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Original article

Growth and fructification of a Norway spruce (*Picea abies* L. Karst) forest ecosystem under changed nutrient and water input

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Abstract – In the mountainous region of a low mountain range (Solling mountains) an ecosystem manipulation experiment with roof constructions underneath the canopy of a 60-year old Norway spruce stand is run since 1991. The responses to artificially prepared, "pre-industrial" through fall and to extended summer droughts with intensive rewetting are investigated in two parallel roof experiments and evaluated against a roof control and an ambient control plot. After long terms of drought distinct reactions of the trees were visible in growth. The reactions of height-increment were more distinct than the effects on diameter-increment. Furthermore, the trees of the dominating social classes (Kraft I and II) reacted more on low water-supply than the dominated trees. So it is probable that a long lasting stress by drought effects changes the stand structure, too: the vertical structure of a stand would get more homogeneous and the diversity in the stand structure would decrease. Reduced input of sulphur and nitrogen did not show any distinct growth reactions within the 9-year observation period.

roof-project / nitrogen / drought / growth / fructification

Résumé – Croissance et fructification d'un écosystème forestier d'épicéa commun soumis à un apport variable d'eau et de nutriments. Dans la partie haute d'une région montagneuse de moyenne altitude (Solling), on procède depuis 1991 à une expérience de manipulation d'un écosystème forestier à l'aide de constructions de toits en dessous des couronnes d'un peuplement d'épicéa commun âgé de 60 ans. Dans le cadre de deux expériences parallèles (de toit), on étudie les réactions à des précipitations « préindustrielles » créées artificiellement et à une sécheresse estivale prolongée, suivie d'une réhumidification intensive, en évaluant et en comparant ces résultats à une placette témoin. Après de longues périodes de sécheresse, on a pu observer des réactions différentes des arbres sur le plan de la croissance. Les réactions au niveau de la croissance en hauteur s'avèrent différentes des effets sur l'accroissement en diamètre. En outre, les arbres dominants (Kraft I et II) témoignent d'une réaction plus prononcée à un faible apport d'eau que les arbres dominés. Ainsi, il est probable qu'un stress de longue durée par l'effet de la sécheresse modifie également la structure du peuplement : la structure verticale d'un peuplement devient alors plus homogène, tandis que la diversité du peuplement diminue. Les effets d'un apport réduit de soufre et d'azote n'ont pas révélé de réactions différentes sur le plan de la croissance au cours de la période d'observation de 9 ans.

projet de toit / azote / sécheresse / croissance / fructification

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1. INTRODUCTION

The effects of environmental parameters on reactions in forest ecosystems can be best investigated under laboratory conditions. Here it is possible to modify single factors while other variables are kept constant. However, the transfer of the results thus obtained to the ecosystem, is problematic. Conditions are required which allow the control of influence factors, but these conditions differ markedly from the natural conditions. In addition, results obtained under laboratory conditions do not give a realistic picture of the complex interactions in an ecosystem. Existing interrelationships and mutual dependencies can not be sufficiently considered. An alternative method is a long term observation of forest ecosystems under field condition with parallel observations of the role of the environmental factors. The disadvantages of this method are the prolonged periods of observation required and the difficulty in determination of those parameters which have a strong effect on the ecosystems among a number of varying factors. In order to avoid these disadvantages, ecosystems as a whole or at least representative parts have to be exposed to controlled changes of the environment. This concept is the basis for the roof-project presented here.

The large scale experiment concentrates on two basic environmental changes, which were simulated by quantitative and qualitative manipulation of element inputs [4, 5]. The effects of an improved deposition quality which can be expected as a result of implementation of air protection measures, were investigated in a de-acidification experiment. The effects of long periods of drought phases were tested in a drought out experiment.

Internationally, the experiments were integrated in the framework of the projects EXMAN (Experimental Manipulation of Forest Ecosystems in Europe, project duration 1987–1995, [3, 24] and NITREX (Nitrogen Saturation Experiments) supported by the EU. In this research co-operation similar projects were carried out on the Danish west coast (Klosterheede), in south-western Ireland (Ballyhooly), in the Netherlands and in Höglwald in Bavaria.

The project was co-ordinated by the Forest Ecosystems research centre, University Göttingen and the work carried out by groups in the Institute of Soil Science and Forest Nutrition, the Institute of Silviculture and the Zoological Institute. The results presented here focus on the work of the group Eco-physiology and Growth, which investigated aboveground reactions of the trees to the manipulations. In particular the investigation shall test whether tree growth would be better under de-acidification and in which extent drought periods affect tree increment.

