

## ADAPTATION TO LOCAL CONDITIONS AFTER ONE GENERATION IN NORWAY SPRUCE

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### ABSTRACT

In this paper we present results from early tests with Norway spruce which indicate that an adaptation to the local climatic conditions may take place even after one generation. Tests of seed lots harvested in planted stands in Norway of origin Harz, Germany, and from Harz and local provenances, were performed both in a growth chamber experiment and in nursery tests. Assessments of terminal bud-set the first year showed that the seedlings from the Norwegian Harz stands set bud considerably earlier in the autumn than those from the original provenance. Seedlings from the Harz stands in West Norway showed a response to the shortening day length intermediate between the Harz and the Norwegian provenance. Seedlings from a Harz stand planted close to latitude 64°N had the same timing of bud-set as the local Central Norwegian provenance. Similar results were obtained with seedlings from seed harvested in a stand established with a provenance transferred from South to Central Norway. The observed results are discussed relative to pollen flow, natural selection and preconditioning caused by the weather conditions during the sexual reproductive process.

**Key words:** *Picea abies*, provenance transfer, bud-set, natural selection, environmental preconditioning.

### INTRODUCTION

Non-local seed sources have played an important role in the reforestation of Norway spruce (*Picea abies* (L.) Karst.) for a long time. In southern Scandinavia, provenances from Central and Eastern Europe have been an important component of the commercial seed supply and are for some climatic zones highly recommended (WERNER & DANELL 1993). Seedlings from both local and transferred provenances have been planted over large forest areas, and it is today not possible to identify the exact origins of the stands. The transfer of more southern provenances to the north have in many cases been successful, but have on sites with severe local climatic conditions resulted in stands with reduced timber quality, mainly due to frost damage (SKRØPPA *et al.* 1993). It is a growing concern that the gene flow from the stands established with transferred provenances will contribute to a reduction of the adaptability of the local provenance. It may influence the adaptive properties of seedlings from cone harvests in both natural and planted stands and also have negative implications for natural regenerations.

Norway spruce is a species with a high level of genetic variability both among and within-populations for most quantitative traits (*e.g.* EKBERG *et al.* 1985, 1991; ERIKSSON 1995). In Scandinavia, rather strong clinal variation patterns have been observed among populations for traits related to the annual growth

rhythm such as growth cessation and terminal bud-set in the autumn. DORMLING (1979) found a strong relationship between the latitude of the provenance and its critical night length for terminal bud-set. DÆHLEN *et al.* (1995), in a test of autumn frost hardiness of Norwegian provenances, could explain as much as 87% of the variation in frost hardiness by the latitude and altitude of the provenance. Considering the young age of the species in the region (MOE 1970) and the extensive gene flow among populations (KOSKI 1970), it has been speculated that this close relationship between the provenance traits and the climatic conditions at the origin of the provenance may not be due to natural selection alone, but also be generated by the climatic conditions during the sexual reproductive process (JOHNSEN & SKRØPPA 1996). If this is the case, then such effects may also have implications for the adaptive traits of offspring from stands established with non-local provenances.

Seed collections were made in Norway spruce stands established after transfers of provenances from Harz, Germany, to West and Central Norway and from a south to north transfer within Norway. The purpose was to compare the performance of the first generation offspring from these stands with that of seedlings of both the original provenance of the mother trees and of the local provenance. We will in this paper make such comparisons for the first year terminal bud-set and discuss the results.

## MATERIALS AND METHODS

### Growth chamber experiment

Cones were collected in the autumn of 1993 from two Norway spruce stands in western Norway. The stands were planted 55 and 65 years ago, respectively, with seedlings of origin Harz, Germany (Table 1). In the youngest stand, located at Førde, latitude 61°20' N, altitude 100 m, the seeds from 3 trees were mixed into a pooled seed lot. From the other stand at Ulvik, latitude 60°35' N, altitude 100 m, 4 seed lots from single trees and one mixed lot from 9 trees were obtained. These 6 seed lots were sown in a growth chamber experiment together with a seed lot of origin Braunlage, Harz, Germany, altitude 700 m (HAR7), and one commercial seed lot of origin Telemark, Norway, altitude 100 m (C1) (Table 1).

