CHLOROPHYLL AND CAROTENOID CONTENT IN NURSERY PLANTS OF ABIES GRANDIS LINDLEY.

N. Lust

State University, Faculty of Agricultural Sciences, Department of General and comparative Silviculture
Research Centre for Silviculture, Forest Management and Forest Policy

1. Aims and methodology

The aim of this research is to get a better knowledge of the pigment content in nursery plants of Abies Grandis Lindley. The examination will pay special attention to the chlorophyll a and b content and to the group of yellow pigments or carotenoïds. The following factors will be examined : the absolute pigment contents, their mutual relations, the evolution in the course of the growing season and the influence of several growing circumstances.

The analyses take place in different plant parts, in order to get a better judgment of the value and the importance of the needles on the different plant parts.

The present research is a complement to a previous one, in which the above ground biomass was analysed (Van Miegroet & Lust, 1983).

The investigation concerns five year old nursery plants of Abies grandis, which have been transplanted as two year old seedlings. The population has been divided into 2 groups, viz. :

Group I : Dominating plants, the most vital plants, which had reached an average height of 59,2 cm at the end of the 5th growing season.

Group II : dominated plants, which have grown less fast, with a height of 41,3 cm.

In each of both groups a distinction has been made between 6 objects, according to age and place of occurence of the needles :

1. one year old needles on one year old stem part ;
2. one year old needles on two year old stem part ;
3. one year old needles on more than two year old stem part ;
4. two year old needles on two year old stem part ;
5. two year old needles on more than two year old stem part ;
6. more than two year old needles on more than two year old stem part.

In each group the objects can be reduced to 3, viz. one year old, two year old and more than two year old needles.

The pigment content has been determined by means of a spectrophotometer (Thas, 1969).

About 1 g of needles has been used for each object.

Practically it was not possible to repeat the experiment for all objects, which a well-founded statistic interpretation would require. In order to cope with this difficulty, each sample was composed of needles of ten different plants. The pigment content is expressed in g per dry weight. Therefore, however, the transition from fresh weight to dry weight has to be examined.

2. Relation fresh weight - dry weight

Fresh weight and dry weight of leaves and needles are depending on many factors, of which water supply, position with respect to light or shadow, and the physiologic situation of the organs are very important.

Lust (1973) determined that especially the environment has an important influence on fresh and dry weight of the needles of young ash plants.

The fresh weight of plants growing in the full light was about 1,94 time higher than it was of plants growing under a dense cover. The differences between the values of the dry weight were even greater, namely 2,92. As a consequence, the relation between fresh weight and dry weight was bigger in shade plants than in light plants. The mean value for the first group was 5,33 whereas it was only 3,54 for the other group. In these ashes the relation in shadow leaves was 1,51 times greater than it was in light leaves.

The relation fresh weight/dry weight in seedlings of Abies Grandis is very variable (table 1). This value is generally the highest in one year old needles. From June till October the mean value is 3, 57 in the dominating group and 3,37 in the dominated one. The differences however are not significant. So, this statement, does not match with the above-mentioned results in ash leaves. The needles of the dominated group are indeed more shade-like than the ones of the dominating group.

One year old leaves have a very high value shortly after their appearance, which is a consequence of the low percentage of dry matter. However these needles evolve rather soon to a lower level.

In both groups the parameter value in one year old needles is considerably higher than it is in the older needles. Apart from the exceptional data for the one year old needles in May, the following results are mainly obtained :

	group I	group II
- one year old needles	3,57	3,57
- two year old needles	2,88	2,80
- > two year old needles	2,74	2,67

There is only a slight difference between 2 year old needles and the older ones. The differences between both groupsalso grow smaller with increasing age. The dry weight of the needles is more important as the needles grow older and as the plants can grow up in the full light.

Table 1 : The relation fresh weight- dry weight.

Object			Point of time			Evolution	
	4/5(1)	6/6(2)	5/7(3)	10/8(4)	1/10(5)	(1)/(2)	(2)/(5)
I, 1 y old needles	5,60	3,61	3,89	3,39	3,38	1,55	1,07
I, 2 y old needles	2,56	2,99	2,91	2,98	2,98	0,86	1,00
I, > 2 y old needles	2,46	2,85	2,77	2,83	2,78	0,86	1,03
II,1 y old needles	5,45	3,31	3,56	3,28	3,32	1,64	1,00
II,2 y old needles	2,57	2,79	2,88	2,83	2,92	0,92	0,96
II,> 2 y old needles	2,91	2,70	2,45	2,60	2,71	1,08	1,00
I,1y n. on 1 y stem	5,96	3,63	3,87	3,26	3,32	1,64	1,09
I,1y n. on 2 y stem	5,14	3,78	3,79	3,20	3,41	1,36	1,11
I, 1 y n. on > 2 y stem	5,70	3,41	4,00	3,71	3,40	1,67	1,00
I, 2 y n. on 2 y stem	2,55	3,06	2,92	3,01	2,82	0,83	1,09
I, 2 y n. on > 2 y stem	2,56	2,91	2,90	2,95	3,13	0,88	0,93
I, > 2 y. n. on > 2y st.	2,46	2,85	2,77	2,83	2,78	0,86	1,03
II, 1y. n. on 1y st.	5,22	3,30	3,54	3,27	3,24	1,58	1,02
II, 1y. n. on 2 y st.	5,69	3,27	3,57	3,22	3,36	1,74	0,97
II, 1y. n. on > 2 y.st.	5,44	3,37	3,57	3,36	3,35	1,63	1,06
II, 2y. n. on 2 y.st.	2,53	2,80	2,88	2,73	2,91	0,90	0,96
II, 2y. n. on > 2 y st.	2,63	2,78	2,88	2,92	2,93	0,94	0,95
II, >2y.n. on > 2 h st.	2,91	2,70	2,45	2,60	2,71	1,08	1,00

There is only a slight difference between 2 year old needles and the older ones. The differences between both groups also grow smaller with increasing age. The dry weight of the needles is more important as the needles grow older and as the plants can grow up in the full light.

There is practically no difference between the needles that are of the same age. In both groups there is hardly any difference between one year old needles appearing on the one year old stem and the one year old needles on the older stem parts. In this respect there is no difference between light needles and shade needles. The age of the needles is of main importance and their social position is of second importance.

