ABOVE GROUND BIOMASS AND BIOMASS DISTRIBUTION IN NURSERY PLANTS OF ABIES GRANDIS LINDLEY

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Abstract

After 3 years significant differences exist between fast (F) and slower growing (R) plants of Abies grandis Lindley. These differences increase, absolutely and relatively, with the passing of time.
In both cases 50 % of all overground biomass is concentrated in the needles, 30 % in the main stem and 20 % in the branches

INTRODUCTION

The aim of the present study is to acquire information about the production and distribution of the above-ground biomass of 5-year old nursery plants of Abies grandis Lindl., transplanted as 2-year old seedlings.
It was further attempted to gain some insight in early differences in growth, which, in the course of subsequent use in afforestation, could have some impact on stratification and early stand development.

METHODOLOGY

At the end of the 5th growing season plants were selected for more thorough analysis, half of them obviously taller than average and the other half obviously below average. The group of F-plants (= fast growing plants) attained, at that moment, an average height of 59.2 cm + 4.59 and the group of R-plants (= retarded or slower growing plants) only 41.3 cm $\pm$ 1.21, indicating a significant difference in height between both groups (t = 9.23 ***).

Basis measurements were the number and dry weight of needles and branches and the length and dry weight of annual shoots.

For needles, branches and stem segments or annual leaders, three-age-classes were considered :

1 year old : Result of the last or 5th growing season.

S.1 = shoot ; N. 1 = needles, B.1 = branches.

2 years old : Result of the growing season before last or 4th growing season.

S.2 = shoot; N.2 = needles; B.2 = branches.

More than 2-years old : Result of the first growing period of 3 years, covering 2 years as seedling and 1 year as transplant.

S.n = shoot; N.n = needles; B.n = branches

For comparative analysis 3 parts or levels were considered in all plants :

Upper part of the plant = Upper crown level UC = S.1 + all latteral branches connected with this shoot.

Middle part of the plant = Middle crown level MC = S.2 + all latteral branches connected with this shoot, whatever their order or degree of branching.

Lower part of the plant = Lower crown level LC = S.n + all latteral branches connected with this part of the stem, whatever their age, order or degree of branching.

GROWTH AND DEVELOPMENT

At the end of the 3rd growing season, one year after transplanting the 2-year old seedlings, a significant difference of 13.7 cm in average height already existed between fast growing plants (hF = 27.1 cm) and slower growing or retarded plants (h_R = 13.4 cm) (t = 5.04) (h-ratio F/R = 2.02).

After the 5th growing season the absolute difference in average height has increased to 17.9 cm (h_F = 59.2 cm ; h_R = 41.3 cm; t = 9.23 ***), but the relative difference is reduced to 43 % (h-ratio F/R = 1.43).

These observations illustrate the ambiguous position of more or less retarded plants in a socially well-structured community. The retarded plants show a tendency toward recuparation during an undefined period of time by, apparently, growing relatively better than the more advanced plants of the same age. Nevertheless, the absolute vertical distance between F-plants and R-plants increases steadily at the same time. This, undoubtly, favours the faster growing plants and permits them to acquire, within a relatively short time, a dominant position or to consolidate and improve such a position, if already attained.

These phenomens confirm observations on natural regeneration in the forest, spontaneous or induced, where maximal relative differen iation was also found to occur during the very first years of community development, absolute differences in height increasing and relative differences decreasing with the passing of time (Van Miegroet, 1980).

It stands to reason, that correct interpretation of the development of natural regeneration in the forest must take into account the continual reduction of the number of seedlings, a phenomen that does not reach the same level of intensity in the nursery.
In the field it tends to decrease the relative differences in height between the remaining plants by the preferential elimination of the weaker individuals.

