Figure 3. — A ten-month-old potted plant.

Figure 4. — An eleven-month-old field established plant.

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Will Traditional Conifer Tree Breeding for Enhanced Stem Production Reduce Wind Stability?

Genetic Variation in Allocation of Biomass to Root Classes and Stem

By C. Ch. N. Nielsen[1]

Abstract

The productivity of different root groups are to a considerable extend influenced by other genes than stem production, which is the basis for a genetic variation in different root/stem-ratios. Traditional selections in conifer breeding programmes for enhanced stem production might reduce the ratio between below and above ground biomass compartments and might as such decrease the wind stability of genetic "improved material".

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Key words: root, root/shoot-ratio, stability, selection, breeding.

Contents

1. The Problem

Main objective of most North European conifer breeding programs is the improvement of stem biomass production. Traits as wood quality, stem form, branch characters and resistance against biotic and abiotic stress factors are given various but usually minor attention.

Tree breeders are concerned about possible negative effects of the selection process. It is though widely expected, that a negative response must be based on a genetic correlation between the affected trait and the stem production capacity. Such genetic correlations are not known to be common. This paper deals with a potential decrease of wind stability caused by traditional breeding for stem production; a negative effect based on the genetic variation of the root/stem-ratio.

2. Theory

2.1. A potential negative effect of breeding on the root/stem-ratio

The selection of "plus trees" with outstanding stem production is carried out in stands or field trials of much different ages. Selections within provenances or progenies may even be carried out in the nursery. Regardless of developmental stage, the selection is usually based on the phenotypic or genotypic value of a *stem production parameter*.

An assessment of *total biomass* would clearly be beneficial compared to the traditional measurements of only *stem volume*, but the effort and resources for complete biomass measurement (including roots) are so substantial, that only easy attainable, above ground parameters are registered. Furthermore, breeders have felt confident to neglect the root biomass, because the auto-correlation between root- and stem-biomass is common known. Thus all breeding programs ignore the question or are based on the assumption that stem biomass is representative for root biomass[2]).

Breeding theory has until now neglected the existence and importance of the genetic variation of root/stem-ratios. The theoretical impact on this parameter by selections for stem biomass will be outlined in *figure 1, 2* and *5*.

Figure 1a presents the phenotypic correlation between root- and stem biomass found in normally distributed pop-

[1]) It is thus assumed that no genetic correlation exists between stem biomass and root/stem-ratio in normal conifer populations. This assumption may be true, and it is maintained in this paper.
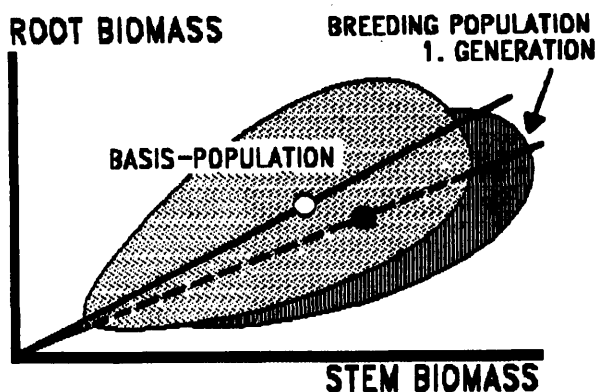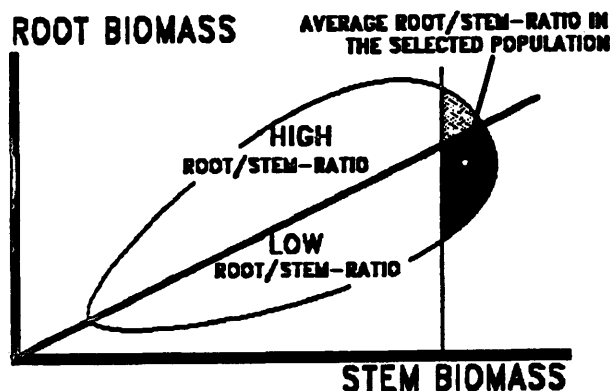
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Figure 1. — a) Phenotypic values of root- and stem biomass in the total and in the selected population. b) Phenotypic correlations between root- and stem biomass after reproduction of the basis and the selected population, assuming some degree of genetic control in root/stem-ratio.

ulations of trees or plants[3]). It is for simplicity assumed that root/stem-ratio is constant for all dimensions of trees, thus the regression line in *figure 1a* intercepts in zero and has a slope equal to the average root/stem-ratio of the population[4]). Trees above and beneath the regression line have phenotypic root/stem-ratios respectively higher and lower than population average.

Owing to the auto-correlation between root- and stem biomass, a selection for stem biomass will cause an indirect selection for root biomass. But because the root-stem-correlation is not 1, the "gain" for root biomass in the selected material will be less than for stem biomass, which causes a change in this biomass relation. This theory is illustrated in *figure 1a*, where a traditional "truncated selection" for stem biomass defines a selected sub-population with a lower average phenotypic root/stem-ratio than the basic population.

[3]) As confirmed in several investigations the variation in root/stem-ratio increase with dimension and age of trees (MELZER, 1962; WILSON, 1975; SANTANTONIO et al., 1977; NIELSEN, 1982 and 1990b).

[4]) Although this assumption is confirmed by the present data (*Figure 6*), it is not valid for all materials. LEDIG et al. (1965) describe root-stem-relation with allometric functions, and NIELSEN (1990b) found an increasing phenotypic "thick root"/stem-ratio with increasing dominance in 92 year old Norway spruce thinning plots. The question of *linearity* of the root-stem regression is of minor importance in respect of the discussed theory. Essential for an unbalanced selection is the slope of the root-stem-curve at the upper-right part of the curve (s. *Fig. 2a*).
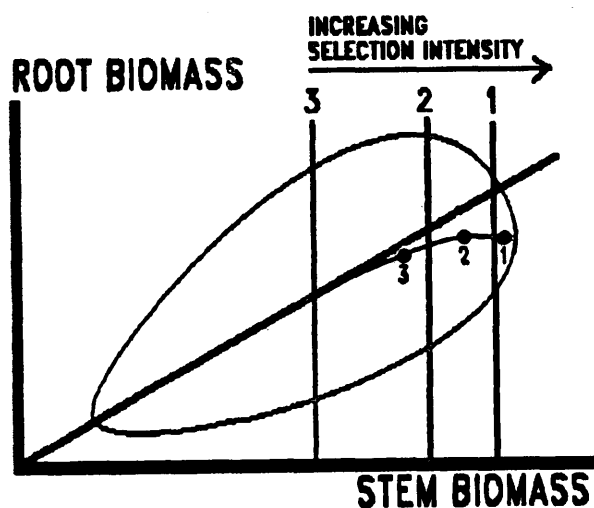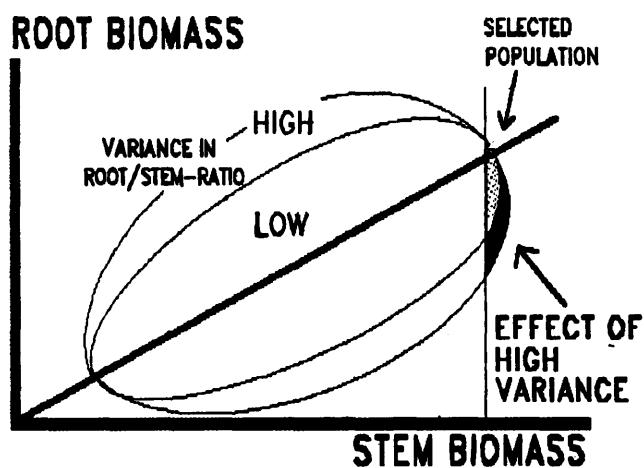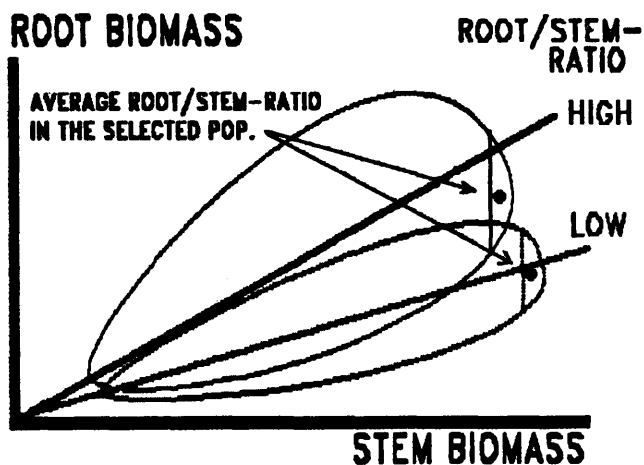
ROOT BIOMASS

ROOT/STEM-RATIO

AVERAGE ROOT/STEM-RATIO IN THE SELECTED POP.

