary mass occurrence of *Semudobia* attacks, especially on *B. pendula*, have been reported from Poland (Kapuscinski 1966).

Apart from a high production of viable seeds, patches of disturbed ground are necessary for successful seed regeneration of *B. pendula* and *B. pubescens* coll. (Miles 1973; Kinnaird 1974). Such patches must have been relatively frequent because of the thin humus layer on the former sand dunes in and around the Røros plantation.

Lethal frost injuries on seedlings and/or saplings may also have decreased the seedling recruitment in the plantation. Frost damage, but only in the upper parts, was common on *B. pendula* saplings planted in an area above the altitudinal limit of the species, between Røros and Koppang (Langehammer 1981). The same type of damage was also found on *B. pendula* saplings planted in northern Finland (Raulo 1977). In both experiments, frost injuries were lower in plants of northern than of southern provenance.

The results show that *B. pubescens* coll. has a greater capacity of sexual reproduction than *B. pendula*, especially in the Røros area. This indicates that the higher elevation of the distribution limit of *B. pubescens* coll. may mainly results from its better sexual reproduction in a harsh climate. But the greater capacity of vegetative reproduction and the more lateral growth form of *B. pubescens* coll. may also influence its higher distribution limit. (Forbes and Kenworthy 1973; Crawford 1982; Stevens and Fox 1991). Even if sexual reproduction was much higher for *B. pubescens* coll. than for *B. pendula* at Røros, the species do not differ in stem growth. An explanation for this may be that *B. pendula* is able to allocate limited resources first to growth and survival,