In the case of the transplants of Abies grandis Lindl. under observation differentiation has not yet had its final effect : No significant difference in length of S.1 between F- and R-plants is observed during the 5th growing season. Maximal differences in annual increment between both groups seem to exist during the very first years. Later on retarded plants are more or less catching up as the ratio of shoot-length between stem segments with a different age indicates :

Ratio	F	R
S.1/S.2	1.39	1.81
S.1/S.n	0.68	1.08

The restricted importance of the difference in shoot length between F and R is however counterbalanced by more important differences in biomass. (Tab. 1). Whereas the relative difference in height attains no more than 43 %, the difference in average total dry weight in g/plant reaches 123 %.
The differences between F and R are nearly the same for all plant parts taken separately. Nevertheless, the differences are maximal for the assimilating needle mass (+ 129 %). The increasing superiority of faster growing plants, due to their higher biomass on all levels, as well as the restricted importance of differences in height growth, is further confirmed by the B/h-ratio (Cannel, 1974 : total dry weight in g/total height in cm) :

	B/h	s	t
F-plants	0.85	0.09	3.95**
R-plants	0.54	0.17	

Dominant or fast growing plants are undoubtly superior :

- they show good crown development and have a greater biomass pro unit of length ;
- they are more densely covered with needles and, consequently, have better opportunities for assimilation, thus continually increasing their relative advance;
- they are less slender and thus show a higher degree of physical stability.

On the other hand, plants in both groups seem to develop in much the same general way, as indicated by analogous biomass distribution over needles, stem and branches (50 to 51 % for the needles, 30 to 31 % for the stem and 19 % for all branches). It is questionable whether this relative biomass distribution will remain unchanged (Hegyi, 1972) and a steady increase for some time of the biomass must be reckoned.

Tab. 1 Biomass (dry weight in g/plant) and its distribution

Components	F - group			R - group			tF/R	Ratio F/R
	%	$\bar{x}$	s	%	$\bar{x}$	s		
Needles	50.8	25.4	3.35	50.6	11.1	3.55	7.18***	2.29
Stems	30.4	15.2	2.51	31.7	7.1	1.76	6.47***	2.14
Branches	18.8	9.4	1.19	18.7	4.2	1.57	6.46***	2.24
Total	100	50.0	6.12	100	22.4	6.75	7.41***	2.23

DISTRIBUTION OF NEEDLE-BIOMASS

1. General pattern of distribution

The needles account for nearly 50 % of the above-ground biomass. They grow on branches and directly on the stem, but 95 % of all needles occur on the branches.

Average dry weight of needles / g pro plant

Type	On branches	On stem	Total	% on branches
F	24.8	0.64	25.4	97.6
R	10.5	0.57	11.1	94.6

Although fast growing plants carry a much higher total needle biomass as slower growing plants, the biomass of needles, developing directly on the main stem, is about the same in both cases. As a consequence of the lower stem-biomass of R-plants, their stems are thus more densely covered by needles pro surface unit.

However, the needle-biomass, directly growing on the main stem represents no more than 2.4 to 5.4 % of total needle-biomass and only 1.3 % (F-plants) to 2.4 % (R-plants) of total above ground biomass.

The greater part of the needles on the main stem grow on the youngest stem segments, both in group F and R (Tab. 2). It amounts to 58 % of this specific form of needle biomass in both groups, against 35 % (R) to 39 % (F) of stem needle biomass on 2-year old segments and only 3 % (F) to 7 % (R) on stem segments older than 2 years. It is evident that needles seldom remain more than 2 years on the main stem. They are relatively more important for retarted plants as the density of covering of the shoots (dry weight of needles in g/shoot length in cm) seems to indicate :

	F	R
S.1	0.020	0.023
S.2	0.018	0.025

Tab. 2. Distribution of dry weight of needles directly growing on central stem segments (g/plant)

Stem segment	F - group			R - group			t F/R	Ratio F/R
	%	$\bar{x}$	s	%	$\bar{x}$	s		
S.1	57.8	0.37	0.10	57.9	0.33	0.11	0.66	1.12
S.2	39.1	0.25	0.07	35.1	0.20	0.06	1.33	1.25
S.n	3.1	0.02	0.03	7.0	0.04	0.08	0.57	0.25
Total	100	0.64	0.13	100	0.57	0.12	0.97	1.12

But nevertheless, needles, directly growing on the main stem are of minor importance in both groups.

2. The number of needles

The taller F-plants have a higher number of needles (7034/plant) than the smaller R-plants (3257/plant), the ratio F/R reaching 2.16 as against 1.43 for the height of the plants (Tab. 3)

The variation among the smaller plants is rather high and more important than the variation in height. The relative uniformity of the F-group, on the other hand, is perceptible. These observations indicate that, even under favourable nursery conditions, social differentiation within the community is not negligible, that unhindered developments promotes uniformity and that suppression or mutual hindrance creates variation.