HIGH

LOW

STEM BIOMASS

ROOT BIOMASS

SELECTED POPULATION

VARIANCE IN ROOT/STEM-RATIO

HIGH

LOW

EFFECT OF HIGH VARIANCE

STEM BIOMASS

ROOT BIOMASS

INCREASING SELECTION INTENSITY

3   2   1

STEM BIOMASS

Figure 2. — Three factors affecting the negative effect on root/ stem-ratio by stem biomass selection:

a) Influence of regression slope,
b) Influence of root/stem-ratio variance,
c) Influence of selection intensity.

Essential for the validity of this theory is the degree of genetic control in the phenotypic variation of the root/ stem-ratio.

If the phenotypic variation in *figure 1a* only to some extent reflects genetic differences in biomass allocation,

will a truncated selection for stem biomass change the genetic values for root- and stem productivity with different proportions. The genetic value for stem production will increase relatively more than the value for root production[5]). According to this theory, the ratio between root- and stem-production will be reduced in the breeding population compared to the basic population, which leads to a change in root-stem-regression as illustrated in *figure 1b*.

Root/shoot-ratios are strongly influenced by environmental factors like nutrient supply (COUTTS et al. 1976, 1977; NIELSEN, 1990b), light intensity (MAGNUSSEN, 1980), wind exposition (JACOBS, 1954; NIELSEN, 1990c), plant spacing (NIELSEN, 1990a and b) and thinning regimes (NIELSEN, 1990c). Less work has been done to clarify the role of genetics in the allocation of biomass within trees, but some publications on young material give evidence of substantial genetic control of the root/shoot-ratio (LARSEN, 1985; NIELSEN, 1992). This question is analyzed in chapter 3.5. The negative effect on root/stem-ratio by selections based solely on above ground measurements might be modified by three factors:

1) Slope. The steeper the regression between root- and stem biomass turns out, the more individuals with root/ stem-ratios below average will be selected (*Fig. 2a*).

2) Variance. The higher the phenotypic variation in root/stem-ratio, the more individuals with root/stem-ratios below average will be selected (*Fig. 2b*).

3. Selection intensity. By increasing selection intensity relative more individuals with root/stem-ratios below average will be selected (*Fig. 2c*).

2.2. Developmental and physiological mechanisms influencing root/stem-ratios

2.2.1. Age of the basic population

Average root/shoot-ratio seems to increase during the first few growth-seasons and to decrease during the rest of the life cycle (*Fig. 3*). The "age-curve" for the root/ stem-ratio probably shows a similar trend. According to the theory expressed in *figure 2a*, selections of "plus-trees" at developmental stages with high root/stem-ratios should be pronounced crucial. A study of *figure 3* with this mechanism in mind indicate, that selections in 2 to 15 year old material should be most unfavorable. However, this conclusion must be modified for different groups of roots, as discussed below.

2.2.2. The impact of selections on different root groups

NIELSEN (1990c) stresses the importance of differentiated analysis of 3 different root groups, according to different physiological behavior of these root groups: *1) "thick roots"* (diameter > 20 mm) are in increment highly influenced by daily mechanical stresses caused by tree swaying, 2) *"thin roots"* (1 < diameter < 20 mm) are in increment affected by root branching pattern and highly hormonally influenced by the water- and nutrient-activity of the connected root tips, 3) *"fine roots"* (diameter < 1 mm) have a much higher rate of turnover than the 2 other root groups (NIELSEN, 1990a). Owing to the different physiology of "thin" and "thick" roots, the long term increment level of the two root groups differ, and thick and thin roots

[5]) With high slope of the root-stem-regression and high variation around this line, the change in genetic value for root productivity may even be negative. This seems to be realized for the "thin root" section within the present Sitka spruce material (*Table 1, Fig. 8a*)
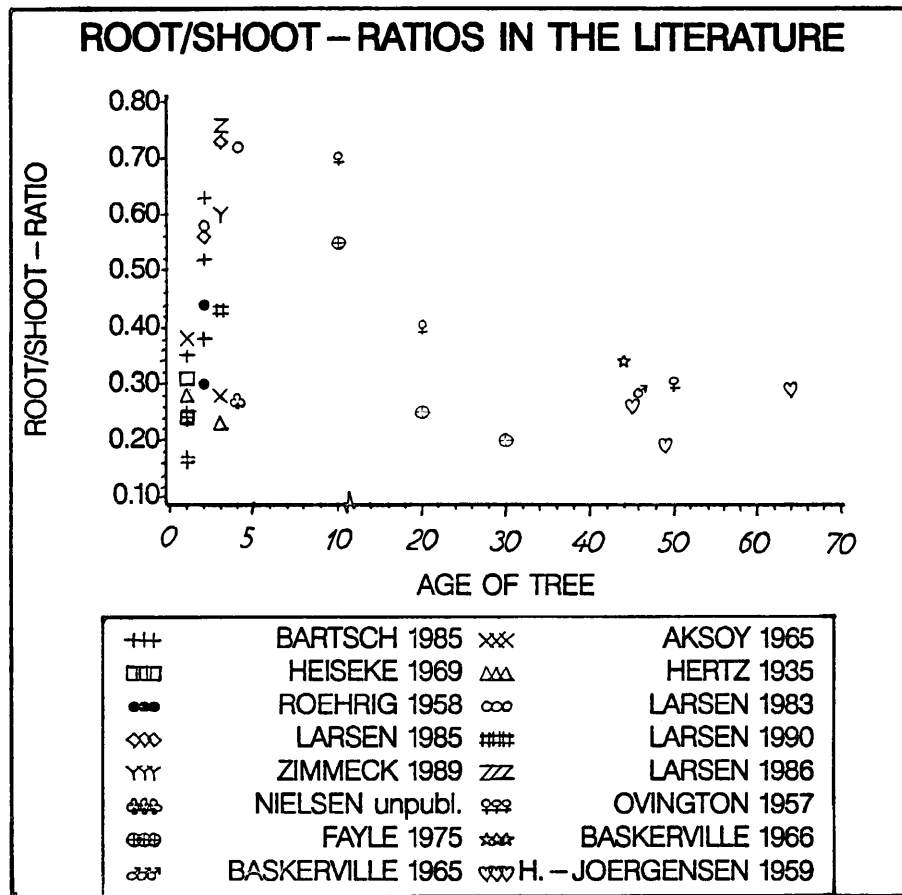
ROOT/SHOOT — RATIOS IN THE LITERATURE

Figure 3. — Root/shoot-ratios calculated or cited from other investigations.