The growth chamber experiment was similar to that described by KOHMANN & JOHNSEN (1994). The seedlings were germinated and grown in 8 individually controlled growth chambers. Each chamber represented a specific fixed night length treatment, programmed from 3 to 10 hours of darkness. The light and temperature conditions and irrigation and fertilisation were as described by KOHMANN & JOHNSEN (1994). Within each chamber each seed lot was replicated 4 times in plots consisting of 50 to 70 seedlings.

Each seedling was classified as having set terminal bud or not after six weeks from sowing. The proportion of seedlings with terminal buds was calculated for each plot within each chamber. The observed proportions for the different night length treatments were fitted to a logistic model (KOHMANN & JOHNSEN 1994). The

night length when 50% of the seedlings had set terminal bud,  $NL_{50}$ , was estimated for each combination of seed lot and replicate. These night length observations were analysed in a two-way analysis of variance, regarding the seed lots as fixed and the replicates within chamber as random factors. For the Ulvik stand, the mean values per replicate of the 5 entries were used in the analysis.

### Nursery experiments

Cones were collected in the autumn of 1995 from 3 planted stands in Verdal, Central Norway, latitude 63°45' N. Two of the stands were established in 1954 adjacent to each other on a slope facing south at an altitude of 400 m. The seedlings in one of these stands were of origin Harz, Germany, and in the other of local origin, but from altitude 200 m (L2). The third stand was established in 1965 with seedlings of origin Buskerud and Oppland counties, Norway, altitude 300 m (B3). This site at altitude 300 m is located next to a bog where frosts frequently occur during the whole vegetation period. In each stand cones were collected from 15 randomly selected trees that were felled. The seeds from each tree were kept separate.

The seedlings of origin Harz were from one of two seed lots that were imported to Norway after seed collections in 1948. One of these lots were from altitude 200–400 m and the other from altitude 400–700 m. Both lots were sown at Sønsterud Nursery, latitude 61°35' N in 1950. Seedlings from one or both of the two lots were planted in Verdal in 1954. However, it has not been possible to identify the exact origin of the seedlings in the seed stand, whether it is from

**Table 1. Materials used in the growth chamber experiments. The provenance is the location of the seed stand. The origin is the provenance of the parents in the seed stand.**

Material	Provenance	Origin
Stand 19	Førde, Norway Latitude 61°30', Altitude 100 m	Harz Germany
Stand 67	Ulvik, Norway Latitude 60°35', Altitude 100 m	Harz Germany
C1	Telemark, Norway Latitude 59°20', Altitude 100 m	Same as provenance
HAR7	Braunlage, Germany Latitude 51°40', Altitude 700 m	Same as provenance

**Table 2. Materials used in the nursery experiments. The provenance is the location of the seed stand. The origin is the provenance of the parents in the stand.**

Material	Provenance	Origin
Harz stand	Verdal, Norway Latitude 63°45', Altitude 400 m	Harz Germany Latitude 51-52°, Altitude 200-400 m, 400-700 m
Harz provenance	Braunlage, Germany Latitude 51°40', Altitude 700 m	Same as provenance
B 3 stand	Verdal, Norway Latitude 63°45', Altitude 400 m	Oppland, Norway Latitude 60°30', Altitude 300 m
B3 provenance	Oppland, Norway Latitude 63°45', Altitude 400 m	Same as provenance
Local stand	Verdal, Norway Latitude 63°45', Altitude 400 m	Nord-Trøndelag, Norway Latitude 63-64°, Altitude 200 m
Local provenance	Verdal, Norway Latitude 63°45', Altitude 400 m	Same as provenance

altitude 200-400 m or 400-700 m in Harz.

In the summer of 1996 seeds from the 45 families, the same commercial Harz seed lot as used in the growth chamber experiment (HAR7), a commercial B3 seed lot and a seed lot of local origin, altitude 200 m (L2), were sown in two nurseries. The materials are summarized in Table 2. One of the nurseries, Stiklestad, is a commercial nursery located approximately 35 km from the stands where the seed was harvested. Each lot was sown in two replicates in multipot containers each with 95 pots. The seedlings were grown in a greenhouse throughout the season and were given the same treatments as the commercial seedlings growing adjacent in the same greenhouse. The other nursery is located at the experimental farm Hoxmark, Ås, at latitude 59°45' N. Here the seedlings were germinated and grown in the greenhouse for 6 weeks and then moved outside on August 8. The cultivation followed standard routines as regards watering and fertilisation (SKRØPPA 1991).

