Photosynthesis and Transpiration in Damaged and Undamaged Spruce Trees

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Dedicated to Professor Horst Senger on the occasion of his 65th birthday

CO_2/H_2O Gas Exchange, CO_2 Compensation Point, Photosynthesis, *Picea abies*, Transpiration, Water Potential, Forest Disease

The investigations presented here focus on the CO_2/H_2O gas exchange in damaged and undamaged spruce trees while using open-air measurements as well as measurements under defined conditions in the laboratory. The studies were performed at two different sites in the Hunsrück and the Westerwald mountains. In the laboratory the CO_2/H_2O gas exchange was measured on detached branches under controlled conditions in the course of two years. CO_2 saturation curves were also generated. In addition CO_2 compensation points were determined employing a closed system. In the natural habitat diurnal course measurements of photosynthesis and transpiration as well as light-saturation curves for photosynthesis were performed. In parallel with the photosynthesis and transpiration measurements, measurements of the water potential were taken at both locations.

The photosynthetic capacity and transpiration rate show a typical annual course with pronounced maxima in spring and late summer and minima in summer and winter. The needles of the damaged trees exhibit higher transpiration rates and a distinct reduction in photosynthesis than the needles of the undamaged trees during two seasons. The diurnal course measurements of net photosynthesis and transpiration show a maximum in photosynthesis and transpiration in the afternoon in May and September, but a characteristic midday depression in July. Photosynthesis was markedly lower and transpiration higher in the needles of the damaged trees. The damaged trees show a lower increase in the light and CO_2 saturation curves and higher CO_2 compensation points as compared to the undamaged trees. The water potential reaches much lower values during the course of the day in needles of the damaged trees.

The reduction of the photosynthetic rate on one hand and the increase in transpiration on the other hand result in an extreme lowering of the water use efficiency in photosynthesis. The damage to the thylakoid membranes and to the guard cells obviously results in a profound disturbance of the physiological homeostasis of the needles and could thus lead to premature needle loss.

Introduction

The damage to coniferous and broadleaved deciduous trees in the forests of Central Europe has been monitored since the late seventies. The extent of damage was predominantly assessed by the loss of needles or leaves. Additionally, the yellowing of needles and leaves has been taken into consideration (Waldzustandsbericht der Bundesregierung 1984–1995). Today, it is widely accepted that this "novel forest decline" is of multifactorial origin, i.e. a multitude of biotic and abiotic factors operating together in various ways at different sites. Atmospheric pollutants play an important part. Here, sulphur dioxide, nitrogen oxides, ozone, and ammonia are the main culprits, effecting organisms in two ways: firstly, by direct impact of pollutants on the plant metabolism, secondly, in an indirect way, by soil acidification due to acid deposition with effects on nutrient availability and root function. The variety of stress factors as well as the variety of interplays of the factors, all changing from place to place, are the reason for the wide range of symptoms and for the irregular progression of the damage that we observe.

In the subalpine mountain ranges of Central Europe, yellowing of the needles – in the light-exposed upper parts of the older needles – is a frequent symptom of spruce tree damage (Siefermann-Harms 1990, 1992). It occurs in particular in regions where the trees' supply with magnesium is sub optimal and where high levels of ozone pollu-

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tion are is present. In these needles we find that a reduced photosynthetic apparatus is affecting the energy supply to the trees. In addition to the reduced chlorophyll content, a drastic reduction in the electron transport rate and in the redox components of the thylakoid membranes can be observed. These phenomena are due to damage and indicate a degeneration of the photosynthetic membranes (Wild *et al.,* 1993).

Fumigation of coniferous trees with air pollutants led in many controlled chamber experiments to impairment of photosynthesis (Skeffington and Roberts, 1985; Guderian 1987, 1993; Keller and Häsler, 1988; Schweizer and Arndt, 1990; Führer *et al.,* 1993; Rebbeck *et al.,* 1993; Willenbrink and Schatten, 1993). In addition, it was discovered that pollutants impair the ability of stomata to control gas exchange in needles (Keller and Häsler, 1984; Selinger *et al.,* 1986; Koch and Maier-Maercker, 1992).

In the natural habitat, the situation for obtaining comparable measurements is more complex. The variables of light, humidity, and temperature have immediate effects on photosynthesis and transpiration. Furthermore, changes in photosynthetic activity over the course of the year need also to be taken into account.

