Establishment and Tending of Subalpine Forest: Research and Management.
H. Turner and W. Tranquillini, eds.
Proc. 3rd IUFRO Workshop P 1.07-00, 1984. Eidg. Anst. forstl. Versuchswes., Ber. 270 (1985): 113-122.

CO_2 UPTAKE IN EUROPEAN LARCH (*LARIX DECIDUA* MILL.) NEAR TREELINE IN SWITZERLAND (STILLBERG/DAVOS)

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ABSTRACT

Gas exchange in young European larches (*Larix decidua* Mill.) on the north- and east-facing slopes of an avalanche gully (2185 m a.s.l.) was measured with climatised gas exchange cuvettes during the summer of 1983. Air and soil temperatures, photon flux density, and leaf-air water vapour pressure differences were recorded concurrently.

The differences in maximum net photosynthesis rates on the two sites were surprisingly great. In the tree on the less favourable N-facing slope, CO_2 assimilation reached at the most only two thirds of that in the tree on the E-facing slope. An even greater difference was apparent in the net balance of CO_2 uptake: average CO_2 uptake during the measuring period was 57.2 mmol CO_2 m^{-2} d^{-1} in the tree on the E-slope but only 28.3 mmol CO_2 m^{-2} d^{-1}, or about half as great, in the tree on the N-slope.

Of the main factors affecting CO_2 uptake, soil temperature seems to be particularly important. Net balance of CO_2 uptake was also greatly affected by the length of the production period, which was 20% longer on the E-slope, and by slow recovery of net photosynthesis in the N-slope larch after a marked temperature drop at the beginning of August. Presumably also differences in soil (nutrient supply) contribute to the observed great photosynthetic differences. A considerable influence on CO_2 uptake is ascribed to the differing physiological states of the trees on the two contrasting habitats.

INTRODUCTION

High altitude afforestation often involves great difficulties. Apart from the many dangers threatening the young trees (snow blight fungi, browsing by game, snow pressure, avalanches etc.), growth rates even on favourable sites at the alpine timberline are very low (Schönenberger, 1975; Turner and Schönenberger, 1981). Various hypotheses and explanations of this have been put forward; Tranquillini (1979) gives a comprehensive survey.

Site exposure and microclimate exert a decisive influence on the growth and survival of young trees at the alpine timberline. While trees grow relatively well on a sunny, east-facing slope, they struggle to survive on a shady, north-facing slope at the same altitude (Schönenberger, 1975). Measurement of gas exchange with climatised cuvettes at the natural growth site has proved a particularly suitable means of studying the relationships between the rapidly changing weather conditions and the plant responses. This method allows the detection of differences in net rates of photosynthesis in young trees after only a few months' growth (Häsler, 1982).

As part of the experimental programme on the ecology of afforestation being conducted at the Stillberg research area near Davos, gas exchange in young conifers growing on different sites has been measured over several vegetation periods in order to study the relationships between growth and microclimate and to determine the main limiting factors.

MATERIALS AND METHODS

The present study was conducted in summer 1983 (26th June - 5th October) on the north- and east-facing flanks of an avalanche gully (horizontal distance between the slopes about 45 m; 2185 m a.s.l.) in the Stillberg research area near Davos, Switzerland. Horak (1963) and Schönenberger (1975) described the area in detail. As a result of the differing microclimates, different soils and plant communities have developed on the paragneiss parent rock. On the east-facing slope, which has a yearly net radiation surplus of 308 kWh m^{-2} and is 3-4°C warmer in the root zones during the growing season (Turner *et al.*, 1982), a slightly podzolic soil has developed under *Junipero-Arctostaphyletum*, while on the north-facing slope there is an iron humus podzol covered by *Empetro-Vaccinietum* (Kuoch, 1970; Blaser, 1980). The measurements were conducted on European larches (*Larix decidua* Mill.) provenance Sils Maria (2050 m a.s.l.), raised from seed in the SFIFR nursery in Birmensdorf and transplanted as 1-year-old seedlings to the study area in 1975. In 1983 the larches had grown up to a height of approximately 60 cm (E-slope) and 25 cm (N-slope).