There is no significant difference between the number of needles directly implanted on the main stem of F- and R-plants. In both cases the greater number of needles is found on the last shoot S.1 (about 60 % of all needles growing on the stem) and only 11 to 14 % of the needles growing on S.n. This facts confirm the rapid deterioration and disappearance of stem-needles, which seldom survive for more than 2 years.

With respect to the number of needles, growing on the branches, the differences between the F- and R-plants are more significant. The taller plants (F) carry a higher total number of needles and also have more needles in each crown level (UC, MC and LC), considered separately (Tab. 3). The distribution of the needles over different crown levels goes however in both groups roughly in the same direction : The ratio UC/MC/MC attains 1 : 3.46 : 7.92 for F-plants against 1 : 2.95 : 4.75 for R-plants. These ratio seems to indicate that the superiority in growth of the F-group is correlated with or determined by better crown development, the higher total number of needles and especially the relatively higher number of needles in the lower crown segments, standing for longer survival of the needles and/or permanent formation of new needles in the lower parts of the crown. In the upper crown part (UC), exclusively carrying recently formed needles, no real difference exists in the actual number of needles between F and R; in the middle crown (MC) a fairly important difference develops

Tab. 3 : Average number of needles/plant

Position of needles		F - plants			F - plants			t F/R	Ratio F/R
		%	$\bar{x}$	s	%	$\bar{x}$	s		
On branches	UC	8.1	554	165	11.5	356	169	2.05	1.56
	MC	27.9	1915	330	33.9	1049	420	3.97***	1.83
	LC	64.0	4386	852	54.6	1691	798	5.56***	2.59
	Tot.	100.0	6855	780	100.0	3096	1204	8.69***	2.21
On Stem	S.1	62.0	111	51.9	59.6	96	21.6	0.65	1.16
	S.2	29.1	52	22.3	29.2	47	12.8	0.48	1.11
	S.n	8.9	16	14.2	11.2	18	15.2	0.17	0.89
	Tot.	100.0	179	68.0	100.0	161	24.8	0.82	1.11
Total :	UC + S.1	9.4	665	216	13.9	452	190	2.46*	1.47
	MC + S.2	28.0	1967	351	33.7	1096	433	5.18***	1.79
	MC + S.,	62.6	4402	864	52.4	1709	813	7.52***	2.58
Grand total		100.0	7034	776	100.0	3257	1208	8.72***	2.16

in favour of F-plants; the difference in the number of needles between F- and R-plants is maximal at the lower crown level (LC). The needles of taller or faster growing plants are not only more abundant, but they also have a longer life-span. These facts explain the increasing dominance of taller and faster growing plants and the further weakening and regression of smaller plants, even under controlable nursery conditions. There is no reason to believe that, in the case of natural regeneration in the forest, development should not proceed in much the same direction.

A last analysis of needle distribution over the different ontogenetic units of each plant, whether a leading shoot or a latteral branch, whatever its position or the degree of branching, shows that the number of shoot units is much higher for F-plants with an average of 60.3 units pro plant than for R-plants with an average of only 40.2 (Tab. 4). In both plant groups the number of needles varies between 1 and 400 pro shoot unit. The F-plants carry an average of 111 needles pro ontogenetic unit against only 80 for the R-plants.

However, 55 % of all shoot units in the F-group carry less than 90 needles and only 4.5 % (= 2.5 shoot units in absolute terms) have more than 300 needles. Variation is less pronounced in the R-group, because up to 75 % of all shoot units carry less than 90 needles and only 7 % (= 2.8 shoot units in absolute

Tab. 4 Frequency (number of shoot units) of different needle classes pro ontogenetic unit (averages pro plant)

Needle class = number of needles pro unit	F - group		R - group	
	n = Freq	%	n = Freq.	%
1 - 30	13.0	21.6	10.3	25.6
31 - 60	11.8	19.6	12.7	31.6
61 - 90	8.7	14.4	6.7	16.7
91 - 120	6.2	10.3	2.7	6.7
121 - 150	3.5	5.8	3.0	7.5
151 - 180	6.0	10.0	1.8	4.5
181 - 210	1.7	2.8	1.0	2.5
211 - 240	1.8	3.0	0.7	1.7
241 - 270	2.2	3.6	0.7	1.7
271 - 300	1.2	2.0	0.5	1.2
301 - 330	2.0	3.3	0.2	0.5
331 - 360	0.3	0.5	0.2	0.5
> 360	2.2	3.6	0.5	1.2
Total	60.3		40.2	

terms) have more than 210 needles.
The superiority of the taller plants results from their higher degree of branching and the more dense covering of all branches with needles.