The investigations presented here focus on the CO_2/H_2O gas exchange in damaged and undamaged spruce trees while using open-air measurements as well as measurements under defined conditions in the laboratory. The studies were performed at two different sites in the Hunsrück (Hattgenstein site) and the Westerwald (Wallmerod site) mountains in Middle-West Germany.

At the Hattgenstein site the goal was to determine how much phenotypically observable damage, the aging of the leaves, and the progression through the seasons would influence photosynthesis and transpiration in relatively healthy looking trees and in damaged trees. At the Wallmerod site, a stand of all healthy spruce trees, comparative measurements performed on only healthy trees addressed the question of how much of the possible variations in gas exchange were explainable by natural fluctuations that might be explained in particular by genetic differences or differences in the delimited immediate habitats of individual trees.

Since a multitude of environmental factors can influence CO_2/H_2O gas exchange, all measurements were performed on paired individuals. This way it was possible to determine the gas exchange in a damaged and a relatively healthy tree growing side by side in Hattgenstein or in healthy pairs in Wallmerod alternating with 15 minute intervals under identical environmental conditions.

A CO_2/H_2O porometer made it possible to follow the daily course of CO_2 assimilation and H_2O transpiration as well as to obtain light-saturation curves for photosynthesis in the open field. In the laboratory the CO_2/H_2O gas exchange was measured on detached branches under the controlled conditions of 150 W/m^2 and 1200 ppm CO_2 utilizing an ultra-red gas analyzer and a water vapor sensor. CO_2 saturation curves were also generated. In addition, CO_2-compensation points were determined employing a "closed system".

The water potential was measured in the field with the help of a portable Scholander pressure chamber.

Materials and Methods

Description of the locations

The studies were carried out on spruce trees (*Picea abies* (L.) Karst) in two open air habitats in the Hunsrück and the Westerwald mountains over the course of three years. The damage classes at the respective trees were assessed according to the criteria of the forest damage report (Waldzustandsbericht der Bundesregierung 1984–1995).

Wallmerod site

This site in the Hoher Westerwald (Wallmerod Forestry Office, Höhn Forest District, Division 1C) is located on a plateau about 495 m above see level. The soil was well supplied with nutrients and showed only weak acidification (pH 4.3 - 4.5) in the upper layer.

The four 15 - 18 year old trees studied were apparently healthy (damage class 0) and served as an undamaged reference for the trees at the Hattgenstein site.

Hattgenstein site

This spruce tree plantation is situated in the western part of the Hunsrück mountains at approximately 660 m above sealevel (Idar-Oberstein Forestry Office, Hattgenstein Forest District, Division 257 b^2). It is characterized by its podsolated highly acidic brown earth (pH 2.7 - 3.8) with low cation-exchange capacity and a low nutrient supply. Concentrations of ozone were between 90 - 110 µg/m^3 during the summer months (monthly average).

Climatic and immission data were registered by the monitoring station of ZIMEN (Central Network for the Measurement of Immissions in Rhineland-Palatinate, 1985–1995).

Apparently healthy trees (damage class 0–1) were standing in close proximity to damaged trees (damage class 1–2). The damage symptoms comprised loss and yellowing of the needles mainly on the light-exposed parts of needles. Older needles were generally more affected than younger ones.

More detailed descriptions of the sites can be found in Wild *et al.* (1993), Richter and Wild (1994), and Schmieden and Wild (1995).

Materials

Studies were performed on spruce needles of the first to the fifth needle age class from the seventh whorl. In Hattgenstein three pairs of spruce trees were selected. Each pair consisted of one tree that was apparently healthy (damage class 0–1) and one that was clearly damaged (damage class 1–2) standing in close proximity to each other. To equalize conditions for the comparison of these trees to the Wallmerod trees, the four apparently undamaged trees (damage class 0) studied at the Wallmerod site were also treated in pairs.

Methods

Gas exchange measurements

Photosynthesis (CO_2 assimilation) and transpiration rates as well as light saturation curves were registered with a CO_2/H_2O porometer (Walz, Effeltrich). These studies were carried out in the natural habitat directly on the trees. At the same time the photosynthetically active radiation (PAR) was measured with a quantum sensor fixed on the porometer probe (LI-COR, Lincoln, Nebraska). The light-saturation curves were obtained under standardized conditions applying light intensities of 0 - 1500 $\mu E{*}m^{-2}{*}s^{-1}$ (a slide projector with gray filters of various transmissions; Schott, Mainz) at a temperature of 20 °C.