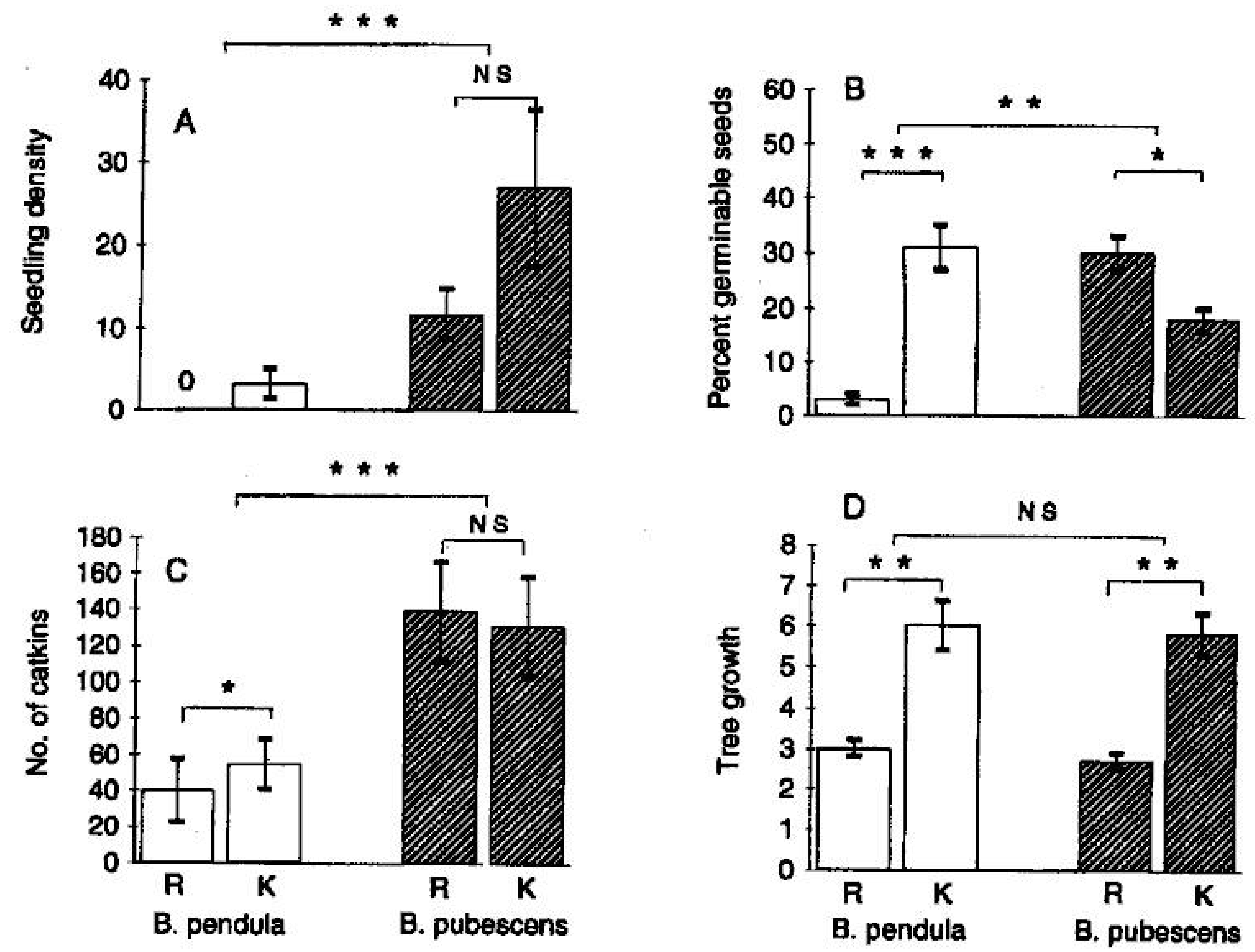

Fig. 3. Seedling density, (A), percentage of germinable seeds (B), number of catkins (C) and tree growth (D) in *Betula pendula* and in *B. pubescens* coll. at Roros and Koppang (K). Seedling density was measured as the number of seedlings + saplings within a 10 m radius from the stem, seed germinability on about 200 seeds per tree, the number of catkins on branchs 3 - 7 from below, and the growth as stem diameter (1.3 m above ground) / tree age (at stem base) (mm). Mean values and SE are shown. n=30. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ (Mann Witney U- test).

and only during climatological favourable periods to reproduction.

The obtained results can only give indicative answers on the questions adressed in the introduction. Differences in treatments (plantation of *B. pendula* in Røros, but not in Koppang), age structures, and soil conditions could also have affected the observed differences in fitness between the studied populations. Strictly, only plants from the same original population planted in different altitudes, and under the same soil conditions, could give a conclusive answer to the questions adressed. However, this could only be done in a 20 to 30 years long experiment in order to get data on seed set.

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Population	Germinated	Filled, not germinated	Partly filled	Empty	*Semudobia* galls	Other insect damages	Unknown reasons
	Seed class						
B. pendula							
Røros (n=5168)	3.0 (0.7)	0.4 (0.2)	7.9 (1.6)	86.4 (2.1)	0.9 (0.2)	0.3 (0.1)	1.1 (0.3)
[Røros vs. Koppang]	***	**	NS	***	*	NS	NS
Koppang (n=5952)	30.9 (3.6)	3.3 (0.9)	11.1 (1.9)	49.9 (4.6)	1.5 (0.3)	0.3 (0.1)	3.0 (0.8)
[*B. pendula* vs. *B. pubescens*]	**	***	***	***	***	NS	NS
B. pubescens							
Røros (n=7703)	29.7 (3.6)	16.6 (2.2)	30.1 (3.1)	20.3 (2.5)	0.7 (0.2)	1.2 (0.4)	1.4 (0.2)
[Røros vs. Koppang]	*	NS	*	***	*	*	NS
Koppang (n=6728)	18.1 (2.6)	17.5 (2.6)	16.3 (2.0)	45.6 (3.3)	0.1 (0.0)	0.1 (0.0)	2.3 (0.7)

Table 1. Percentages of seeds classified as germinated, filled not germinated, partly filled, empty, *Sebudomia* infected (galls), other insect damages and damages due to unknown reasons, for *Betula pendula* and *B. pubescens* coll. from Røros and Koppang, respectively. Means and within parantheses SE, are shown. Asterisks denote significant differences as follows: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, Mann Whitney U - tests. n=number of seeds analysed per population.

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