3. Age of the needles

The distribution of needles over age-classes and without regard for the part of the plant on which they occur, indicates that 64.4 % of all needles on F-plants and even 73.2 % on R-plants are only 1 year old (Tab. 5). The share of 2-year old needles is modest : 31.1 % for F-plants and 23.7 % for R-plants. Needles of more than 2 years are an exception in both cases : 4.5 % of the number of needles and 2.8 % of needle biomass for the F-group against 3.1 % of the number of needles and 2 % of needle biomass for the R-group. Older needles seem to deteriorate rapidly and are not very well developed : Their role in assimilation is restricted.

There is no real difference in the average age of all needles between faster and slower plants (1.40 yr for F-group against 1.30 yr for R-group).
A certain superiority of F-plants is only due to several aspects of relative development :

Tab. 5. Average number of needles and dry weight of needles on branches in g/plant according to age and position

Age Needles	Position	Number of needles on branches/plant								Dry weight of needles on branches in g/plant							
		F - plants			R - plants			t	Ratio	F - plants			R - plants			t	Ratio
		%	$\bar{x}$	s	%	$\bar{x}$	s	F/r	F/R	%	$\bar{x}$	s	%	$\bar{x}$	s	F/R	F/R
1	UC	8.0	554	165	11.5	356	169	2.05	1.56	12.1	3.0	0.86	18.6	1.9	0.95	2.10	1.58
	MC	19.6	1341	201	26.8	830	371	4.06**	1.62	24.9	6.2	0.93	27.5	2.8	1.09	5.81***	2.21
	LC	36.7	2519	781	34.9	1080	650	3.46**	2.33	28.5	7.1	2.45	28.4	2.9	1.24	3.75**	2.45
2	MC	8.4	574	478	7.1	220	89	1.78	2.61	8.0	2.0	0.63	9.8	1.0	0.34	3.42**	2.00
	LC	22.7	1560	332	16.6	513	189	5.89***	3.04	23.7	5.9	1.42	13.7	1.4	0.67	7.02***	4.21
> 2	LC	4.5	307	283	3.1	97	80		3.16	2.8	0.7	0.52	2.0	0.2	0.16	2.25*	3.50
1 yr.		64.4	4414	697	73.2	2266	1043	4.61***	1.95	65.5	16.3	2.66	74.5	7.6	2.71	5.61***	2.14
2 yr.		31.1	2134	299	23.7	733	251	7.43***	2.87	31.7	7.9	1.18	23.5	2.4	1.03	7.98***	3.29
>2yr.		4.5	307	284	3.1	97	80	1.73	3.16	2.8	0.7	0.52	2.0	0.2	0.16	2.25*	3.50
	UC	8,1	554	165	11.5	356	169	2.78*	1.56	12.1	3.0	0.86	18.6	1.9	0.95	2.85**	1.58
	MC	27.9	1915	679	33.9	1050	459	3.50**	1.82	32.9	8.2	1.56	37.3	3.8	1.39	6.98***	2.16
	LC	64.0	4386	1395	54.6	1690	918	5.55***	2.60	55.0	13.7	4.38	44.1	4.5	2.07	6.30***	3.04
Grand total		100	6855	2238	100	3096	1546	4.58***	2.21	100	24.9	7.33	100	10.2	4.26	5.75***	2.44

* F- plants carry more needles all over the crown and in each crown level separately.
* Recent formation of new needles is more abundant.
* Needles remain longer on the plant and in greater numbers.