In the laboratory CO_2-saturation curves and CO_2 compensation points were measured on detached twigs with the help of an ultra-red gas analyzer (URAS 2T, Hartmann & Braun, Frankfurt a. M.). To avoid emboli, these twigs had been cut under water and were kept in water at 20 °C throughout the experiments. The measurement of the CO_2-compensation points was performed in a closed system. The CO_2-saturation curves were obtained under conditions of 150 $W{*}m^{-2}$ and with CO_2 concentrations ranging from 0 to 1500 ppm. Furthermore, in the course of two years, the capacity of photosynthesis and transpiration was also investigated in the laboratory with cut-off twigs under constant conditions of CO_2 (1200 ppm) and light (150 W/m^2).

The technical details of the procedures in the field and in the laboratory have been described in previous publications (Benner and Wild, 1987; Benner *et al.,* 1988).

Water potential

The total water potential (Ψ) was measured with a self-made portable pressure chamber (Scholander *et al.,* 1965) according to Rosenkranz *et al.* (1989).

Leaf area

The total leaf area was determined with a computerized planimetry device (Videoplan, Kontron). The average needle length and needle perimeter were used to calculate the total needle area of the sample.

Results

The annual course of photosynthetic capacity and transpiration rate

Figures 1 and 2 show the pattern of the CO_2 assimilation capacity and of transpiration over the course of the year for needles from an undamaged and a damaged tree at the Hattgenstein site. Data from the Wallmerod site are not shown. Over the course of two years the capacity of photosynthesis and transpiration rate were investigated in the laboratory with cut-off twigs under conditions of CO_2 and light saturation. Five needle generations were

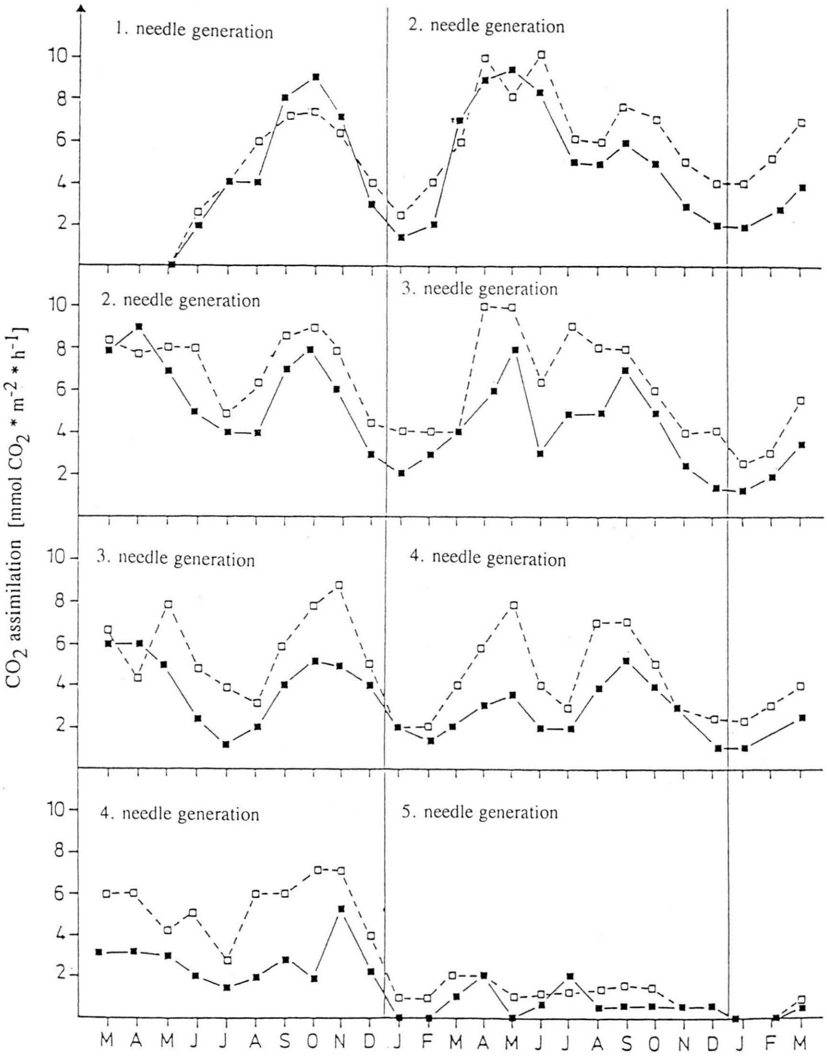

Fig. 1. CO_2 assimilation capacity over the course of two years for needles of five needle generations from an undamaged and a damaged spruce tree at the Hattgenstein site. The measurements were carried out two times; the deviations were < 10%; □, Undamaged tree; ■, damaged tree.

examined from both sites. A typical annual course with pronounced maxima in spring and late summer and minima in summer and winter was observed for the undamaged as well as for the damaged spruce trees.

