Original article

Gas exchange in young Scots pine following pruning of current shoots

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Summary — A pine shoot beetle attack was simulated by cutting all current shoots in the upper crown of 2 20-yr-old Scots pines (*Pinus sylvestris* L) while gas exchange was followed continuously before and after the shoot removal. Net photosynthetic rate and mesophyll conductance of the 2-yr-old shoots decreased by $\approx$ 50% immediately after pruning but recovered within 10 d after the shoot removal. The quantum yield was also much lower after cutting. Water status and transpiration rate were not systematically affected by the treatment.
Possible explanations of the photosynthetic decrease could be an accumulation of assimilation products decreasing the mesophyll conductance of carbon dioxide to the chloroplasts or changes of the carbon allocation pattern.

Scots pine / shoot-pruning / photosynthesis / quantum yield / field performance

Résumé — Échanges gazeux chez des jeunes pins sylvestres après élagage des pousses de l'année. *Une attaque du scolytide* Tomicus piniperda *a été simulée en coupant toutes les pousses de l'année dans la partie supérieure de la couronne de 2 pins sylvestres (*Pinus sylvestris *L) de 20 ans. Pendant le même temps, les échanges gazeux ont été suivis de façon continue avant et après l'opération. Le taux net de photosynthèse et la conductance du mésophylle des pousses de un an décroît d'environ 50% immédiatement après l'élagage, mais récupère dans les 10 jours suivant le retrait des pousses. Le rendement quantique diminue aussi beaucoup après la coupe des pousses. L'état hydrique et le taux de transpiration ne sont pas affectés systématiquement par le traitement. La diminution de la photosynthèse pourrait être expliquée par une accumulation d'assimilats ayant pour effet de diminuer la conductance du mésophylle pour le dioxyde de carbone vers les chloroplastes ou par des modifications dans le shéma d'allocation du carbone.*

pin sylvestre / élagage des pousses / photosynthèse / rendement quantique / performance sur le terrain

INTRODUCTION

It is known that insects can cause growth losses in forest trees, eg by consuming foliage and buds (for references, see Kulman 1971). Besides quantitative losses in terms of reduced stem growth, insect activity also has qualitative effects on physiological processes in the tree. Such reported effects include increased nitrogen (Piene and Percy, 1984; Ericsson et al, 1985) and reduced carbohydrate levels (Ericsson et al 1980a, 1985) in remaining needles, increased photosynthetic capacity in regrowth foliage (Heichel and Turner, 1983), and increased amounts of defensive chemicals such as tannins and phenolics (eg Wagner, 1988). It has also been suggested that water and light conditions for remaining foliage may at least temporarily be improved as a result of defoliaton (Ericsson et al, 1980b). Altogether, some of these physiological changes counteract the detrimental effects of the foliage loss, and may be important in the recovery process of the defoliated tree.

In a field experiment comparing induced beetle attacks on caged trees and artificially pruned trees, both treatments produced unexpectedly small growth losses in young Scots pine (Pinus sylvestris L) trees as compared to previously reported natural attacks by the pine shoot beetle, Tomicus piniperda (L) (Coleoptera, Scolytidae) (Ericsson et al, 1985). The pruning pattern as well as the induced attacks were very similar to the attack pattern observed under natural conditions. The discrepancy in growth reduction as compared to earlier studies was thought to be a result of younger trees being used in the experiment. A later study confirmed that older trees react comparatively more strongly to needle loss than young trees (Langström et al, 1990). Among different compensatory mechanisms discussed in these studies,

increased photosynthetic capacity of remaining needles was hypothetically considered to be one likely explanation for the observed results. Thus, combining such a simulated attack with continuous gas exchange measurements in trees in situ could improve the understanding of carbohydrate dynamics and growth responses of attacked trees.

To test this hypothesis, we simulated a pine shoot beetle attack by cutting all current shoots in the upper crown of 2 20-yr-old Scots pines while in situ gas exchange of 1-yr-old needles was followed continuously before and after the "attack".

MATERIAL AND METHODS

The experiment was carried out in a 20-yr-old stand of Scots pine (Pinus sylvestris L) situated at Jädraas, Sweden (60° 48' N, 16° 30' E, altitude 180 m). The stand, growing on glacifluvial sand, has been described by Flower-Ellis et al, (1976) and details of the site have been given by Axelsson and Brakenhielm (1980).