2. MATERIALS

2.1. Investigation area and experimental site

The experimental sites of the roof project are about 50 km north-west of Göttingen (51° 46' 09" N; 9° 34' 52" E), 510 m above sea level in the department 4257j of the forestry administration Dassel (Lower Saxony). The suboceanic climate prevalent in the area Hoher Solling is characterised as cool humid. The average annual temperature is 6.9 °C, the average temperature during the vegetation period (May–September) is 13.5 °C. About 120 days were with frost (temperature minimum below 0 °C). The relatively high amount of precipitation (1040 mm/year) is evenly distributed over the course of the year (*figure 1*). December the month with the highest precipitation of 105 mm exceeds February the month with the lowest rainfall by only 30 mm. Long term measurements showed marked differences between the years: The annual sums fluctuated over the past 30 years between 400 mm (1959, 1983) and 1500 mm (1960, 1970) [8].

Measurements of air pollutants showed that the SO_2-pollution was very high during winter months. It reached an average concentration of more than 0.1 mg m^{-3} which is comparable to the conditions in densely populated regions. Ozone was determined at high concentrations of

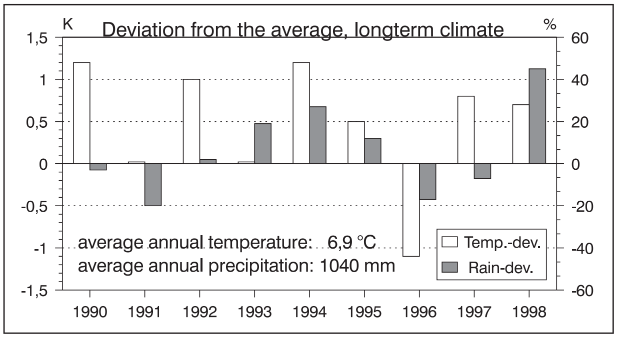

Figure 1. Average temperature and precipitation development during the observation period, presented as deviation from the average, long term climate.

more than 0.1 mg m^{-3} (= 100 µg). The average nitrogen concentration in the air during the winter months was mostly more than 0.05 mg m^{-3} (50 µg). In total the sulphur input has considerably decreased. After a maximum input was reached in the middle of the 1970s with more than 100 kg ha^{-1} yr^{-1} it decreased to below 50 kg at the beginning of the 1990s and today to just above 30 kg. In contrast, the total amount of nitrogen deposition, composed almost of equal amounts of ammonium ($N\text{-}NH_4$) and nitrate ($N\text{-}NO_3$) nitrogen, increased over the same period of time from just 30 kg to 40 kg ha^{-1} yr^{-1}.

The experimental sites are on the slightly sloped Solling Plateau. The geological parent material is a Triassic sandstone on which slightly podsolic, weakly pseudogleyic brown-earth layers have formed [11]. The nutrient potential of the sites is mainly determined by loess layers of a varying thickness. In the investigation area the loess is up to one meter, but shows large differences over small spatial areas [1]. The organic layer varying in deep thickness between 6 and 9 cm, corresponds to an average dry substance of 114 t ha^{-1} [11] , of which just over half of the total amount can be allocated to the OL and OF layer. Probably due to the high atmospheric nitrogen inputs, the C/N-ratio of 25 found in all humus layers is less than that normal for the fine-humus-rich moder humus form [2]. The low magnesium and calcium contents in the humus layer are evidence of the generally poor nutrient conditions (*table I*, [13]).

The very low pH-values in the upper soil of around 3 (pH $CaCl_2$) are within the aluminium and iron buffer ranges [21]. The pH increases to values of more than 4 at deeper soil depths. As a result the contents of sodium, potassium and magnesium in the mineral soil at all soil depths are very low, contributing only 6% to the total cation exchange capacity. The highest amounts are found in the soil layers at 20 to 40 cm depths. Relatively high amounts of some nutrients have accumulated in the organic layer: nitrogen and magnesium contribute one third and calcium a quarter to the total amount.