As a result, the share of older needles is relatively more important in the F-group, as indicated by

* The increasing value of the F/R-ratio with progressing age for the number of needles as well as for their biomass.
* The relative importance of the age classes within each group.
* The higher share of older needles in each crown level for F-plants compared to R-plants :

		Distribution of needles	
Crown level	Age of needles	F-group	R-group
MC	1	70.0%	79.0%
	2	30.0%	21.0%
LC	1	57.4%	63.9%
	2	35.6%	30.4%
	3	7.0%	5.7%

It is difficult to ascertain whether the relative dominance of 1-year old needles is due to increasing annual needle formation with the passing of time or to quick shedding of needles. However, in both groups, needle formation seems to progress more intensely than the increase in length and biomass of the main stem :

Ratio		F	R
Biomass of shoot	S.2/S.2	0.40	0.95
Length of shoot	S.1/S.3	1.34	1.81
Number of needles	N.1/N.2	2.07	3.09
Biomass of needles	N.1/N.2	2.06	3.17

Retarded plants seem to recuperate after some time and should therefore not prematurely be considered as a loss. The annual growth rate of the needles and the density of their cover are, in fact, better parameters for qualification as the actual height growth of plants.

A last important difference concerning the age of needles between F-plants and R-plants, resides in the fact that, although the lower crown level carries the highest number of needles in both groups(64 % for F and 55 % for R) and as the highest share in each needle age-class, older needles are relatively more important in the F-group over the whole crown and on each crown level separately. At the same time the lower crown level is more strongly represented, absolutely and relatively, in F-plants :

Age class	Crown level	F-group	R-group	
1	UC	12.6%	15.7%	
	MC	30.4%	36.6%	
	LC	57.0%	47.7%	100.0
2	MC	26.9%	30.0%	
	MC	73.1%	70.0%	100.0

4. The biomass of needles

The characterization of the needle biomass by its dry weight roughly produces the same general picture as its expression by the number of needles :

a. The average dry weight of all needles pro plant is considerably higher for fast growing plants (24.9 g for F-plants against 10.2 g for R-plants).

b. The share of each age-class in needle biomass is about the same, whether expressed by dry weight or by the number of needles : 2/3 (F) to 3/4 (R) of needle biomass is concentrated in 1-year old needles, 1/3 (F) to 1/4 (R) in 2-year old needles and older needles represent no more than 2 to 3 % of the total needle biomass.

c. The needle biomass is concentrated in the lower level, but with a relatively greater share in the F-group as in the R-group. The share of the upper crown level is restricted to 12 % of needle biomass for fast growing plants against up to nearly 19 % for slower growing plants.

In interpreting these facts, it should be kept in mind that F-plants carry a higher absolute needle biomass on all crown levels, but that younger needles and the needles in the upper crown have a relatively greater share in total needle biomass in the R-group as in the F-group.

This situation can be explained by the different degree of branching and, as a consequence, by differences in the formation of new needles in MC and LC. On these points fast growing plants are in a better position. The greatest mass of 1-year old needles occurs in LC (7.1 g or 28.5 % of needle biomass in the F-group and 2.9 g or 28.4 % in the R-group) and the lowest in the upper crown level, where the differences between F- and R-plants are minimal (3.0 g or 12.1 % for F against 1.9 g or 18.6 % for R). As a consequence of better branching and crown development the F/R-ratio for needle dry weight is higher in LC than in UC (3.04 against 1.58). It is also much higher for older needles as for 1-year old needles (3.50 against 2.14).

It is evident that the distribution of needle dry weight, as compared to the distribution of the number of needles, indicates a certain shifting in the direction of UC, but not in het direction of 1-year old needles. This shifting is rather more important in the R-group. On the other hand, all F/R-values indicate a clear shifting in the direction of the F-group on nearly all counts : The relative superiority of fast growing plants is still better expressed by the dry weight of the needles as by their numbers. The physiological consequences of this situation are obvious.

Rather puzzling remains the modification of growth relationship during the last growing year as compared to the previous one :

		F-group	R-group
Ratio	Dry weight N.1/N.2	2.06	3.17
	Dry weight S.1/S.2	0.47	0.51
	Dry weight B.1/B.2	1.22	1.28

In both groups development is more concentrated in needle growth as in branching, height growth practically remaining the same. The higher values of the rates for the R-group, especially concerning the relation between younger and older needles, indicates a certain degree of recuperation of the retarded plants.

5. The weight of the needles

The picture of relative plant development is incomplete without an acceptable characterization of the needles themselves. Fröhlich (1969) considers, in this sense, the dry weight of 1000 needles as the most important and suitable parameter.

