Rooting Success of Cuttings from Young *Picea abies* in Transition to Flowering Competent Phase

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Abundant flowering occurred in a central Swedish trial with 10-yr-old *Picea abies* L. (Karst.) cuttings, taken on 4-yr-old seedlings. Large deviations in cone-set between clones were assumed to reflect different stages in transition from juvenile to flowering competent phase. Rooting success and first-yr growth performance (leader length, leader origin and plagiotropic growth) were studied on cuttings originating from the upper and lower parts of the crown in 15 clones with heavy cone-set and 15 clones without cones. Twigs from the lower part of the crown had a significantly higher rooting percentage. Cone-set did not have an effect on any of the variables analysed. The results suggest that flowering ability and rooting capacity are independent age-related processes, implying that selection for high rooting capacity in clonal forestry does not reduce flowering competence. The results will have a great impact on breeding of *P. abies*, since both early flowering and high rooting ability are important traits for reducing the turnover time of the breeding cycle. *Key words: clonal variation, crown position, cuttings, flowering capacity, maturation, Norway spruce, plagiotropism.*

INTRODUCTION

The concept of maturation is of fundamental importance in forest tree breeding and propagation of genetically improved trees. In woody plants, maturation involves a reduced capacity to form adventitious roots and an increased ability to form flowers (Doorenboos 1965). Several other important physiological and morphological changes also take place during maturation (see review, Hackett 1985), e.g. reduced seasonal duration of growth (von Wühlish & Muhs 1986, Ununger et al. 1988), declined annual growth of individual shoots (Borchert 1976) and a changed growth pattern, with predetermined growth becoming increasingly more important than free growth (Jablanczy 1971, Ununger et al. 1988). Rooting ability in Norway spruce (*Picea abies* L. (Karst.)) has been found to decrease gradually until the trees are over 20 yrs old (Roulund 1975). This decline also involves a stronger tendency towards plagiotropic growth of the cuttings (Roulund 1979, Dekker-Robertson & Kleinschmit 1991). Norway spruce generally starts to flower late, after 15–20 yrs under good conditions (Wareing 1958) and cone-set reaches an appreciable extent after 30–40 yrs in Scandinavia (Wright 1964). Flowering ability changes gradually with age in Norway spruce (Dormling et al. 1976). In

other conifer species, flowering competence is reached faster and more abruptly, e.g. in black spruce (Tousignant et al. 1995), white spruce (Wright 1964) and radiata pine (Sweet 1973). The interrelation between the various changes observed to occur with age has required a characterization of maturation stages. Greenwood (1987, 1995), Poethig (1990) and Meier-Dinkel & Kleinschmit (1990) defined four phases: embryogenic, juvenile, transition and mature reproductive. Maturation is, however, a complex web of simultaneous processes that take place at different rates and in different parts of the organism. A generalized definition of the various phases would imply that the processes are highly correlated. This generalization is in contrast to the idea that age-related processes are largely genetically independent (Borchert 1976, Poethig 1990). From a breeder's point of view, it is essential to clarify the relations. If rooting ability and flowering capacity are genetically linked, there is a risk that selection for one trait may lead to a negative correlated response in the other trait.

The relation between rooting and flowering was studied in young black spruce (*Picea mariana* [Mill.] B.S.P.) by Tousignant et al. (1995). They suggested that flowering and rooting were two independent

maturation processes. Topophysis effects, i.e. crown position of the cutting, were much larger than effects due to flowering capacity (cyclophysis effects). A Norway spruce clonal experiment in central Sweden flowered for the first time in 1995 at a cutting age of 10 yrs, or 14 yrs from seed. Weather conditions the previous year were optimal for inducing reproductive organs, but there were still large deviations among clones, some with abundant cone-set and others without cones. The variation was hypothesized to reflect different stages among clones in transition from juvenile to flowering competent phase. An experiment was conducted to determine how rooting success and cutting performance were correlated with flowering capacity and crown position of the donor plant.