The relation fresh weight:dry weight is quite stable during the growing season. An exception to this is made by one year old needles, as their relation quickly decreases in the beginning of the growing season. The relation between the content on 6/6 and the one on 1/10 equals 1,01 for all objects together.

3. Content and evolution of the chlorophyll pigments

According to Egle (1960) the mean value of the chlorophyll content in light leaves equals 11,80 mg/g dry weight, whereas this value is 15,80 for shade leaves, that means 33,8 % more. The results obtained by Van Miegroet (1970) are similar. He stated for five hardwood species that the chlorophyll content/g fresh weight is meanly 37 % higher for the dominated level than for the dominating level. However he noted a much lower pigment content.

Lust (1971), '73) noted that the chlorophyll content in seedlings of ash was, 13, 72 mg/g dry weight under a dense cover, whereas the same plants in the open field only had a content of 3,10 mg/g dry weight.

In 5 year old seedlings of Abies alba, Paule (1977) found for all pigments a higher percentage in plants growing under a cover. Fomichev (1973) examined the chlorophyll content in seedlings of Pinus sylvestris and Larix siberica. It increased as the number of seedlings decreased. " The quality and yield of seedlings were directly related to chlorophyll content ".

Blintsov and Tsai (1977) determined the chlorophyll content in 6 and 7 year old plants of Pinus sylvestris. In doing so, they noted that soil cultivation and fertilisation had a positive influence.

When examining 40 year old trees of Picea abies Tsaregorodtseva and Novitskaya (1975) in their turn stated that the pigment content increased with the application of fertilizers.

During research on Metasequoia glyptostroboides, Laudi and Lanzini (1975) pointed out that " leaves from vegetative buds, that had been completely shielded from light, contained about half as much chlorophyll as normal leaves. The ultrastructure of plastids grown in darkness was little changed, except for the absence of starch. It is concluded that the capacity to become green without exposure to light is a primitive characteristic which is expressed in both leaves and cotyledons. "

3.1. Chlorophyll a per dry weight

The chlorophyll a content, as an average of all needles and all points of time, amounts to 4,16 mg/g dry weight for dominating plants and 3,70 mg/g dry weight for dominated plants. (Table 2).

Table 2. Content and evolution of chlorophyll (mg/g. dry weight).

Object	Point of time				
	4/5	6/6	5/7	10/8	1/10
I, 1 y. old needles	4,20	3,68	3,91	4,19	4,32
I, 2 y. old needles	4,13	4,56	3,75	4,96	3,47
I, > 2 y. old needles	3,94	4,82	3,98	4,49	4,00
II, 1 y old needles	3,31	3,38	3,50	3,07	4,57
II, 2 y old needles	4,26	3,57	3,51	4,26	3,86
II, > 2 y old needles	4,83	3,49	2,88	3,61	3,35
I, 1 y old needles on 1 y old stem	4,11	3,55	3,75	3,45	3,96
I, 1 y old n. on 1 y old st.	3,29	3,71	3,91	3,33	4,19
I, 1 y old n.on > 2 y old st.	5,19	3,79	4,07	5,78	4,81
I, 2 y old n.on 2 y old st.	4,03	5,04	3,58	5,52	2,65
I, 2 y old n.on 2 y old st.	4,22	4,07	3,92	4,39	4,28
I, > 2 y old n. on > 2 y old st.	3,94	4,82	3,98	4,49	4,00
II, 1y old n. on 1 y old st.	2,40	3,77	3,71	2,23	5,01
II, 1y old n. on 2 y old st.	4,15	2,84	3,46	2,90	4,81
II, 1y old n. on > 2 y old st.	3,37	3,53	3,32	4,07	3,88
II, 2y old n. on 2 y old st.	3,74	3,38	3,34	3,72	2,82
II, 2y old n. on> 2 y old st.	4,78	3,75	3,68	4,79	4,89
II >2 y old n.on > 2y old st.	4,83	3,49	2,88	3,61	3,35

The differences between both groups are significant, despite the periodical variations. This means that the chlorophyll a content, expressed per dry weight, is higher in vital plants than in less vital plants.

This confirms the results of Banecke (1972), Fomichev (1973), Tsaregorodtseva (1975) and Blintsov (1977), who all noted that growth-stimulating products had a favourable effect on the chlorophyll content. In this case the differences are not so big -hardly 12%- although the dominating group is 43 % higher than the dominated one, and the differences in biomass between both groups amount to 123 % (Van Miegroet, Lust, 1983).

Within the same group of plants the shade position of the needles increases as the needles grow older : the more than 2 year old needles are overgrown by the 2 year old ones and the latter are overgrown themselves by the most recent needles.

According to the above-mentioned results, the pigment content should be the highest in more than 2 year old needles. However this is not the case : in both groups there is no significant difference between the chlorophyll a content per dry weight of one year old needles, two year old needles and more than 2 year old needles. The mean values for the whole season are :

	group I	group II
1 year old needles	4,06	3,57
2 year old needles	4,17	3,89
> 2 year old needles	4,25	3,63

In the first group the mean value might indicate a certain trend, but the variations on different points of time are too large to be significant.

Needles of the same age appear on stem parts of different ages.

The result of this fact on the chlorophyll a content is not clear. The following mean values were stated for the whole season :

	group I	group II
1 year old needles		
- on 1 year old stem	3,77	3,42
- on 2 year old stem	3,69	3,63
- on > 2 year old stem	4,73	3,71
2 year old needles		
- on 2 year old stem	4,16	3,40
- on > 2 year old stem	4,18	4,38

In the first group the content of the 1 year old needles is significantly the largest on the more than 2 year old stem. This fact however is not confirmed by the second group. Yet, in the latter group, there are significant differences between the two year old needles, which is not true in the first group.

The differences in the chlorophyll a content per dry weight are, generally speaking, not very big. The most vital plants have the greatest content. Shade needles do not have clearly higher values.Under normal circumstances, the high chlorophyll a content of shade leaves indicates an increased intensity of the leaves. It is possible that the rather low values, determined in these nursery plants of Abies grandis, point to a small efficiency of the older needles.