Gas exchange was simultaneously measured on both sites with two climatised gas exchange cuvettes (Walz, FRG). The method used is described in detail by Koch *et al.* (1971), Schulze *et al.* (1972) and Häsler (1982), with the difference that here the cuvettes were fitted with curved heads to preclude shading of the

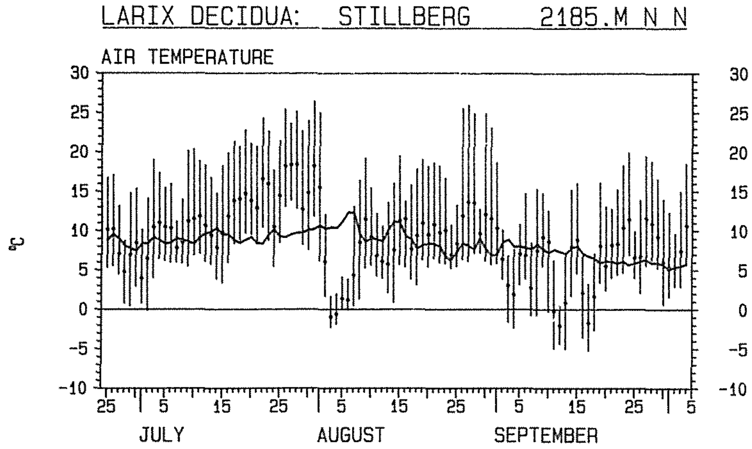

Figure 1. Daily mean values of air temperature measured between 1971 and 1980 at Stillberg meteorological station, NE aspect, 2090 m a.s.l. (——). Measurement H. Turner. Daily mean and extreme values of air temperature on the E-facing slope during the period of CO_2 gas exchange measurements in 1983 (ǂ).

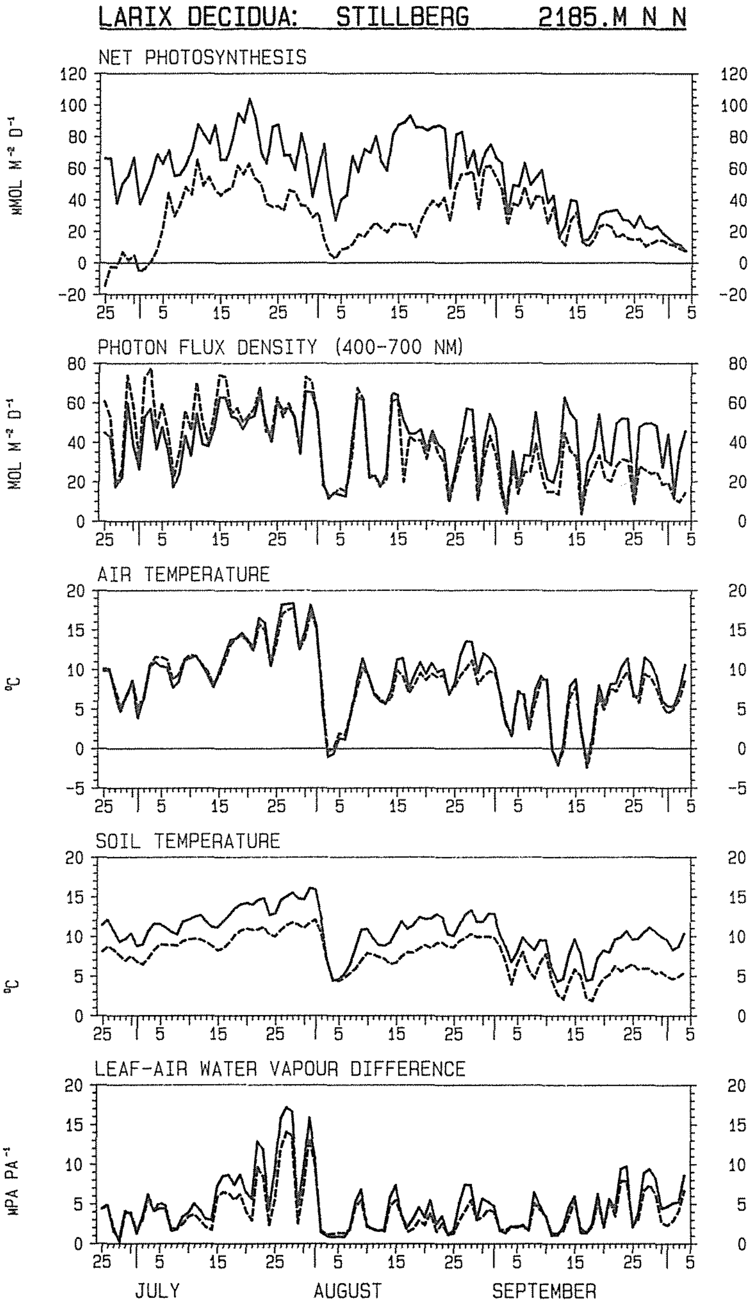

Figure 2. Part of the annual course (1983) of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

