Effect of Spacing on Growth, Especially Predetermined and Free Shoot Growth of Norway Spruce (Picea abies (L.) Karst.)

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Abstract

Four year old Norway spruce stecklings of 12 clones in total (4 clones each of 3 provenances) were grown at 22 × 22, 35 × 35, 50 × 50, and 65 × 65 cm for two years in the nursery. Shoot growth was distinctively larger on densely spaced trees while diameter growth was reduced. Free growth occurred much more frequently and also predetermined growth elongated more and quicker on densely spaced trees, although at the different spaces an equal number of primordia had been initiated (at least in the first year of the experiment). Denser spacing caused the trees to flush earlier. Between clones in provenances and provenances differences in several characters were found. There seem to be different modes of adaptation. While plants from the provenance Istebna prefer the predetermined growth pattern, plants from the other provenances switch more easily to the free growth pattern if conditions are favourable.

Key words: *Picea abies*, shoot growth, predetermined growth, free growth, spacing, mode of adaptation.

Zusammenfassung

Vierjährige Fichtenstecklinge von drei Provenienzen mit jeweils 4 Klonen wurden in 22 × 22, 35 × 35, 50 × 50 und 65 × 65 cm-Abstände gebracht und über zwei Jahre beobachtet. Während das Höhenwachstum bei den engen Abständen größer war, sind bei den weiteren Abständen größere Durchmesser gebildet worden. Freies Wachstum wurde bei eng stehenden Pflanzen häufiger gebildet und prädeterminiertes Wachstum wurde größer und schneller gestreckt, obwohl (zumindest im ersten Beobachtungsjahr) in den einzelnen Abstandsstufen eine gleiche Anzahl von Nadelprimordien initiiert worden war. Engere Pflanzenabstände bewirkten einen früheren Austrieb. Zwischen Klonen in Herkünften und zwischen Herkünften wurden deutliche Unterschiede bei verschiedenen Wachstumsmerkmalen gefunden. Zwischen Herkünften scheint es verschiedene Formen der Anpassung zu geben. Während Pflanzen der Herkunft Istebna eher die Form des prädeterminierten Wachstums vorziehen, können die Pflanzen anderer Herkünfte leichter zum freien Wachstum überwechseln, wenn die Umweltbedingungen günstig sind.

Introduction

Predetermined and free growth are shoot growth characters which occur on *Pinus, Picea, Abies, Pseudotsuga,* and other species. The most frequent of these forms of shoot growth is predetermined growth while free growth occurs in the seedling and juvenile stage (von Wühlisch and Muhs 1986). Research has been focused on predetermined and free growth for different reasons. One was to find ways to manipulate shoot growth for instance to accelerate it (Dormling *et al.* 1968, Farrar 1961) or to terminate it early enough so shoots can harden off before winter (Rosvall-Åhnebrink, 1982). Another reason was to use these characters to find provenance differences to possibly be able to identify provenances or even to use these characters for early tests (Schmidt-Vogt 1964, Hoffmann 1965, Holzer 1967, 1975, Magnesen 1971, Pollard and Logan 1974, Cannel and Johnstone 1978, Ununger 1981). All of these studies showed that besides genetic control predetermined and free growth are controlled by the prevailing environmental conditions. Of these, the length of the daily photoperiod has an overruling control over the termination of free growth. There are many further environmental factors which influence predetermined and free shoot growth, in fact, probably all growth influencing factors affect free and predetermined growth, as for instance nutrient supply (Schmidt-Vogt 1964, Dormling *et al.* 1968, von Wühlisch and Muhs 1987), water supply (Walters and Soos 1961) or even humidity (unpublished data).