Gas exchange was measured in situ by an open system with cylindrical assimilation chambers made of thin perspex. The chamber was attached to a base-plate fixed in a bifurcated holder, which enabled the chamber to be mounted in the natural position of the shoot to be studied. The chamber temperature followed ambient temperature by an air-cooling system. Carbon dioxide was measured by an infra-red gas analyzer (UNOR 2, Maihak, Hamburg, Germany) and water vapour concentration by dew point mirrors (Walz Mess- und Regeltechnik, Effeltrich, Germany). Air temperature was measured by thermocouples (copper/constantan) and photon flux density was recorded by quantum meters (LI-190 Lambda Instruments, USA). Each chamber was provided with a separate quantum meter placed horizontally outside the chamber. Rates of photosynthesis and transpiration were expressed on a projected needle area basis, the needle area of each branch being determined at the end of the experiment by a leaf area meter (LI-300, Lambda Instruments, USA). Stomatal conductance for the flux of carbon dioxide

through the stomata and mesophyll conductance for the flux from the stomatal cavity to the chloroplasts were calculated according to Ludlow and Jarvis (1971). Further details of the gas exchange measurement system are given by Linder *et al* (1980). Gas exchange data together with climatic data were collected, stored and processed by a computer (PDP 11/40) at the field site (*cf* Engelbrecht *et al*, 1980).

Needle water potential was measured occasionally (table I) with pressure chamber technique based on the design of Waring and Cleary (1967) and further developed by Hellkvist *et al* (1980). For these measurements, 1-yr-old needles from the third whorl from the top on the south side of the trees were collected in the middle of the day.

In 1982 budbreak occurred at the end of May. Shoot growth finished at the beginning of July while needles reached their final length in the middle of August. Three trees of height 2.5–2.8 m standing close to each other were used for the study. Assimilation chambers were mounted on last year's needles on the main branch axis of south-facing branches of the third whorl from the top. Gas exchange measurements started on June 16, 1982 and on July 27, most current shoots of the 6 uppper whorls, including the branches with the assimilation chambers, were pruned from 2 of the trees while the third tree was kept intact as a control. The total needle biomass was thus reduced by ≈ 25%, and that of the current shoots by ≈ 70%, simulating a heavy attack of the pine shoot beetle. The clipping procedure has been described in detail

by Langström *et al* (1990). Gas exchange was then followed continuously to September 4th. To evaluate gas exchange data, the average diurnal course of 4 periods of 10 d before and after pruning as well as daily photosynthetic input were calculated for each branch. The apparent quantum yield was calculated from the linear part of the photon flux density response curve obtained from field data. The daily light use efficiency was calculated from average daily values of photon flux density and the net CO_2 uptake during the 24-h period, thus including the respiration losses during the night hours (*cf* Troeng and Linder, 1982).

The total number of records from each assimilation chamber varied between 3 100 and 3 335. Separate data from each of the chambers were collected at least every 45 min throughout the measurement period and later condensed to average values. By comparing gas exchange data between trees and between periods before and after the pruning treatment, some general information was obtained concerning the reactions of gas exchange to a large reduction of needle biomass.

RESULTS

The period before shoot pruning was characterized by low precipitation and above average air temperature (*cf* Lindroth 1985). Water stress in the stand increased slowly

Table I. Needle water potential of the experimental trees and the control tree at noon on 4 days.

Date	Needle water potential (MPa)		
	Experimental tree 1	Experimental tree 2	Control tree
16 July	−0.98 ± 0.04	−0.96 ± 0.03	−1.02 ± 0.06
29 July	−1.10 ± 0.02	−1.14 ± 0.04	−1.38 ± 0.05
7 Aug	−0.40 ± 0.02	−0.38 ± 0.05	−0.38 ± 0.05
19 Aug	−0.52 ± 0.01	−0.51 ± 0.03	−0.55 ± 0.04

The values represent the mean of 5 replicates ± standard error. Shoot pruning of the experimental trees took place on July 27.

during July and reached a maximum at the beginning of August, as indicated by partial stomatal closure and midday depression (Troeng, 1985). Precipitation during the period July 5–August 5 was < 5 mm and soil water potential (Jansson and Halldin, 1979) at the end of July was ≈ 0.1 MPa in the layer 0–30 cm (Lindroth, 1985). The water stress conditions disappeared after 40 mm rainfall on August 6.

Daily net photosynthetic performance was similar for the 3 shoots during the period before pruning (fig 1). The control shoot had slightly higher photosynthetic performance during all periods before July 27. This was due to the fact that photon flux density was ≈ 10% higher for the control branch due to less shading from surrounding trees. Since calculated quantum yields from photosynthetic light response curves from each tree were not significantly different, net photosynthetic efficiency was considered to be equal before shoot pruning. The records of daily photosynthetic input showed a drastic decrease during

the first days after pruning (fig 1) and the daily quantum yield was considerably lower for the cut trees during the first 10 d after shoot pruning (fig 2). The decrease after pruning was primarily caused by low photosynthetic rates towards the end of the day while photosynthesis during morning hours was similar to that of the control (fig 3). Transpiration data were analysed for the 3 trees before and after pruning, but since no drastic changes nor any systematic trends in transpiration were found, data are not reported in detail here. Water potential measurements (table I) indicated a similar water stress situation for all trees before shoot-pruning. After pruning, the control tree showed slightly lower water potential records while the general water stress disappeared after the heavy rain fall on August 6.