2.2. The spruce stand

The spruce stand is the second generation of this tree species, which replaced the natural wood-rush/beech forest (Luzulo-Fagetum). The spruce stand was planted in 1933 and as a result of several silvicultural measures was thinned to 900 trees ha^{-1} by the beginning of the project (1990). The stand was then 57 years old and had an average DBH of 27 cm (d) where the strongest trees already exceeded 40 cm. The mean height of the stand was 19.7 m (h) in which the highest tree measured 25 m. The h/d ratio, the quotient calculated from tree height and DBH used to determine the stand stability, showed a favourable average value of 73. The average annual increment was 9 m^3 ha^{-1} yr^{-1}. Almost all trees showed old peeling scars at the stems caused by red-deer, noticeable to varying degrees as wound occlusions. At the start of the experiments the spruce were allocated to the damage classes 2 (according to the international tree damage class system, this means medium damage) and partly damage class 3 (severe damage). In addition to needle loss, older needles were chlorotic.

3. METHODS

3.1. Experimental design

The spruce stand was divided into several experimental sites, of which the three sites D1, D2 and D3 were roofed in order to be able to manipulate the water and element inputs. The roofs are self-supporting wooden structures spanning over 17 m and with a 3.5 m ridge height. A central maintenance building was built on concrete foundations. Each roof is covered with transparent polycarbonate sheeting and covers a ground area of 300 m^2. The total precipitation falling on the roofs in the stand was directed by pipes to collecting tanks in the

Table I. Average storage of nutrients in the humus and mineral soil up to a depth of 80 cm (LAMERSDORF 1998).

Element storage	C	N	P	K	Ca	Mg	Mn	Fe	Al
in humus (t/ha)	48	1.9	0.11	0.22	0.16	0.08	0.02	0.91	1.0
in the mineral soil (t/ha)	55	3.5	0.86	1.14	0.46	0.17	0.98	0.85	13.7
sum (t/ha)	103	5.4	0.97	1.38	0.62	0.25	1.00	1.76	14.7
proportion in the humus (%)	46	35	11	16	26	31	2	52	7

maintenance building. Here the chemical composition of the water could be manipulated by an installed desalination and subsequent dispensing equipment. It was also possible to deviate water for a temporary storage in the storage tanks (42 $m^3 \approx 140$ mm precipitation). Finally the precipitation of the stand – depending on the roof area and experiment in natural or chemically changed form – was transported via a pipe system back underneath the roofs and released as rain using sprinklers. The three quadrangular roof structures could be used from spring 1991. In order to carry out the necessary measurements in the crown area, in spring 1992 a crane 30 m high was installed in the center of the roofed area. This was equipped with a special transport system for persons (a cabin with a floor space of 100 × 70 cm) which made it possible to reach the crown area of all of about 100 trees which belonged to the experimental sites.

3.2. The experimental treatments

Under the de-acidification roof (D1) an unchanged amount of precipitation, but in a changed composition was sprinkled. In doing so the conditions were to be simulated which compared to the composition of pre-industrial precipitation. In order to attain this result the water was first de-mineralised in the desalination device and subsequently a nutrient solution and sodium hydroxide was added, thus the manipulated through fall only contained half of the normal concentrations of sulphate, nitrate and phosphate. Considering the severely reduced ammonium nitrogen content to 16% of the normal concentration, this manipulation reduced the total nitrogen input to almost one third. At the same time the pH-value was increased from an ambient 4.1 to between 6.0 and 6.4, while the contents of aluminium and iron ions were markedly reduced (20–25% of the normal input). The similarly strong increase of the calcium (150% of the ambient input) and magnesium inputs (200%) certainly does not correspond to a simulation of pre-industrial inputs. However, it means an optimisation of the site conditions as it can be expected to result from a reduction of the pollutant inputs in connection with soil amelioration measures (liming, fertilisation).

Another roof (D3) was used for the investigation of responses to drought. The precipitation during the vegetation period in the years of 1991 until 1994 were collected in large storage tanks and after a drought phase normally lasting for several months sprinkled under the roof over the space of a few days (*table II*). The average amount of sprinkled water was 10 $dm^3\ m^{-2}\ day^{-1}$ (= 10 mm), however, the daily amounts differed strongly. Especially in 1992 strong variations occurred: Very high amounts of sprinkled water such as at the 11th Sept. with 28 mm were corrected with extremely low amounts during the following day (1 mm at the 12th Sept.). This experiment was carried out to clarify the question, whether drought and rewetting phases result in intensive acidification pushes. Due to the marked drought stress responses observed at the trees in the years of 1993 and 1994 subsequent to a drought over several months in 1995 no further drought experiments were carried to give the stand a chance to recover, instead the phase of recovery was monitored by continuous measurements.