For the development of early tests it is important to know the influence of environmental effects on predetermined and free shoot growth. The better the knowledge of these factors is, the better can early tests be adjusted and the more distinct are the results (von Wühlisch and Muhs 1986). This study investigates the influence of spacing on shoot growth. From the well known fact that densely spaced trees grow higher but less in diameter than solitary trees, it may be postulated that densely spaced trees produce longer shoots than widely spaced trees. The questions raised are: does this bigger shoot growth result from free or predetermined growth or both, and how strong is the influence of spacing on predetermined respective free growth? Can free growth be induced by dense spacing? Are there differences in the patterns of shoot growth between provenances?

Material and Methods

4-year old stecklings (rooted cuttings) of three provenances were used: Tännesberg, Federal Republic of Germany; Istebna, Poland; and Nødebo, Denmark (a provenance probably originating from the Black Forest, according to informations of the Arboretum at Hørsholm, Denmark). Of each of these provenances 4 clones were included in the experiment. Before the experiment, the plants were kept in 2-liter pots spaced at 20 × 20 cm. Im January they were potted into 5-liter pots and in March they were arranged into 4 different spaces: 22 × 22, 35 × 35, 50 × 50 and 65 × 65 cm. Except for the densest spacing, the pots (with the plants) were put into larger clay pots to keep them from heating up more than pots of the denser spaced plants because more sunshine can reach these pots. Before the second year of the experiment, the plants were repotted in wintertime into 7.5 liter pots.

The experimental design comprised 4 square blocks, one for each spacing. The blocks were divided into 4 randomized repetitions. Each block was surrounded by one row of plants of the same material and at the respective spacing.

Plant heights, lengths of predetermined as well as free growth, and root collar diameters were measured. Elongation of the leading shoot was measured in weekly intervals. Frequency of terminal free growth on the leading shoots was recorded, taking also lateral free growth on leading shoots into account where terminal free growth did not occur. Furthermore, date of bud break and termination of shoot elongation were recorded.

Results

The stecklings appeared to be healthy and in good condition throughout the experiment. At the beginning of the experiment (year n - 2) the branches of the plants of the smallest spacing overlapped and there was such a small amount of light reaching the bottom that some of the lower branches died during the first year (n - 1) of the experiment. In the second-smallest spacing (35 × 35 cm) branch tips of neighbouring plants were just touching, letting enough light through for bottom branches to grow. By growth of the plants in the first year, spaces became smaller in the second year (n) of the experiment and branches of plants in the second-smallest spacing were now also interlocking and the branch tips of the 50 × 50 cm plants were touching. Only between the plants spaced at 65 × 65 cm there were still distinct gaps.

Height Growth

Height growth was strongly affected by the treatments already in the first year of the experiment, with the stecklings at a dense spacing growing in total about 10 cm higher than those spaced widely. In the second year this difference increased to 28 cm (*Table 1*). This response is mainly due to predetermined growth with densely spaced stecklings elongating their predetermined growth about 1.5 times more than widely spaced plants in the first year and about twice as much in the second (*Table 1*). The differences in height between the provenances remained about equal during the experiment with Tännesberg and Istebna having similar heights and Nødebo being significantly smaller (*Table 1* and 2).

Table 2. — **F-Values of Different Characters in the Second Year (n).**

	Source of variance				
	Treat- ments (T)	Provenan- ces (P)	Clones in P	T x P	T x C in P
Height	29.4***	11.8***	4.9***	1.7 -	0.6 -
Length of predet. growth	70.3***	0.0 -	6.7***	0.8 -	0.8 -
Root collar diameter	38.3***	10.0***	4.6**	2.0 -	0.6 -
Flushing date	22.6***	2.4 -	14.8***	0.4 -	1.0 -
Term. of shoot elongation	0.9 -	1.0 -	3.6***	3.1***	1.1 -
Duration of shoot elongation	3.2 -	3.5 -	2.9**	2.2 -	1.0

*** = significant at P < 0.001, ** = significant at P < 0.01.
- not significant.

Free growth occurred generally very little. In the first year there was no terminal free growth on plants at the two wider spaces and only on some trees (4 resp. 6%) there was lateral free growth on the leading shoots. On the densely spaced trees frequency of free growth was much larger (12.8 resp. 31%) and also there occurred some terminal free gowth. This can add significantly to the yearly shoot increment of some plants but averaged over all plants of the treatment, free growth length is insignificant compared to the length of predetermined growth (1,0 resp. 0,4 mm). In the second year, there was altogether a little more free growth than in the first but the most frequent and longest free growth occurred on the second smallest spacing (50 × 50 cm) and not on the most densely spaced plants.

