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SEASONAL CHANGES IN PHOTOSYNTHETIC PARAMETERS OF

PICEA ABIES (L.) KARST.

Abstract. Internal conductance to carbon dioxide diffusion (g_m) at saturating light intensity and the initial slope of the curve of photosynthesis light response were studied in a young and an old open-grown Norway spruce (*Picea abies* (L.) Karst.). In the young tree, internal (mesophyll) conductance recovered after winter depression a month earlier than in the old one. In both trees, g_m started to decline in October. The initial slope of the photosynthesis light curve increased steadily from spring to autumn and then decreased abruptly. Seasonal variation in photosynthetic performance, expressed on the needle area and on the needle dry-weight basis, differed due to rapid changes in the needle specific area during the intensive growth of new shoots.

Key words: Photosynthesis, *Picea abies*, light response curve, seasonal changes.

Introduction

Evergreen conifers display a remarkable seasonal variation of photosynthesis (Pisek and Winkler, 1958; Fuchs et al., 1977; Troeng and Linder, 1982; Teskey et al., 1984). The reasons for this seasonal change in photosynthesis may generally be divided into two groups. First, the variation of external climatic conditions to the extent that does not result in structural alterations of the photosynthetic apparatus. These responses are relatively quick and have no residual effects. Second, the prolonged influence of unfavourable conditions, which causes long-term structural changes in the photosynthesizing system.

In a cold winter, the photosynthetic apparatus of conifers undergoes big structural changes both at biochemical and cell levels (Koch, 1976; Senser and Beck, 1977; 1979; Öquist, 1986). These changes cause pronounced depression of photosynthetic capability and stomatal activity (Neilson et al., 1972; Kaufmann, 1976). The recovery from winter depression may take several months (Leverenz and Öquist, 1987; Lundmark et al., 1988). Unfavourable weather conditions, e. g. frozen soil (Turner and Jarvis, 1975; Troeng and Linder, 1982), low nighttime temperature, combined with high daytime radiation, may influence the recovery rate and daily photosynthetic efficiency.

In summer and early autumn, photosynthesis is mostly limited by external factors. Although the daily photosynthetic production may change by more than an order (e. g. Troeng and Linder, 1982), it is possible to model these changes using microclimatic data as driving variables (Lohammar et al., 1980; Korpilahti, 1988). However, when combined with high daytime radiation, night frosts may bring about an essential internal depression of photosynthesis (Lundmark and Häll-

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gren, 1987). In autumn photosynthesis starts to decline due to the decreased photosynthetic photon flux density and low temperature (Troeng and Linder, 1982). Seasonal changes in the photosynthesis of conifers have frequently been studied in field conditions. In these conditions, it is not easy to define to what extent photosynthesis is limited by external versus internal factors. Teskey et al. (1984) studied photosynthesis and respiration of detached *Abies amabilis* shoots in a controlled environment. They revealed the temperature dependences and foliage-age-related changes in photosynthesis. So far little is known about the seasonal variation of the parameters of the photosynthesis light curve in conifers.

The aim of the present study was to investigate the seasonal changes of photosynthetic parameters in Norway spruce in order to assess the role of internal limitation. In our previous study (Kull and Koppel, 1987), we found the differences in photosynthetic properties that were related to the size (or age) of the trees. Another objective of this study was to investigate seasonal differences of photosynthetic parameters of old and young trees.

Material and Methods

Plant material. The measurements were carried out from December 1984 through November 1985 at Vooremaa Ecology Station, Estonia. A detailed climatological and phytographic description of the site has been given by Frey (1977). Two open-grown trees were investigated. The first was 66 years old and 22 m in height and the other was 9 years old and 2.5 m in height.

The sample shoots were excised mostly in the morning and their proximal ends were immediately recut under water. Before the measurements the shoots were stored for half a day in order to eliminate the possible influence of water deficit on stomatal conductance. In winter the shoots were stored for a day at 20 °C for the stomata to open. Despite this preconditioning, in February the stomata remained closed on the second day. At each measurement cycle two shoots flushed in 1984 were investigated per tree. The shoots were taken from the southwestern side of the crown, at a height of 2 m from the ground.

Experimental procedure. The measurements were made under controlled conditions in a system based on an "Infralyt-4" IRGA (Junkalor, Dessau, DDR). The conditions in the assimilation chamber were: air temperature — 20 °C; CO_2 concentration in the inflowing air — 350 $\mu l \cdot l^{-1}$; leaf-to-air water vapour pressure deficit — not exceeding 0.9 kPa; the incident radiation intensity — 1400 (saturating light), 80, and 0 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The equipment and measurement procedure have been described earlier in more detail by Kull and Koppel (1987).