MATERIALS AND METHODS

Field experiment

The Norway spruce clones in this field study were selected and propagated from 4-yr-old seedlings of Belorussian provenances in 1985. Original selection was based on seedling height, vigour and growth rhythm. The experimental trial was planted in 1988 with 3-yr-old container-grown cuttings. It was established as a demonstration plot with 200 clones and 5 ramets per clone. The ramets for each clone were planted in a five-tree row plot, with no replicates within the trial. The experiment is located on a former farm-field in central Sweden (60°16′ N, 16°47′ E, 50 m a.s.l.). The same clones were tested under field conditions in other trials, e.g. for height growth and growth rhythm.

The number of cones on each ramet was assessed in November 1995. On average, 58% of the clones were bearing cones, and in the whole trial there were 3.7 cones ramet^{-1}. Comparison with clonal values for height in field trials, indicated that cone-set and height growth were not correlated ($r < 0.03$). A weak ($r = 0.21$) but significant ($p = 0.003$) correlation between cone-set and timing of bud burst was found. Late-flushing clones had a higher frequency of cone-bearing trees than early-flushing clones (Fig. 1). A plausible explanation is that, for early-flushing clones, bud differentiation occurred too early in 1994 to take advantage of the warm period that started in early July 1994 in central Sweden. The warm weather in July could have contributed substantially to the abundant flowering in 1995. There was also a large variation in flowering capacity among clones with the same date of bud burst.

Because of the probable impact of phenology on flowering, clones for this particular study were selected only from among those with an intermediate flushing date. Selections were divided into two groups: 15 clones with no cone-set and 15 clones with a heavy cone-set (6–45 cones ramet^{-1}). Each of the selected clones had five living ramets. The selected clones were randomly distributed in the experiment. There were no indications that flowering varied with location in the trial. A clone with prolific cone-set could often be located next to a clone without cones.

Rooting study

From each of the 30 selected clones, dormant cuttings were taken from both the upper third and the lower third of the crown. At least 50 twigs were harvested from each clone and crown position. Twigs were evenly distributed over all of the five ramets. Harvesting took place on February 2 1996. The twigs were immediately packed in sealed plastic bags and transported to SkogForsk's field station at Brunsberg, where they were cold-stored until inserted in rooting medium in a greenhouse on February 8–9.

The greenhouse area was divided into four blocks. Each treatment (cone-set group, clone and crown position) was represented by plots with 12 cuttings in a row per block. The total experiment comprised 15 clones × 2 cone-set groups × 2 crown positions × 4 blocks × 12 cuttings, i.e. 2880 cuttings in total. Surplus cuttings were added for destructive control of rooting rate. The average length of the twigs was measured for each plot. Rooting was performed in Styrofoam containers (Cellpot III with 130 cm^3 cavity
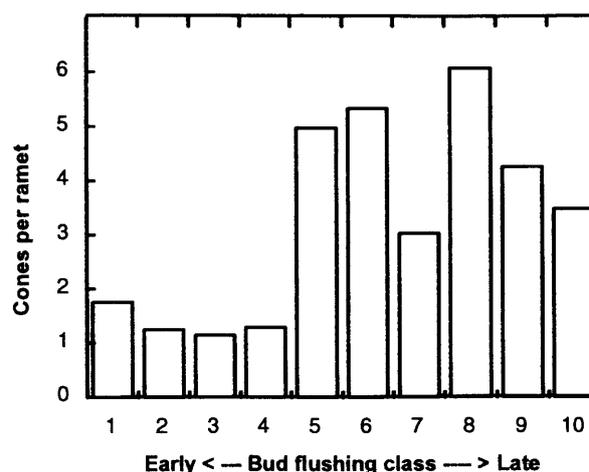

Fig. 1. Cone-set (number of cones per ramet) in clones separated in bud-burst classes. Clones for the rooting experiment were selected within classes 5–9.