+++	BARTSCH 1985	✕✕✕	AKSOY 1965
◫◫◫	HEISEKE 1969	⋀⋀⋀	HERTZ 1935
••••	ROEHRIG 1958	∞∞	LARSEN 1983
⟨✕✕⟩	LARSEN 1985	⧉⧉⧉	LARSEN 1990
⋎⋎⋎	ZIMMECK 1989	zzz	LARSEN 1986
⊕⊕⊕	NIELSEN unpubl.	♀♀♀	OVINGTON 1957
⊕⊕⊕	FAYLE 1975	☆☆☆	BASKERVILLE 1966
♂♂♂	BASKERVILLE 1965	▽▽ H. – JOERGENSEN 1959	

respond differently to environment (NIELSEN, 1990a). NIELSEN (1990c) found pronounced changes in the "thin root/thick root"-ratio due to changes in spacing or thinning regime. Age of the tree also has a marked effect on this ratio, since the amount of thick roots equals zero until an age of 8 to 10 years. The ratio of "thin roots" to total root mass thus changes from 100% in young material to less than 10% in old stands (NIELSEN, 1990b). Hence research on biomass allocation should distinguish between the mentioned root groups. According to this, two root/stem-ratios will be examined in the present paper: the *"thick root"/stem-ratio* and the *"thin root"/stem-ratio*.

The above discussion reveals *that not the age-curve for the "root/stem-ratio" (as indicated in Fig. 3) but the separate trends for the "thin root/stem-ratio" respectively the "thick root/stem-ratio" are central subjects of concern.* Data for such curves are not available, but trends based on own research data are shown in *figure 4*. These trends are rough guesses on how such age-curves might look like; in nature are substantial deviation from these curves bound to exist.

Figure 4 indicates that the "thin root/stem-ratio" reaches a maximum in the very young stages, whereas the "thick root/stem-ratio" reaches high values in the middle and last part of a trees existence. *All theory discussed above finally lead to the hypotheses, that selection of "plus trees" in young populations tends only to be unfortunate in respect of the gene frequencies controlling the "thin root" productivity,* because trees in young stages have not differentiated in respect of "thick root/stem-ratio". This

can be understood if expressed in terms of slope of the root-stem-regression *(Fig. 2a)*: In young plants the slope will be very high for the "thin root"-stem-regression and very low for the "thick root"-stem-regression *(Fig. 5)*. Thus the productivity for thick roots may not be affected by selection in the youth *(Fig. 5b)*. *For selections of "plus*
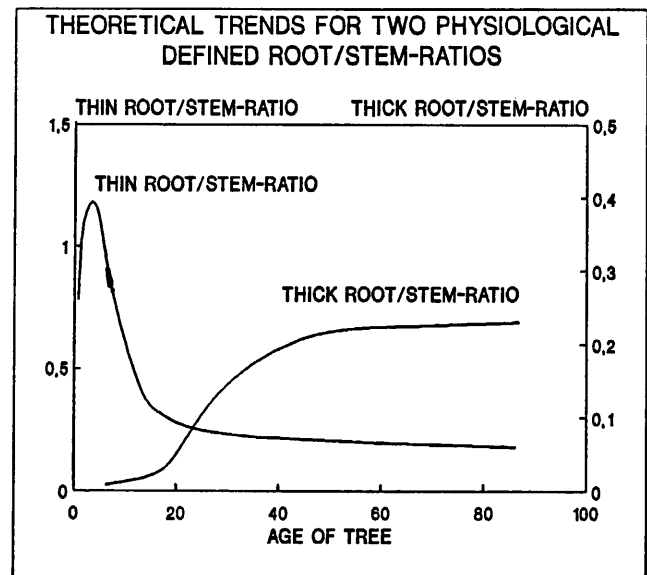

Figure 4. — Theoretical curves for development of the "thin root/stem-ratio" and "thick root/stem-ratio" over age for a tree.

THIN ROOT BIOMASS

YOUNG STANDS

OLD STANDS

STEM BIOMASS

THICK ROOT BIOMASS
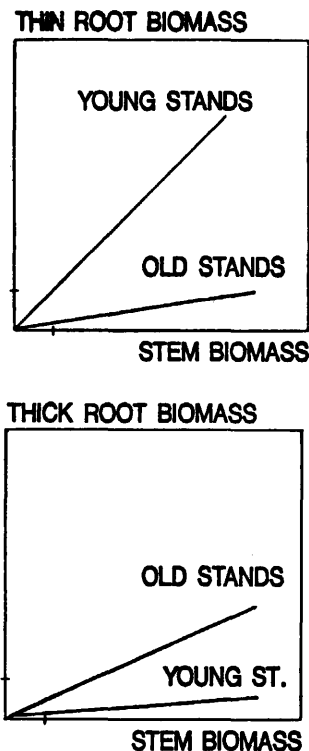
OLD STANDS

YOUNG ST.

STEM BIOMASS

Figure 5. — Hypothetical slopes of root-stem-regressions for populations of trees as function of root group and age of the population.

trees" in old stands a different hypotheses is derived: negative effects on the "thin root/stem-ratio" may be negligible (Fig. 5a), whereas the "thick root"-stem-regression shows a relative high slope in old stands (fig. 5b), which could lead to a decreased "thick root/stem-ratio" in the breeding population.

3. Investigations

3.1. Material and method

In order to investigate the above presented hypotheses, biomass investigations were carried out in the autumn 1989 in 2 clonal trials at the "Hörsholm" State Forest District in Denmark. Field trial number F141a contains one commercial seed standard (Ry Nörreskov, F 299) and ramets from 8 clones of Sitka spruce, originally selected for height growth in an eight-year old stand (Rude Forest, Dept. 578). Trial F141b contains a commercial seed standard (Nödebo, F.71) and ramets from 7 clones of Norway spruce, selected for height growth in a 9 year old stand (Dept. 495) in Rude Forest (ROULUND, 1977). Clones and standards were organized in 64 m^2 plots with 16 cuttings or seedlings per plot planted at distances of 2 meter by 2 meter, all plots replicated in 4 blocks. The trees had late 1989 an age of 20 in both field trials.

After a complete registration of the "breast height diameters" (BHD), 3 soil cores per plot covering an area of each 1600 m^2 were dug out in the central part of the research plot to a depth, were roots no longer occurred, and the root biomass was sieved from the soil material. The roots were washed, sorted to diameter classes, dried and weighed. The total dry weight of roots between 1 mm and 10 mm diameter are referred to as "thin root" biomass in this investigation. Stem form factors were determined on five trees per plot, and structural root systems were ex-

cavated by tractor and winch from three trees per plot, which formed samples of 12 structural root systems per clone or seed standard. Trees of all dimensions were represented due to a stratified sampling. Vertical and horizontal diameters of horizontal roots were measured in distances of 25 cm and 50 cm from the center of the stump. The sum of the "cross sectional areas" (CSA) at 25 cm radius from all horizontal roots of a tree is used as indicators of "thick root" biomass in this work. Due to the extraction method, "thin root biomass" could only be quantified as research plot sums, whereas "thick root biomass" could be estimated for single trees. Stem volume was calculated using tree height, breast height diameter and stem form factor.

3.2. Computations

Clonal differences in "stem form factor" and "tree height"-curves (height over BDH) were determined by analysis of covariance. In the first case only BHD, in the second case both BHD and BHD^2, were used as covariates. The solutions of these analyses were used with the BHD-frequencies to calculate *total stem volume* in every plot. From the three root cores per plot, total *"thin root"* biomass were estimated on every research plot. Regressions of "thick root CSA" over respectively "stem volume" and "stem basal area" were calculated; these regressions were identical in all blocks but significantly deviating for different clones. On the basis of the known BHD-frequencies and the "thick root-stem basal area-regressions" an indication of total *"thick root biomass"* were calculated as the total horizontal root CSA from all trees in a research plot.