A directly adjacent non-roofed part of the stand (ambient control D0) and a roofed control (D2) served as the controls. Here the collected precipitation was sprinkled without changing the amount or the composition and thus the environmental conditions simulated. Thus it was possible to test the validity of probable "roof effects".

3.3. Measurements

Over a total period of nine years, from all 74 spruce trees of the three roofed sites yield data were collected (27 trees from roof 1, 24 from roof 2 and 23 from roof 3). The control tree group analysed from the start of the project, but did not grow within the range of the crane, were thus replaced by a new control group in 1995. These 22 reference trees (16 original control trees at the side of the roofs and 6 close to the crane foundation) are all within reach of the crane. The radial growth was measured with radial measuring bands, which were permanently fixed at a tree height of 1.3 m in 1989. Using this

Table II. Average annual element inputs (kg/ha) in the stand via precipitation at the control site D0 (mean of the time period 1990–1994).

Na	K	Ca	Mg	Fe	Mn	Al	H	NH_4-N	NO_3-N	SO_4-S	PO_4-P	Cl
18.7	26.1	17.4	3.9	0.4	3.0	1.0	1.1	17.6	18.9	42.4	0.2	36.5

method the radial growth of each tree was registered monthly with an accuracy of ±0.2 mm. The annual radial increment was estimated using the data obtained in October. By October the transpiration rate of the trees was already markedly reduced, so that expansion and shrinking processes of the stems did not play an important role. Selected sample tree were additionally equipped with a home made microdendrometer which registers changes in radial growth of the stem at a differentiated level providing information about the growth and water budget of the trees.

The measurement of the annual height increment was also carried out in October. In order to do this the lengths of the newly grown apical shoots had to be determined. This was not possible until the crane could be used in 1992. For the previous years after 1988 the height increment could be estimated on the basis of the distance between the branching nodes. The total height of the trees was first measured in October 1992 at the beginning of the experiments. The subsequent annual height increment rates were used to update this measurement. The reproduction rate of the trees was determined by counting the cones in autumn. The crane was used for this work, and also for the visual assessment of the crowns at different heights and perspectives.

4. RESULTS

4.1. Height growth

The course of the annual height growth showed similar trends for all experimental variants. The mean height increment decreased continuously since the beginning of the measurements in 1988 from an average of 37 cm on all sites to a minimum in the fifth year of monitoring in 1992 (*figure 2*). At this date the mean shoot length was only 14 cm. After which, up to 1996, a marked increase in growth was again observed. In the years 1993 and 1994, an influence of the experimental treatments on the height increment of the trees was shown. As a result of the long dry periods during the summer months of previous years the mean height increment on the D3-site was significantly reduced by about half compared to the other sites (analysis of variance, $\alpha < 0.05$). After 1995 on the basis of all trees, no effects were shown induced by the drought in previous years. By contrast, the effect of the de-acidified precipitation on the trees of the D1-site for the total period monitored were statistically not significant.

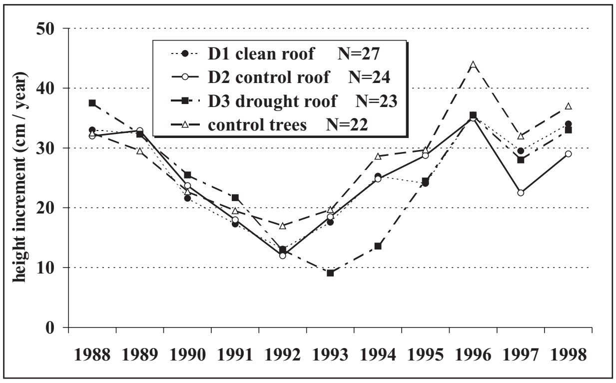

Figure 2. Development of the annual height growth.

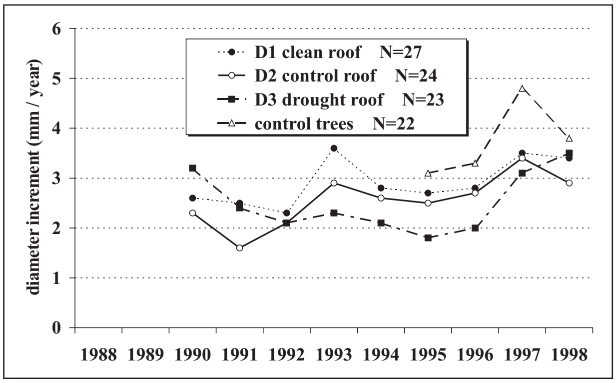

Figure 3. Development of annual diameter increment.

