Acta Bot. Neerl. 41(1), March 1992, p. 89–101

Ecophysiological relations in two Douglas fir stands in the Netherlands

P. W. EVERS, E. G. STEINGRÖVER and W. W. P. JANS

IBN-DLO, Institute for Forestry and Nature Research, P.O. Box 23, 6700 AA, Wageningen, The Netherlands

SUMMARY

Parameters such as crown architecture and biomass were combined with data on gas exchange, nutrient concentrations and biochemical changes to investigate the influence of air pollution in two Douglas fir stands (Garderen and Kootwijk). Most branch parts were found in the middle level on third-order branches: in Garderen there were twice as many as in Kootwijk and therefore there were twice as many needles. Current-year needles in the middle canopy accounted for 40% of the total number of needles. Under certain environmental conditions ozone was found to reduce photosynthetic production by 7–25%. The most significant changes in nutrients were found in the concentrations of K and Ca in the current year's needles.

Key-words: crown architecture, forest decline, nutrients, ozone, photosynthesis, *Pseudotsuga mensiezii.*

INTRODUCTION

An important part of the Dutch National Program on Acidification (APV) involved a forest ecosystem study, called ACIFORN (ACIdification of the FORests in the Netherlands, Evers *et al.* 1988), which used Douglas fir (*Pseudotsuga mensienzii* Franco L.) as the model species. The central aim was to assess the relationship between doses of air pollution and their effects and to find the threshold values for damage by air pollution. This was done for individual trees and forest ecosystems.

Forest decline is generally assessed through geographical vitality assays. The final vitality classification, using EC standards, is dominated by the presence of needle-year classes on sun-exposed first-order branches and on discolouration of needles (Anonymous 1985–1989). A firm link is assumed between tree condition and disfunctioning of needles and/or increased needle cast. However, early needle cast resulting in transparent crowns can be normal on some sites, and does not always imply impaired growth or inferior condition (Niehaus 1989; Roloff 1989). The needle density of young-age classes in certain canopy depths may be more important for growth than needle class presence. Also, this method of assessment does not take account of the physiological quality of the needles that remain on the tree (Cape & Mathy 1988). Therefore, to enable the value of different needle classes to be evaluated, it was decided to combine long series of data with biometrical and physiological parameters distributed widely through the tree.

It is reasonable to assume that air pollution influences more mechanisms in the tree than abscission alone (McLaughlin 1985). By the time actual needle loss occurs, serious physiological damage may already have been done, having more implications for growth and tree condition than abscission *per se*. Biochemical parameters may be crucial in determining pre-visible damage by air pollution (Cape & Paterson 1988). Gas exchange and nutrient dynamics in needle-age class level were chosen as the main parameters for assessing the physiological quality of the needles. Biometrical parameters were used to gather information on branching patterns, carbon partitioning and needle area distribution. In this way information on carbon balance, on water relations, on the hormonal balance and on nutrient dynamics can be collected to evaluate the effects of air pollution and other types of stress. Whole tree physiology approach (Bervaes *et al.* 1988) was applied in this project. It intended to combine primary energy production, nutrient dynamics and biometrics so that visual parameters of vitality and the understanding of tree physiology can be improved.

We assumed that the extra stress imposed by air pollution would sooner or later become visible in parameters of growth and/or of crown architecture (Kramer & Dong 1985; Thiebaut 1988; Roloff 1989). Biomass development depends on photosynthesis. The impact of air pollution on this relation, either directly, or indirectly via nutritional and/or biochemical disruptions, was the core of the present study.

MATERIALS AND METHODS

Two Douglas fir (*Pseudotsuga mensiezii* [Franco] L.) stands (Kootwijk and Garderen) of average vitality, located in the Veluwe area, the central part of the Netherlands, were selected. Two-year-old Douglas fir trees, provenance Arlington, were planted in 1953 in Kootwijk and in 1962 in Garderen. The soil in Kootwijk is that of old farmland on sand, while Garderen consists of preglacial undisturbed soil. The weather conditions are described in Vermetten *et al.* (1990). The Kootwijk stand has a stem density of 994 trees per hectare, in Garderen the stem density is 785 trees per hectare. Both a remote sensing based classification system, developed by Van den Ancker (1987, 1989) and on-the-spot assessment were used to select trees from the stands that were used for measurements. The distribution of wood and needle biomass is based on a classification of needles and branches in crown depths, orders, year classes and branch parts, as described by Jans *et al.* (1991).

Architecture and growth

Tree height, the number of whorls, first-order branches and branch parts and the length of first-order branches were determined in 1988 on 75 trees. Diameter at Breast Height (DBH) and crown projection area were measured on all trees. Stem and crown volume and crown overlap were calculated. The length and diameter of branch parts and number and surface area of needles were measured every year in December at three crown depths on three second-order branch samples from 75 trees. Total branch and needle biomass, Needle Surface Area (NSA) and Leaf Area Index (LAI) were calculated (Jans *et al.* 1991).

Gas exchange and nutrients

In 1988 and 1989 in Garderen, photosynthesis and transpiration were measured continuously in branch assimilation chambers. No measurements were done in Kootwijk. A field gas exchange laboratory was used to ensure that the conditions inside the chambers closely resembled ambient conditions (Steingröver *et al.* 1991).