Analysis of variance was performed on plot sums of the above mentioned and other parameters. Adjusted clonal means from analysis of variance with block- and clonal-effects are presented in *table 1* for central parameters (SAS Institute, 1987). The differences between clones are pronounced and highly significant for all listed characters.

3.3. Thick root/stem-ratios

The physiological auto-correlation between root and stem biomass was discussed thoroughly in chapter 2.1 (*Fig. 1a*). This correlation is examined for the "thick root"-stem-regression in the present research material, as shown in *figure 6a* and *6b*. The figures show a strong linear correlation between thick root CSA and stem volume in both research materials.

An important subject of the investigation was the behavior of the selected clones compared to the seed standards. Unfortunately, the seed standards may not be representative for the basic stands, where the clones were selected. It must though be expected, that average "root/stem"-ratios of different Danish seed stands may not differ more than at most 5%, and it shall in all further analysis be assumed that the seed standards may represent the basis populations of the selected clones.

The "thick root"-stem-regressions for the seed standards are calculated and drawn in *figure 6a* and *6b*. They obviously seem to represent the total material quite well. On an average the selected clones tend to show the same thick root-stem-regression as the seed standards. In terms of the theory in *figure 1b*, no negative downward change in the "thick root"-stem-regression has occurred due to the selection of the clones. The Norway spruce clones even show a slight but not significant higher slope than the seed standard.

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Species	Clone	Stem height	Stem basal area	Stem volume	Thin root biomass	Thick root CSA *	Thin r./ Thick r. -ratio
		m	m^2	m^3	t/ha	m^2/ha	kg/m^2
Norway spruce	Seed	9.4	25.7	135.8	5.67	32.6	176.1
	3795	10.1	29.3	151.1	5.94	36.6	164.8
	3796	10.9	29.2	168.5	5.68	35.9	159.4
	3797	10.2	26.8	148.9	7.38	33.4	228.0
	3798	10.9	28.3	158.0	7.02	45.7	153.8
	3799	10.8	28.2	142.3	5.45	39.1	140.5
	3800	10.8	31.6	171.1	5.64	55.3	102.9
	3802	11.2	35.1	197.3	7.27	61.4	118.5
	ALL	10.6	29.3	159.1	6.26	42.5	155.5
Sitka spruce	Seed	12.0	26.6	166.2	3.67	39.4	93.4
	3803	14.8	43.9	306.9	2.52	82.2	30.5
	3804	12.8	25.6	168.2	3.40	41.5	82.8
	3805	15.2	37.6	288.7	3.49	79.7	43.5
	3806	14.5	35.8	264.6	3.17	57.2	55.5
	3807	15.1	54.5	401.0	3.89	95.4	40.9
	3808	13.0	47.9	308.9	3.09	114.4	27.0
	3809	13.4	41.4	266.3	4.06	63.9	63.0
	3810	15.3	49.5	395.1	4.05	75.6	55.9
	ALL	14.0	40.3	285.1	3.48	72.1	54.7

*) CSA = Cross sectional area af horizontal roots at 25 cm dist. from center of stump

This fact is confirmed in *figure 7a* and *7b*, where adjusted clonal means from analysis of variance on research plot values of "thick root/stem-ratios" and stem volume are presented: *the thick root/stem-ratio of the seed standards are situated around the averages of the selected clones, and no correlation to stem volume production becomes evident.*

Thick root biomass over stem volume
F141a, Sitka spruce, 8 clones
Single tree values

Thick root biomass over stem volume
F141b, Norway spruce, 7 clones
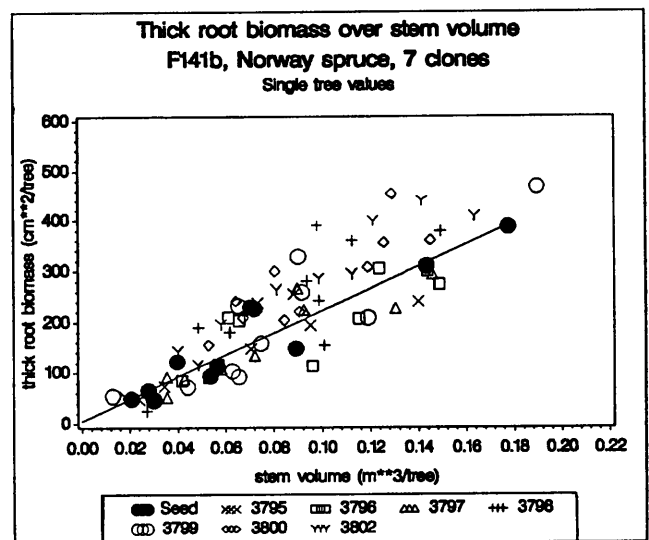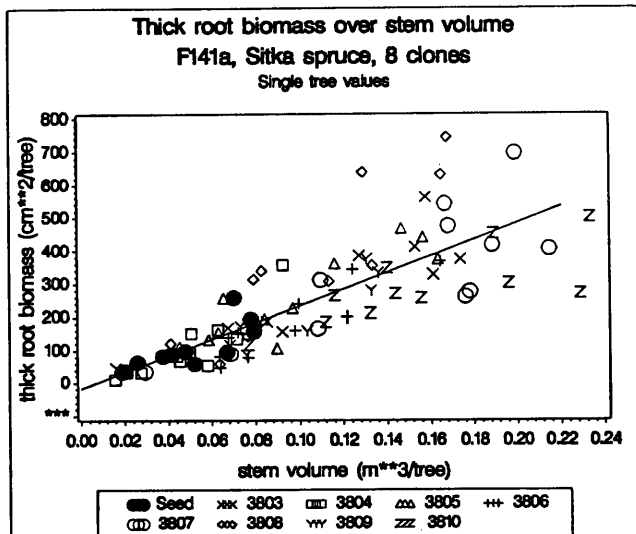Single tree values

Figure 6. — The relation between "thick root cross sectional area" and stem volume for seed standards and clones. Regressions through the seed samples. Single tree values.