The evolution of the chlorophyll a content in the course of the season is not clear. On an average there is practically no difference in both groups between the initial values in May and the final values in October. The first group evolves from 4,09 mg/g dry weight to 3,93 and the second group from 4,13 to 3,93. From May to October, however, the values of all objects fluctuate so irregularly, that no clear trend can be indicated.

3.2. Chlorophyll b per dry weight

In seedlings of ash, Lust (1973) stated a chlorophyll b content per g dry weight, varying from 0,52 mg in the open field to 4,72 mg under a dense cover.
In comparison to the chlorophyll a, the content was 2,5 to 6 times smaller. The value of plants grown in the light reached only 15 % of the value of shade plants.
In the present research, the very high value of chlorophyll b is especially remarkable. For all objects and points of time together, the chlorophyll b content is 4,5 mg/g dry weight. (Table 3). This value is 15 % higher than the chlorophyll a content, which can be considered to be quite exceptionnal. The meaning of this phenomen is not clear.
The most vital group I has an average value of 4,66, whereas the smaller plants have a content of 4,33. Opposed to chlorophyll a, the difference is not significant.
As in chlorophyll a, so in chlorophyll b there is no significant difference between the needles of different ages. The differences in both groups are not significant.

	group I	group II
- one year old needles	4,56	4,20
- two year old needles	4,66	4,49
- > two year old needles	4,77	4,45

Table 3. Content and evolution of chlorophyll b (mg/g.dr.weight).

Object	Point of time				
	4/5	6/6	5/7	10/8	1/10
I, 1y old needles	6,12	3,78	3,67	4,62	4,64
I, 2 y old needles	4,80	5,07	4,34	5,41	3,67
I, > 2 y old needles	3,47	5,64	4,87	5,53	4,35
II, 1 y old needles	4,40	4,03	4,14	3,25	5,19
II, 2 y old needles	4,51	4,20	4,02	5,02	4,69
II, > 2 y old needles	5,47	3,94	3,78	4,92	3,46
I, 1 y old n. on 1 y old st.	6,44	3,44	3,11	3,77	4,41
I, 1 y old n. on 2 y old st.	4,73	3,58	3,61	3,75	4,66
I, 1 y old n. on > 2 y old st.	7,18	4,33	4,29	6,34	4,85
I, 2 y old n. on 2 y old st.	4,74	5,78	4,12	6,33	2,68
I, 2 y old n. on > 2 y old st.	4,86	4,35	4,55	4,49	4,66
I, > 2 y old n.on > 2 y old st.	3,47	5,64	4,87	5,53	4,35
II, 1 y old n. on 1 y old st.	3,13	4,67	4,36	2,01	6,04
II, 1 y old n,on 2 y old st.	6,03	3,39	4,31	3,74	5,58
II, 1 y old n. on > 2 y old st.	4,03	4,02	3,75	4,00	3,95
II, 2 y old n. on 2 y old st.	3,57	4,40	3,81	4,12	3,01
II, 2 y old n.on > 2 y old st.	5,45	4,00	4,23	5,91	6,37
II, > 2 y old n.on > 2 y old st.	5,47	3,94	3,78	4,92	3,46

Contrary to the general rule, shade needles do not have a higher chlorophyll b content per dry weight than do light needles. A more detailed examination for possible differences in needles of an age, grown on different stem parts, does not indicate certain trends, except for the general equivalence with temporary or local remarkable variations which are probably a consequence of the taking of samples.

The mean values of the season are :

	group I	group II
1 year old needles		
- on 1 year old stem	4,23	4,04
- on 2 year old stem	4,07	4,61
- on > 2 year old stem	5,40	3,95
2 year old needles		
- on 2 year old stem	4,73	3,78
- on > 2 year old stem	4,58	5,19

There are only significant differences in the second group in 2 year old needles : the needles on the > 2 year old stem part, that is on the lowest and shadiest part, have a higher clorophyll b value per dry weight.

The evolution of chlorophyll b per dry weight in the course of the season is indistinct, as it is for chlorophyll a.

The fluctuations from month to month are so irregular for all objects, that no general rules can be fixed. For all objects together, the highest values were noted in May and August, namely 4,80 mg/g dry weight, and the lowest value, noted in July, was 4,13.

3.3. The total chlorophyll content (a+b) per dry weight

Wood (1974) determined the chlorophyll content of needles of different ages in 6 year old Pinus radiata plants. " In relation to dry weight of the needles, chlorophyll decreased with increasing age and was unaffected by height in the tree. "

El Aouni and Mousseau (1974) also stated in Pinus nigra var. austriaca that the chlorophyll efficiency decreased with increasing age of the needles.

Linder (1972) stated in seedlings and transplanted plants of Scots Pine and Norway Spruce that the pigment content was influenced by several factors, such as the quality of the station, the age of the plants, the age of the needles and the provenance of the seed. In both species important differences according to the seasons were noted as well.

In seedlings of Pinus mugo and Picea abies in North Tyrol, Benecke (1972) also determined seasonal differences in the chlorophyll content, with a minimum in late winter. Moreover the content decreased with the altitude.

Several authors proposed a hypothesis on the degradation of the destruction of chlorophyll. El Aouni and Mousseau (1974) pose that " the drop in winter of the total chlorophyll content appears to be correlated with a chloroplast degradation as a result of low temperatures. This degradation becomes less and less reversible with age. The renewed activity during the growing season is due in part to an increase in the photoreceptor pigment content. " Öquist et al. (1978) on their part concluded in their study of Pinus silvestris that " photosensitized oxidation is the most probable cause of chlorophyll destruction. "

The results found in 5 year old transplanted plants of Abies alba correspond only in small measure with the above-mentioned researches. (Table 4).

The chlorophyll content of the more vital plants from the first group is not significantly higher than the one of the second dominated group : the first average value is 8,82 mg/g dry weight. In the same way it is not possible to show a significant difference between the needles of different ages. The one year old needles do not have higher values than the 2 year old or older ones, as was stated by Wood (1974) and El Aouni and Mousseau. The mean seasonal values are :

	group I	group II
- one year old needles	8,63	7,77
- two year old needles	8,83	8,38
- > 2 year old needles	9,02	7,95

A more detailed examination of the one year old and 2 year old needles shows the following mean values :

Table 4. Content and evolution of the total chlorophyll (mg/g. dry weight).