Calculated conductances showed that the mesophyll conductance was generally

Fig 2. Daily light use efficiency for each 10-d period for the control tree (open symbols) and the 2 experimental trees (filled symbols). The broken line is the regression line ($y = 0.242$ $e^{-0.006 \, x}$) of the relation between photon flux density and daily quantum yield ($r^2 = 0.77$). If the 2 lowest light use efficiency values representing the first 10-d-period after pruning are omitted, then $r^2 = 0.87$.
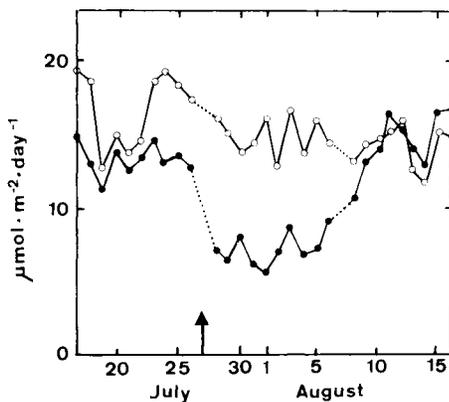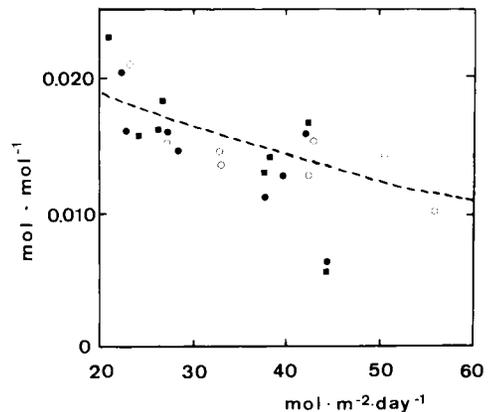

Fig 1. Daily net photosynthetic values of the control tree (open symbols) and average value of the experimental trees (filled symbols) before and after shoot pruning. The arrow indicates the day when shoot pruning took place.
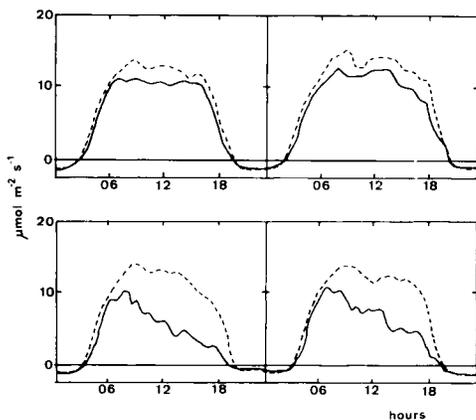
Fig 3. Daily net photosynthetic performance of 1-yr-old needles 2 d before (upper diagram) and 2 d after (lower diagram) pruning of current shoots of the control tree (broken line) and average value of the experimental trees (solid line).
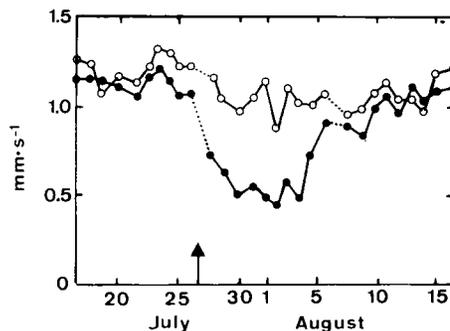

Fig 4. Daily mean values of mesophyll conductance of the control tree (open symbols) and average value of the experimental trees (filled symbols) before and after shoot pruning. The arrow indicates the day when shoot pruning took place.

lower than stomatal conductance and was the limiting factor for photosynthesis. Average stomatal conductance during daytime was between 2 and 4 $mm.s^{-1}$ while mesophyll conductance seldom exceeded 1.5 $mm.s^{-1}$. This was in accordance with earlier results obtained on the same stand (Troeng and Linder, 1982). Even during the water stress period in the end of July mesophyll conductance was lower than stomatal conductance. Daily mean values of mesophyll conductance decreased considerably after the shoot pruning on July 27, but increased again to levels before pruning within 10 d (fig 4). The photosynthetic decrease after pruning was in good agreement with the decrease of mesophyll conductance (cf figs 1, 4).

DISCUSSION

Previously, a similar experiment in the same stand demonstrated that photosyn-thesis of current shoots under attack by a beetle declined drastically as a result of wilting of the damaged shoot, whereas the 1-yr-old needles on the same axis reacted with reduced photosynthesis soon after the collapse of the current shoot (Troeng et al, 1979).