plants by the chamber edges. Temperature was measured with platinum resistance thermometers, and air humidity with dew point mirrors. Photon flux density (400-700 nm) was determined with LI-COR quantum sensors with spherical heads. Wind speed in the chambers was kept at c . 1 m s^{-1}, the average for the two sites (Nägeli, 1971). Matric soil water potential was measured using tensiometers with electronic registration (after F. Richard, unpublished). Soil temperatures were taken at a depth of 10 cm. A Solartron Datalogger (Schlumberger) recorded all values on magnetic tape every 3 minutes; Central European Time (CET) was used. The water potential of the twigs was determined by the pressure chamber method of Scholander *et al.* (1965).

RESULTS

To facilitate interpretation of the gas exchange results, the mean daily temperatures measured at the Stillberg meteorological station between 1971 and 1980 are shown in Figure 1, together with the daily mean and extreme values recorded on the sunny E-facing slope during the measuring period in 1983. There are considerable deviations from the 10-year mean. On the E-facing slope, minimum temperatures during the extremely warm month of July exceeded the 10-year mean by more than 5°C, but maximum temperatures fell to almost 10°C below it at the beginning of August. Three days after the highest temperature was recorded (26°C), the very warm period ended with a snowfall.

How did the plants respond to these extreme weather conditions? At the end of June, when measurements began, net photosynthesis in the larch on the E-facing slope had already reached a relatively high level, whereas the larch on the N-facing slope still had a negative CO_2 balance (Figure 2). On both sites, CO_2 uptake increased in the first half of July, but net photosynthesis was somewhat limited by the very warm conditions in the second half of the month. At 13.00 h on 29th July water potential in the tree on the E-facing slope rose to 2.5 MPa and matric soil water potential reached some 45 kPa, while on the N-facing slope the values were only 2.0 MPa and 30 kPa respectively. The marked fall in temperature at the beginning of August caused a considerable reduction of net photosynthesis on both sites. Recovery of net photosynthesis was relatively rapid in the tree on the sunny slope but took some 3 weeks in the tree on the shady slope. In September CO_2 uptake in the tree on the shady slope almost equalled that on the tree on the sunny slope, but the daily CO_2 balance was slowly beginning to fall on both sites. After two intervals with temperatures below zero in mid-September, some needles gradually began to turn yellow and the first needle fall occurred at the beginning of October. The greatest climatic differences between the two sites are exhibited by solar radiation and soil temperature; here it must be borne in mind that shading of the slopes by the horizon began at different times in the afternoon according to the time of year.

Daily sequences (Figures 3-7) provide additional information on the course of net photosynthesis and those climatic parameters considered. At the end of June, the tree on the N-facing slope just barely achieved positive values for net photosynthesis (Figure 3), even though that slope receives some 2 hours more afternoon sunlight at that time of year. The sun's rays, however, fall almost parallel to the slope and have little warming effect. At the end of June, the snow cover had only recently disappeared and the larch needles were still closely packed and only some 5 mm long. On the E-facing slope, on the other hand, the snow cover had long since disappeared, the tree's needles were almost fully developed, and net photosynthesis had already reached a high level. In mid-July net photosynthesis was still considerably higher in the tree on the E-facing slope (Figure 4). In consequence of the generally greater warming and the higher leaf-air water vapour difference, a certain degree of water stress had already developed on the sunny slope; during the extremely warm period towards the end of the month it increased and also became apparent in the tree on the N-facing slope. After the drop in temperature at the beginning of August, net photosynthesis in the tree on the E-facing slope rapidly returned to higher levels, whereas the tree on the N-facing slope had obviously been more severely affected and, in spite of the subsequent warmer weather, recovered only slowly (Figure 5). From September onwards photosynthetic rates on the two sites differed only slightly, although the rates on the E-facing slope remained higher than those on the N-facing slope (Figure 6). In addition, the N-facing slope was now shaded earlier in the day, a circumstance which lead to increasing differences in daily CO_2 uptake as autumn advanced. Photosynthesis on both sites was further limited by the yellowing of the needles and by needle fall, which started in early October (Figure 7).