To characterize the photosynthetic properties of the shoots the internal (mesophyll) conductance to CO_2 diffusion at saturating light intensity and the initial slope of the CO_2 uptake curve versus light intensity were calculated.

The internal conductance (g_m) was calculated according to Jarvis (1971) as the slope of the photosynthesis versus intercellular CO_2 concentration curve. The internal CO_2 concentration was calculated from the data on leaf conductance to water vapour and ambient CO_2 concentration. The ratio of CO_2 and water vapour diffusivities was taken 0.623. For CO_2 compensation concentration (Γ) the mean value from our previous research (Kull and Koppel, 1987), 43 $\mu l \cdot l^{-1}$, was assumed. In case of negative CO_2 exchange maximum, the internal conductance was not calculated.

The slope of CO_2 uptake light curve was calculated from dark respiration (at the sixth minute after darkening) and CO_2 uptake at an incident radiation intensity of 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At such a low radiation intensity the CO_2 uptake response to light is almost linear and the stomatal conductance has relatively little influence on the CO_2 uptake. In winter, when photosynthesis was saturated at the radiation intensity of 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$, the value of the initial slope was not calculated.

The needle surface area was calculated on the basis of the geometrical parameters of the needles from subsamples of 10 needles per shoot. Total needle surface area was used in the calculations. The needle dry weight was measured after drying at 80 °C for 48 hours.

Results

In winter mesophyll conductance became very low and in February the net gas exchange of the old tree was negative (Fig. 1). Stomatal conductance remained rather low (minimal values of 1—3 $mmol \cdot m^{-2} \cdot s^{-1}$) in winter, though the shoots were kept at 20 °C for 24 hours. In spring mesophyll conductance started to increase with increasing ambient temperature. In the young tree, the rise of g_m was much more rapid and its maximum was achieved about a month earlier than in the adult tree. A brief depression in g_m recovery was detected in April (in the younger tree) and in May (in the older one). After peaking in early summer, the mesophyll conductance decreased slowly. In October, after the first night frost mesophyll conductance decreased rapidly.

The initial slope of the curve of photosynthesis light response varied also during the season (Fig. 2). Unlike the mesophyll conductance, the initial slope tended to increase until the end of the growing season, when it dropped rapidly.
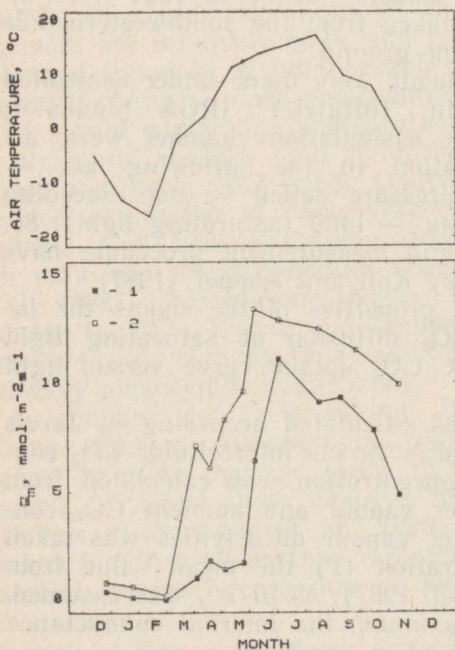

Fig. 1. Seasonal changes in the internal conductance to CO_2 diffusion in the old (1) and the young tree (2) and the average monthly air temperature, recorded at Tartu.
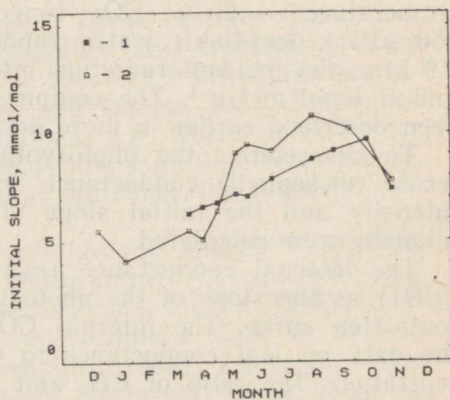