In the present study, where we cut the current shoots, we observed a similar drastic but transient drop in photosynthesis and mesophyll conductance. Apart from cutting the shoots instead of using beetles, the main difference was the whole-tree-approach in the present study as compared to one single attack in the previous study. However, knowing the independence of individual branches (Langström et al, 1990), the similar outcome of the 2 studies is not surprising. Simulating a pine shoot beetle attack by artificial pruning has been shown earlier to be a good mimic of natural attacks (Ericsson et al, 1985; Langström et al, 1990).

One possible explanation for the decrease in photosynthesis after pruning

could be the carbon balance of the tree. It is known from other investigations in the same stand (Ericsson, 1978; 1979) and elsewhere (Senser *et al*, 1975) that current needles accumulate starch as long as they are still growing. As needle growth finished in the middle of August, current needles were still a strong sink at the time of pruning at the end of July. Consequently, when the current shoots were cut off, the main sink for photosynthetic products of 1-yr-old needles disappeared and an accumulation of carbohydrates may have taken place, thereby inhibiting net photosynthesis (*cf* Neales and Incoll, 1968). Lake (1967) suggested that assimilate accumulation may decrease mesophyll conductance and Rackham (1966) has stated that such a decrease could be an effect of accumulated starch grains in the chloroplasts. Thus, this source–sink relationship could explain the decrease of photosynthesis and mesophyll conductance immediately after pruning. Also, the diurnal pattern of photosynthesis during the days after pruning (fig 3) supports this hypothesis. During the second 10-d period after cutting photosynthetic rates and mesophyll conductances were back to normal. This could be due to carbohydrate transport to new sinks (*eg* the root system), thus decreasing accumulated carbohydrates in the source needles. However, no attempt was made to follow the carbohydrate flow or carbohydrate content in different organs of the trees.

Removing most current shoots decreased the transpiring needle area considerably and improved the water balance of the experimental trees as shown by needle water potential measurements carried out 2 d after cutting. Midday values of needle water potential of 1-yr-old needles were then ≈ 0.2–0.3 MPa lower for the control tree than for the experimental trees. Unfortunately, measurements were carried out only once before shoot-pruning, the results being similar for all trees. This observation is supported by the transpiration data which did not indicate any differences in stomatal conductance between the trees either before or after pruning. Also, it is known from the same stand that transpiration and stomatal conductance between individuals vary more than photosynthesis (Troeng and Linder, 1982). Thus the most likely conclusion is that the marked decrease in net photosynthesis of the experimental trees just after cutting was not caused by water stress, but merely by the shoot pruning treatment. Similar results have been obtained for defoliated trees in the same stand (Ericsson *et al*, 1980b).

After partial defoliation, remaining leaves or needles may increase their photosynthesis (Maggs, 1965; Sweet and Wareing, 1966). Heichel and Turner (1983) found that regrowth foliage of defoliated maples displayed increased photosynthesis capacity. On the other hand, King *et al* (1967) has suggested that photosynthesis of a specific wheat leaf can be regulated by the demand for assimilates from that leaf. In such a case a low demand due to loss of a strong sink would decrease photosynthesis.

Our results support the latter view. Also, the results of a previous study in the same stand support the same hypothesis (Troeng *et al*, 1979), where net photosynthesis of 1-yr-old needles decreased simultaneously with the photosynthetic collapse of the beetle-attacked current shoot. The observed decrease in photosynthesis was, however, transient and may well have been compensated for by a possible later increase in net photosynthesis due to an increase in needle nitrogen of remaining needles. The fertilizing effect of shoot-pruning (*ie,* a clear and lasting increase in needle nitrogen) has been documented in the same stand (Ericsson *et al*, 1985;

Langström et al, 1990), as has the relationship between needle nitrogen concentration and photosynthetic performance (Linder and Ingestad, 1977). Since no increase of net photosynthesis was observed in the cut branches towards the end of the study period we postulate that the possible compensatory photosynthetic effect develops more slowly than the increase in needle nitrogen (cf Langström et al, 1990). This is in contrast to defoliation experiments where remaining needles reacted with an increased uptake of ^{14}C within a week after needle removal (Ericsson et al, 1980b). Hence, the different photosynthetic reaction to defoliation as compared to shoot pruning may be caused by other reasons.

In conclusion, we found a drastic but transient decrease in photosynthetic performance and a minor improvement in water status of the shoot-pruned trees. No evidence of increased compensatory photosynthesis due to improved nitrogen, water or radiation status was found during the months following shoot pruning. Such a development may well have occurred during the next growing season, but studies did not cover that period.

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