Object	Point of time 4/5	6/6	5/7	10/8	1/10
I, 1 y old needles	10,31	7,47	7,58	8,81	8,96
I, 2 y old needles	8,93	9,62	8,09	10,37	7,14
I, > 2 y old needles	7,41	10,46	8,85	10,02	8,35
II, 1 y old needles	7,70	7,41	7,64	6,32	9,76
II, 2 y old needles	8,77	7,77	7,53	9,27	8,55
II, > 2 y old needles	10,30	7,43	6,66	8,53	6,81
I, 1 y old needles on 1 y old st.	10,55	6,99	6,87	7,22	8,37
I, 1 y old n. on 2 y old st.	8,02	7,29	7,52	7,08	8,85
I, 1 y old n. on > 2 y old st.	12,37	8,12	8,36	12,12	9,66
I, 2 y old n. on 2 y old st.	8,77	10,82	7,70	11,85	5,33
I, 2 y old n. on 2 y old st.	9,08	8,42	8,47	8,88	8,94
I, > 2 y old n. on > 2 y old st.	7,41	10,46	8,85	10,02	8,35
II, 1 y old n. on 1 y old st.	5,53	8,44	8,07	4,24	11,05
II, 1 y old n. on 2 y old st.	10,18	6,23	7,77	6,64	10,39
II, 1 y old n. on > 2 y old st.	7,40	7,55	7,07	8,07	7,83
II, 2 y old n. on 2 y old st.	7,31	7,78	7,15	7,84	5,83
II, 2 y old n. on > 2 y old st.	10,23	7,75	7,91	10,70	11,26
II, > 2 y old n. on > 2 y old st.	10,30	7,43	6,66	8,53	6,81

	Group I	Group II
- 1 year old needles		
- on 1 year old stem	8,00	7,47
- on 2 year old stem	7,75	8,24
- on > 2 year old stem	10,13	7,58
- 2 year old needles		
- on 2 year old stem	8,89	7,18
- on > 2 year old stem	8,76	9,57

These results do not show a clear trend. In the first group there are only significant differences between the 1 year old needles on the 2 year old stem part and the ones on the more than 2 year old stem.

In the second group on the other hand, there is no significant difference between the 1 year old needles, but there is between the two year old needles. The lowest needles, the ones in the shadiest position, have the largest chlorophyll content. However this can not be considered as a general rule.

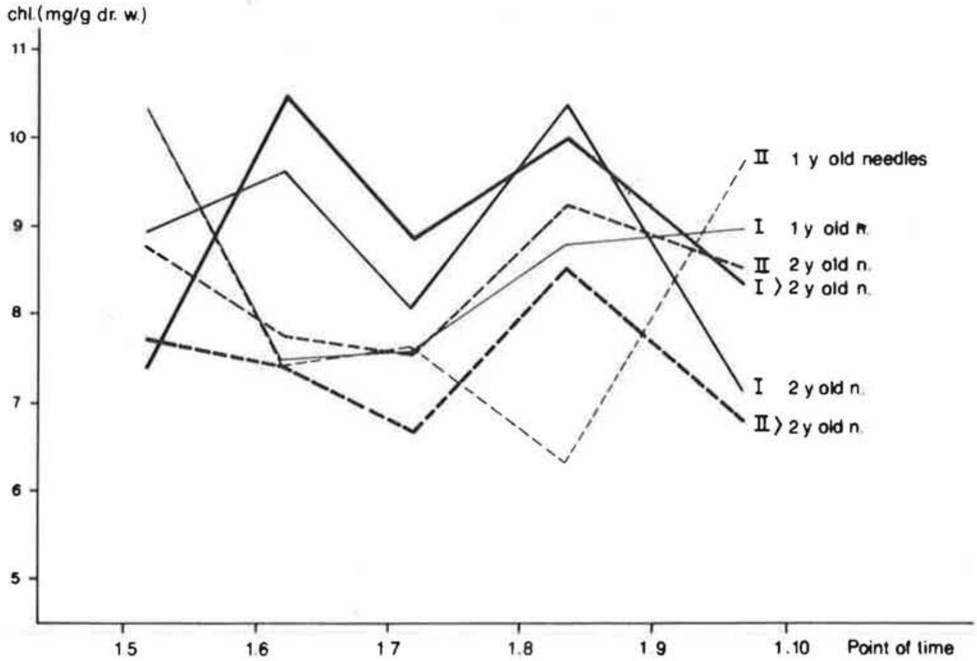

Fig. I. The evolution of the chlorophyll content in the course of the season in dominating (I) and dominated (II) plants.

The evolution in the course of the season is very variable (fig. 1). Clear differences can not be determined. Higher values follow on lower ones, or vice versa. The following mean values were noted :

	4/5	6/6	5/7	10/8	1/10
group I	8,88	9,18	8,17	9,73	8,15
group II	8,92	7,54	7,28	8,04	8,37
total	8,90	8,36	7,73	8,86	8,26

The initial value for the young needles in May is quite high, but in the beginning of October it is still high. The lowest values were noted in July, but the differences with other data are not significant.

4. Content and evolution of carotenoïds

Egle (1960) mentions that the mean carotenoïd values in light leaves equal 2,10 mg/g dry weight and 2,76 mg/g dry weight in shade leaves. So the content in shade leaves is 31 % higher, which is about the same as for chlorophyll.

Lust (1971, '73) stated similar results in ash. The carotenoïd content was higher in plants grown under a cover than in plants grown in the open field.

The relation was 3,80-1,43 for natural seedlings and 4,76-1,17 for nursery plants.

The carotenoïds were meanly composed of 77 % xantophylls and 23 % carotens.

Popov and Popova (1978) studied the carotenoïd content of the needles of Scots pine in pure pine plantations and in pine/birch strip mixtures. The plantations in central Russia were 12 and 23 years old. Needle carotenoïd content was higher in pine/birch strip mixtures than in pure pine plantations, and increased from the centre of the pine strips towards the birch strips.