and 400 plants m^{-1}) with a 50/50% mixture of peat and Leca grains (2–6 mm diameter). To enhance rooting, the twigs were given a fresh cut prior to being inserted. The cuttings were stuck directly into the substrate, without a pre-formed hole. Temperature in the substrate was maintained at 20–22°C, and in the air at less than 10°C during the rooting phase. Irrigation was applied through mist nozzles. No additional light was applied. To increase air humidity surrounding the cuttings, small plastic tents were built 1 month (March 11, 1996) after the cuttings were stuck. Fungicides were applied on two occasions, in early March and mid April. Despite the ambition to keep air temperature low, many of the cuttings burst their buds. Average rooting was consistently controlled during the greenhouse period, and the rooting rate was found to be uneven and correlated with the visual vigour of the twigs. In the later phase of the rooting, during late April and May, there was an obvious conflict between cuttings with developed root systems, that suffered from excessive watering and those that had not rooted and still needed moist conditions. Over-watering of early-rooted cuttings might have contributed to low vigour and mortality after the cuttings had been transferred outdoors. In May, when rooting was assumed to be completed, rooting success was assessed by pulling. Based on preliminary tests, all cuttings that were attached to the substrate were regarded as rooted. The rooted cuttings were transferred outdoors on June 28, where they were kept and maintained with watering and fertilization. Overwintering also took place outdoors.

In late spring 1997, before bud burst, assessment was made of plagiotropism in five classes, modified from Kleinschmit & Schmidt (1977) (Fig. 2). The length of 1996 year's leading shoot was measured and leader origin was recorded in two classes: if the leading shoot emerged from the apical bud (1) or from a lateral bud (0).

Statistical analysis

The effects of clone, cone-set group and crown position on rooting success were calculated from plot-mean values with the following statistical model:

$$y_{ijkl} = \mu + a_i + b_j + c_{k(i)} + d_l + ab_{(ij)} + e_{ijkl}$$

where y_{ijkl} is the mean rooting percentage in block l of cuttings harvested in cone-set group i on crown position j in clone k; μ is the overall mean rooting percentage; a_i is the effect of cone-set group i ($i < 1$,
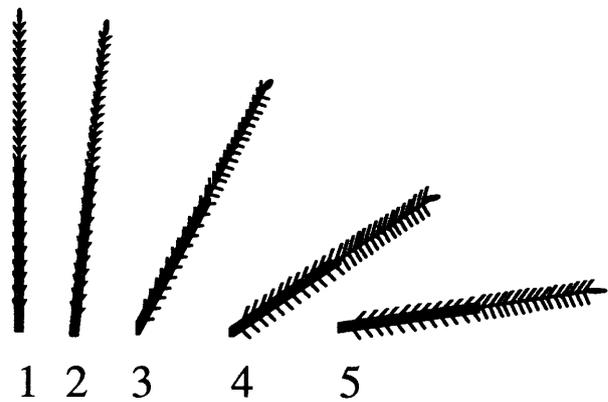

Fig. 2. Classification of plagiotropism. The angle refers to a line between apical bud and stem base in relation to the vertical line. Class 1 is fully ortotropic cuttings; class 2 has an angle divergent from the vertical of maximum 22°; class 3 has an angle between 22 and 45°; class 4 has an angle between 45 and 66°; class 5 has an angle of more than 66° (fully plagiotropic cuttings). Modified from Kleinschmit and Schmidt (1977).

2); b_j is the effect of crown position j ($j < 1$, 2); $c_{k(i)}$ is the effect of clone k nested in cone-set group i ($k < 1, ..., 15$); d_l is effect of block l ($l < 1, ..., 4$); $ab_{(ij)}$ is the interaction effect between cone-set group and crown position; and e_{ijkl} is the random residual error. Factors a_i, b_j, d_l and $ab_{(ij)}$ were regarded as fixed and $c_{k(i)}$ as random.