To allow better comparison of weather conditions and plant responses on both sites, scatter diagrams were constructed of the simultaneously measured daily sums of net photosynthesis and photon flux density, together with mean daily values of photon flux density, air and soil temperatures, and leaf-air water vapour pressure differences (Figure 8). Net photosynthesis exhibits considerably greater deviation from the angle bisector than the other factors, although its scatter is also greater. It must further be borne in mind that the daily means of weather conditions were influenced by the differences in sun and shade on the two sites during the measuring period. Figure 9 also shows clearly that the greatest differences occurred in soil temperature and leaf-air water vapour pressure difference. These factors may thus have contributed significantly to the difference in the plant responses.

Curves of light dependence (Fig. 9) also reveal the marked difference in net

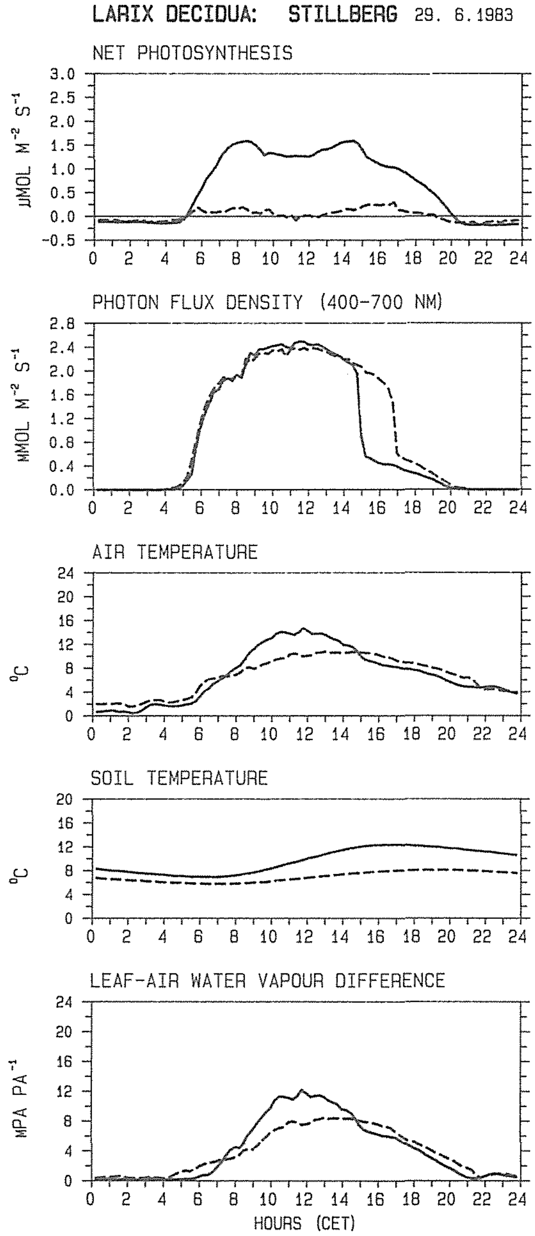

Figure 3. Diurnal course of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

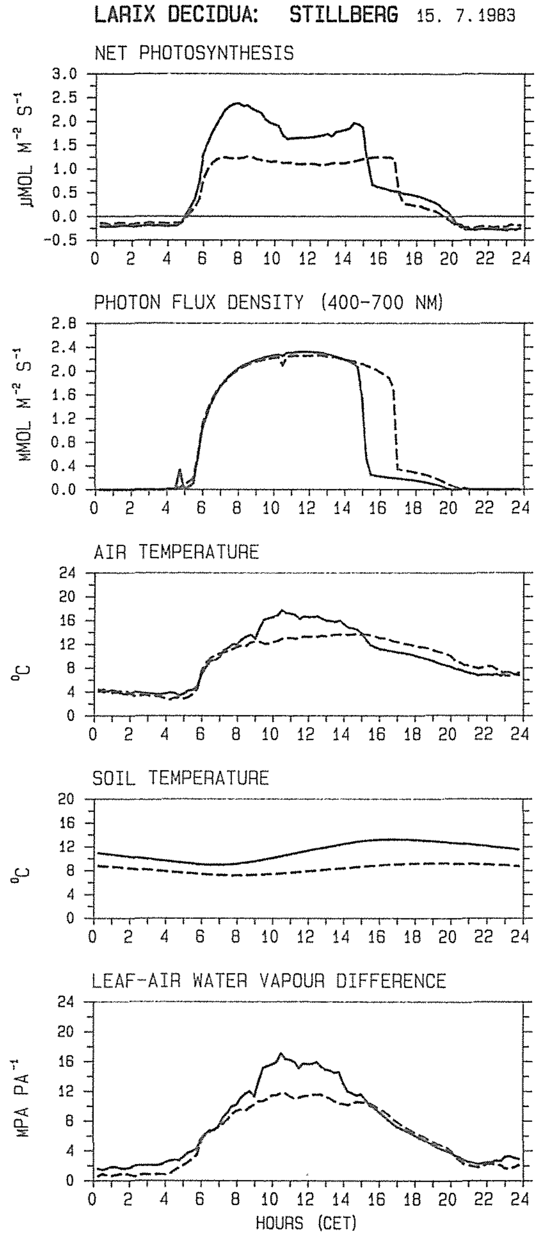

Figure 4. Diurnal course of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

photosynthesis. The lowermost curves comprise all measured values and thus all naturally occurring combinations of climatic factors. The scatter for each mean computed is also shown. The mean curves (designated as mean (T)) are based on all measurements of net photosynthesis for which air temperature was barely limiting ($T > 10^oC$). This curve may well correspond closely with the mean light dependence curve. The upper (max) curves represent maximum values for net photosynthesis recorded during the measuring period. Comparison of the curves for the E- and N-facing slopes shows that maximum net photosynthesis values on the N-facing slope reach only approximately two-thirds of those on the E-facing slope, and mean values only about half. In both cases, the difference between the mean values (stippled area), which were differently determined, is relatively small. In other words, the influence of air temperature was probably very limited.

Figure 10 shows net photosynthesis in relation to air temperature. As before, the lowermost curves represent all recorded values. This curve shows the average response of net photosynthesis under natural conditions, as well as the scatter for each computed point. The central curves comprise only the figures for more or less optimum light conditions ($IP > 1$ mmol m^{-2} s^{-1}). These curves probably correspond more closely to mean temperature dependence. The uppermost curves show the highest absolute values (max) for net photosynthesis recorded in each temperature interval. The stippled areas give a measure of the influence of light, although