Differences between provenances in predetermined growth became smaller during the experiment and the values are almost equal at the end of the experiment (*Table 1*). However, between the different clones in provenances there are distinct differences (*Table 2*). Also in free growth no distinct provenance differences were found, al-

Table 1. — **Means and Standard Deviation of Different Characters of Young Norway Spruce Trees of Different Provenances Growing at Different Spaces.**

	Spacing (cm)				Provenances		
	22 x 22	35 x 35	5C x 50	65 x 65	Nodebo	Tännesberg	Istebna
Height (n - 2) (mm)	709 ±129	705 ±142	706 ±126	707 ±129	547 b	796 a	776 a
Height (n - 1) (mm)	1026 ±125 a	970 ±139 b	948 ±139 b	929 ±163 b	791 b	1055 a	1058 a
Height (n) (mm)	1355 ±199 a	1278 ±150 b	1149 ±144 c	1077 ±153 d	1038 b	1297 a	1309 a
Length of pred. gr. (n - 1) (mm)	313 ± 61 a	264 ± 57 b	242 ± 49 c	222 ± 56 d	243	258	281
Length of pred. gr. (n) (mm)	323 ± 62 a	299 ± 79 b	195 ± 51 c	141 ± 45 d	235	235	239
Length of free gr. (n - 1) (mm)	1,0 ± 0,4	0,4 ± 0,2	0	0	0,3	0,7	0,0
Length of free growth (n) (mm)	6 ± 5,2	18 ± 20	6 ± 4,1	7 ± 5,1	8	7	11
Frequency of free gr. (n - 1) (%)	31,2	12,8	4	6	21,0	9,7	10,9
Frequency of free gr. (n) (%)	44	57	29	15	45	40	23
Root collar diameter (n - 1) (mm)	14,8 ± 2,1 d	15,9 ± 1,1 c	16,7 ± 1,9 b	17,1 ± 2,4 a	14,4 b	17,2 a	17,0 a
Root collar diameter (n) (mm)	21,4 ± 3,8 d	24,5 ± 3,4 c	28,1 ± 3,1 b	28,5 ± 2,5 a	22 b	28 a	26 a
Flushing date (n - 1)	May 14 ± 7,7	May 14 ± 6,5	May 15 ± 7,2	May 15 ± 7,1	13.5.	11.5.	20.5.
Flushing date (n)	May 14 ± 8,2 a	May 16 ± 7,7 b	May 17 ± 7,4 c	May 21 ± 7,8 d	14.5.	14.5.	23.5.
Terminat.of shoot el.(n - 1) (date)	July 9 ± 7,4	July 10 ± 8,5	July 6 ± 5,5	July 4 ± 7,8	5.7.	8.7.	9.7.
Terminat. of shoot el.(n) (date)	July 15 ± 5,0	July 17 ± 7,8	July 14 ± 12,0	July 9 ± 9,9	18.7.	11.7.	13.7.
Duration of shoot el. (n - 1) (days)	57 ± 7,8	56 ± 8,9	52 ± 4,1	50 ± 5,8	54 a	58 a	50 b
Duration of shoot elong. (n) (days)	63 ± 7,2	62 ± 11,8	59 ± 12,9	50 ± 11,3	64	58	52

The length of free growth is given as average of all plants. For the frequency of free growth lateral free growth has been included when there was no terminal free growth on the leading shoot. Standard deviation of flushing date and termination of shoot elongation is given in no. of days. (n - 2) = beginning of the exp., (n - 1) end of the first year of the exp., (n) = end of the second year of the exp. Values associated by different letters are significantly different at P < 0,5.

though Istebna showed a different pattern than the other two provenances. With 23% occurrence of free growth it had only half the frequency of the other provenances but with averagely 11 mm free growth length it had the longest free growth increment. Once terminal free growth is initiated in Istebna it apparently grows to a much greater length than in the other provenances.