Only 14.7% of all the inserted cuttings, or 53.1% of all the rooted cuttings, were still alive in spring 1997. Among cuttings from the upper crown position, 3.4% of inserted cuttings were alive, and from the lower crown position 25.9%. With respect to the low remaining number of cuttings from the upper part of the crown, plagiotropic growth, leader origin and leader length were only analysed for cuttings from the lower crown position (in total, 374 living cuttings). The effect of crown position b_j and the interaction effect $ab_{(ij)}$ between cone-set group and crown position were therefore excluded from the model above. Plagiotropism was treated as a continuous variable, because the distribution was found to be close to normal. The calculations were based on plot-mean values weighted with the number of trees per plot to compensate for imbalance due to mortality (Williams & Matheson 1994).

Plot-mean values of the binary variables rooting percentage and leader origin were transformed to arcsine-values prior to the analysis. All analyses of variance were run in the procedure Mixed (SAS Institute Inc. Cary, NC, USA).

Table 1. *Rooting percentage of cuttings by cone-set group and crown position*

Pooled standard errors from mean square error in the analysis of variance were 4.2% for each combination of cone-set and crown position, 3.9% for the means over crown positions and 3.0% for the means over cone-set groups

Crown position	Cone-set		
	No Cones	Cones	Mean
Upper	11.1	8.5	9.8
Lower	48.4	42.3	45.4
Mean	29.8	25.4	27.6

Correlation between clonal means (estimated as least square mean values) for rooting success, cones per ramet, twig length, leader origin, plagiotropism and leader length were determined as Pearson's correlation coefficient. Only twigs from the lower crown position were considered.

RESULTS

The average rooting percentage was slightly, although not statistically significantly, higher for clones without cone-set than for clones with cone-set (Tables 1 and 2). At the lower crown position, the rooting success was 4–5 times higher than at the upper position for both the non-flowering clones and for the flowering clones. Among cuttings from the lower crown position, there was no difference in survival between clones with or without cone-set (25.6% and 26.2% surviving cuttings of all inserted, respectively). The analysis of variance on mean rooting percentage showed no effect of cone-set group, but a strong significant effect of crown position (Table 2). Interaction effect between cone-set group and crown position on rooting percentage was not significant.

Among cuttings from the lower part of the crown, rooting percentage was significantly and positively correlated with twig length before rooting, with leader origin and leader length, but not with number of cones per ramet or with plagiotropic growth (Table 3, Figs. 3 and 4).

The average frequencies of leaders from apical buds were 62% and 58% for clones with and without cones, respectively, and leader lengths were 40 and 46 cm for each of the two groups. The average plagiotropism class was 2.9 for clones with and 2.8 for clones without cone-set. None of these differences between the two groups were significant. There was no effect of cone-set group on leader length, leader origin or plagiotropic growth (Table 3). Block had a significant effect on plagiotropism. Correlations between cones per ramet, leader origin and plagiotropism were non-significant (Table 4).

The effect of twig length before rooting on rooting success was not included in the ANOVA since the twigs were both longer ($\bar{x} = 69$ mm) and more vigorous in the upper part of the crown than in the lower part ($\bar{x} < 52$ mm). The main effect of crown position therefore includes the effect of twig length on rooting rate. As noted above, the correlation with rooting rate was significant when only cuttings from the lower part of the crown were considered. Twig length before rooting also correlated with leader length (Table 4).

DISCUSSION

The main result of this study was the absence of a cone-set effect on the variables rooting success, plagiotropism, leader origin and leader length of the cuttings. The relatively strong clonal effects on rooting success and leader length were independent of flowering abundance. The crown position of the twigs was most important for the rooting result, even more

Table 2. *Test of fixed effects on rooting percentage of cuttings harvested at two crown positions on Norway spruce clones with and without cone-set*

Source of variation	NDF[a]	DDF[b]	F[c]	p < F
Cone-set group	1	28	0.39	0.54
Crown position	1	205	285.9	0.0001
Cone-set group × crown position	1	205	0.39	0.53
Block	3	205	3.32	0.021

[a] Degrees of freedom in the nominator.
[b] Degrees of freedom in the denominator.
[c] Type III F-value from SAS.