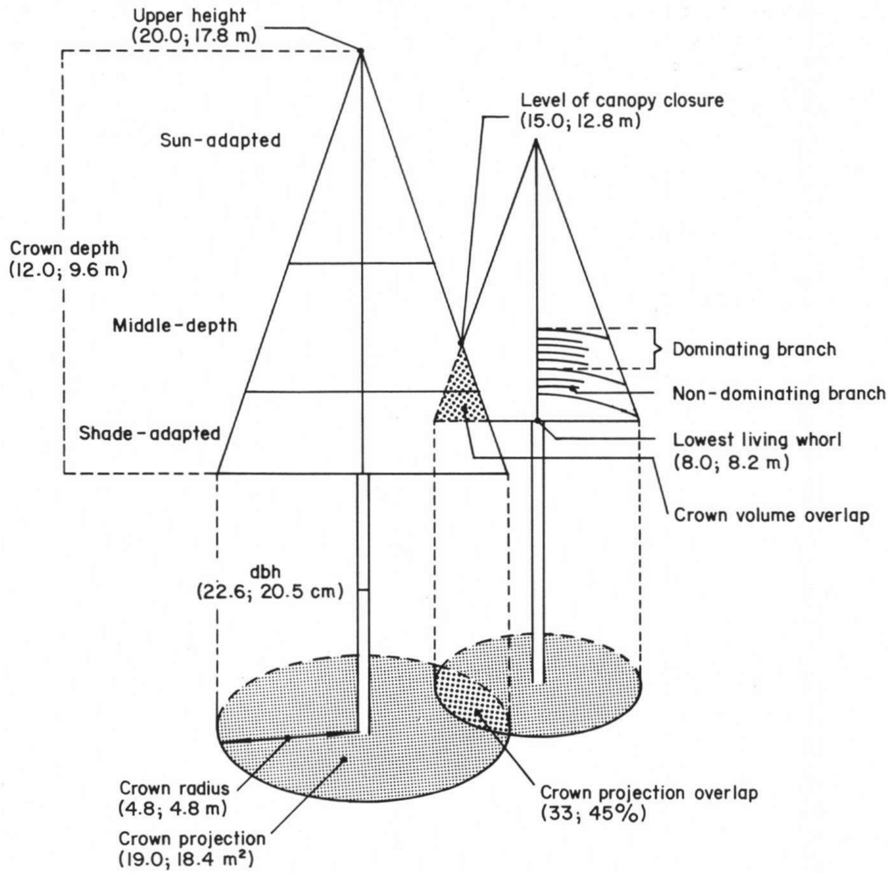

Fig. 1. Diagram of architectural parameters used. Crown depth classification based on the difference between the upper height and the lowest living whorl, and divided into three levels in which the point of canopy closure was set as the middle of the middle level. First value Garderen, second value Kootwijk.

In both stands, N, P, K, Mg, Ca, S and Fe were measured in needles of three age classes from 10 trees nine times per year between March and November (Evers *et al.* 1991), by either autoanalysis or atomic absorption spectrophotometry (AAS).

Air pollution

Air pollution components, including ozone, were measured every 30 min at different heights between 5 and 25 m from the forest floor by Vermetten *et al.* 1990.

RESULTS

Architecture and growth

In Garderen, average DBH and average stem height were greater than in Kootwijk, and therefore average stem volume was also greater in Garderen than in Kootwijk (Fig. 1). The height of canopy closure was significantly different between the stands, reflecting a different distribution of the branches over the three canopy depths. The main difference

Table 1. Percentage branch parts in each of the three crown depths, in an average tree of *Pseudotsuga mensiezii* per order and year class measured in 1988 in Garderen (Ga) and Kootwijk (Ko). SU = sun-adapted level; MI = middle level and SH = shade-adapted level

		Year class					Order			
		0	1	2	3	4	2	3	4	5
Ga	SU	48·2	25·7	14·5	7·4	4·2	36·6	58·2	4·8	0·3
	MI	37·8	27·5	19·1	9·7	5·9	16·4	63·7	17·8	2·1
	SH	33·7	28·6	19·1	10·4	8·2	21·1	60·6	17·7	1·2
Ko	SU	58·3	26·1	11·9	3·8	0·0	45·5	48·6	5·9	0·0
	MI	45·0	29·0	16·9	6·2	2·8	27·2	66·5	6·2	0·1
	SH	35·6	29·4	19·8	9·3	6·0	27·3	62·0	9·7	1·0

Table 2. Average DBH increase (cm) in *Pseudotsuga mensiezii* in 1987, 1988 and 1989 in Garderen and Kootwijk. SE 2%–5%

	1987	1988	1989
Garderen	0·67	0·61	0·51
Kootwijk	0·83	0·39	0·22

was found in the number of dominating branches in the shade (SH) level; there were fewer such branches in Kootwijk than in Garderen (Fig. 1). The number of non-dominating branches decreased from the sun-adapted level (SU) down to the SH level by roughly 80% in Garderen and by 91% in Kootwijk. Estimation of the percentage crown projection overlap area showed that because average crown projection did not differ significantly between the stands, the difference in percentage crown projection area overlap was caused by the difference in stem density.