3.4. Thin root/stem-ratios

Because of the differences in extraction method, thin root biomass could not be analyzed on single tree level as done for thick roots. Hence the observations presented in
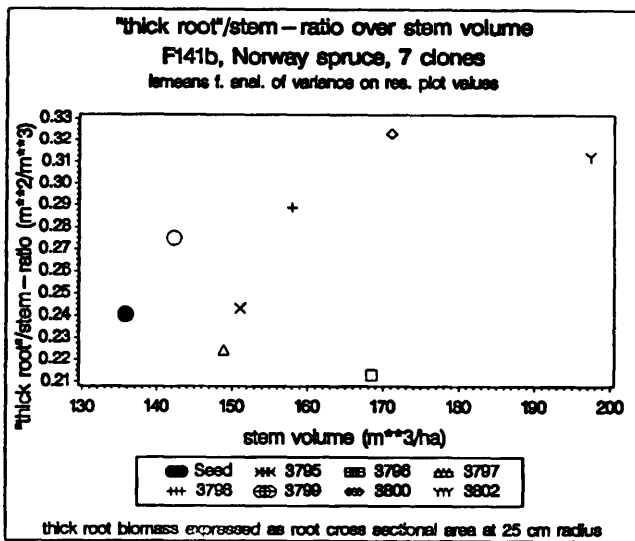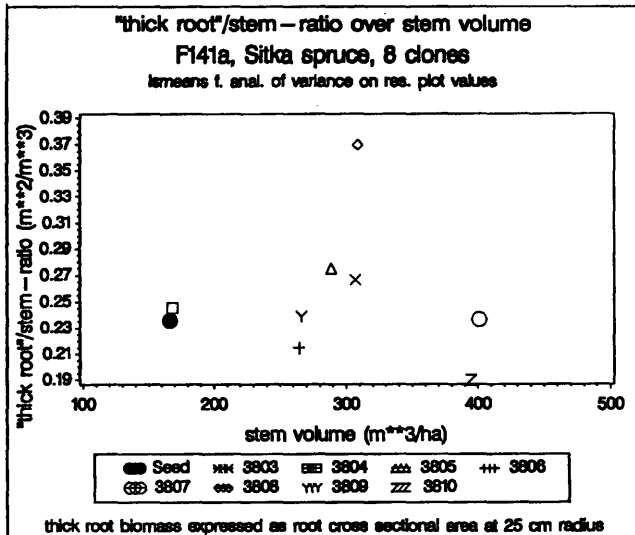
Figure 7. — The "thick root"/stem-ratio over stem volume production for seed standards and clones. Adjusted clonal means from analysis of variance based on plot values.
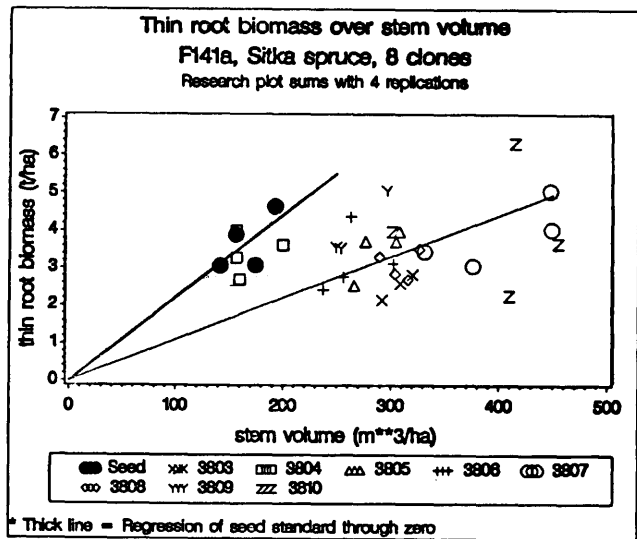
approximately the same biomass of thin roots. This figure shows that the reproduction of the selected clones causes a downward movement of the "thin root"-stem-relationship (compared with the seed sample). These results confirm the theory expressed in *figure 1b*. The consequence is illustrated in *figure 9a*: with increasing selection intensity for stem volume production an increasing part of total biomass is allocated to the stem, hence "thin root/stem"-ratio decreases with increasing gain in stem production, which confirms the theory behind *figure 2c*. The average "thin root"/stem-ratio of all Sitka spruce clones is leveled 45⁰/o below the seed standard.

Although the *Norway spruce* clones in average did not show a such marked differentiation from the seed sample as did the Sitka spruce clones, they defined a "thin root"-stem-regression leveled about 7⁰/o lower than the seed sample regression (*Fig. 8b*), causing an average reduction in "thin root"/stem-ratio of 7⁰/o. *Figure 9* presents the average "thin root"/stem-ratio over stem volume production for the genetic units of Norway spruce. The figure shows a decrease in "thin root"/stem-ratio with increasing gain in stem production. The four clones with lowest stem

figure 8a and *8b* are total thin root biomass over total stem volume in field plots from 4 replications.

The "thin root"-stem-regressions for the seed samples were forced through zero in *figure 8* (as in *Fig. 6*), because this must be logically true. The regressions are linear of convenience, because the plots did not differentiate enough between blocks to indicate the biologic true character of the "thin root"-stem-relationship at this stage of development. This relationship might be curvilinear, but „a kind of saturation" of the soil in respect of thin roots is not realistic: The amount of woody roots with secondary thickening (diameter > 2 mm) will certainly increase with age and dimension at this stage. Even the concept of "fine root saturation" of soils is questioned by NIELSEN et al. (1991b). Even if a curvilinear relationship is assumed, will the theory in chapter 2.1 not be affected (See footnote 5), and the following evaluation and the interpretation of the data (See footnote 9) will only be affected to a minor degree.
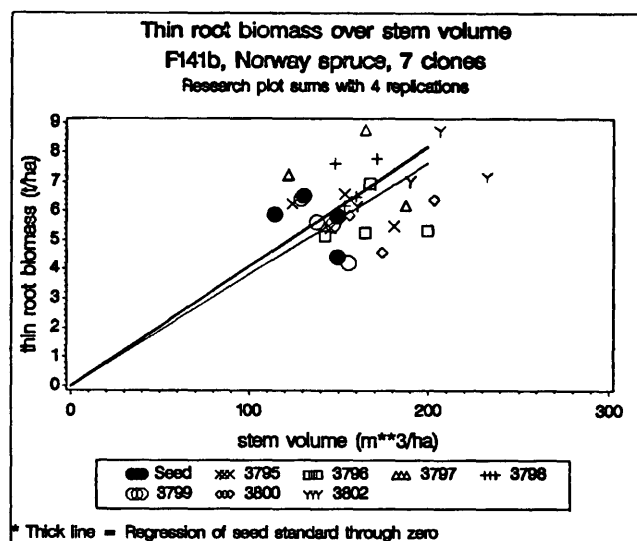
The *Sitka spruce* clones show in *figure 8a* a definite higher stem volume production than the seed sample, but

Figure 8. — The relation between thin root biomass and stem volume production for seed standards and clones. Regression through seed sample.

"thin root"/stem—ratio over stem volume
F141a, Sitka spruce, 8 clones
lsmeans f. anal. of variance on res. plot values

"thin root"/stem—ratio (kg/m**3)

stem volume (m**3/ha)

| ● Seed | ⋈⋈ 3803 | ⊞⊞ 3804 | ⋈⋈ 3805 | +++ 3806 |
| ⊞⊞ 3807 | ⋙⋙ 3808 | ⋙⋙ 3809 | zzz 3810 | |

"thin root"/stem—ratio over stem volume
F141b, Norway spruce, 7 clones
lsmeans f. anal. of variance on res. plot values

"thin root"/stem—ratio (kg/m**3)

stem volume (m**3/ha)

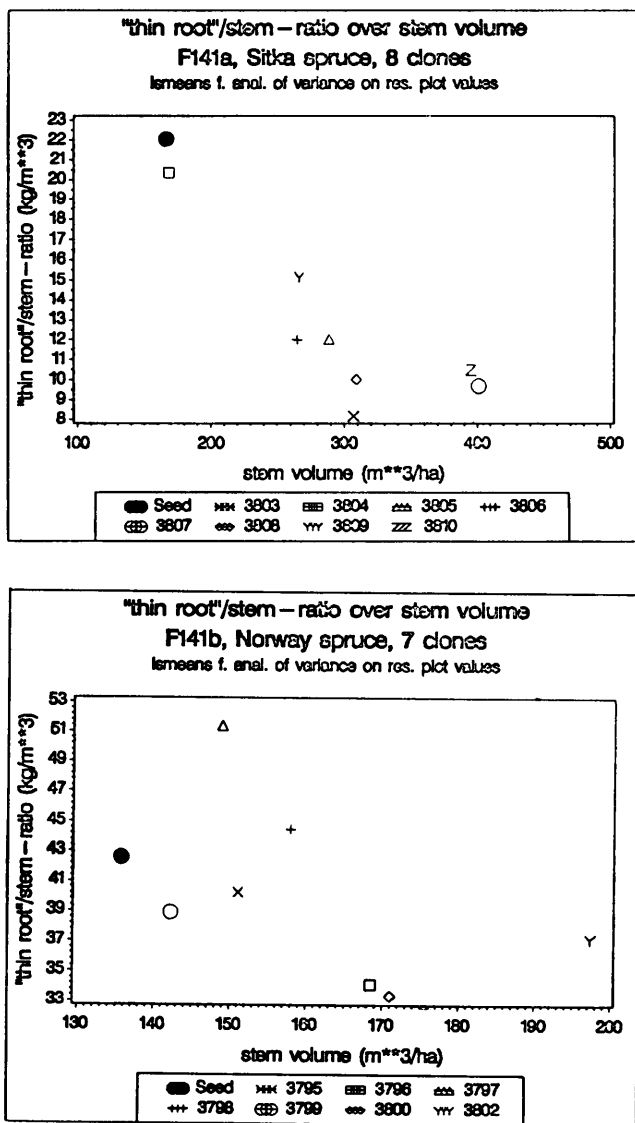| ● Seed | ⋈⋈ 3795 | ⊞⊞ 3796 | ⋈⋈ 3797 |
| +++ 3798 | ⊞⊞ 3799 | ⋙⋙ 3800 | ⋙⋙ 3802 |