Fig. 2. Seasonal changes in the initial slope of the photosynthesis light curve in the old (1) and the young tree (2).
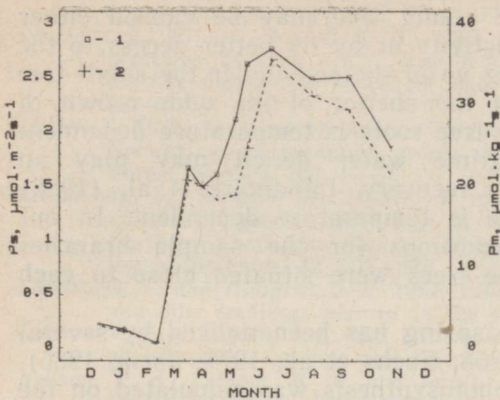
Fig. 3. Seasonal changes in the net photosynthesis rate, expressed on the basis of the needle total area (1) and of the needle dry weight (2).
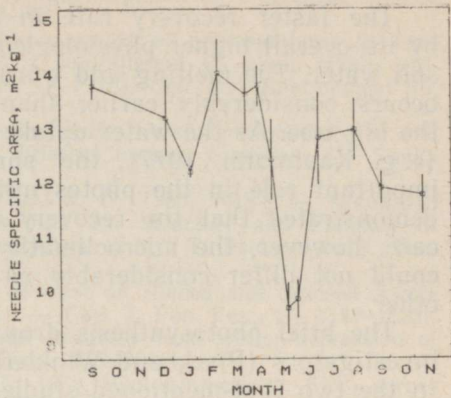
Fig. 4. Seasonal course of the needle specific area. Bars indicate standard errors of mean.

The character of seasonal changes in photosynthetic parameters depends to some extent on whether the calculations are made on the basis of the needle surface area or the needle dry weight (Fig. 3). The biggest differences between these parameters were in May and June. These differences are caused by seasonal changes in the needle specific area (Fig. 4). The changes in the needle specific area were especially rapid in early summer, during the budbreak and the growth of new shoots. In May the needle specific area fell rapidly by about 30%. But by the end of June, when the new shoots had completed their intensive growth, needle specific area of one-year-old shoots almost reached the previous value. Beside the rapid changes in May and June the needle specific area declined constantly with the needle's aging.

Discussion

Our results demonstrate that for the slow recovery rate of photosynthesis after winter depression both the slow rate of biochemical recovery of the photosynthesizing apparatus and the limitation by climatic conditions are important.

The first argument is proved by the fact that all the parameters, the maximum photosynthesis, mesophyll conductance, and the initial slope of the light curve of detached shoots increased almost steadily during the growth period. This may be caused by the slow recovery of the damaged photosynthetic structures. Our earlier field studies on Norway spruce demonstrated the same phenomenon — a gradual increase of maximum photosynthesis towards the end of summer (Кулл and Коппель, 1984). Troeng and Linder (1982) noticed, however, that in Scots pine it took about 12 weeks in spring to achieve the maximum photosynthesis rate.

The initial slope of the photosynthesis light response curve is closely related to the leaf chlorophyll content (Gabrielsen, 1948; Leverenz, 1987). The gradual increase of the initial slope in the progress of the season coincided with the similar trend of chlorophyll fluorescence in *Pinus sylvestris* (Lundmark et al., 1988). This phenomenon can to a great extent be attributed to the seasonal variation of photosynthetic pigments (Linder, 1972).

The faster recovery rate in the young tree may be caused either by its overall higher physiological activity or by its better access to the soil water. The melting and warming up of the soil under the small tree occurs considerably earlier than in the shelter of the wide crown of the big tree. As the water uptake by tree roots is temperature dependent (e. g. Kaufmann, 1977), the springtime water deficit may play an important role in the photosynthesis recovery. Lundmark et al. (1988) demonstrated that the recovery rate is temperature dependent. In our case, however, the microclimatic conditions for the sample branches could not differ considerably as the trees were situated close to each other.

The brief photosynthesis drop in spring has been noticed by several investigators (Pisek and Winkler, 1958; Fuchs et al., 1977; Jurik, 1986). In the two first-mentioned studies photosynthesis was calculated on the needle dry weight basis. Fuchs et al. (1977) explained this drop with the changes in the needle specific area. Our results demonstrate that this drop likewise exists, though to a smaller extent, if photosynthesis is calculated on the needle surface area basis.

Probably in May, prior to budbreak, reserve carbohydrates accumulate in the old needles. This results in the decrease of the specific leaf area. Ivask (Иваск, 1983) showed a similar decrease in the needle caloric content. Carbohydrates have lower energy content than the needles on the average. Cordon and Larson (1970) demonstrated that in *Pinus resinosa* the last-year shoots were the main exporters of assimilates to the growing shoots. The fact that photosynthesis and mesophyll conductance decrease in May even if these parameters are calculated on the basis of the needle surface area, may be explained as inhibition by the high concentration of assimilates (Azcón-Bieto, 1983) or by photoinhibition as a result of high daily solar radiation and low night temperatures (Lundmark and Hällgren, 1987).

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