In both stands most branch parts are third-order and current year and are in the middle (MI) level. In Garderen the average tree had twice as many branch parts as in Kootwijk. This was mainly because of a difference in third-order branch parts in the MI level, and because relatively more fourth- and fifth-order branch parts were present in Garderen than in Kootwijk (Table 1). Therefore, the trees in Garderen are more branched.

In general, DBH increment decreased from 1987 to 1989 (Table 2). In 1987, DBH increment was 0·16 cm greater in Kootwijk, in 1988 and 1989 however, it was 0·22 and 0·29 cm greater in Garderen. DBH increase was similar to the increment expected on the basis of the growth class of the trees (LaBastide & Faber 1972), except in 1987 when DBH increment was greater than predicted.

The diameter and volume increase of the branches did not differ significantly between 1987, 1988 and 1989, because the increase was too small to measure. The branches made

Table 3. Total branch volume (cm^3) of an average tree of *Pseudotsuga mensiezii* per crown depth and per order, measured in 1989 in Garderen and Kootwijk. SU = sun adapted level; MI = middle level and SH = shade adapted level

	Garderen			Kootwijk		
Branch order	SU	MI	SH	SU	MI	SH
1	7381	16 353	15 740	6675	12 378	6639
2	2304	5890	1806	1402	4777	827
3+	438	3138	892	197	1603	360

Table 4. The total number of needles (*1000), the total NSA (m^2) of an average tree of *Pseudotsuga mensiezii* per crown depth (SU, MI, SH) and the LAI, measured from 1986 to 1989 in Garderen (Ga) and Kootwijk (Ko). SU = sun adapted level; MI = middle level and SH = shade adapted level

		1986		1987		1988		1989	
		Ga	Ko	Ga	Ko	Ga	Ko	Ga	Ko
Nr	SU	1073	982	878	877	949	796	976	808
	MI	4808	2812	4395	2614	4461	2628	4135	2844
	SH	1649	691	1318	705	1181	558	1192	639
NSA	SU	23·3	24·5	17·8	17·2	19·1	14·3	20·4	16·6
	MI	94·3	63·1	91·7	57·3	92·4	51·9	87·7	61·3
	SH	40·1	17·0	29·0	16·4	25·8	11·7	26·5	14·2
LAI		12·4	10·4	10·9	9·1	10·8	7·7	10·6	9·2

up 29% of the total wood volume in Garderen, the comparable figure for Kootwijk was 12%. In both stands a major part of the branch volume was located in the MI level on first-order branches (Table 3). The contribution of second- and third-order branch parts to the total branch volume was greater in Garderen.

The distribution of needles and of needle surface area (NSA) within the crown depended on the number of branch parts, because this number was multiplied by the number of needles on an average branch part of a certain age and order, to calculate crown totals. Most of the needles were on third-order, current-year branches of the MI level. In Garderen the contribution of the number of 2, 3 and 4-year-old needles to the total amount of needles was relatively greater than in Kootwijk. In general, first-order branch parts in Garderen had eight needle-year classes, whereas in Kootwijk they had seven. Between 1986–1989, 40% of the needles were lost on average each year, mostly from the MI level. Comparing the loss from the different levels, most needles were lost from the SU level relatively speaking: 53% from the SU, 40% from the MI and 35% from the SH level respectively. In 1987 and 1988 in Kootwijk and in 1987 in Garderen fewer needles were formed than were lost (data not shown), which resulted in a decrease in total needle biomass and thus in total NSA and in LAI (Table 4).

Table 5. Transpiration per day (absolute minimum and maximum values) in Mol H20 m^{-2} needle surface area of *Pseudotsuga mensiezii*. Averages of 2 (SH), 2 (MI) and 2–4 (SU) branch assimilation chambers at Garderen. SU = sun-adapted level; MI = middle level and SH = shade-adapted level

	March	April	May
SH	5–14	4–12	8–11
MI	5–15	4–10	9–40
SU	5–20	5–31	9–43

Table 6. Characteristics of the light response of photosynthesis of needles of *Pseudotsuga mensiezii* in Garderen. Am and Ad in µmol CO_2 m^{-2} s^{-1} and max PAR reached in µmol E m^{-2} s^{-1}. Am = maximum photosynthetic rate and Ad = dark respiration. SU = sun-adapted level and MI = middle level

		Morning		Afternoon		Night
Level		Am	PAR	Am	PAR	Ad
SU	NY	5·0	300	5·7	700	0·75
SU	SO	8·6	900	8·5	1400	1·09
SU	SW	7·0	1100	7·3	1100	0·97
SU	S	5·0	250	4·6	1000	0·77
MI	SW	6·2	500	7·9	700	0·84
MI	NO	3·7	250	3·6	250	0·74

Gas exchange and nutrients

The presented results on gas exchange were all collected in the first 6 months of 1989 in the Garderen stand. In general, needle transpiration (E) increased from the SH level up to the SU level of the tree (Table 5). Transpiration of needles in the MI level of the tree was comparable to SH or to SU needles, depending upon their position relative to the point of canopy closure. In the SU level, the maximum value of E increased from March to May. In general, E was strongly coupled to photo-active radiation (PAR), average temperature and vapour pressure deficit (VPD) (data not shown). Stomatal resistance showed a diurnal pattern, with values well above 2000 s m^{-1} during the night, indicating closure of the stomata. Stomatal resistance during the day was similar in March and April, but decreased in May to values around 200 s m^{-1}. In needles from the SH level however, values around 600–800 s m^{-1} were found and these values did not decrease in May.