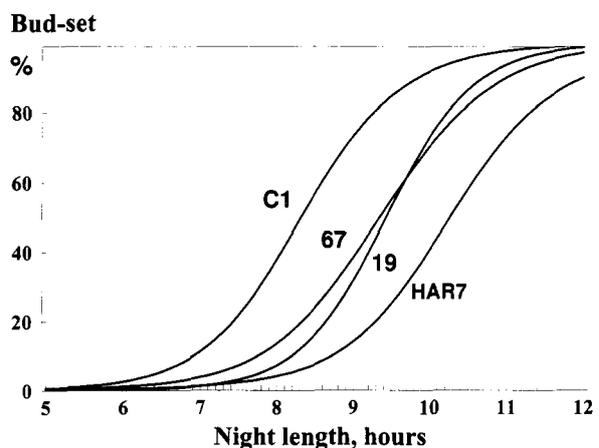
In both nurseries, the seedlings were classified as having set terminal bud or not on three or four occasions, starting at the end of August. At each date, the proportion of seedlings with terminal buds was calculated for each plot. The transformed proportions by the arcsine transformation were subject to analyses of variance. These analyses were done for each of the three pairs of stand and commercial provenance across the two experimental nurseries, and for the three stands. Nursery and provenance were treated as fixed effects and family and replicates as random.

At Hoxmark frost damage and subsequent mortality occurred during the autumn and winter, and assessment of survival was made in the spring of 1997.

## RESULTS

### Growth chamber experiment

Considerable differences were found between the mean photoperiodic response curves of the Norwegian C1 and the German HAR7 provenance (Fig. 1), and with intermediate curves for the two stand seed lots. The seedlings from the C1 provenance showed the fastest



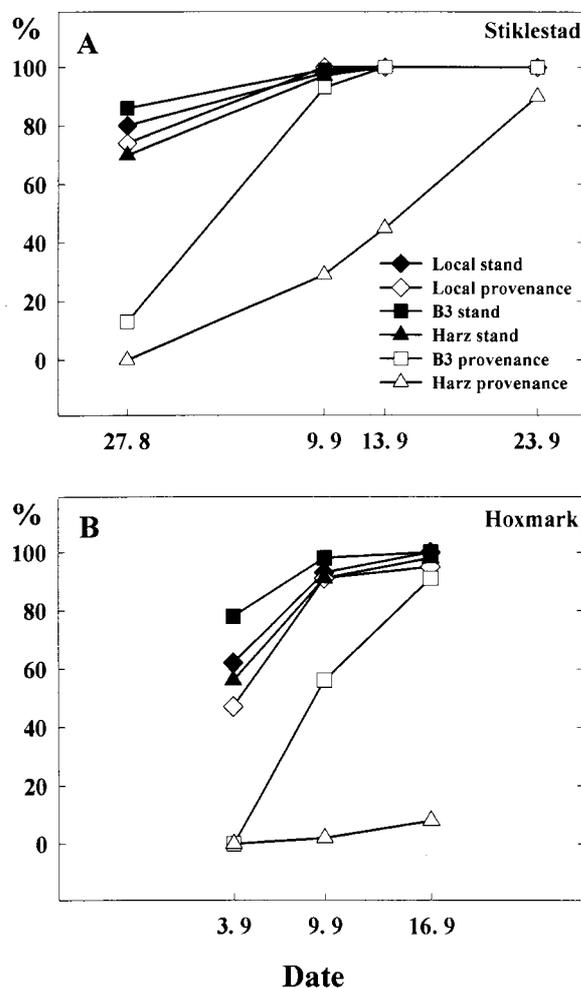
**Figure 1.** Photoperiodic bud-set response for the seed lots from the provenance from southern Norway (C1), the two stands of origin Harz in western Norway (19 and 67) and the Harz provenance (HAR7).

response to the shortening night lengths, with an estimated  $NL_{50}$  of 8.4 hours. The corresponding estimate for HAR7 was 10.3 hours and for both stands 9.4 hours. In the analysis of variance these differences were significant at the 0.1% level.