The research of Ollykaynen (1969), also executed on needles of Scots pine, is very significant. In the needles of the latest growing season, the carotenoïd content was 0,29 mg/g in September, 0,210 mg/g in November and 0,206 mg/g in March. In the needles of the last but one growing season, the value was 0,376 mg/g in September, 0,254 mg/g in November and 0,218 mg/g. The carotenoïd content was depending on the age and the surroundings of the needles, and it varied according to the different phenological phases. The maximum value was determined at the end of the summer in two year old needles, the minimum value at the end of the winter.

The mean carotenoid value for Abies grandis for all objects and for the whole season is 0,94 mg/g dry weight (table 5). In the same way as it was for the chlorophyll content, the value of the most vital plants is slightly higher than the one of the less vital plants, but the difference is not significant (0,98 - 0,90). No significant differences were found between the needles of the different growing season. The mean seasonal values were :

	group I	group II
- one year old needles	0,90	0,92
- two year old needles	0,97	0,91
- > 2 year old needles	1,02	0,87

These results do not match with the above-mentioned data of Ollykaynen (1969) for Scots pine.

The search for possible differentiations in needles of an age did not bring up significant differences.

The carotenoīd content in one year old needles is independent of the occurence on the stem.

The content of needles appearing on the older stem parts, is not essentially different from the one on the youngest stem parts.

The mean seasonal values are :

	group I	group II
- 1 year old needles		
- on 1 year old stem	0,88	0,89
- on 2 year old stem	0,90	0,90
- on > 2 year old stem	1,05	0,98
- 2 year old needles		
- on 2 year old stem	0,97	0,82
- on > 2 year old stem	0,87	0,98

Table 5. Content and evolution of carotenoïds (mg/gr/dry weight)

Object	Point of time				
	4/5	6/6	5/7	10/8	1/10
I, 1 y old needles	0,93	0,67	1,12	1,01	1,00
I, 2 y old needles	1,16	0,93	0,87	1,04	0,86
I, > 2 y old needles	1,18	1,01	0,95	1,08	0,86
II, 1 y old needles	1,20	0,74	1,01	0,83	0,83
II, 2 y old needles	1,07	0,81	0,93	0,84	0,88
II, > 2 y old needles	1,16	0,92	0,73	0,80	0,75
I, 1 y old n. on 1 y old st.	0,77	0,71	1,14	0,95	0,83
I, 1 y old n. on 2 y old st.	0,93	0,66	1,09	0,88	1,01
I, 1 y old n. on > 2 y old st.	1,08	0,65	1,14	1,20	1,16
I, 2 y old n. on 2 y old st.	1,22	0,98	0,86	1,06	0,72
I, 2 y old n. on > 2 y old st.	1,10	0,87	0,87	1,01	0,99
I, > 2 y old n. on > 2 y old st.	1,18	1,01	0,95	1,08	0,86
II, 1 y old n. on 1 y old st.	1,04	0,64	1,05	0,90	0,81
II, 1 y old n on 2 y old st.	1,31	0,75	1,00	0,59	0,83
II. 1 y old n. on > 2 y old st.	1,25	0,82	0,99	0,99	0,86
II, 2 y old n. on 2 y old st.	0,94	0,67	0,92	0,82	0,77
II, 2 y old n. on > 2 y old st.	1,20	0,94	0,94	0,65	0,75
II > 2 y old n. on > 2 y old st.	1,16	0,92	0,73	0,80	0,75

The evolution of the carotenoïd content in the course of the season is, alike the chlorophyll content, very variable (Fig.II). The clearest survey is obtained by joining together all objects.

	4/5	6/6	5/7	10/8	1/10
group I	1,09	0,87	0,98	1,04	0,91
group II	1,14	0,82	0,89	0,82	0,82
Total	1,12	0,85	0,94	0,93	0,86

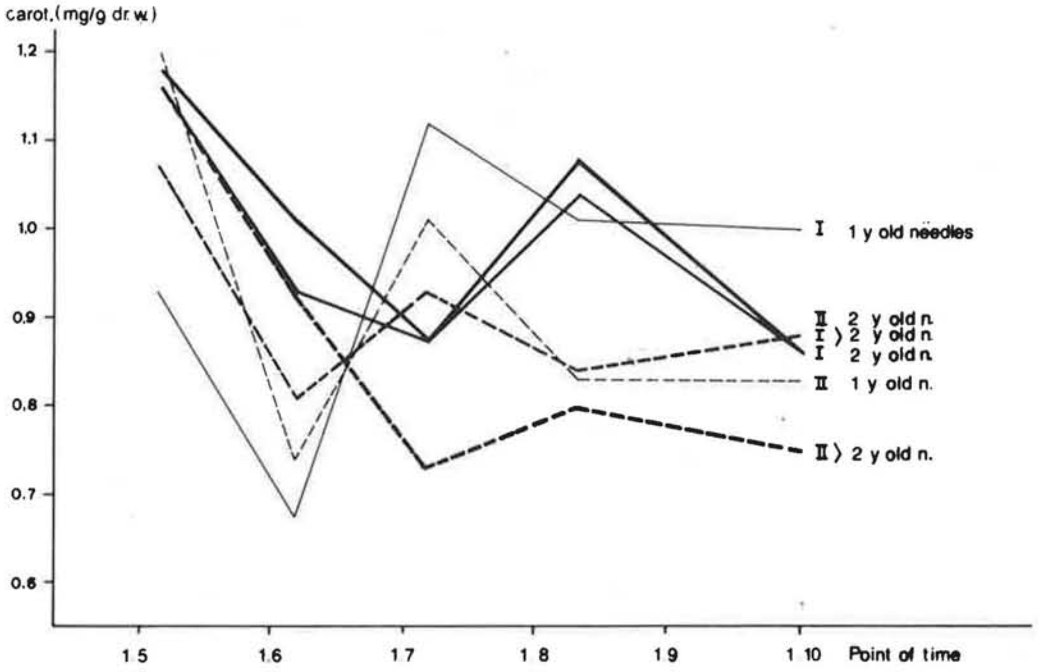

Fig. II. The evolution of the carotenoïd content in the course of the season in dominating (I) and dominated (II) plants.