The characteristics of the light response of photosynthesis are shown in Table 6. PAR levels up to 300 µmol E m^{-2} s^{-1} increased the photosynthetic rate. Calculated from the

Table 7. Light response and calculated photosynthetic reduction by ozone of needles of *Pseudotsuga mensiezii* in Garderen in three SU chambers. MO = morning; AF = afternoon; MO > 40: T > 14C, VPD > 275Pa and O_3 > 40ppb; MO < 40: rest MO data; AF > 70 or 80: T > 14C, VPD > 275Pa and O_3 > 70 or 80 ppb; AF < 70 or 80: T < 14C, VPD < 275Pa and O_3 < 70 or 80 ppb; * = significant difference between much and little ozone ($P = 0{\cdot}025$); Red = reduction in %; e (light use efficiency) in mol/mol and Am (maximum photosynthesis rate) in $\mu mol\ CO_2\ m^{-2}\ s^{-1}$

	1		2		3	
Chamber	e	Am	e	Am	e	Am
MO > 40	0·044*	4·8	0·076*	10·0	0·049*	8·9
< 40	0·081	4·8	0·051	9·1	0·094	8·6
AF > 70	0·030*	7·1	0·070	9·4	0·070*	7·8
< 70	0·041	7·3	0·094	9·6	0·087	8·4
AF > 80	0·032*	6·5*	0·090	8·6*	0·053*	8·7
< 80	0·037	7·5	0·088	9·8	0·094	8·2
	Red		Red		Red	
40 + 70	21		7		15	
40 + 80	25		10		16	

light response curve (Landsberg 1986), not all needles reached the maximum rate of photosynthesis in the morning, depending upon their position in relation to the sun and upon their height in the tree. Light use efficiency varied between 0·05–0·12 mol mol^{-1}. Dark respiration of SH needles was greater than that of SU or MI needles.

Ozone concentrations are strongly correlated with irradiance, temperatures and VPD. To distinguish the effect of ozone on photosynthesis from the effects of the other environmental variables, a correlation diagram was designed, dividing the data into different data ranges. For the morning and the afternoon separately, the light response curve was used to describe the selected ranges. The reduction, by ozone, in needles from the sun level of the tree was calculated (Table 7). Ozone concentrations may reduce photosynthetic production by 7–25%.

The needles from both stands were found to contain moderate concentrations of N and low concentrations of P. Both stands showed high differences in K concentration between canopy depth levels. The new needles in the SU level of 1986 and 1987 in Garderen decreased in K concentration throughout the years, even falling below the 0·3% threshold (Van den Burg 1988) (Figs 2 and 3). Comparable needles in Kootwijk reached a more or less constant K level at the end of the summer 1986, and this level remained constant in the following years. The same changes in K concentration were not found in the SH level. The average K concentration of all needle types together increased slightly through the years in Kootwijk (SE 0·01%). The accumulation of Ca in current-year needles in the SH level increased through the years in Garderen, while in Kootwijk the opposite occurred: a drop to far below 0·25% occurred in 1989 (Figs 4 and 5). At this canopy depth, the Ca concentration in Kootwijk was higher than in Garderen in 1986, but this was fully reversed by 1989. The Mg concentration was 0·1% in both stands, which is considered normal (Van den Burg 1988). The Mg concentration increased slightly in the SH level through the years (data not shown).

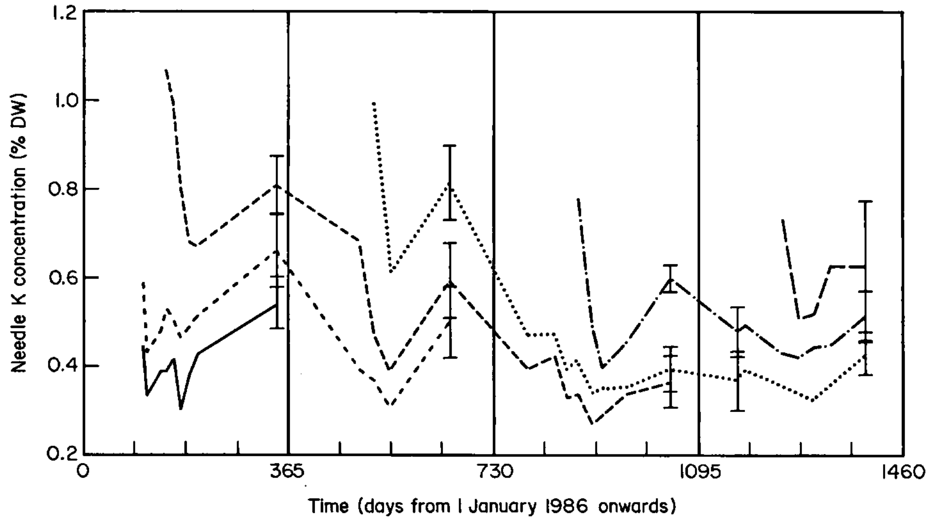

Fig. 2. Potassium concentration as % dry weight (±SD) in the sun-adapted level in current-year, one-year-old and two-year-old needles of *Pseudotsuga mensiezii* in Garderen, sampled in 1986–1989. Year of flushing: —— 84; - - - - 85; — — — 86; · · · · 87; — · — · — 88; —— — 89.