4.2. Radial growth

Figure 3 clearly shows that the pattern of radial growth at a height of 1.3 m does not correspond to the course of the height increment (*figure 2*). During the whole monitoring period of nine years not even a trend towards a change is detectable. The highest radial growth increment was determined in 1997 for most of the sites. In general, the non-roofed control trees showed a higher radial growth than the roofed trees. That the control trees are first shown in 1995 is as the control trees used until then belonged to a different collective.

It was not possible to show conclusively an effect of the treatments on the radial growth of the trees. Although the drought experiment differed from the control under the roof during the years of intensive drought by an average of more than 0.5 mm radial increment, this was not statistically significant at any point in time. Only the differences determined for the year 1995 between the de-acidification and the drought experiment were significant (analysis of variance, $\alpha < 0.05$).

Marked recovery effects were observed in the annual radial growth of the trees under drought conditions. During 1993 to 1995 the radial growth compared to the control was still significantly reduced, while in 1996 the growth of the trees exposed to drought was markedly lower with 1.9 mm compared to an average of 2.6 mm of other sites. In 1996 the growth on the de-acidification site with 2.8 mm was highest, the difference at all sites was not statistically significant (analysis of variance, $\alpha < 0.05$). From the cumulated monthly increment rates since 1989, it is noticeable that droughted trees show a strongly reduced growth after 1993. The trees of the de-acidification experiment showed an increased radial growth of the stem. However, this improvement was not statistically significant at any point in time.

4.3. Effects on the stand structure

When the experimental treatment effects are regarded separately for different sociological tree classes, an obvious effect on tree growth could be shown. This was based on the hypothesis that non-dominating trees are less affected by changes in the abiotic site factors. On the one hand they are exposed to smaller amounts of immission than the larger trees. On the other hand the competitive conditions probably represent a stronger limiting factor for their growth potential. Thus a worsening of the environmental conditions (compare D 3) or an improvement (compare D1) will have lesser effects than for dominating trees.

Figures 4 and *6* show the mean values for height and radial increment of the dominating and codominating trees (tree classes 1 and 2 based on Kraft). The values for the trees which are at least partially overshadowed (tree classes 3 to 5) are shown in *figures 5* and *7*. The classification of the trees according to their sociological order was based on the stand condition, before the two experiments began in 1990.

The effects of the drought experiment were clearly observable in the dominating and codominating trees from 1993. At the D3-site the lack of growth was significant compared to all other sites. On average the height increments (*figure 4*) of these trees was reduced by 50% and the increments of radial growth (*figure 6*) by 20%. This development could be observed over a period of four

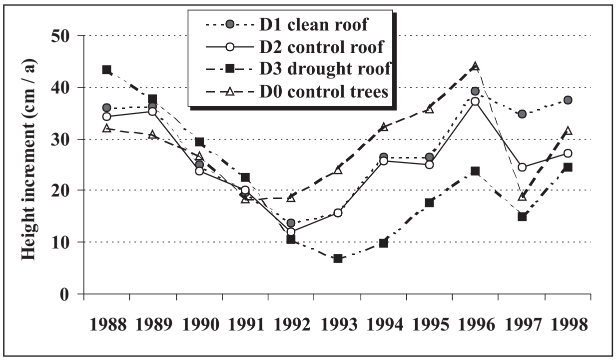

Figure 4. Development of height increment for the dominating trees (tree classes 1 and 2 based on Kraft).

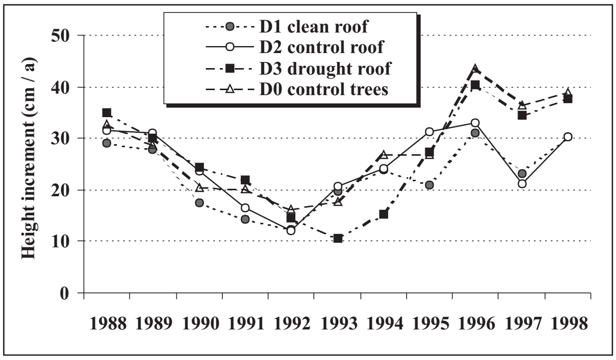

Figure 5. Development of height increment for the dominated trees (tree classes 3 to 5 based on Kraft).