There are clearly significant differences between the content of the beginning of May and the one of all other points of time. The carotenoïd content is clearly the largest in the beginning of the growing season, independent of the position of the needles and of the trees. These results are again completely opposite to the observations of Ollykaynen (1969).

5. Relation between the different pigments

Several authors have paid attention to the relations between the different pigments, such as

- chlorophyll a/ chlorophyll b ($Q\ \frac{a}{b}$)
- chlorophyll/caratenoïds ($Q\ \frac{a+b}{x+c}$)

At first, it was assumed that these values were almost constant and independent of the environment in which the plants were growing. The value $Q\ \frac{a}{b}$ equalled 3 and the value $Q\ \frac{a+b}{x+c}$ was meanly 3,56 (Willstätter & Stoll, 1913). The research of Egle (1960) proved however that these values were positively dependent on the growing circumstances. He stated that the ratio $Q\ \frac{a}{b}$ was greater for light leaves than for shade leaves, that the ratio $Q\ \frac{x}{c}$ (xantophylls/carotens) on the other hand was greater for shade leaves than for light leaves and that the relation $Q\ \frac{a+b}{x+c}$ was quite variable.

These data were confirmed by the research of Hepburn (1972) about the effect of shadow on the pigments of Pinus sylvestris ssp. scotica. " It is shown that there is a marked increase in the ratio of chlorophyll a to chlorophyll b as light intensity increases. "

Lust (1971,1973) stated that the ratio $Q\ \frac{a}{b}$ in ash was meanly 5,89 for young plants under cover and 2,73 for plants in the open field.

Wood (1974) examined the spatial variation in leaf chlorophyll within the crown of a Radiata Pine sampling. The ratio chlorophyll a : b was greater in younger than older needles and increased with increasing height up to the mid-crown.

The chlorophyll : carotenoïd ratio in seedlings of Pinus spp. was examined particularly by Venator, Howes & Telek (1974). " Molar chlorophyll/carotenoïd ratios after three to five months establishment in the field were : var. bahamensis 5.71, var. caribaea 6,53 and var. Hondurensis 4,57 (high altitude) and 4,87 (low altitude). These figures are taken as confirming the greater adaptability of var. hondurensis in the tropics, since a low ratio indicates greater protection against chlorophyll breakdown. It is concluded that the chlorophyll carotenoïd ratio is an important physiological and genetic parameter for prediction of adaptability ".

As a consequence of the very high value of chlorophyll b the ratio $Q\frac{a}{b}$ is verly low in young plants of Abies grandis. (Table 6). It amounts meanly to 0,40 for dominating plants

Table 6. Relations between the different pigments.

Object	$Q\frac{a}{b}$		$\frac{a+b}{c+x}$	
	4/5	1/10	4/5	1/10
I, 1 y old needles	0,69	0,93	11,26	9,06
I, 2 y old needles	0,86	0,96	7,12	8,22
I, > 2 y old needles	1,14	0,92	6,28	9,71
II, 1 y old needles	0,77	0,89	6,34	11,75
II, 2 y old needles	0,97	0,86	8,16	3,53
II, > 2 y old needles	0,88	0,97	8,88	9,08
I, 1 y old n. on 1 y old st.	0,64	0,90	13,70	10,08
I, 1 y old n. on 2 y old st.	0,70	0,90	8,62	8,76
I, 1 y old n. on > 2 y old st.	0,72	0,99	11,45	8,33
I, 2 y old n. on 2 y old st.	0,85	0,94	7,19	7,40
I, 2 y old n. on > 2 y old st.	0,87	0,92	8,25	9,03
I, > 2 j old n. on > 2 y old st.	1,14	0,92	6,28	9,71
II, 1 y old n. on 1 y old st.	0,77	0,83	5,32	13,64
II, 1 y old n.on 2 y old st.	0,69	0,86	7,77	12,53
II, 1 y old n. on > 2 y old st.	0,84	0,98	5,92	9,10
II, 2 y old n. on 2 y old st.	1,05	0,94	7,78	7,57
II, 2 y old n. on > 2 y old st.	0,88	0,77	8,53	11,49
II, > 2 y old n. on > 2y old st.	0,88	0,97	8,88	9,08

in the beginning of the season. These values are almost identical for the less fast growing plants from group II. This ratio exceeds 1 only excemtionally.

exceeds 1 only exceptionally. In the beginning of the growing season, the ratio is the smallest in one year old needles. In the first group this is a consequence of the high chlorophyll b content. Later on in the growing season there is no more difference to be noticed between one year old and older needles. So the statements of Wood (1974) are contradicted.

The relation between green and yellow pigments ($Q\frac{a+b}{x+c}$) is very high. This is a consequence of the high chlorophyll content as well as of the low carotenoïd content. The values are quite variable, and group I and group II do not have the same course.

Due to the high content of yellow pigment in the beginning of the growing season, the ratio $Q\,\frac{a+b}{c+x}$ is meanly lower in May than it is later on. In May the mean values were 8,42 for the first group and 7,79 for the second group, whereas they amounted to 9,00 and 10,12 in the beginning of October.

6. The pigment content per plant

Van Miegroet & Lust (1983) noted the total above ground dry weight (in g) of the same plants as in the actual research as follows :

	Group I	Group II
- needles	25,4	11,1
- stem	15,2	7,1
- branches	9,4	4,2
	50,0	22,4

About 95 % of the needles appears on the branches, the rest occurs on the stem. In the first group the needles on the branches take up 24,8 g, which means 94,5 %.

By joining the results of the dry weight of the needles occuring on the different stem parts (Van Miegroet & Lust 1982) and the actually obtained results on pigment content, the total pigment content for the whole plant may be calculated (table 7).

Table 7. The content of pigments per plant at the end of the growing season.