Table 3. *Test of fixed effects on leader length, leader origin and plagiotropic growth of cuttings harvested on Norway spruce clones with and without cone-set*

All cuttings were harvested from the lower part of the crown

Source of variation	NDF[a]	DDF[b]	Leader origin		Leader length		Plagiotropism	
			F^c	$p < F$	F^c	$p < F$	F^c	$p < F$
Cone-set group	1	26	0.03	0.87	1.12	0.30	0.14	0.71
Block	3	52	0.62	0.61	1.44	0.24	9.26	0.0001

[a] Degrees of freedom in the nominator, the same for all variables.
[b] Degrees of freedom in the denominator, the same for all variables.
[c] Type III F-value from SAS.

so when considering that the twigs in the lower position were shorter and visibly less vigorous. The results support other reports on Norway spruce, e.g. Dormling et al. (1976) and Roulund (1979), showing that twigs from lower branches generally form adventitious roots more easily than from upper branches. This indicates that the lower branches are ontogenetically younger than the upper branches (Hackett 1985).

The lack of relationship between cone-set and the other variables is in accordance with the results on black spruce by Tousignant et al. (1995). They presented two hypotheses to explain the lack of relationship. First, female cone production might not be a good indicator of sexual maturity. Second, sexual maturity might not be directly correlated with other aspects of maturation. In our study, there were large differences in flowering capacity among clones, even if they were of the same chronological age and had received the same conditions during bud differentia-

tion in the year before flowering. This indicates that the difference in cone production was of genetic origin rather than due to different conditions promoting flowering. The source of the genetic variation could be variation in the length of the juvenile phase (flowering precocity) or variation in flowering capacity (fruitfulness). These two traits have been suggested to be under separate genetic control, at least for *Pinus taeda* (Schmidtling 1981) and *Pinus contorta* (Ying & Illingworth 1986). In our study, we cannot exclude the possibility that the clones differed in flowering capacity. However, the relatively low age of the clones and the separation of a group of clones with no reproductive organs present at all (no-cone group) and a group with abundant flowering, are arguments for the groups differing in their length of the juvenile phases. In birch, Stern (1961) observed a genetic variation in the length of the juvenile phase. According to the hypothesis of Robinson & Wareing (1969) and formulated by Greenwood & Hutchison
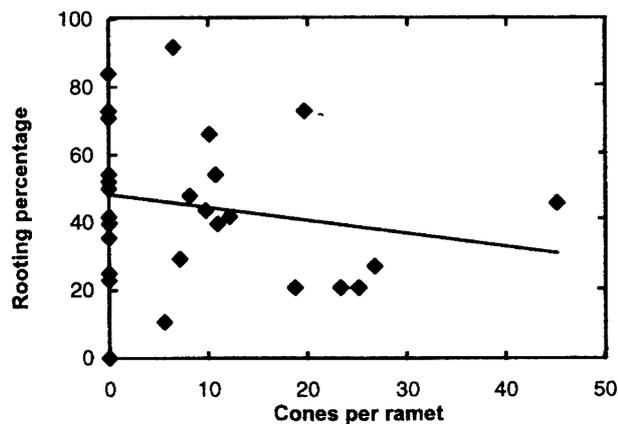

Fig. 3. Relationship between rooting percentage and cones per ramet based on clonal mean values ($r = -0.19$). Cuttings from the lower part of the crown only.
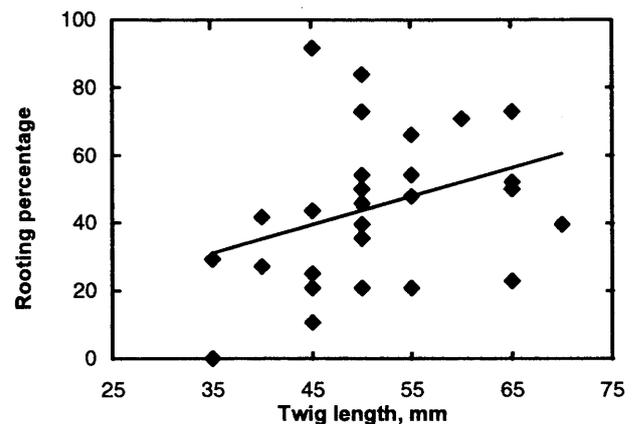

Fig. 4. Correlation between rooting percentage and twig length before rooting based on clonal mean values ($r = 0.37$). Cuttings from the lower part of the crown only.