When comparing damaged and undamaged spruce trees at the Hattgenstein site with regard to the CO_2 assimilation rates, needles of damaged trees exhibited a distinct reduction in net photosynthesis (with the exeption of the first needle generation). With increasing needle age the annual average as well as the maxima of the CO_2 assimilation rate decreased in both, the damaged and the undamaged tree; but the discrepancy between the absolute values for the undamaged and the damaged spruce tree also increased with the age of the needles.

When comparing the transpiration rates of needles of the undamaged tree with needles of the damaged tree, the latter showed – beginning with

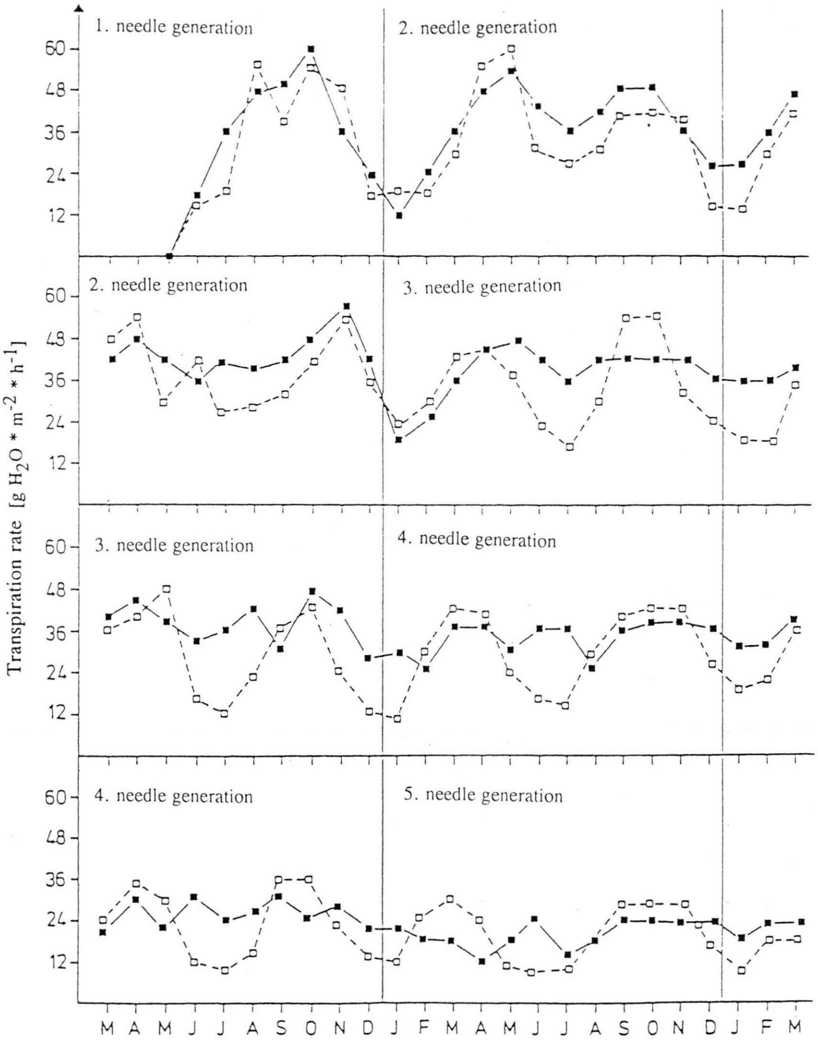

Fig. 2. Transpiration rate over the course of two years for needles of five needle generations from an undamaged and a damaged tree at the Hattgenstein site. The measurements were carried out two times; the deviations were < 10%; □, Undamaged tree; ■, damaged tree.

the third needle generation – a far less distinct fluctuation over the course of the year with no or only small reductions in summer and winter. In other words, the needles of the damaged tree exhibited higher transpiration rates than the needles of the undamaged tree during those two seasons.

Among the healthy trees at the Wallmerod site there were no differences in the yearly patterns of CO_2 assimilation and transpiration rates between individual trees (data not shown). When the undamaged trees at the Hattgenstein site were compared to the undamaged trees at the Wallmerod site, they followed a similar yearly course with regard to photosynthetic capacity and transpiration.