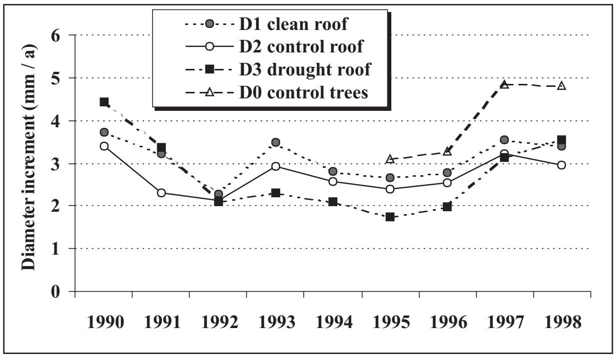

Figure 6. Development of diameter increment for the dominate trees (tree classes 1 and 2 based on Kraft).

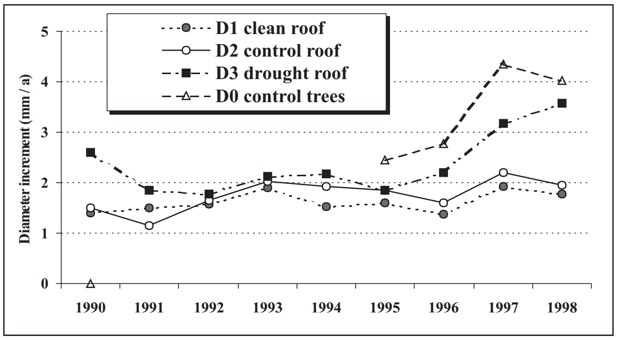

Figure 7. Development of diameter increment for the dominated trees (tree classes 3 to 5 based on Kraft).

years up to and including 1996. Thus the influence of the drought experiment, which was finished in 1994 on the D3-site, continued to be effective for two years after the treatment was stopped. The trees showed no signs of a quick regeneration. A visual assessment of the tree crowns also suggests that although a regeneration process had actually taken place, the damage in some cases is however irreversible.

For the dominated trees on the D3-site a reduced increment in height development was only determined (*figure 5*) during the years of severe drought (1993 and 1994). However, in the absolute volumes there were marked differences which were statistically not significant (Scheffé, $\alpha < 0.05$). After a fast adjustment of the shoot length growth to the values of the control trees as early as one year after the drought, the dominated roofed trees on D3 developed better in the following years than the trees of the other two roofs. The radial growth of the dominated trees was not affected by the experimental treatment (*figure 7*).

The results obtained have confirmed the hypothesis, that a worsening of the environmental conditions mainly affects the prevalent and dominating trees of a stand, while the dominated trees hardly show any reaction. A reason for this could be the more intensive contact of the dominating tree crows with the polluted atmosphere compared to the dominated trees. In addition, the dominated trees can take an advantage of the decline of dominant trees due to reduced leaf area, more light reaching the lower canopy and less competition for water and nutrients. If the conditions continue over several years the structure of the stand may become more homogenous. However, a complete adjustment and formation of stands composed of one growth layer is unlikely to occur.

The evaluation of the results obtained from the de-acidifying experiment did not show any significant effects on tree growth (analysis of variance, $\alpha < 0.05$). The development of the height and radial growth increments on the D1-site was similar to the development on the control site D2. The investigation based on the sociological classes could also not show any differences between the dominating and dominated trees. The absence of a reaction is probably due to the compensating effects of the changes in the input. Although as a result of the de-acidification a better nutrient supply and thus a higher growth rate was expected, the high reduction in nitrogen inputs may have had the opposite effect. In addition on the D1-site, which has a total of 27 trees, providing a much smaller rooting area for each tree, which may have resulted in a stronger competition than on the other roofed sites (with 24 or 23 trees respectively per 300 m^2). Also comparing the density dependent basal area, the value for D1 with 56 $m^2\ ha^{-1}$ is 10% higher than that of the two other sites. These comparatively very high stocking rates are also the result of bark stripping damage which occurred on almost all stems. Wound occlusion leads also to the formation of asymmetrical stem cross sections and hollows, which prevented a more accurate determination of the diameter of the stem. The typical symptoms of thickened trunk bases due to butt rot damage from Heterobasidion annosum induced by bark stripping damage also lead to systematically increased DBH.