Object	dry weight/g	Content of pigments (mg/g/dr weight) chl (a+b)	carotenoïds	Content of pigments per plant of needles on branches chl.(a+b)	carot.	Total
I, 1 y old needles on 1 y old stem	2,99	8,37	0,83	25,03	2,48	27,51
I, 1 y old n. on 2 y old st.	6,18	2,85	1,01	54,89	6,24	61,13
I, 1 y old n. on > 2 y old st.	7,08	9,66	1,16	68,39	8,21	76,60
I, 2 y old n. on 2 y old st.	1,99	5,33	0,72	10,61	1,43	12,04
I, 2 y old n. on > 2 y old st.	5,89	8,94	0,99	52,66	5,83	58,49
I, > 2 y old n. on > 2 y old st.	0,70	8,35	0,86	5,85	0,60	6,45
II, 1 y old needles on 1 y old stem	1,93	11,05	0,81	21,33	1,56	22,89
II, 1 y old n.on 2 y old st.	2,84	10,39	0,83	29,51	2,36	31,87
II, 1 y old n. on > 2 y old st.	2,94	7,83	0,86	23,02	2,53	25,55
II, 2 y old n. on 2 y old st.	1,04	5,83	0,77	6,06	0,80	6,86
II, 2 y old n.on > 2 y old st.	1,45	11,26	0,98	16,33	1,42	17,75
II, > 2 y old n. on > 2 y old st.	0,25	6,81	0,75	1,70	0,19	1,89
I, 1 y old needles	16,25			148,31	16,93	165,24
I, 2 y old needles	7,88			63,27	7,26	70,53
I, > 2 y old needles	0,70			5,85	0,60	6,45
II, 1 y old needles	7,41			73,86	6,45	80,31
II, 2 y old needles	2,49			22,39	2,22	24,61
II, > 2 y old needles	0,25			1,70	0,19	1,89
	10,45					

The results can be summarized as follows :

	group I	group II
- chl total (a+b) of the needles on the branches (mg)	217,43	97,95
- carotenoïd total of the needles on the branches	24,79	8,86
- total pigment content of the needles on the stem (mg)	5,95	6,21
- total pigment content per plant (mg)	248,17	113,02
- % pigment content of one year old needles	66,6	71,0
- % pigment content of two year old needles	28,4	21,8
- % pigment content of > 2 year old needles	2,6	1,7
- % needles on stem	2,4	5,5
- mg pigment content per gr. plant	4,96	5,04
- mg pigment content per gr. 1 y. old n.	10,17	10,47
- mg pigment content per gr. 2 y.old n.	8,95	10,09
- mg pigment content per gr. > 2 y. old n.	9,21	7,56

The pigment content is meanly 5 mg/g plant and is equal for both groups. It is confirmed again that in the actual research the pigment content of all needles, in whatever circumstances they occur, is practically the same and varies very little.

The young plants of Abies grandis are very photostable. They react in no way on the different light circumstances which occur in the course of the season. The pigment content per weight unit is not hight in the more vital plants than it is in the less vital plants.

The one year old needles take up about 70 % of the pigment content. This is completely in correspondence with the biomass distribution in these plants. In the same way, most of the pigments appear in the one year old or older stem part. Per weight unit there is no clear difference according to the age of the needles. In the less vital plants however, the pigment content of the oldest needles is considerably lower.

If we assume that there are about 320.000 such plants per ha (Krüssmann) in a nursery, which corresponds to a planting distance of 20x20 cm, and that the mean above-ground biomass equals 36g, then the pigment content/ha equals :

320.000 x 36 x 5,00 mg/g plant = 57,6 kg

With a planting distance of 25 x 25 the pigment content for the same plants would be 36,7 kg/ha.

In Japan, Kirita and Hozuni (1973) made an estimation of the total chlorophyll amount and its seasonal change in a warm-temperate evergreen Oak forest. Estimated chlorophyll increased from the new-leaf stage in June throughout the summer to a maximum value (ca. 40 kg/ha) in winter, and reached a minimum (ca 20 kg/ha) in June, when most of the leaves were shed.

As in the actual research of Abies grandis the chlorophyll takes up about 90 % of the total pigment content, the chlorophyll content/ha for the following planting distances can be estimated :

- 20 x 20 cm : 57,6 x 0,9 = 51,8 kg
- 25 x 25 cm : 36,7 x 0,9 = 33,0 kg

These values are high when compared with the results of Kirita and Hozuni (1973).

7. Conclusions

The results, registered for 5 year old nursery plants of Abies grandis Lindley, do in most cases not correspond to the results noted in other plants grown up in more or less similar circumstances.

The total chlorophyll content is meanly 8,42 mg/g dry weight, which can be considered as normal. However the chlorophyll content is composed for the greater part of chlorophyll b, which is quite exceptional. The mean value of chlorophyll b amounts to 4,50 mg/g dry weight, that is, 53 % of the total chlorophyll content.

The carotenoïd content, which is meanly 0,94 mg/g dry weight, may be considered as low.

The carotenoïd content only takes up meanly 10 % of the chlorophyll content.

Most authors have stated in similar researches that the pigment content was dependent on all kinds of circumstances, such as the age of the needles, light or shadow position of the needles, the vitality of the plants, the period in the growing season, etc.

The present research however is characterized by its independence of almost all values. In most of the cases the pigment content is practically identical for different growing circumstances. Normally the pigment content decreases as the needles grow older. This is not the case in the present research. There is no difference in pigment content/dry weight between one year old, 2 year old and older needles.

On the whole the pigment content of the most vital plants is not higher than the one of the less vital plants. The total chlorophyll content and the carotenoïd content are identical in group I and group II. Only the chlorophyll a content was higher in the most vital plants.

A distinction according to the light or shadow position of the needles can nowhere be shown, although the pigment content in shade leaves should normally be higher than in light leaves, especially when it concerns the chlorophyll content.

It was also impossible to indicate clear seasonal differences. Usually the values in the beginning of the growing season are not significantly different from the ones at the end of the growing season. In the course of the growing season, the values still can vary very much. Only for the carotenoïd content the greatest value was clearly determined in the beginning of the growing season, but this is exactly in contradiction with the results of other researchers.

The pigment content, expressed per g plant is meanly 5 mg.

Once again this value is the same both for the vital and for the less vital group. The one year old needles contain about 70 % of the total pigment content, which corresponds exactly with the biomass distribution in these plants. The pigment content per ha is calculated on 57,6 kg for a planting distance of 20 x 20 cm and on 36,7 kg for a planting distance of 25 x 25 cm. These values are to be considered as high.