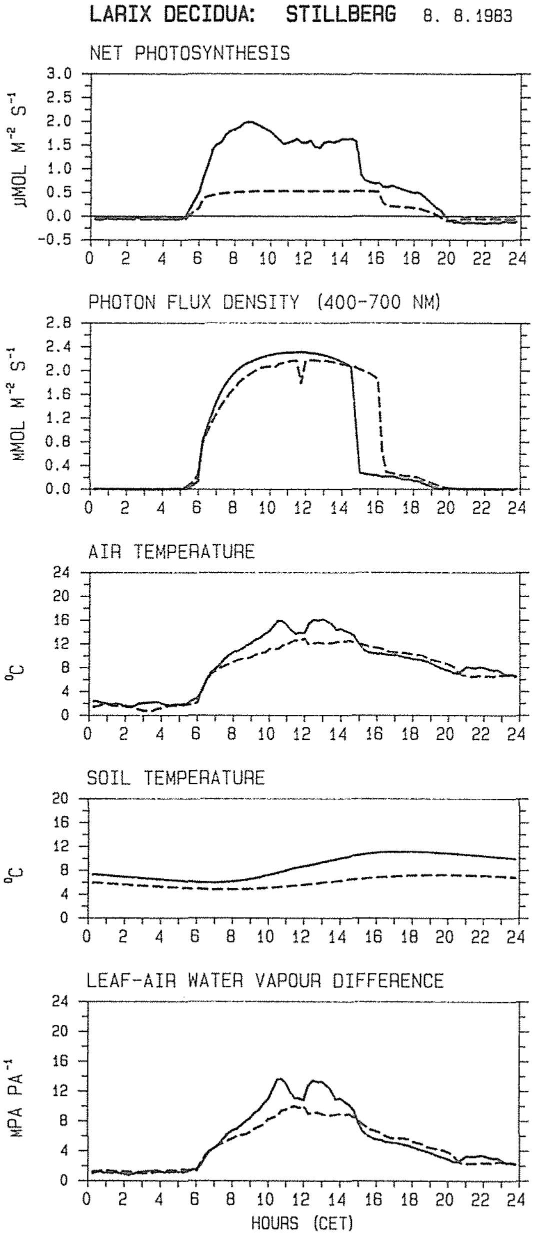

Figure 5. Diurnal course of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

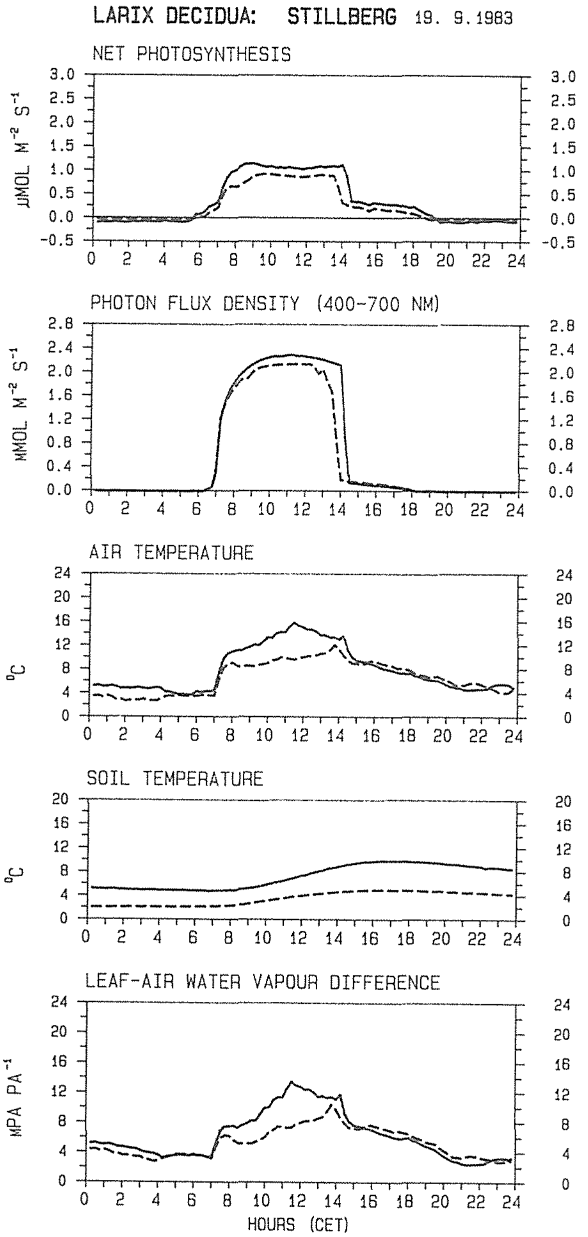

Figure 6. Diurnal course of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

they include values measured at dusk. Photosynthesis responds very rapidly to temperature changes between something under 10°C. Above 10°C there is very little influence on CO_2 uptake.

Figure 11 shows the mean curves of net photosynthesis in relation to leaf-air water vapour pressure difference. These curves include all external factors, but the relation to air humidity cannot be directly seen. In contrast, the curves of maximum values clearly show the inhibitory effect of dry air. Response to leaf-air water vapour pressure differences above 15 mPa Pa^{-1} seems to have been considerably stronger in the tree on the E-facing slope than in the one on the less favourable N-facing slope.

Figure 12 shows the sums of CO_2 uptake during the measuring period at different levels of photon flux density and temperature. The marked differences in CO_2 gain on the two sites are particularly evident. Over the measuring period, the tree on the E-facing slope fixed an average on 57.2 mmol CO_2 m^{-2} d^{-1}, whereas that on the N-facing slope fixed only 28.3 mmol CO_2 m^{-2} d^{-1}, or only about half as much. In these diagrams two photosynthetic maxima are noticeable, particularly for the tree on the E-facing slope. The first occurs at low photon flux densities and average temperatures, the second at higher photon flux densities and high temperatures.