4.4. Seasonal growth developments

The permanently fixed rings for radial growth measurements permitted not only the determination of the annual values but also the monthly changes. In the years of 1993 and 1994 on D3 for several months of the vegetation period strong drought conditions were simulated. *Figure 8* shows the mean growth values of the radial growth.

In both years by far the highest growth rate was determined in June, July and August. In 1994, a relatively wet (20% more precipitation above the long term average), and very warm year (+ 1 °C above the long term average), changes in radial growth were shown from May onwards. The control trees outside the roofed area had a higher annual growth over the whole year which began at the start of the vegetation period

The effects of the extreme drought in 1993 lasting from April to September did not become apparent until July, when the radial growth was markedly reduced. Compared to the other roofed trees the increment in July

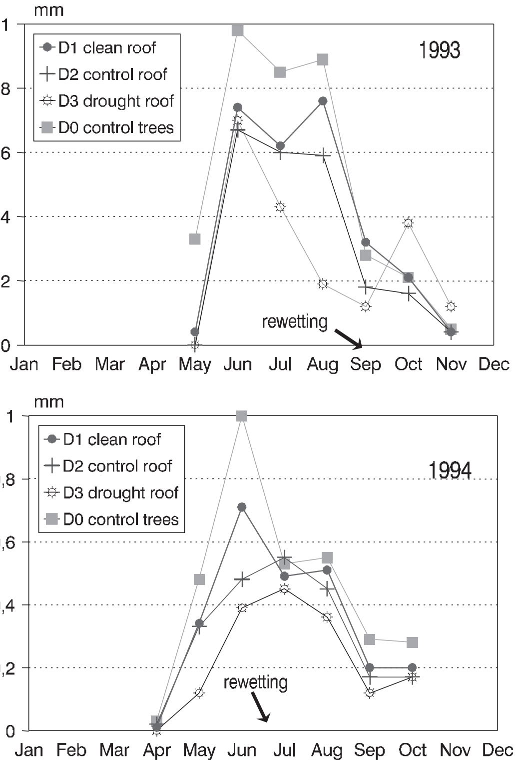

Figure 8. Development of monthly diameter increment in 1993 and 1994.

was lower by one third. In August growth stagnated to 0.2 mm, while the values at the other sites varied between 0.6 and 0.9 mm. Towards the end of the vegetation period in September, a seasonally related decrease in growth of all trees decreased to the low levels of the droughted trees was shown. However, after an intensive rewetting was carried out an opposite reaction began. It may be assumed that the trees on the D3-site in September still had an unused growth potential which had not been activated during the drought. This could be used to compensate for a part of the losses in growth. To what extent the increase in radial growth by 0.4 mm in October 1993 was related to an actual gain in growth or only to temporary swelling processes of the stem and bark could not be determined. When the drought experiment was repeated in the following year, it was terminated by rewetting in July 1994. However, although climatic conditions were very warm, no extreme changes in growth were determined for the trees on the D3 site at the peak of the summer. Rather, a continuous reduction of growth was observed lasting over the whole of the vegetation period.

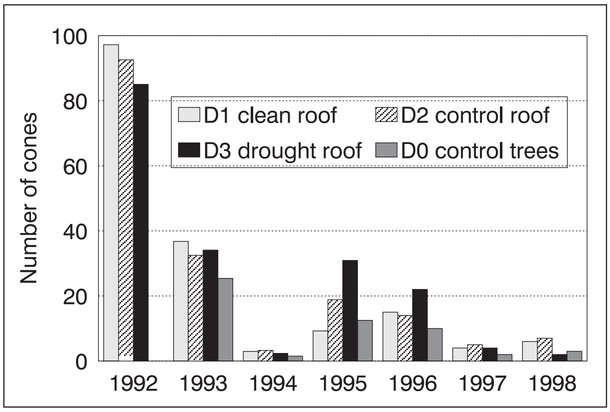

Figure 9. Development of cone number.

4.5. Fructification

Figure 9 shows the average number of cones in the years 1992 to 1998. The first count in late summer 1992 showed a large number of cones with an average between 93 and 97 per tree. However, the mean values on an area basis conceals marked differences between individual trees. While some trees had several hundred cones, others had none. During the following two years the amounts dropped to 30 cones in 1993 or 5 cones 1994, respectively. After a new increase in the years 1995 and 1996 the number of cones in 1997 reached similar amounts to those of 1994.