Figure 9. — The "thin root"/stem-ratio over stem volume production for seed standards and clones. Adjusted clonal means from analysis of variance based on plot values.

production have the highest, and the three best producing clones have the lowest "thin root"/stem-ratio. The variation between the clones is interesting, because it illustrates a big variation of the "thin root"/stem-ratio within a population.

In spite of the strong phenotypic selection intensity, it is obvious that the genotypic values for stem production of the clones 3795, 3797, 3798 and 3799 are not much above population average. As a consequence of this, the "thin

root"/stem-ratio of these clones are positioned around the level of the seed standard.

Both examined materials show a *downward replacement of the "thin root"-stem-regression for the selected clones compared to the seed standard,* which causes a reduction in "thin root"/stem-ratio. *The reduction in "thin root"/ stem-ratio increases with increasing genetic gain for stem production.* This effect is recognized as well within the two research materials as by a comparison between the two materials (*Fig. 9a* and *9b*).

3.5. The genetic component of the variation around the root-stem-regression lines

A precondition for reduced root/stem-ratios, due to selections, is some degree of genetic control of the phenotypic variation around the root-stem-regression line (*Fig. 1a*). To test this prerequisite on the present research material, regressions were calculated for thin root biomass and for thick root CSA over stem volume for observations of the seed standards. These regression lines are drawn in *figure 6* and *8*. The deviation of all observations from these regression lines (a kind of "residuals") were calculated, and the genetic component of variance of the residuals was estimated after the formula (FAULKNER, 1981): $V_p = V_g + V_e$ (V_p = phenotypic, V_g = genotypic and V_e = environmental variance). These components of variance were estimated by analysis of variance, using genetic units and blocks as random effects (SAS Institute, 1987). From the components of variance the heritability (FAULKNER, 1981) was calculated to express the degree of genetic control in the phenotypic root-stem-correlation: heritability = h^2 = (V_g/V_p). The results are presented in *table 2*. To control the above described method a traditional analysis of covariance with equal weight to all genetic units were calculated with the stem volume production as covariate for all four groups of observations. The heritability derived from this method is also presented in *table 2*, and no essential differences in degree of genetic control could be found between the 2 methods. *The analysis of heritability documents a height degree of genetic influence on phenotypic root/stem-ratios.* A study of *figure 6a* and *6b* visualize the genetic control in allocation of woody increment: the clones 3800, 3802 and 3808 show high thick root production, whereas the clones 3806 and 3810 are positioned below the regression line.

A comparison of clones in respect of root production is complicated by the different levels of stem production. To solve this problem adjusted clonal means from analysis of covariance (stem volume being covariate) are presented in *table 3*; the values illustrate the differences between genetic units by equal values of the covariate. *Table 3* shows that the clonal differences in root production per unit stem volume are quite large: the ranges between

Table 2. — Heritabilities for the variation around root-stem-regressions tested with two methods.

| Species | Residuals from | Number of | | P-values | | h² from residual-method | h² from analysis covariance |
		genetic units	blocks	genetic units	blocks		
Norway spruce	thin roots	8	4	8.1 ***	26.8***	0.88	0.85
	thick roots	8	4	3.7 **	n.s.	0.73	0.72
Sitka spruce	thin roots	9	4	13.8 ***	n.s.	0.93	1)
	thick roots	9	4	4.2 ***	n.s.	0.76	0.78

¹) The covariate not significant

Species	Clone	Thick roots cm²/tree		Thin roots kg/ha	
		Adj. mean	%	Adj. mean	%
Norway spruce	Seed	184	100	6.29	100
	3795	185	101	6.16	98
	3796	168	91	5.43	86
	3797	171	93	7.65	123
	3798	224	123	7.05	112
	3799	196	107	5.90	94
	3800	241	131	5.32	85
	3802	242	132	6.25	99
Sitka spruce	Seed	251	100	4.32	100
	3803	245	98	2.50	58
	3804	251	100	4.04	94
	3805	261	104	3.47	80
	3806	196	78	3.28	76
	3807	204	81	3.25	75
	3808	341	134	2.96	69
	3809	224	89	4.27	99
	3810	129	51	3.44	80

the highest and lowest producing clones are for thick roots 41% (Norway s.) and 83% (Sitka s.), and for thin roots 38% (Norway s.) and 41% (Sitka s.).

3.6. Clonal differences in biomass allocation within the root system

The different impact of selections on thin and thick roots was documented in part 3.3. and 3.4., which stresses the importance of separate analysis of different root classes and different root/stem-ratios. This statement is supported in *figure 10a* and *10b*, where total *thin root* production is plotted against total *thick root* production. It is evident that no relationship can be established between the production of the 2 root groups by a comparison of clones[6]. Certain clones show high thick root and low thin root production, other clones behave in the opposite way, whereas some clones show high or low production of both root groups. *This analysis leads to the conclusion, that the production of the two root groups to a fairly large extend are controlled by different genes.*

3.7. Influence of tree species and soil moisture on biomass allocation

Marked differences between the 2 tree species and between blocks within the Norway spruce trial were analyzed. Differences between species and blocks in the "thick root"/stem-ratio were in most cases not significant and did not exceed 7%.

The "thin root" biomass per hectare was 44% lower in the Sitka spruce than in the Norway spruce trial, although

[*] Narrow correlations between thin and thick root biomass will presumably be found in replicated ramets *within* clones. But regressions for different clones would have different slopes (according to *Fig. 10*).

stem volume in the Sitka spruce trial was in average 79% higher than in the Norway spruce trial (*Table 1*). According to this, average "thin root"/stem-ratio was 13.3 kg/m³ and 40.3 kg/m³ in the Sitka and in the Norway spruce trials, respectively. This huge difference must be interpreted with caution: 1) In spite of the small distance between the two trials (150 meter), soil moisture was higher in the Sitka spruce area, which is known to influence "thin root" productivity pronounced (NIELSEN, 1990b), and 2) All Sitka spruce trees had intensive vertical roots with pronounced fine root branching, whereas vertical roots was almost absent on the Norway spruce trees. Because the estimation of "thin roots" was carried out in soil columns between the trees, the "thin root" biomass may be underestimated in the Sitka spruce plots. Further studies of the fine root distribution around trees require root samples closer to the stems, which enables the calculation of fine root "concentration bells" (NIELSEN, 1991).