On a general level, there seems to be no difference in the average 1000-needle dry weight and consequently, in the individual basis physiological characteristics of the needles, developing on fast and on slower growing plants, as well as between the needles on branches and those growing on the main stem in both groups (F and R) :

	Dry weight of 1000 needles/g	
	On branches	On the stem
F-group	3.63	3.52
R-group	3.39	3.52

On the other hand, significant differences in needle weight are observed, if the age of the stem segment, on which they develop, is considered :

	Dry weight of 1000 needles / g					
	On S.1		On S.2		On S.n	
	g	%	g	%	g	%
F-group	3.33	100	4.81	144	1.25	38
R-group	3.44	100	4.26	124	2.22	65
F/R	0.97	100	1.13	116	0.56	58

In both groups the needles on the 2-year old segments are heavier than those on the actual leading shoot. The difference is more important in the F-group as in the R-group. The needles on older stem segments are feebly developed, especially in the F-group, and, therefore, of restricted importance. The variation within the F-group is greater as within the R-group.

The comparison of 1000-needle weight growing on branches and according to position and age of the needles, confirms that no real differences in needle weight exist, also not for each crown level and each age-class separately, between fast and slow growing plants. (Tab. 6). It thus appears that the differences in growth between F-plants and R-plants are mainly caused by differences in needle mass or crown development and practically not by differences in needle quality.

Within each group, however, equivalent differences in needle weight are caused by differences in position of the needles and, to a lesser degree, by differences of age of the needles. In both groups needle weight rapidly diminishes from UC over MC to LC. Differences attain 43 % for F-plants against 50 % for R-plants. On the other hand, general differences in weight do not exist between 1-year old and 2-year old needles in both groups, but older needles show a rapid decrease in weight and, consequently, in needle quality.

Growing results and collective differences in growth are thus mainly determined by the total needle-biomass and by the presence of younger needles in the uppercrown level.

The intricate interference of age and position of the needles, as far as their weight is concerned, can be summarized as follows :

- Within each group (F and R) needle weight decreases along the line UC — MC— LC.
- In the middle crown MC and the lower crown LC 2-year old needles are superior in weight, and probably also in physiological activity, in comparison to 1-year old needles.
- Needles, more than 2-years old and existing only in LC, are less heavy and, on account of their lower individual weight and the modest share of total needle biomass they represent, of minor importance.

Needles reach their maximal degree of development in the second year and in the middle part of the crown (MC). After 2 years, needles deteriorate rapidly. Recently formed needles in the lower part of the crown (LC) do not develop well.

THE BIOMASS OF STEM AND BRANCHES

As indicated before (Tab. 1), needles account for about 50 % of above-ground biomass, the main stem for 30 % and the branches for roughly 20 %. In respect to this proportion 5 : 3 : 2, no significant differences exist between F-plants and R-plants. Neither stimulation nor slowing down of height growth does affect the proportional development of nursery plants of Abies grandis Lindl.

1. Stem biomass

Stem dry weight is significantly higher for F-plants as for R-plants and this applies to total stem biomass as well as to each stem segment separately.(Tab.7).

Tab.6 : Average dry weight/g of 1 000 needles according to age and position

Age needles	Position	F - plants				R - plants				t F/R	Ratio F/R
		%	$\bar{x}$	s	t	%	$\bar{x}$	s	t		
1	US	100	5.47	0.98	3.57**	100	5.57	1.07	3.99**	0.17	98
	MC	72	3.96	0.34	5.56***	62	3.44	0.75	1.17	1.55	115
	LC	52	2.82	0.37		52	2.89	0.88		0.18	98
2	MC	100	5.93	1.02	3.45**	100	4.95	0.80	2.55**	1.85	120
	LC	66	3.90	1.02		72	3.54	1.31		0.53	110
2	LC	100	1.89	0.10		100	2.42	0.68		1.89	128
1		100	3.51	0.34	2.22*	100	3.45	0.60	1.47	0.21	102
2		121	4.23	1.02	7.57***	114	3.93	0.90	4.44***	0.54	108
2		54	1.89	0.10		70	2.42	0.68		1.71	128
	UC	100	5.52	0.96	9.04***	100	5.57	1.07	3.75**	0.08	99
	MC	78	4.28	0.18	6.62***	67	3.71	0.71	1.75	1.91	115
	LC	57	3.14	0.51		50	2.78	0.52		1.21	113

Other t-values :

F - plants : 1.MC/2.MC = 6.08***
1.LC/2.LC = 2.44**

R-plants : 1.MC/2.MC = 4.57***
1.LC/2:LC = 1.37

Tab. 7 : Distribution of dry weight / g over different stem segments.