Diurnal course measurements of photosynthesis and transpiration

The results from one pair of spruce trees from the Hattgenstein and the Wallmerod sites each are shown in figures 3 and 4. They are representative for all our measurements of diurnal changes in net

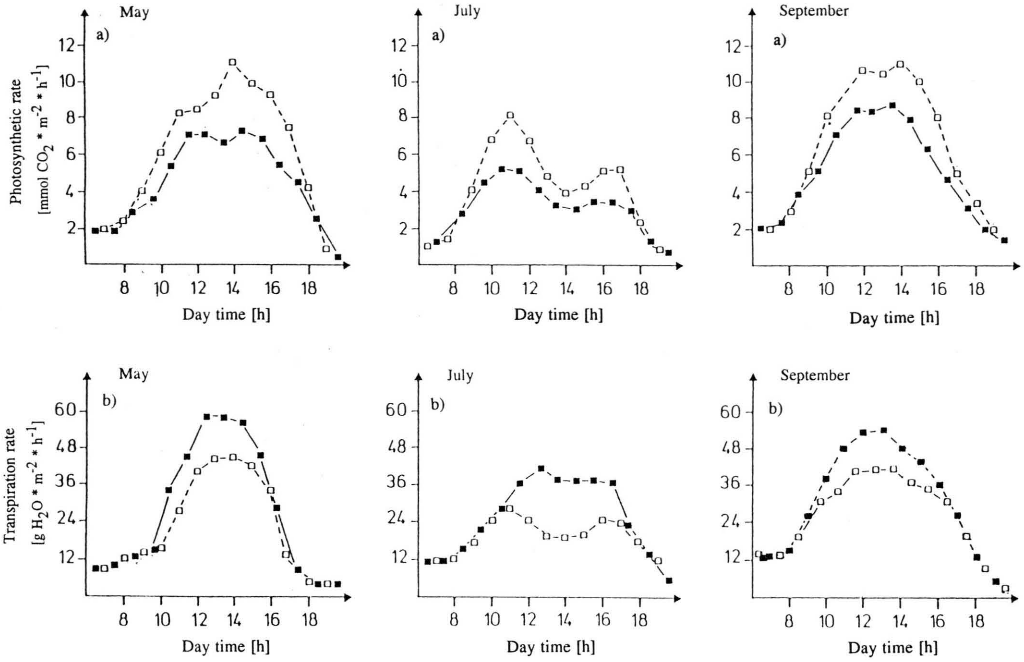

Fig. 3 a/b. Diurnal course measurements of photosynthesis (a) and transpiration (b) from one pair of spruce trees (biannual needles) at the Hattgenstein site in May, July and September. The measurements were performed in two following years and showed the same results; □, Undamaged tree; ■, damaged tree.