### Nursery experiments

At Stiklestad Nursery, the first bud-set assessment was made on August 27. Hardly any of the seedlings of the Harz provenance and less than 20% of the seedlings of the B3 provenance had set terminal bud at that date (Fig. 2 A). In contrast, more than 65% of the seedlings of the local provenance and of the three northerly located stands had produced buds. Their further development was fast and so was that of the seedlings of the B3 stand. The seedlings of the Harz provenance continued the slow bud-set development.

### Bud-set



**Figure 2.** Mean bud-set development at Stiklestad Nursery (A) and Hoxmark (B) for families from the three stands and the three provenances.

At Hoxmark, similar results were obtained (Fig. 2 B). Here frost occurred on September 12, and a large proportion of the Harz seedlings showed visible sign of frost damage. This fact most likely retarded their further development. Statistical tests were made on the basis of transformed bud-set percentages on August 27 at Stiklestad and September 3 at Hoxmark. Significant differences were present between stand and provenance seedlings for Harz and B3 lots ( $p < 0.005$ ), but not for the local stand and local provenance comparison ( $p = 0.46$ ).

A considerable mortality occurred at Hoxmark during the autumn and winter. In the spring of 1997, only 21.4% of the Harz provenance seedlings had survived compared to 54.9% for the Harz stand families. No difference in survival was found between the provenance and stand seedlings of Norwegian origin, which had a mean survival of 64.5%.

The analyses of variance showed significant variation among the families within all three stands ( $p < 0.001$ ), but no family  $\times$  nursery interaction. The variability was in particular large among the families from the Harz stand, with family bud-set means ranging from 21 to 94% for the mean values from Stiklestad (August 27) and Hoxmark (September 3). The estimated variance components among families within stands, based on transformed values, were 0.075, 0.019 and 0.020, for the Harz, B3 and L2 stand, respectively.

### DISCUSSION

The timing of terminal bud-set is a trait that frequently has been used to characterise the growth cessation of Norway spruce provenances (*e.g.* DORMLING 1973; HOLZER 1975; KRUTZSCH 1986). The seedlings of a northern population react to very short night lengths and produce their terminal buds early, whereas longer periods of darkness are required by the more southern origins to set bud (DORMLING 1973, 1979). This photoperiodic reaction is thought to be an important component of the climatic adaptation of tree species in the boreal and temperate zones (VAARTAJA 1959; EKBERG *et al.* 1979). It allows the individuals of the northern populations to attain hardiness before the occurrence of the first autumn frosts which is a main selective factor. Several studies have demonstrated close relationships between the bud-set parameters of provenances and their latitude and altitude (*e.g.* DORMLING 1979; KRUTZSCH 1986; KOHMANN 1996). However, a substantial variability is also present within populations for the same trait (SKRØPPA & THO 1997). The importance of bud-set as a trait characterising climatic adaptation is shown by the variation in mortality observed at Hoxmark in the spring of 1997.

The timing of bud-set of the seedlings from the stands was in both experiments considerably different from that of seedlings from the same origin as the stand trees. The seedlings from the stands in West Norway of origin Harz set buds approximately intermediately between the Harz and Norwegian provenance. The offspring of parents that had been subject to transfers to the sites close to latitude 64°N had a considerably earlier bud-set than seedlings from the original provenance. The seedlings from the three stands in Central Norway were also similar in their timing of bud-set, which did not differ from that of the local provenance. Several factors may contribute to the explanation of these observations.

The identities of the planted seedlings were recorded at the establishment of the stands and were noted on maps kept by the forest owner. In Verdal, the mean diameter of the 15 seed trees of Harz origin was 24% larger than that of the 15 trees sampled in the adjacent stand of local provenance. This is consistent with what is known of the superior growth of trees of Harz origin when growing under good local climatic conditions even at a northern site.

A large proportion of successful crosses may take place with pollen from surrounding stands (KOSKI 1970). The two localities in West Norway, however, are outside the natural range of Norway spruce and all planted stands in that area are established with seedlings of origin Harz. In Verdal, on the other hand, it is likely that a large proportion of the offspring in the Harz stand are from fertilisation with pollen of local origin. In the extreme case that all seedlings are provenance hybrids, then their average timing of bud-set should take place intermediately between the time of bud-set of the seedlings of local and Harz provenance, as additive inheritance is dominating for this trait (ERIKSSON *et al.* 1978; SKRØPPA & THO 1997). However, the mean bud-set of the seedlings from the Harz stand was close to that of the local provenance and far from being intermediate. This shows that pollen flow from local stands cannot be the main reason for the observed results, even if it may have been a contributing factor.