Table 4. *Pearson's correlation coefficients based on clonal mean values (n = 30). Only cuttings from the lower crown position*

Significance levels are given below the coefficient: ns, not significant; $^a p < 0.05$; $^b p < 0.01$

	Twig length before rooting	Cones per ramet	Leader origin	Plagiotropism	Leader length
Rooting percentage	0.37^a	-0.19 ns	0.50^b	0.10 ns	0.58^b
Twig length before rooting	–	-0.31 ns	0.28 ns	-0.19 ns	0.40^a
Cones per ramet		–	-0.33 ns	-0.02 ns	-0.08 ns
Leader origin			–	-0.36 ns	0.16 ns
Plagiotropism				–	0.30 ns

(1993) as "continuing cell division of an apical meristem may be the actual mechanism that drives the maturation process", the interpretation of our results could be that there is a genetic variation in the number of cell divisions of the apical meristems needed to pass the juvenile phase or that the cell-division activity varies among the clones. For reaching the stage when rooting ability decreases, fewer cell divisions seem to be needed.

Rooting success and vigour of the cuttings may have been physically affected by the flowering, i.e. abundant flowering might result in lower vigour of the twigs. This should lead to an increase in the differences in rooting, leader length, leader origin and plagiotropism between cone-bearing and non cone-bearing clones but, instead, the differences were very low in this study. The hypothesis of independence of onset of flowering and vegetative maturation is supported by Borchert (1976), who stated that "there is good evidence of independent genetic control with respect to their quantitative expression and rate of change during aging". Rooting ability and onset of flowering were given as examples of characters covered by the statement. Maturation may proceed more rapidly for vegetative traits than for onset of flowering (Meier-Dinkel & Kleinschmit 1990).

In clonal forestry, rooting performance is an economically important trait to select for (Högberg et al. 1995). Clonal propagation is also an important tool in many tree improvement programmes (Danell 1991). Conversely, the age of reaching flowering competence governs the turnover time in tree breeding, and the breeder therefore struggles to reach as early a flowering as possible (e.g. Wright 1964). Mass propagation by means of seed is another measure that favours selection for early flowering competence and seed production. If rooting and flowering competence are genetically independent, the risk of undesired

correlated responses after selection will be diminished, and this would have important implications for breeding and mass propagation. One example is that cutting propagation could replace grafting when establishing Norway spruce seed orchards. In Sweden, cuttings are generally far cheaper to produce than grafts.

The absence of a correlation between clonal values for field height and cone-set supports the results obtained by Nienstaedt (1985), who examined fruitfulness of 9–10-yr-old white spruce. In that study, family differences in female strobili production were highly significant, and ranking between families in flowering was consistent among years. The number of female strobili was weakly but positively correlated with height, and Nienstaedt concluded that there is no conflict between selection for fast early growth and early production of female and male strobili. Similar conclusions were also reached by Chambers et al. (1997) for early flowering and early growth in *Eucalyptus globulus*.

In conclusion, the results suggest that flowering ability and rooting capacity are two independent age-related processes. The lack of correlation implies that selection for high rooting capacity in clonal forestry does not necessarily lead to reduced flowering competence. The results will have a great impact on breeding of *P. abies*, since both early flowering and high rooting ability are important traits for reducing the turnover time of the breeding cycle. The lack of correlation between height and cone-set are also encouraging, as this indicates that selection for height growth does not affect flowering ability. However, the genetic relationship between flowering precocity and flowering abundance on one hand, and growth on the other hand, need to be studied further in Norway spruce.

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