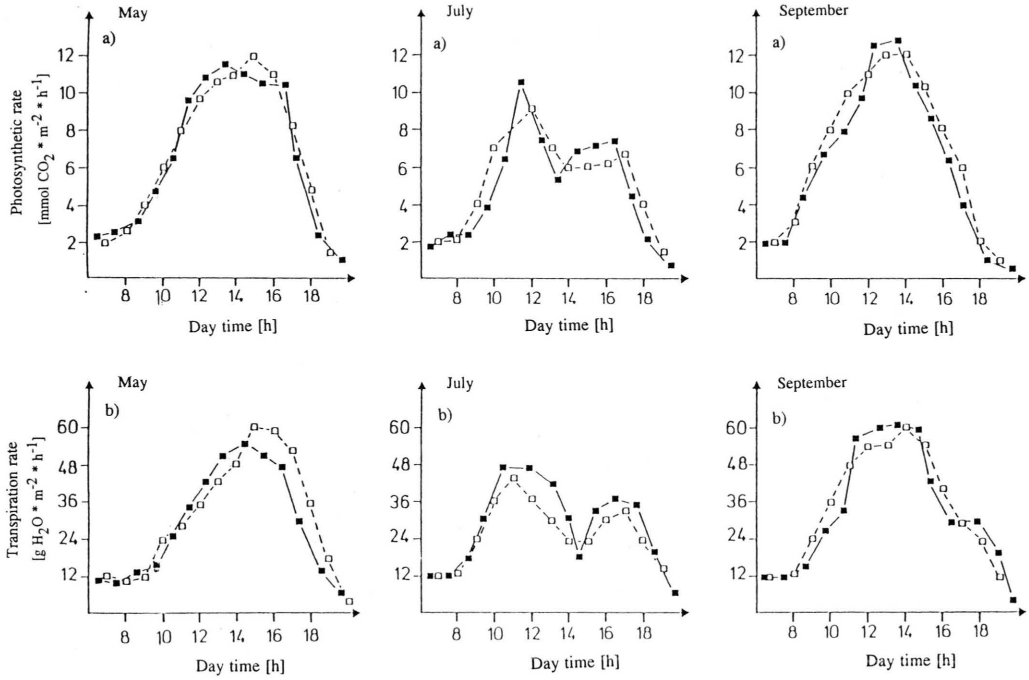

Fig. 4 a/b. Diurnal course measurements of photosynthesis (a) and transpiration (b) from one pair of spruce trees (biannual needles) at the Wallmerod site in May, July and September. The measurements were performed in two following years and showed the same results; (□, ■, undamaged tree).

photosynthesis and transpiration. The measurements were carried out in May, July, and September over two years with 6 trees at the Hattgenstein site and 4 trees at the Wallmerod site. At both sites the conditions in terms of temperature and light intensity were similar on all experimental dates.

In May and September the spruce trees at both sites showed a maximum in photosynthesis and transpiration in the afternoon, in parallel to the diurnal course of the photosynthetic active radiation (data not shown). In July, however, when temperature, light intensity, and ozone concentration reached their highest level, all trees showed a lower photosynthetic rate and a clear midday depression of photosynthesis and transpiration.

At the Hattgenstein site net photosynthesis was distinctly lower in needles of damaged spruce trees than in needles of undamaged trees (Fig. 3a). In contrast, transpiration was distinctly higher in the needles of the damaged trees (Fig. 3b). The midday depression in net photosynthesis and transpiration, occurring in July, appeared more clearly in the undamaged spruce trees than in the damaged trees.

The four apparently healthy spruce trees examined at the Wallmerod site exhibited similar net photosynthesis and transpiration rates on all three experimental dates (Fig. 4 a,b).

Light and CO_2 saturation curves

In figures 5 and 6 the dependence of photosynthesis on light and CO_2 concentrations is shown in a representative manner. While the light saturation curves were investigated directly on twigs of the trees in the open air on site, the CO_2 saturation curves were obtained from cut-off twigs in the laboratory. The results show a lower increase in the light and CO_2 saturation curves and essentially smaller light and CO_2 saturation values for the damaged trees as compared to the undamaged trees. Thus, the damaged trees have lower photosynthetic rates during CO_2 and light saturation, a decreased carboxylation efficiency, and reduced apparent photorespiration.

No differences were apparent between the four healthy spruce trees at the Wallmerod site (data not shown). All had light and CO_2 saturation curves that were similar to the undamaged spruce trees at the Hattgenstein site.

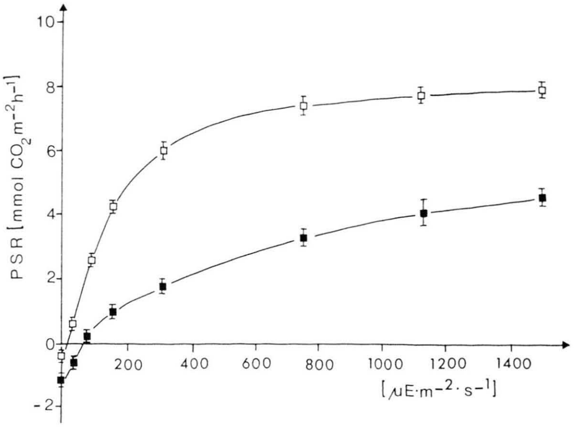

Fig. 5. Light saturation curves, investigated directly on twigs of the trees in the open air at the Hattgenstein site. The measurements were repeated three times; ☐, Undamaged tree; ■, damaged tree; PSR, photosynthetic rate.

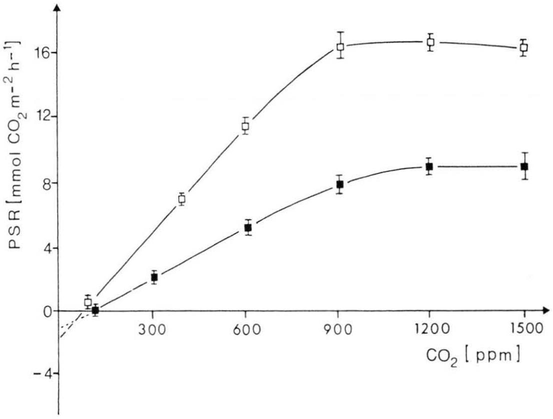

Fig. 6. CO_2 saturation curves, obtained from cut-off twigs in the laboratory, Hattgenstein site. The measurements were repeated three times; ☐, Undamaged tree; ■, damaged tree; PSR, photosynthetic rate.