Within the Norway spruce trial, block 4 had lower elevation and higher soil moisture than the other three blocks. Block 1 had highest elevation and dryer soil. A comparison of these two blocks stresses the pronounced
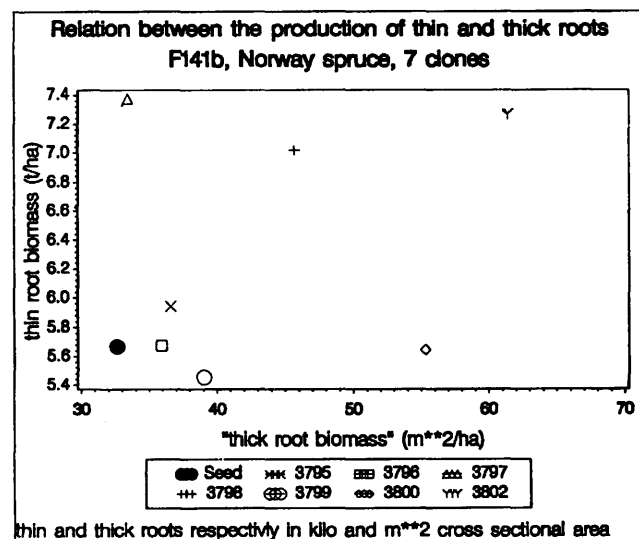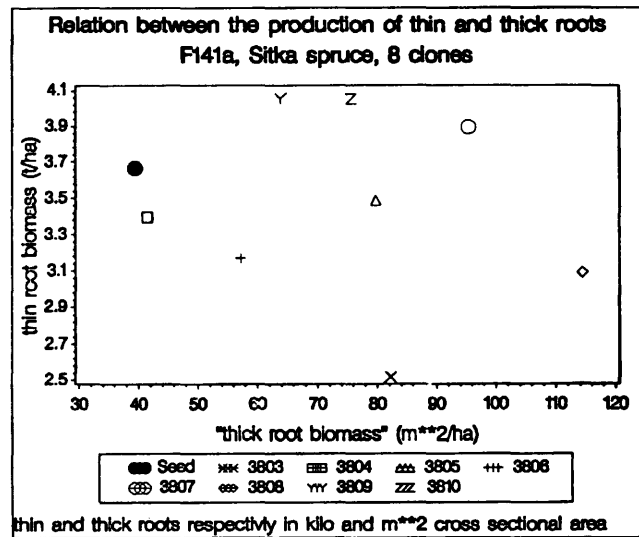

Figure 10. — The production of thin and thick roots for seed standards and clones. Adjusted means based on plot sums.

influence of available soil water on stem and "thin root" production. Stem volume was 22% *lower* in block 1 than in block 4, but "thin root" biomass was 20% *higher*. According to this, "thin root"/stem-ratio is heavily reduced from block 1 to block 4 (*Fig. 11*)[7].

4. Discussion

The theory in chapter 2 revealed, that the slope of the root-stem regression is relative high for "thin roots" in early and for "thick roots" in the later stages of a trees life cycle (*Fig. 5*.). Because a downward displacement of the root-stem-regression line depends on a relative high slope of this regression in the basic stand at the time of selection (*Fig. 1a* and *2a*), following hypotheses was formulated in chapter 2.2.2:

1) only "thin root productivity" is influenced by "plus tree" selections in young material,

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[7] Thick root biomass was proportional to stem volume within clones, with no significant effect of blocks.
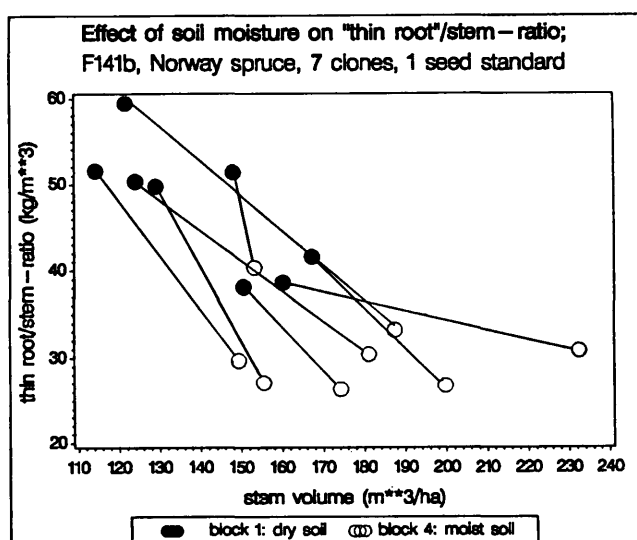

Figure 11. — Influence of soil moisture on the stem production and the "thin root"/stem-ratio in the Norway spruce trial. Research plot values from block 1 and 4.
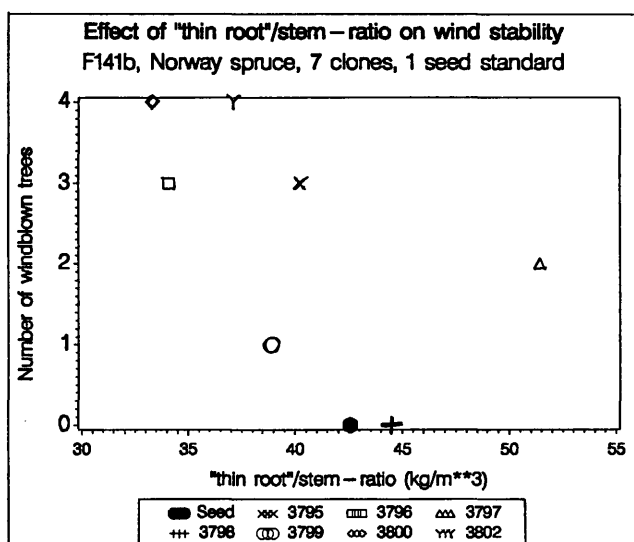

Figure 12. — Influence of the "thin root"/stem-ratio on the number of windblown trees for 7 clones and 1 seed standard in the Norway spruce trial.

2) whereas mainly "thick root productivity" could be reduced by selections in older stands.

The first hypotheses is confirmed by the present results: all investigated clones were selected in 8- to 9-year old stands, and the root-stem-regressions showed a downward displacement for the "thin root" section (*Fig. 8*)[8], whereas this regression was unchanged for the "thick root" section (*fig. 6*)[9].

The second hypotheses, concerning the impact on the "thick root"/stem-ratio by selections in old stands, still has to be verified or falsified in other research materials.

The negative correlation between the "thin root"/stem-ratio and the gain in stem production (*Fig. 9*) confirm the theory, that the *injuring effect on root growth, caused by selections for stem biomass, is enhanced by increasing selection intensity (Fig. 2c).*

The plots in *figure 10* show, that the *productivity of "thin roots" respectively "thick roots" to a wide extend are controlled by different genes.* Thus selections and breeding efforts may affect the frequency of genes controlling the production of one root group without changing the genetic basis for increment of the other root group. This stresses the importance of the theory presented in chapter 2.2.2: *the age of the population, in which selections are carried out, may determine the root classes affected by the selection.* The great importance of separated analysis of root groups with different physiology becomes evident in the present work, where the analysis of "thick" and "thin" roots showed very different results. If the *total* root mass had been analyzed and compared with stem production, differences between clones might have been undetectable.