Stem segment	F - group			R - group			t F/R	Ratio F/R
	%	$\bar{x}$	s	%	$\bar{x}$	s		
S.1	6.6	1.0	0.29	8.4	0.6	0.19	2.83*	1.67
S.2	16.4	2.5	0.60	15.5	1.1	0.35	5.29***	2.27
S.n	77.0	11.7	2.25	76.1	5.4	1.42	5.80***	2.17
Tot.	100	15.2	2.51	100	7.1	1.76	6.47***	2.14

Within each group stem-segment biomass, quite normally, decreases along the line S.n — S.2 — S.1.

The ratio F/R is practically the same as for needles and branches, conforming equivalent relative development in both groups. Applied to individual stem segments however, the F/R-value is relatively lower for S.1 as for S.2 and S.n. This leads primarely to the acceptance of a fundamental and possibly genetic difference between both groups. More important, however, is the constation of the increasing superiority of fundamentally faster growing plants, due to the cumulative effects of their better potential for growth and their aptitude to obtain a dominant position in a simply structured community, characterized by equal distribution of growing space and egalization of growing conditions.

The lower stem segment (S.n) accounts for no less than 3/4 of total stem biomass in both groups, S.2 for about 16 % and the actual leading shoot S.1 for only 6 to 8 %. The relative distribution of dry weight over the three stem-segments is roughly the same for F-plants and R-plants. The higher relative share of S.1 in the R-group and the fact that the F/R-ratio is minimal for S.1, are indicative for the recuperative power of slower growing plants, even if significant absolute differences in shoot weight must be taken into consideration.

As S.1 is the result of 1 growing season, S.2 of 2 growing seasons and S.n of an average of [illegible] growing seasons, the mean annual increment in dry weight pro shoot segment can be calculated :

	F-plants	R-plants
S.1	1.00	0.60
S.2	1.25	0.55
S.n	2.93	1.35
Total	3.04	1.42

The lower part of the stem clearly shows the highest yearly increment in mass. The relative differences between both groups are confirmed.

2. Biomass of branches

F-plants have a considerably higher number of branches of first order as R-plants (Tab. 8). The difference is nearly exclusively due to significant differences in the number of branches in the lower crown level. The relative dominance of faster growing plants is determined by their better branching during the very first growing years and the longer survival of branches, with a higher total and needle biomass as a direct consequence and increasing their dominance.

Tab. 8 : Number of branches of 1st. order and their distribution

Position	F - group			R - group			t F/R	Ratio F/R
	%	$\bar{x}$	s	%	$\bar{x}$	s		
UC/S.1	13.9	4.3	0.82	14.4	3.3	1.21	1.68	1.30
MC/S.2	25.8	8.0	2.53	29.7	6.8	2.23	0.87	1.18
LC/S.n	60.3	18.7	2.34	55.9	12.8	3.54	3.41**	1.46
Total	100	31.0	2.97	100	22.9	3.29	4.42**	1.35

Fast growing plants build, as a matter of fact, stronger branches with a higher biomass in each age-class, the degree of branching not taken into consideration (Tab. 9). The superiority in branch dry weight is more outspoken than the superiority in number of branches (cfr. F/R tab. 8 and tab. 9). It increases with progressing age of the branches, more due to the quicker weakening of older branches in the R-group than to a relatively better development of younger branches in the F-group. However, in both groups, older branches are less well developed than the younger ones and the t-value for the differences in dry weight between branches with a different age are highly significant :

Age of branches	F-group	R-group
1 year / 2 years	2.22*	1.25
2 years / 3-5 years	4.31**	3.92**

Tab. 9 : Dry weight of branches (g/plant)

Age/yr branches	F - group			R - group			t F/R	Ratio F/R
	%	$\bar{x}$	s	%	$\bar{x}$	s		
1	100	3.98	0.53	100	1.96	0.79	5.15***	2.03
2	82	3.26	0.56	78	1.53	0.58	5.47***	2.13
> 2	52	2.08	0.39	25	0.49	0.23	8.66***	4.24

These observations are not incompatible with the fact that the greater part of the total branch biomass is concentrated in the lower crown level LC, which represents between 45 and 54 % of dry weight of all branches (Tab. 10). The differences between crown segments as well as between plant groups for each segment are significant. The superiority of F-plants is complete, as also the average weight pro branch is higher :