CO_2 compensation point

Figure 7 presents the CO_2 compensation points of the spruce trees at the Wallmerod and the Hattgenstein sites. The investigations were carried out on four different needle generations. While the undamaged trees at the Wallmerod site exhibit the lowest compensation points, the damaged trees at the Hattgenstein site have the highest compensation points. With increasing needle age the differences between the undamaged spruce trees at the

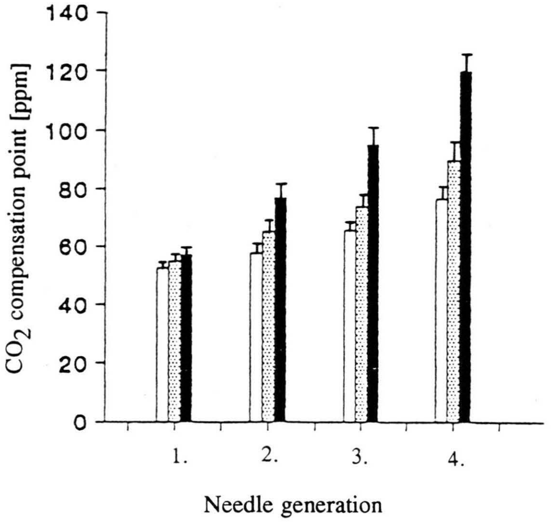

Fig. 7. CO_2 compensation points of the trees at the Wallmerod and the Hattgenstein site for four different needle generations. The measurements were repeated three times; □, Undamaged Wa; ▨, undamaged Ha; ■, damaged Ha.

Wallmerod site and the damaged trees at the Hattgenstein site become even more pronounced.

Water potential

In parallel with the photosynthesis and transpiration measurements, measurements of the water potential were taken during the course of the day at both locations. As can be seen in figure 8, a definite daily circle is evident and obviously driven by the extend of the transpiration. At the Hattgenstein site the water potential reaches much lower values during the course of the day in needles of the damaged trees while it matches the values of the undamaged trees in the morning and in the evening (Fig. 8).

No significant differences were evident between individual healthy trees at the Wallmerod side (data not shown).

Discussion

With the help of year-round measurements it was possible to uncover a pronounced yearly rhythm in photosynthetic performance and transpiration in spruce. Surprisingly, a rather strong depression was found during the summer months. In healthy trees, this depression occurs in 2–5 year old needles in photosynthesis as well as in transpiration. In 3–5 year old needles of damaged trees, though, the reduction occurs only in photosynthesis, while the transpiration rate stays high. The summer depression in the two processes is mirrored in the daily course of measurements during July. The finding that photosynthesis is reduced in needles of damaged trees, while transpiration remains unusually high, points to an independent rhythm for photosynthesis. The summer depression also doesn't seem to be directly dependent on environmental conditions, since it also appears in the laboratory where the measurements are performed in a constant environment.

The comparative measurements of photosynthesis done on damaged and undamaged trees at the Hattgenstein location show clearly that the photosynthetic yield declines progressively in needles

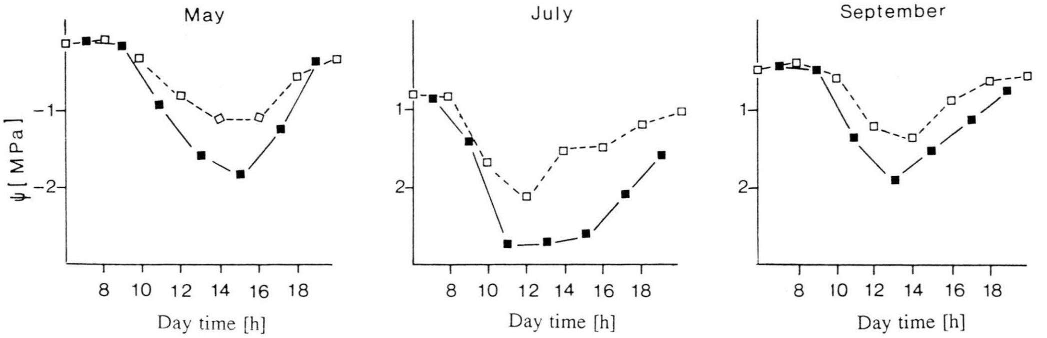

Fig. 8. Water potential measurements during the course of the day at the Hattgenstein site. The measurements were performed in two following years and showed the same results; □, Undamaged tree; ■, damaged tree; ψ, water potential; MPa, Mega-Pascal.