An important precondition for a shift in average root/stem-ratios, due to traditional selection practice, is the existence of a *genetic variation* of such ratios. Significant

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[8] Two reservations to this interpretation shall be pointed out:
1) The number of clones in the investigated field experiments are limited.
2) *Figure 4* sketches a decreasing "thin root"/stem-ratio with increasing age. This trend is more likely to be a function of physiologic development than of time, of which the former could be expressed by tree height or stem biomass. An alternative explanation to the negative correlations between "thin root"/stem-ratio and stem production in *figure 9* could according to this be "different stages of development". This interpretation of *figure 8* and *9* would reject the hypotheses formulated in chapter 2.2.2. A valid test of this alternative interpretation requires though a comparison of clones at equal stages of "development", which is not practicable. But the following analysis and arguments allows the rejection of this alternative interpretation: A) An approach for clonal comparison at equal stages of stem biomass was carried out by the calculation of adjusted clonal means for root biomasses in an analysis of covariance with stem volume as covariate. Adjusted clonal means express the root biomasses for different clones at an *equal level* of stem biomass (*Table 3*). The adjusted clonal means showed big and highly significant clonal differences. B) A further precondition for this alternative explanation is a complete decline of the thin root increment towards zero after a stem production level of 200 m³ (*Fig. 8a*), which is not feasibly. (The rate of "thin root" turnover is very low at this stage of development). C) Different developmental stages are furthermore characterized by different ratios of thin roots from 1 mm to 2 mm to those of 5 mm to 10 mm of diameter (NIELSEN, 1990b), and such differences could not be confirmed in the present material. Although the alternative interpretation of the data in *figure 8* and *9* discussed here may be valid to minor extend, it is certainly not sufficient to explain the results.
[9] The results also support the assumption, that the seed standards are representative for the basic populations in which the clones were selected.

differences in root/shot-ratios between provenances and individuals were found by several authors in young research material (Köstler et al., 1968; Larsen, 1985), and the present investigation confirm clonal differences in older material (Table 3). The range between clones in "thin root"/stem-ratio and "thick root"/stem-ratio reaches values of 160 respectively 95% in figure 7 and 9. Such variations of root/stem-ratios within populations enables large negative changes of the root-stem-regressions (Fig. 1b and 2b).

However, the damage on root/stem-ratios depends on the degree to which environment overrides genetic differences. Increasing environmental heterogeneity will decrease the genetic gain in stem production and diminish the shift in root/stem-ratio. A comparison of the two investigated breeding materials in chapter 3 might illustrate the difference between phenotypic and genetic values. The selection intensity implemented in the two basic populations of Norway respectively Sitka spruce was comparable, but the realized genetic gain in stem production was much higher for Sitka than for Norway spruce. The stem production of the selected Sitka clones was averagely 81% above the seed standard, whereas this difference was only 20% for Norway spruce. According to this are the displacement of the "thin root"-stem-regressions much different in the 2 materials (Fig. 8). This illustrate that phenotypic values may differ strongly from the genetic values, and that the negative impact on the root-stem-regression through selections depends much on the environmental component of variance in the basic population.

The importance of the root/stem-ratios for wind stability shall finally be stressed[10]. Intensive studies have revealed, that the primary "strength" of an undamaged anchorage system ("primary elasticity") to a high extend depends on the magnitude of the root ball, which again depends on the mass and spatial arrangement of the "thick roots". After initiation of the "anchorage loosening process", the amount of "thin roots" is essential for the long term secondary "strength" ("plasticity") of the anchorage system (Nielsen, 1990c). In the youth, where root balls are small or not yet existing (as in case of the present Norway spruce material), "thin root" biomass becomes even important in the primary stages of the "anchorage loosening process" (Nielsen, 1990a). It must be concluded, that a reduced allocation of biomass to thick roots as well as to thin roots will reduce the long term wind stability. This was confirmed by the frequencies of windblown trees in different clones in the Norway spruce trial. This parameter is plotted against the "thin root"/stem-ratio in figure 12, where a decrease of wind damage with increasing "thin root"/stem-ratio is visualized[11].

5. Conclusions

1. Selections of "plus trees" in young populations (1 year to 20 years) for height, diameter or stem biomass production, are likely to cause a severe reduction of the average "thin root"/stem-ratio, due to a shift in the genetic control

of "thin root"-increment. This statement is supported by results from both investigated materials.

2. A selection of "plus trees" in older stands is likely to cause a reduction of the average "thick root"/stem-ratio in the breeding population compared to traditional seed material. This part of the theory still has to be examined in future investigations.

3. The "damage" on the root/stem-ratios will increase with increasing selection intensity, with increasing genetic variation of root/stem-ratios in the basic population and with increasing slope of the "root-stem-regression" (Fig. 2).

4. By selections in nurseries and young stands it is recommended to investigate stem- and root-production and to select for total biomass production (or even only for root production in order to breed for wind stability). This strategy might secure a genetic gain for stem as well as for thin root production of even magnitudes, so that the ratio between these two biomass compartments is not changed by the selection. Such a strategy could be neutral in respect of thick root productivity.

5. By selections in old stands it could be necessary to investigate the "thick root"-stem-regression of the basic stand. After harvest of cones and grafts from plus trees, these could be excavated and tested for their position in the regression mentioned. Because this demands extreme resources, research should be invoked to establish early test methods for thick root productivity[12]).

6. Summary

The existence of a genetic variation of "root/stem-ratios" in conifer populations may cause a negative change of such ratios in breeded material compared to normal seed populations, if "plus trees" are selected for outstanding stem production (Fig. 1a). Such a shift in root/stem-ratio in disfavor of the roots depends on a positive slope of the root-stem-regression, and it is assumed, that only steep slopes will change the frequency of genes controlling allocation of biomass (Fig. 2a).

Since the increment of thin roots (1 mm to 20 mm of diameter) and thick roots (above 20 mm) to a wide extend are controlled by different genes (chapter 2.2.2 and 3.6), 2 "root/stem-ratios", defined by these root groups, should be analyzed separately. Curves for "thin root"/stem-ratio and "thick root"/stem-ratio over age (Fig. 4) indicate, that regressions between root- and stem biomass alter drastically with age. According to the changing slopes of such regressions over time (Fig. 5), a traditional "plus tree" selection in young stands should cause a severe reduction of the average "thin root"/stem-ratio in the breeding population. This is based on a particular high slope of the "thin root"-stem-regression in youth. This mechanism was confirmed by biomass investigations in two field trials of Norway spruce and Sitka spruce, where the mentioned ratio was reduced with 7% respectively 45% due to a traditional selection for height growth. The "damage" on the "thin root"/stem-ratio increased among clones with increasing gain of stem productivity (Fig. 9). Because the tested clones were selected in 8 to 9 year old stands, where the slope of the "thick root"-stem-regression is almost 0, no effect on the frequency of genes

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[10]) To exclude the windload from the discussion, it is assumed, that biomass allocation between crown and stem varies independent of the allocation between roots and stem (Nielsen, 1990a and 1990c). This prerequisite has been confirmed in two materials of different age (Nielsen, 1991).

[11]) Clone 3797 has the second lowest "thick root"/stem-ratio, which explains the wind damages within this clone.

[12]) Because the thick root production is strongly influenced by mechanical stresses (Nielsen, 1990a, 1990c), the genetic variation in the ability to create reaction wood might be coupled to the variation in "thick root"/stem-ratio. Such mechanisms might be the basis for development of early test methods for the "thick root"/stem-ratio.

controlling "thick root" productivity could be found in the 2 tested materials.

The need for further research on the subject and the limitations of the present test material was stressed. Still the investigation confirmed the hypotheses, that traditional breeding selections for above ground production will cause reductions in the ratios between root- and stem-biomass. By selections in young material only the "thin root" productivity is reduced, by selection in old stands mainly "thick root" productivity should be diminished. By selections in young material at present, it is suggested also to investigate the root biomass and select for total biomass production. On longer term, early test methods for the 2 physiologic different behaving "root/stem-ratios" should be developed.

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Genetic Control of Eighth Year Traits in Pinus patula Schiede and Deppe

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Summary

Polycross, factorial and diallel mating designs were used in the genetic improvement programme for Pinus patula SCHIEDE and DEPPE in Zimbabwe. Their function was to elucidade genetic structure and control in economically important traits, to investigate genotype-environment interaction, to identify the best general combiners and to provide information on the efficiency of mating and experimental designs. Productivity, stem form and wood density traits were measured in the eighth year from planting in the field. Analysis of the data indicated that all traits were principally under multigenic control with dominance, maternal and reciprocal effects of no practical significance. Heritabilities were highest for wood density (up to 0.82

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