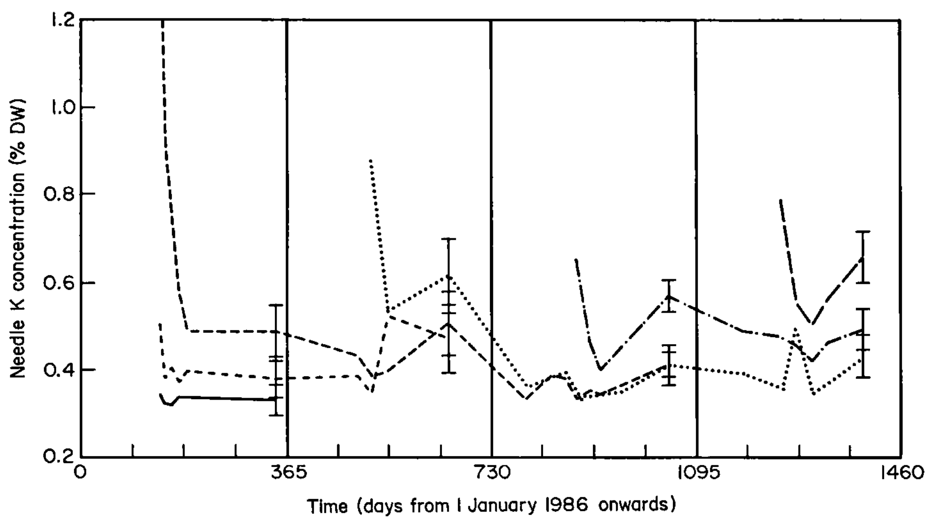

Fig. 3. Potassium concentration as % dry weight (±SD) in the sun-adapted level in current-year, one-year-old and two-year-old needles of *Pseudotsuga mensiezii* in Kootwijk, sampled in 1986–1989. Denotations as in Figure 2.

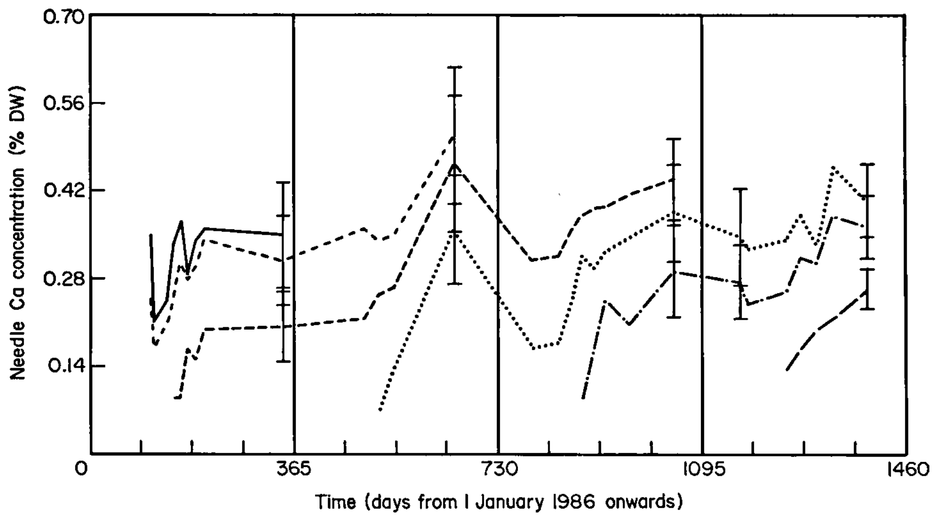

Fig. 4. Calcium concentrations as % dry weight (±SD) in the shade-adapted level in current-year, one-year-old and two-year-old needles of *Pseudotsuga mensiezii* in Garderen, sampled in 1986–1989. Denotations as in Figure 2.