An explanation of the observed results by natural selection implies that strong selective events causing an early bud-set must have taken place either in the nursery, in the establishment and further development of the stand or during the reproductive phase in 1995. Early autumn frost is the selective factor that can be directly related to early growth cessation in Norway spruce (LANGLET 1960; DIETRICHSON 1964). In West Norway such selection is rather unlikely both in the nursery and in the stand as frost events very seldom occur in the early autumn. During the development of

the stand the number of trees is reduced due to competition and specific provenance characteristics may gradually disappear (FISCHER 1949). We have problems, however, to relate the observed directional change in bud-set to the competitive process in these stands.

Natural selection may have played a more important role for the adaptive traits of the seed lots harvested in the stands in Verdal, Central Norway. No records are available of the mortality in the two Harz provenances grown at the Sønsterud Nursery in the period 1950-54. Official temperature statistics (Det Norske Meteorologiske Institutt 1950-54), however, show that frost damage and mortality could have occurred. A possible effect of directional selection in the nursery for early growth cessation can therefore not be excluded. However, the large variability in bud-set percentages among the families from the Harz stand indicates that such selection has not been very efficient. This variation corresponds to what has earlier been observed within German stands for physiological traits (SAUER-STEGMANN *et al.* 1978). In the Harz and L2 seed collection stands in Verdal few trees have died and no visual difference can be observed between the two stands in climatic damage. The conditions in the B3 stand are different. Mortality has occurred in patches, and a large proportion of the surviving trees show signs of having been damaged by frost. The seedlings from this stand showed the earliest bud-set in both nurseries, even earlier than the seedlings of local origin.

Little information is available about a possible occurrence of selection during the reproductive phase. In an experiment exposing the pollen parent grafts to different temperatures and photoperiods during male meiosis and pollen development, JOHNSEN *et al.* (1996) found no effects of the treatments on the autumn frost hardiness of the offspring. The potential effects of gametophytic and sporophytic selection are rather limited due to the low number of pollen grains that can be accommodated in each pollen chamber and the few embryos in a developing seed (OWENS & BLAKE 1985).

In summary, in the B3 stand in Verdal natural selection may have contributed largely to the observed differences in timing of bud-set between the stand offspring and their original provenance. However, selection alone does not explain the results with the Harz stands seedlings from West Norway and Verdal.

Recently, several independent tests have shown that the climate and weather conditions during sexual reproduction influence the adaptive properties of Norway spruce progenies, see review by JOHNSEN & SKRØPPA (1996). Growth cessation and autumn frost hardiness are among the traits that are affected when the parents are moved from a cold to a warm climate

where reproduction takes place. The progenies have a later growth cessation and bud-set and a delayed development of autumn frost hardiness compared to progenies reproduced in the colder native environment. The influencing cause is not known, but the most likely explanation is a regulatory mechanism affecting the expression of genes controlling adaptive traits (JOHNSEN & SKRØPPA 1996). Temperature and photoperiod and/or a possible interaction between the two seem to be the triggering factors. Our observations can be explained by the same mechanisms taking place during sexual reproduction, but this time after transfers to a colder climate than at the site of origin. The weather conditions during reproduction in 1995 in Central Norway were cold, and pollination took place 15 days later than normal. A regulatory mechanism should therefore have ample possibilities to precondition the progenies of the north-transferred provenances to the northern climatic conditions. The extreme variation in bud-set percentages among the Harz families may reflect that selection for early bud-set most likely has not been an important selective factor within the Harz provenance. It may also be that there is variation among trees in response to the climatic conditions during reproduction.

Several influencing factors may explain the observed results from these experiments. Most likely both pollen flow, natural selection and the weather conditions during sexual reproduction in the stands have contributed, but with different importance in the seed stands. The possibility of responses to environmental signals during the reproductive process will have implications for the understanding of the evolution of Norway spruce in the boreal zone and for the interpretation of provenance differences. This should be considered when stand seed is collected in areas with stands of introduced provenances and in the development of strategies for conserving the genetic resources of the species.

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