The meaning of the obtained results is not always clear. Undoubtedly this is due in part to the object itself. In the young nursery plants the differences between light and shade needles, between young and old needles are physiologically not so important. Yet, an equal pigment content does not mean that the efficiency of the needles is the same. Due to a lack of light, older needles, and shade needles in general, do need more pigments/weight unit than do younger needles and light needles.

The Abies grandis does not react in a special way to varying light and growing circumstances, and it can therefore be considered as a very photostable species.

B a u e r, I. & G r i l l D., 1977 : Zur Problematik der Pigmentanalyse als Rauchschadendiagnose. Angew. Botanik, Berlin, 51, 5/6, 241-250.

B e n e c k e, U, 1972. Growth, CO2 exchange and content of pigments in some tree species after planting out at different altitudes. Angew. Botanik, 46, 1/2, 117-135.

Blintsov, I.K. & Tsai, V.V., 1977. Effect of soil cultivation and fertilizers on the chlorophyll content in pine needles. Lesnoe Kho zyacstvo, 10, 24-26.

B r e t t, W.J. & S i n g e r, A.C., 1970. Lòng term chlorophyll fluctuation in an evergreen-juniperus virginiana. Proceedings of the Indiana Academy of Science. 80,95.

E g l e, K. , 1955. Die Farbstoffe. Handbuch der Pflanzenphysiologie, I, 565-573.

E g l e K., 1960. Menge und Verhältnis der Pigmente. Handbuch der Pflanzenphysiologie, V, I, 444-497.

E l A o u n i, M.H. & M o u s s e a u, M., 1974. Relation of CO2 exchange in needles of Austrian Black Pine to age, chlorophyll content and reassimilation. Photosynthetica, 8 (2), 78-86.

F o m i c h e v, A.V., 1972. The chlorophyll content in the needles of seedlings in relation to plant density and fertilizing. Les geobotan. i. biol. dreves rast. Vyp. 1 Bryansks, U. S.S.R. 160-65.

G u a r d i g a n, V.N., S h a b e l ' S k a y a, E.F. & G o d n e v, T.N. 1973. Content and ratio of green pigments in plants of various kinds under conditions of prolonged darkness. Vestsi Akad. Navuk. B.S.S.R. Buyal Navuk, 1, 113-117.

H e p b u r n, A.G. 1972. The effect of shade on the photosynthetic pigments of needles on trees of Pinus sylvestris sp. scotica grown under field conditions. Transactions, Botanical Society of Edinburg, 1972, 41,4, 461-467.

H e r z m a n n, H. 1962. Pflanzenfarbstoffe, Wittenberg, Lutherstadt.

K i r i t a, H. & H o z u m i, K. 1973. Estimation of the total chlorophyl amount and its change in a warm temperate evergreen oak forest at Minimata, Japan. Japanese Journal of Ecology, 23, 5, 195-200.

K r a m e r, P.J.& K o z l o w s k i,T.T., 1960. Physiology of trees. New-York - Toronto-London.

K r e u t z e r, K., 1972. Die Wirkung des Manganmangels auf die Farbe, die Pigmente und den Gaswechsel von Fichtennadeln. Forstw. Cbl. Hamburg u. Berlin, 91, 2, 80-98.

K r ü s s m a n n, G. 1978. Die Baumschule. Paul Parey.

L a u d i, G. & M a n z i n i, M.L. Chlorophyll content and plastic ultrastructure in leaflets of Metasequoia glyptastroboides.

L i n d e r, S. 1973. Seasonal variation of pigments in needles. A study of scots Pine and Norway Spruce seedlings grown under different nursery conditions. Studia forestalia Suecica, 100.

L u s t, N. 1973. Etude sur la teneur en pigment de frênes qui croissent dans des conditions différentes. Sylva Gandavensis, 37, 1-19.

L u s t, N. 1971. Onderzoek naar de structuur, de morfologische kenmerken en het groeireaktievermogen van langdurige onderdrukte essenverjongingen. Gent, Thesis Fakulteit Landbouwwetenschappen.

O l l y k a j n e n, A.M. 1969. Über den Karotinoïdgehalt in den Nadel der Waldkiefer. Bljulleten ' Glawnogo Botaniceskogo sada. Moskau, 72, 81-84.

Ö q u i s t, G. & M a r t e n s s o n, O., M a r t i n, B, M a l m b e r g, G. 1978. Seasonal effects on chlorophyll-protein complexes isolated from Pinus silvestris. Physiologia Plantarum, 44,3, 187-192.

P a u l e, L. 1977. Content of pigments in assimilatory organs of silver fir. Biologica, Czechoslovakia, 32,10, 729-737.

P o p o v, V.K. & P o p o v a, N.M. Seasonal changes in the content of carotenoïde in Scots Pine needles in pure and mixed plantations.

S e y b o l d, A. 1957. Die Pflanzenpigmente als physiologisches Problem. Jb. Akad. Wiss. u.d. Literatur in Mainz, 1957, 213-229, Wiesbaden : Franz Steiner.

T h a s, J. 1964. A quantitative determination of the plastic pigments in higher plants. Silva Gandavensis, 14, 1-10.

T s a r e g o r o d t s e v a, S.O. & N o u t s k a y a, Y u.E. 1975. Pigments of coniferous trees. Lesnoe Khozyaistov, 4, 45-57.

V a n M i e g r o e t, M. 1970. On the reactivity of some hardwood species studied by their leaf characteristis. Silva Gandavensis, 23.

V a n M i e g r o e t, M. & L u s t, N., 1983. Above ground biomass and biomass distribution in nursery plants of Abies grandis Lindley. Silva Gandavensis, 49, 1-18.

V e n a t o r, C.R., H o w e s, C.D. & T e l e k, L. 1974. Chlorophyll : carotenoïd ratio as a parameter to predict plant adaptability. Genetics, 77, 1, II.

W i l l s t a t t e r, R. & S t o l l, A. 1913. Untersuchungen über chlorophyll. Berlin, Springer.

W o o d, G.B. 1974. Spatial variation in leaf chlorophyll within the crown of a Radiata Pine saipling. Australian Forest Research, 6,4, 5-14.