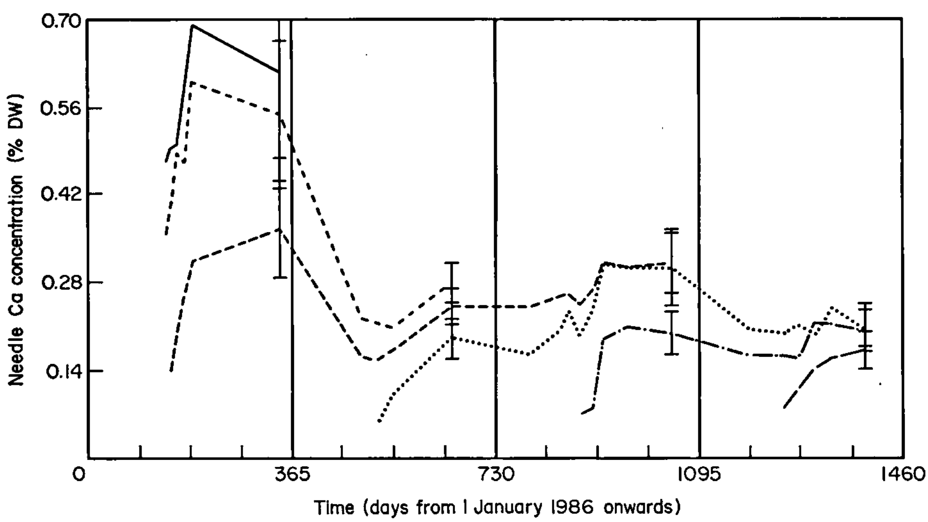

Fig. 5. Calcium concentration as % dry weight (±SD) in the shade-adapted level in current-year, one-year-old and two-year-old needles of *Pseudotsuga mensiezii* in Kootwijk, sampled in 1986–1989. Denotations as in Figure 2.

DISCUSSION

Several authors have reported the effects of air pollution on branch and crown architecture of conifers (Lesinski & Landmann 1988; Roloff 1989). Both stands of Douglas fir used were of the same provenance, so no major differences in architecture were expected.

Considering the age difference between the stands, more first-order branches would be expected in Kootwijk. However, more first-order branches and twice as many branch parts were found in Garderen. Moreover, the branching density was also greater in Garderen. The difference in number of first-order branches between the stands accounted for only about 12% of the difference in the total number of branch parts. The lower stem density in Garderen may also have contributed to the larger number of branch parts in this stand. Thus the major cause of the difference in branch parts between the stands is not clear: difference in bud formation or in bud and/or branch abortion may have contributed. The difference in the total number of branch parts is echoed by the difference in number of branch parts found in the SU level. Assuming that branch formation has not changed over the years, it is unlikely that branch abortion caused the difference in total number of branch parts. The difference in bud formation or in bud abortion between the stands may have been caused by a difference in competition between trees, in air pollution, in water relations and/or in the nutritional status of the trees.

As needle density per branch part is the same in Garderen and Kootwijk, the difference in the total number of branch parts fully determines the difference in the total number of needles. Although Garderen contains twice as many needles as Kootwijk, EC vitality-based classification indicates no differences between the stands. This is not necessarily contradictory: the EC classification is based on counting the needle-year classes on first-order branches in SU level, and not on assessing needle density and/or needle numbers in any part of the tree. In general, tree growth is thought to reflect the condition of the tree (Landmann 1988; Kenk 1989). If tree growth is considered in terms of DBH increment (Kramer & Dong 1985; Athari & Kramer 1988), the condition of trees in Garderen and Kootwijk is the same. However, there are twice as many needles in Garderen as in Kootwijk and yet there are no differences in DBH increment between the two stands. The DBH increment found in Garderen and Kootwijk can be considered as normal (LaBastide & Faber 1972). The amounts of needles found in Garderen and Kootwijk probably do not limit tree production. This raises questions about possible differences in condition between Garderen and Kootwijk and about the importance of DBH increment and the total number of needles as indicators of the condition of the tree (Cape & Mathy 1988). Needle quality might be more important than needle numbers. More information on the condition and the adaptability of the tree can be obtained from physiological research on the quality of needles from different needle classes, especially current-year needles on third-order branches in the MI level of the tree, which may contribute up to 40% of the total number of needles.

Direct effects on Douglas fir photosynthesis were observed with ozone concentrations below the threshold levels found in most laboratory experiments (Gorissen & van Veen 1988; Smeets *et al.* 1990). Because ozone is strongly correlated with irradiance, temperature and vapour pressure deficit, the effect of ozone could only be demonstrated during certain periods of the day. This does not imply that ozone effects are limited to these periods, but that the interdependency with other environmental parameters is too great. Both the magnitude of the ozone effect and the number of days on which effects were found indicate that direct effects of ozone in a Douglas fir forest can be substantial in the long run. The great interdependency between ozone and other environmental variables strongly suggests that future forest ecosystem and laboratory studies should not be restricted to one air pollution factor only and that the ambient variation in environmental parameters should be included (Gudriaan 1985; McLaughlin 1985, Dueck *et al.* 1986, Prinz 1987, Steingröver *et al.* 1991).

Little is known about the mechanisms and time scales in which the nutrient status within the crown changes (Miller 1986; Cape 1989). No indications were found for excessive nutrient losses from the needles as a result of the impact of stress. Attempts to correlate needle concentrations and throughfall have already been made (Van der Maas *et al.* 1990; Steingröver *et al.* 1990). Potassium increases in the throughfall were less than expected from the described decrease in needle potassium concentrations. The spatial distribution of needles and thereby of nutrients may have important implications for throughfall. The described differences between SU and SH levels, as well as between young and old needles show the necessity of including needle quality in throughfall studies (see also Houdijk & Roelofs 1991).