Diameter Growth

The development of the root collar diameter was vica versa as in height growth with significantly larger diameters on wide-spaced trees than on densely spaced trees. In the second year this difference increased from 2.3 to averagely 7.1 mm (*Table 1* and *2*). Between provenances and clones in provenances root collar diameter is distinctly different. According to their height growth performance, Tännesberg and Istebna had the biggest diameters while Nødebo was distinctly smaller.

Phenological Characters

Time of bud break was influenced very little in the first year by the treatments but in the second year a distinct influence became apparent. The widely spaced plants flushed averagely about one week later than plants spaced densely. Provenance differences in flushing were small but between clones in provenances they are distinct (*Table 2*).

Termination and duration of shoot elongation were influenced only little by the treatments. However, there is a tendency recognizable that shoot elongation terminates a little earlier in widely spaced than in densely spaced plants (*Table 1*). As in flushing, no provenance but clone-in-provenance differences were found in these characters. In termination of shoot growth an interaction between treatments and provenances shows that the provenances terminate shoot growth differently at different spacings (*Table 2*).

Correlations

Correlations were calculated between all characters recorded in the different years at the clone level for each treatment separately using Pearsons's product-moment correlations. Between the two years of the experiment heights, root collar diameter, and flushing date are auto-correlated in each of the treatments. Shoot length of predetermined growth is auto-correlated only in the 35 × 35 and 50 × 50 spacing and free growth frequency determined over all treatments is weakly auto-correlated between the two years of the experiment. Among the growth characters correlations between height and root collar diameter as well as height and predetermined shoot length were found in both years and in each treatment. Among phenological characters correlations were found only between termination and duration of shoot growth. Between phenological and growth characters sporadic correlations were found in individual treatments. For instance termination of shoot growth is positively correlated with heights, predetermined growth, and root collar diameter indicating that larger growth is connected with late termination of shoot growth. However, there is no such correlation in the 35 × 35 spacing treatment and in the 50 × 50 and 65 × 65 spacing there are fewer correlations between these characters and one correlation in both treatments between height in the year before the experiment (n - 2) and termination of shoot growth in the second year (n) is negative indicating the complete opposite of the other correlations. No general trend is observable if at a wider or a denser spacing more or closer correlations can be found. More results are given in VON WÜHLISCH (1984a).

Discussion

Predetermined and free growth show a clear response to spacing which fits well into the general picture that densely spaced plants grow higher but less in diameter than solitary plants. Especially in predetermined growth a pronounced response was observed. In free growth the response was even larger but since generally only little free growth occurred, the difference between treatments in absolute values was by far not as large as in predetermined growth.

Very remarkable is the immediate response of predetermined and free growth stating in May after the plants had been put into the different spaces only by March. This demonstrates that besides free growth also predetermined growth is flexible in its response to changing environmental conditions even though it is a two-year process with the development of primordia in one year and their elongation occurring in the following year. The criticism concerning the term "fixed growth" for predetermined growth is supported by these results (SWEET and BOLLMANN, 1976).

The most striking feature is that predetermined and free growth reacted in a similar way to the treatments. Thus, the endogenous control over both forms of shoot growth is similar in response to this treatment. Accordingly, where there is large predetermined growth there is also more free growth and where there is little predetermined growth there is little or no free growth. This agrees with the reactions caused by other treatments such as fertilization, defoliation or short photoperiods (VON WÜHLISCH and MUHS 1987).