During the total monitoring period no significant differences were found between the experimental sites (analysis of variance, $\alpha < 0.05$). Independent of the site however, there is a close relationship to the sociological order of the tree, and thus the parameter DBH. A highly significant, negative correlation was determined between the annual height growth and the fructification intensity in the same year. The higher the number of cones formed during the vegetation period, the smaller was the growth in height of the trees.

5. DISCUSSION

The growth increment of trees must be considered to be the result of several factors which underlie complex interrelations. Thus it is very difficult to investigate individual aspects and their effects separately. This applies especially to the investigations of environmental changes carried out in the roof experiments. A result is that continuous drought stress resulted in marked increment losses. In contrast, the amelioration treatments of the soil chemical conditions carried out in the de-acidification experiments resulted in an increment increase especially in dominant trees. It has often been observed that water supply is a stronger influence than nutrient supply if site conditions are improved [17].

The effects of drought stress were investigated by Wiedemann [22] in several medium aged spruce stands in Saxony. A relationship was determined between the observed increment losses in the trees and the number of months with drought (precipitation of less than 40 mm) during the vegetation period. This corresponds with the results of Gross [9] who determined a significantly reduced increment growth rate under drought stress conditions in 10 to 15 year old spruce trees. A decrease in shoot length growth in 4 to 5 year old spruce trees after a drought period was shown by Michael et al. [15]. Nilsson and Wiklund [19] describe a reduction of needle size as a direct result of drought stress. Gross and Pham-Nguyen [10] relate this process to the shorter shoot lengths. In addition, effects ranging from a thinning of needles to a total loss of older needle generations may occur. Thus it may be concluded that the rate of photosynthesis decreases in spruce trees exposed to drought stress. This is postulated by Gross [9] and Gross and Pham-Nguyen [10]. However, not only the inhibition of the assimilating system has a negative effect on the increment rate of the trees. It must also be assumed that the growth of the root system is reduced or altered [2]. As particularly the fine root system is affected, water and nutrient uptake by the trees is decreased. On the D3-site the radial and height increment regenerated within two years subsequent to the termination of the drought experiment. Considering the severe damage in some trees the regeneration time seems remarkably short. Wiedemann [22] investigated spruce stands and reports a time span of 2 to 20 years before a regeneration of the increment rate sets in.

A comparison of the de-acidification site D1 with the roofed control site D2 allows conclusions to be drawn about the effects of soil acidification. Despite a markedly stronger intraspecific competition (higher density of the stand at the beginning of the experiment) the trees on the de-acidification site showed continuously better growth. This is most certainly due to the experimental treatments carried out which improved the nutrient supply to the trees. Widstrom and Ericsson [23] emphasise the importance of nitrogen and magnesium for the growth of spruce and birch. Both elements play a key role under the prevailing site conditions in the higher Solling uplands [16]. The consequences resulting from magnesium deficiency are reported [14]. Here it is assumed that as a result of the reduced transport of assimilates in the trees growth is inhibited. It also appears that the formation of chlorophyll strongly depends on the magnesium supply to the needles.

An assessment of the importance of nitrogen for the growth rate of spruce trees is more problematic. On the one hand, as Rosengren-Brinck and Nihlgard [20] point out, an increase of nitrogen input provides better growth conditions, but at the same time it might represent a stress factor for the trees. However, some site and regional differences render it difficult to determine the amount of nitrogen available [6]. High concentration of nitrogen can be responsible for the appearance of decline symptoms [7]. It could be shown that high atmospheric nitrogen input has a depressive effect on tree vitality during dry periods [7]. Furthermore, a Norway spruce canopy can uptake especially NH_4^+ nitrogen directly from the atmosphere [12]. This makes it more difficult for a balanced nutrient composition of the tree. An increase of the nitrogen supply thus does not automatically increase the increment rate. On the D1 site the increment rate even increased although the nitrogen inputs were shown to be markedly reduced. Only on the sites with an insufficient supply of nitrogen can specific fertilisation treatments with nitrogen result in an increase of the growth rate. This was shown by Nilsson and Wiklund [19] in a 25 year old spruce stand in southern Sweden. For sites with a sufficient N-supply a balanced level of nutrient elements is required, independent to a large extent of the total amount of available nitrogen [18]. This seems to be confirmed by the results obtained in the de-acidification experiment on the D1-site.

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