Average dry weight / g pro branch

Grown level	F-group	R-group	F/R
UC	0.3186	0.2333	137
MC	0.3662	0.2205	166
LC	0.2684	0.1500	179
All levels	0.3006	0.1829	164

Tab. 10 : Distribution of branch biomass (g/plant) over different crown levels

Crown level	F - group				R - group				t	Ratio
	%	$\bar{x}$	s	t.CL*	%	$\bar{x}$	s	t.CL*	F/R	F/R
UC	14.7	1.37	0.41		18.4	0.77	0.38		2.63*	1.78
				.32***				2.49^{+}		
MC	31.4	2.93	0.59		35.8	1.50	0.61		4.13**	1.95
				3.61**				0.93		
LC	53.9	5.02	1.29		45.8	1.92	0.92		4.79***	2.61

* t.CL = t-value for mean differences between crown levels.

Maximal average branch weight for F-plants is found in the middle crown level; for R-plants it decreases continually from upper to lower over the middle crown level. The superiority of F-plants is however maximal in the lower crown level due to the higher number of branches, the higher branch and needle biomass and the higher individual branch weight, although in all cases average branch weight is lower in LC than in UC.

It is growth during the very first years that provokes the big differences in crown structure and branching. Fast growing plants dominate and increase their dominance because they carry a far higher branch biomass in each crown level and in each branch age-class pro crown level (Tab. 11). Their superiority is especially pronounced in all age classes belonging to the lowest crown level. In the F-group the biomass of 2-year old branches is higher in LC than in MC; the biomass of 1-year old branches is higher in MC than it is in UC; branches of more than 2 years old have the highest biomass compared to all other classes; even the 1-year old branches in LC, although less well developed than the same age class on other levels, still reaches 86 % of the biomass of recent branches in UC, meaning that formation of new branches is still going on and that the biomass they represent, is not neglectable. In the R-group quite the contrary occurs : the biomass of 1-year old branches decreases from UC to LC and the biomass of 2-year old branches from MC to LC; the biomass of the branches, older than 2 years, is the lowest of all classes; the biomass of recent branches in LC reaches but 68 % of the biomass of 1-year old branches in UC.

Tab. 11 : Distribution of branch biomass (dry weight g/plant) according to age of branches pro crown level.

Crown level	Age of branch / yr.	F - group		[illegible] - group		t F/R	Ratio F/R
		$\bar{x}$	s	$\bar{x}$	s		
UC	1	1.37	0.41	0.77	0.38	2.63*	1.78
MC	1	1.43	0.38	0.68	0.30	3.79**	2.10
	2	1.50	0.22	0.82	0.35	4.03**	1.83
LC	1	1.18	0.34	0.52	0.28	3.67**	2.27
	2	1.76	0.64	0.71	0.28	3.68**	2.48
	>2	2.08	0.39	0.49	0.23	8.60***	4.24

CONCLUSION

In a random sample of nursery material of Abies grandis Lindl. an early and significant distinction can be made between fast (F-plants) and slower growing (R-plants) After 3 years they are already characterized by significant differences in height, that increase absolutely and decrease relatively with the passing of time.

In both groups 50 % of all overground biomass is concentrated in the needles, 30 % in the main stem and 20 % in the branches. Needles of more than 2 years old are an exception, accounting for less than 3 % of needle biomass. More than 2/3 of all needles are only one year old. Needles reach their maximal development in the second year and deteriorate rapidly afterwards.

Fast growing plants possess a higher number of needles and branches; their superiority is still more clearly expressed by the dry weight of these components.

Fast growing plants show a better survival of older crown elements than slower growing or retarded plants. They manifest a higher potential for the formation of new elements, both needles and branches. This fact is amply illustrated by the much higher number of 1-year old needles, present in the lower crown level.

The superiority of taller plants exists in all crown levels, but especially in the lower crown level. The higher biomass of fast growing plants corresponds with a more intense physiological activity in all crown levels, particularly in the lower of the crown, where the greater part of needle-biomass is concentrated and which represents a higher share of biomass in F-plants in comparison with R-plants.

The selection of material, suitable for afforestation, must take these differences into account. In all cases, where no fundamental objections against the use of taller plants are formulated, due preference must be given to F-plants.

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