Between the provenances only insignificant differences in predetermined growth were found. This agrees with results found by POLLARD and LOGAN (1974). It is difficult to draw a conclusion from this finding. POLLARD and LOGAN found quite some variation in free growth length and concluded that rank changes might be explained by the capacity to produce free growth which would favour early growth of those provenances which are able to produce much free growth (LOGAN and POLLARD, 1975). However, in other experiments (VON WÜHLISCH, 1984a) highly significant provenance differences in predetermined growth were found. Furthermore, distinct differences in this character were found between clones in provenances which indicate that there is genetic variation in predetermined growth. Also the little differences in free growth between provenances or clones in provenances which are smaller than in predetermined growth let the rank-change theory of POLLARD and LOGAN seem to be not very plausible for Norway spruce, even if provenances prove to have adapted to local environments by different shoot growth patterns as is demonstrated by Istebna. Due to missing supportative data a preliminary assumption is that the lacking variation in predetermined growth in the three provenances included is probably a random incidence.

It was intended to treat the material in such a way that free growth should neither be accelerated nor reduced to study the way of induction of free growth. Why generally only little free growth occurred may have different reasons. For instance climatic influences or the choice of provenances (provenances which happen to produce little free growth) or the circumstance that the 4-year-old ramets had reached an age where free growth occurs less frequently (VON WÜHLISCH and MUHS 1986) may be the cause. Furthermore, due to cyclo- respective topophysis effects (SEELIGER 1924, MOLISCH 1929, VON WÜHLISCH 1984b) the stecklings may in a physiological sense be much older than 4 years and may therefore be little inclined to produce much free growth. However, the fact that in the second year free growth occurred more frequently than in the first with 15 to 57% of individuals with free growth may indicate that the environmental influences or even the treatments are responsible rather than physiological age.

The effect of the more densely spaced trees flushing distinctly earlier than widely spaced ones may have different causes. One could be the microclimate which might be a little warmer in the more densely spaced plants. As ERIKSSON *et al.* (1978), CAMPBELL (1980), NIENSTAEDT (1967), WORRALL and MERGEN (1967), and TRANQUILLINI *et al.* (1980) observed, the time of flushing depends largely on the prevailing spring temperatures. Similarly, a larger nutrient supply which caused bigger shoot growth was highly correlated with an earlier flushing of the buds (DORMLING *et al.* 1968, VON WÜHLISCH and MUHS 1987).

Termination and duration of shoot elongation was later and respectively a little but not significantly longer on densely spaced plants. This result may be connected with the larger shoot growth of these plants caused by competition but also the favourable microclimate may have caused a later termination of shoot elongation (DORMLING *et al.* 1968).

It is remarkable that spacing affected growth much more than phenological characters. In almost the same number of days the shoots of the densely spaced trees elongated averagely about twice as fast and grew to about twice the length than the shoots of the widely spaced trees. Thus termination of shoot growth occurred at nearly the same time in all treatments. This indicates that the amount shoot growth has little influence on its termination. However, the variation between clones and provenances and the significant interaction beetween provenances and treatments in termination of shoot growth reveales a certain interpendency (*Table 2*).

The variation found between the 3 provenances and between the 4 clones in each of these provenances reflects a result which has often been found in Norway spruce: a high variation within provenances (SAUER *et al.* 1973, WORRAL 1975, KLEINSCHMIT and SAUER 1976, GÄRTNER 1975, POLLARD and LOGAN 1977). In all of the characters recorded, clear differences were found between the clones in provenances but also between the provenances differences were found which were to be expected with the seed sources being so far apart. Between the provenances Istebna and Tännesberg differences in height and diameter growth are not large. However, growth of the provenance Nødebo is smaller. The presumption that this provenance originates from one of the less well growing Black Forest seed sources (KÖNIG 1981) is not contradicted by this result.

The provenance from Istebna stands out from other provenances in the respect that it flushed late but terminated shoot growth early and yet showed the largest height growth. Furthermore, this provenance developed less frequent free growth compared to its predetermined growth component. This behaviour may be explained by the adaptation to the continental climate in southern Poland with long winters and little precipitation in summer which would not be favourable for a late termination of shoot growth as well as free growth.