The N concentration in needles from Kootwijk increased both with the ageing of the needles and throughout the years. In Garderen however, the N concentration of the needles did not increase with age. The N concentration in the needles of both stands was qualified as sufficient and far from supra-optimal (Van den Burg 1988; all criteria are based on current-year needles on first-order branches from the SU level). Based on a 0·1% threshold level (Van den Burg 1988) the P concentration in the needles from Kootwijk was qualified as poor, while the P concentration in needles from Garderen was deficient. However, at the end of the measuring period, the P concentration increased in both stands, but faster in the needles from Kootwijk. Also, the current-year needles formed in 1986 and 1987 in Kootwijk contained a higher concentration of P than the needles from Garderen. In both stands the needles from the SH level in the canopy had the highest P concentration.

In general, the change in N, P and K concentrations found in needles from Garderen resulted in a poorer nutrient status than the Kootwijk stand. The fact that needle biomass in Garderen was double that in Kootwijk might have contributed to the differences in nutrient concentration.

In conclusion, the direct effect of air pollution on photosynthesis was proven to be significant. No disruption of the biochemical status of the trees by air pollution was apparent. The changes in nutritional status of the trees and the observed differences between the stands could not be correlated with air pollution. It is still unclear whether the observed direct effects on photosynthesis correlate with the observed changes in nutritional status of the trees. The reason for the significant structural differences found between the stands remains unclear.

ACKNOWLEDGEMENTS

The authors would like to express their special gratitude to Hans van der Beek, Wim Swart, Hannie Relou and Jacqueliene Donkers (project participants). We also thank Joke Belde, Geurt van Roekel, Wim van Orde and Herman Oostendorp (sampling), Rikie Kemperman and Azadeh Pilon (analyses), Henk Blom and Sjoerd van Eeden (technical assistance), Bert van der Werf and Eit van der Meulen (statistical assistance), Aart Vermetten for supplying the air pollution data and Joy Burroughs-Boenish for editing the English text.

This research was funded by the Department for Agricultural Research (DLO) and for Forestry (BLB) of the Ministry of Agriculture, Nature Management and Fisheries, by the Dutch National Program on Acidification, and by the Environment Protection Program of the EC.

REFERENCES

Anonymous (1985, 1986, 1987, 1988, 1989): *Verslagen van de landelijke inventarisatie van de vitaliteit van het Nederlandse bos*. Pp. 18–24. SBB, Utrecht.

Athari, S. & Kramer, H. (1988): Problematik der Zuwachsuntersuchungen in Buchenbeständen mit neuartigen Schadsymptomen. *Allg. Forst. Jagd. Zeit.* **160:** 40–45.

Bervaes, J.C.A.M., Mathy, P. & Evers P.W. (eds) (1988): *Relationships between above and below ground influences of air pollutants on forest tree physiology*. CEC air pollution report 16, Brussels, ISBN 2-87273-005-8.

Cape, J.N. (1989): Variability within forests in throughfall and stemflow. In: Bresser, A.H.M. and Mathy, P. (eds): *Monitoring air pollution and forest ecosystem research*. Pp. 155–162. CEC, Brussels.

Cape, J.N. & Mathy, P. (1988): *Scientific base of forest decline symptomatology*. CEC, Brussels.

Cape, J.N. & Paterson, I.S. (1988): Early diagnosis of forest decline. In: Mathy, P. (ed.): *Air pollution and ecosystems*. Pp. 609–616. Riedel, Dordrecht.

Dueck, Th.A., Ernst, W.H.O. & Pasman, F.J.M. (1986): Effects of SO_2, NO_x and O_3 in combination on the yield and reproduction of *Silene cucubalus* populations. *J. Plant Physiol.* **122:** 97–106.

Evers, P.W., Jans, W.W.P. & Steingröver, E.G. (1991): *Impact of air pollution on ecophysiological relations in two Douglas fir stands in the Netherlands*. Rapportnr. 637, Rijksinstituut voor bosbouw en groenbeheer 'De Dorschkamp', Wageningen, ISSN 0924-9141.

Evers, P.W., Konsten, C.J.M. & Vermetten, A.W.M. (1988): Acidification research on Douglas fir forests in the Netherlands. In: Mathy, P. (ed.): *Air pollution and ecosystems*. Pp. 887. Riedel, Dordrecht.

Gorissen, A. & van Veen, J. (1988): Temporary disturbance of translocation of assimilates in Douglas Firs caused by low levels of ozone and sulphur dioxide. *Plant Physiol.* **88:** 559–563.

Gudriaan, R. (ed.) (1985): *Air pollution by photochemical oxidants*. Springer Verlag, Berlin.

Houdijk, A.L.F.M. & Roelofs, J.G.M. (1991): Deposition of acidifying and eutrophicating substances in Dutch forests. *Acta Bot. Neerl.* **40:** 245–256.

Jans, W.W.P., Evers, P. & Relou, H. (1991): Stand and branch architecture. In: Evers, P.W. (ed.): *Impact of air pollution on ecophysiological relations in two Douglas fir stands in the Netherlands*. Rapportnr. 637, Rijksinstituut voor Bosbouw en Groenbeheer 'De Dorschkamp', Wageningen. ISSN 0924-9141.