from damaged trees starting with the second year needles. This trend towards diminished photosynthetic performance had been already realized in earlier measurements (Benner and Wild, 1987; Benner *et al.*, 1988). The reduction of CO_2 assimilation cannot be explained by a clogging or closing of the stomata, since the needles of damaged trees exhibit significantly higher transpiration. The loss of photosynthetic capacity is rather caused by the damage to and loss of thylakoid membranes. A premature damage and reduction of thylakoids has been demonstrated by electron microscopy (Jung and Wild, 1988; Forschner *et al.*, 1989) as well as by measurements of the redox components in the photosynthetic electron transport chain (Wild *et al.*, 1993) and of the electron transport capacity (Dietz *et al.*, 1988).

The measurements of transpiration over the length of a day show much higher water loss by needles of damaged trees. Correspondingly, the water potential, which serves as a measure of water saturation of the system, becomes increasingly more negative in damaged trees during the midday. In addition, the measurements over the course of a year reveal that in damaged trees – in contrast to undamaged trees – the older needles do not show a reduction in transpiration during the summer and winter months. The high water loss by the needles leads to a deterioration of the water status in the trees, as we have demonstrated in comprehensive studies of the water economy (Rosenkranz *et al.*, 1989). During a dry spell in the weather the high water loss can develop into extreme water stress and finally lead to a premature dropping of the needles.

The underlying cause for the increased transpiration by the needles of damaged trees probably lies anywhere from disturbed regulation of the stomata to serious cell structure damage to the death of the guard cells as attested to by electron microscopy (Schmitt, 1991).

The reduction of the photosynthetic rate on one hand and the increase in transpiration on the other hand result in an extreme lowering of the water use efficiency in photosynthesis (mg assimilated CO_2/g transpirated H_2O). Koch and Maier-Maerker (1992) demonstrated that branches of spruce trees growing in polluted ambient air exhibit a lower water use efficiency on days with high light-intensities as compared to branches growing in filtered air. It was shown that the midday transpiration was not reduced under ambient conditions. Independently, Schweizer and Arndt (1992) reported that the water use efficiency of 22-year-old spruce trees in an open-top chamber experiment was significantly reduced in trees exposed to ambient conditions. Both locations were characterized by high ozone concentrations. Maier-Maercker and Koch (1991) succeeded in showing that this kind of impairment of stomatal regulation occurs after ozone fumigation. Keller and Häsler (1987) also found increased transpiration rates of some spruce tree clones after an exposure to 50–150 ppb ozone for several months under saturating light conditions.

Control over this relationship between assimilated CO_2 and transpirated H_2O is of utmost importance for a tree's survival at its location. The damage to the thylakoid membranes and to the guard cells obviously results in a profound disturbance of the physiologic homeostasis. The drastic reduction in water use efficiency can therefore be taken as an indicator of the deterioration of a tree's ability to survive. Temporary water deficits due to a loss of stomatal regulation could be an important triggering factor for the disturbance of hormonal balance and therefore for premature needle loss.

Gruber (1987, 1991) showed that the abscission of needles is primarily regulated by the endogenous water status. According to him, older needles are not at all or often incompletely connected to the secondary xylem and are therefore threatened by poor water supply. A blockage in the transport system, or an interruption of the transport ways in the cambial zone and the zone of xylogenesis, can also be responsible for a poor water supply to the needles. These processes are mostly regulated endogenously by plant growth substances.

By comparing undamaged and damaged trees, a decrease in free endogenous IAA could be observed following damage (Wessler and Wild, 1992). According to Dörffling (1982), auxin produced in leaves delays abscission. IAA is involved in the regulation of cambial activity and xylem development (Little and Savidge, 1987; Sundberg and Little, 1987). Therefore, the decreased IAA concentrations in the case of damage, as outlined in the studies of Wessler and Wild (1992), could be responsible for the incomplete connection of the needles to the secondary xylem or for a blockage in the transport system. A decrease in IAA concentration following damage could thus indirectly lead to premature needle loss.

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