As the experiment clearly shows, some of the characters are influenced strongly by spacing. For testing provenances, clones, progenies, etc. this influence may be disturbing. On the other hand it can be used to induce or reduce certain characters as for instance free growth. If for some reason free growth is to be increased the plants should be spaced densely. If better test results can be achieved by a reduction in free growth, a wider spacing should be chosen. However, consideration should be given that not only free growth but also other characters are affected by spacing such as predetermined and diameter growth as well as time of flushing and termination of shoot growth.

The different correlations found between growth and termination of shoot elongation at the clonal level support the theory that provenances which terminate shoot growth late grow higher (VON WÜHLISCH 1984c). This theory however, cannot be generalized for all provenances. As the behaviour of Istebna shows, the mode of adaptation of the provenance has to be considered indicating that this theory may be applicable only to provenances of a certain region. As the differing correlations between the different years and treatments show, the environmental conditions should be controlled carefully to get useful results when implementing this character in early tests.

- To conclude from these findings, shoot growth in Norway spruce can occur in two different forms, namely predetermined and free growth, which basically show the same response to the treatments.
- Thus free growth is not assumed to be "additional" growth, but rather an integrated, complementary part of the annual shoot growth which of course may be reduced to zero in favour of predetermined growth. Free growth can be induced by dense spacing. There seems to be an optimum spacing depending on plant size. Very dense spacing in this study has not increased but decreased frequency of free growth. Even plants from the provenance Istebna which is known to produce little free growth have been stimulated to induce free growth.
- Growth patterns of plants from Istebna (Istebna type) is different from those of both other provenances: they flush later, have a faster growing speed, terminate earlier and seem to have a higher threshold value for inducing free growth which however extends to greater lengths once it has been induced.
- Seasonal growth pattern and especially free growth cannot explain the rank changes of height growth of clones or provenances. This seems to be much more influenced by the life cycle of the tree rather than by the seasonal growth pattern or free growth pattern of young plants.
- Free growth is highly affected by spacing and therefore only of restricted use in early tests except the threshold value at which free growth is induced which may be of interest.

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Differences in the resistance of Douglas fir provenances to the woolly aphid Gilletteella cooleyi

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Summary

Four year old plants of 165 Douglas fir provenances (*Pseudotsuga menziesii*) from the IUFRO seed collection 1966/69 have been evaluated for the resistance against the woolly aphid *Gilletteella cooleyi*. Large differences were found which correspond with the geographical groups within the species *Pseudotsuga menziesii:* northern coastal provenances (green form of Douglas fir) were infested severely, southern coastal provenances from southern Oregon and California were less attacked. Low attack was observed also in northern interior provenances (grey form of Douglas fir). Almost resistant were southern interior provenances (blue form of Douglas fir). The mean values of woolly aphid attack were strongly correlated with the percentage of infested trees within a provenance. — The results correspond very well with the differentiation of terpene types of Douglas fir by other authors.

Key words: Douglas fir, provenances, woolly aphid, resistance, terpene types.

Zusammenfassung

Vier Jahre alte Douglasien (*Pseudotsuga menziesii*) von 165 Herkünften aus der IUFRO-Einsammlung 1966/69 wurden auf ihre Resistenz gegenüber der Douglasien-Wollaus *Gilletteella cooleyi* bonitiert. Dabei ergaben sich Unterschiede, die weitgehend der geographischen Gruppierung innerhalb der Douglasien entsprachen: nördliche Küstenherkünfte (grüne Form der Douglasie) waren sehr stark befallen, südliche Küstenherkünfte aus Oregon und Kalifornien waren schwächer befallen. Geringen Wollaus-Befall hatten die nördlichen Interior-Herkünfte (graue Form der Douglasie). Als weitgehend resistent erwiesen sich die südlichen Interior-Herkünfte (blaue Form der Douglasie). Der

Dedicated to Prof. Dr. W. Langner on his 80th birthday.