Kenk, G. (1989): Zuwachsuntersuchungen im Zusammenhang mit den gegenwaertigen Waldschaeden in Baden-Wuerttemberg. In: Bucher, J.B. and Bucher-Wallin, I. (eds): *Air pollution and forest decline*. Pp. 263–271. EAFV, Birmensdorf, Switzerland.

Kramer, H. & Dong, P.H. (1985): Kronenanalyse für Zuwachsuntersuchungen in immissionsgeschädigten Nadelholzbeständen. *Forst. Holzw.* **5:** 40.

LaBastide, J.G.A. & Faber, P.J. (1972): *Revised yield tables for six tree species in the Netherlands*. Uitvoerig verslag. Stichting bosbouwproefstation 'De Dorschkamp', Wageningen. Bd. 11, no. 1.

Landmann, G. (1988): Preventive and curative measures for terrestrial ecosystems, in particular forests. In: Mathy, P. (ed.): *Air pollution and ecosystems*. Pp. 420–422, Riedel, Dordrecht.

Landsberg, J.J. (1986): The carbon balance of leaves. In: Sutcliffe J.F. (ed.): *Physiological ecology of forest production*. Academic Press, London.

Lesinski, J.A. & Landmann, G. (1988): Crown and branch malformation in conifers related to forest decline. In: Cape, J.N. and Mathy, P. (eds): *Scientific base of forest decline symptomatology*. Pp. 92–106. CEC, Brussels.

McLaughlin, S.B. (1985): Effects on air pollution on forests: a critical review. *J. Air Poll. Contr. Ass.* **35:** 516–534.

Miller, H.G. (1986): Effects of dry and wet deposition on tree canopies—in particular mineral and nutritional status. In: Andersson, F. and Mathy, P. (eds): *Direct effects of dry and wet deposition on forest ecosystems—in particular canopy interactions*. Pp. 10–25. CEC, Brussels.

Niehaus, G. (1989): Terrestrische Zustandserfassung von Kiefernkronen. *Forst. Holz.* **8:** 23–26.

Prinz, B. (1987): Causes of forest damage in Europe. Major hypotheses and factors. *Environment* **29:** 11–15.

Roloff, A. (1989): Entwicklung und Flexibilität der Baumkrone und ihre Bedeutung als Vitalitätsweiser. *Schweiz. Zeitschr. Forstw.* **9:** 67–74.

Smeets, W.L.M., Kropff, M.J. & Meijer, E.M.J. (1990): Effects of ozone on photosynthesis, stomatal control and drought sensitivity of Douglas fir (*Pseudotsuga menziesii*) seedlings. In: Smeets, W. *et al.* (eds): *Quantitative analysis of the uptake of SO_2 and O_3 by plants and effects on physiological processes and plant growth*. IPO report R-89-11, Wageningen, the Netherlands.

Steingröver, E.G., Belde, J.J.M., van der Maas, R., Evers, P.W. & van Breemen, N. (1990): Direct and indirect effects of acid deposition on growth and mineral status of Douglas fir. In: Ulrich, M. (ed.): *International congress on forest decline research*, 232–235.

Steingröver, E.G., Swart, W., Evers, P.W., Vermetten, A. & van der Meulen, E. (1991): Effects of ozone, PAR, temperature and VPD on photosynthesis. In: Evers, P.W., Bouten, W., van Grinsven, J.J.M. and Steingröver, E.G. (eds): *CORRELACI, Identification of traditional and air pollution related stress* *factors in a Douglas fir ecosystem: the ACIFORN stands*. Dorschkamp report 623, ISBN 0924–9141.

Thiebaut, B. (1988): Tree growth, morphology and architecture, the case of beech. In: Cape, J.N. and Mathy, P. (eds): *Scientific basis of forest decine symptomatology*. Pp. 49–73. CEC, Brussels.

Van den Ancker, J.A.M. (1987): *Een vitaliteitsbeoordeling met behulp van kleuren infrarood luchtfoto's (schaal 1:2500) van twee percelen douglas*. Rapport Rijksinstituut voor Bosbouw en Groenbeheer 'De Dorschkamp', Wageningen, no. 492, ISSN 517072.

Van den Ancker, van den Werf, B., van de Voet, H., Jans, W. & Relou, H. (1989): *Relatie tussn boomfysiologie en multispectraal—en kleurenfotografie—eerste fase*. BCRS report no. 89–39, 198 pp.

Van den Burg, J. (1988): *Voorlopige criteria voor de beoordeling van de minerale voedingstoestand van naaldbomen op basis van de naaldsamenstelling in het najaar*. Rapport 520 Rijksinstituut voor onderzoek in de Bosen Landschapsbouw 'De Dorschkamp', Wageningen.

Van der Maas, M.P., Belde, J.J.M., Klap, J. & Olsthoorn, A.F.M. (1990): Dynamics of the potassium status of two Douglas fir stands. In: Ulrich, M. (ed.): *International congress on forest decline research*. Pp. 227.

Vermetten, A.W.M., Hofschröder, P. & Versluis, A.H. (1990): *Air pollution in forest canopies*. Report DAPV no. 101–9, projects 101.1 and 101.2, RIVM, Bilthoven, September 1990.