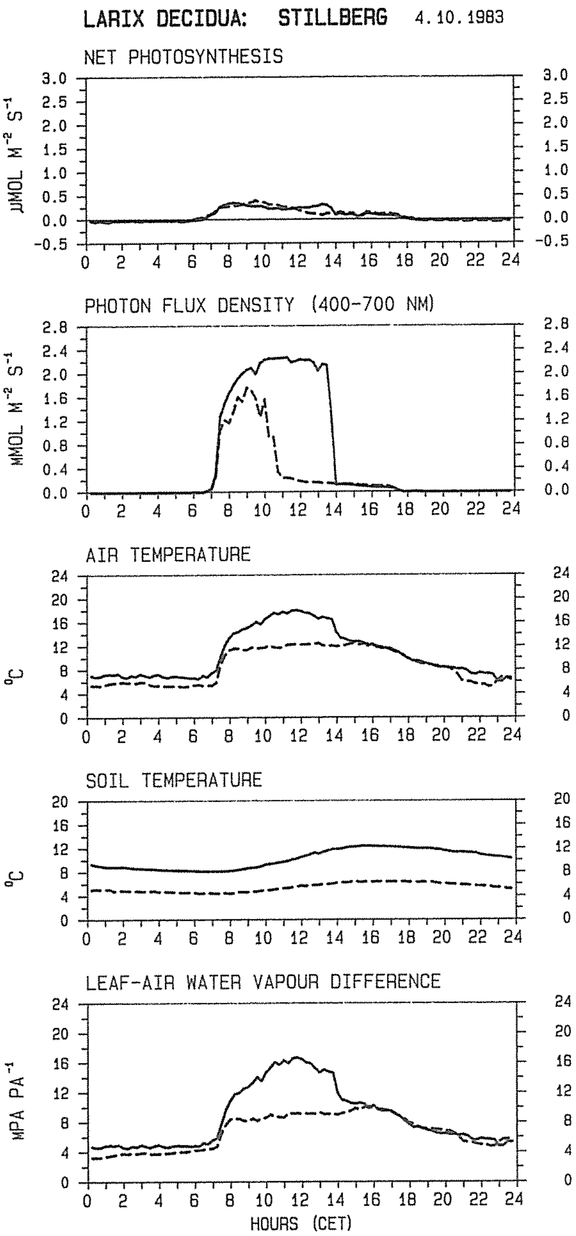

Figure 7. Diurnal course of net photosynthesis, photon flux density, air and soil temperature and leaf-air water vapour pressure difference, measured on an east (——) and a north (---) facing slope.

DISCUSSION

The different growth rates of young trees on the two sites with their different exposures may result from a number of factors (Turner and Schönenberger, 1981; Turner *et al.*, 1982). Even at the end of June, when measurements began, one particular site factor was obviously crucial; the fact that the snow cover disappears two to three weeks earlier on the E-facing slope than on the N-facing one means that the trees on the E-slope have a 20% longer production period. Tranquillini (1979) points out that this has a decisive influence on growth and survival at timberline. As can be seen from Figure 2, however, frosts during the development period may depress photosynthesis for some time, a danger which increases with earlier disappearance of the snow cover.

Consequently, the practically permanent differences in rates of photosynthesis (Figures 3-7) can be at least partly explained by the differing physiological states of the trees. The lapse between growth phases on the two sites precludes direct comparisons, but constitutes a characteristic difference in the course of development on the two sites.

The maximum photosynthetic rates of the larch on the E-facing slope are of the same order of magnitude as those reported by Larcher (1969a) and confirmed by Benecke *et al.* (1982) and Matyssek (1982) for a variety of sites. Photosynthesis in the tree on the N-facing slope never attained these values, remaining considerably below the order of magnitude of 3 µmol m^{-2} s^{-1} throughout the whole season (cf. Häsler and Blaser, 1981). Apart from the colder, less favourable microclimate on the N-facing slope and the time lapse mentioned above, the occurrence of a cold spell at what was obviously a particularly disadvantageous moment for the tree must have contributed to this difference. The needles of this tree had not yet fully developed; Havranek (1983) reports that needle maturation continues for some weeks after completion of longitudinal growth (increase in weight).

The direct comparison given in Figure 8 makes the difference in daily CO_2 uptake of the two larches particularly evident. The deviation of the regression lines from the angle bisector is considerably greater than that found by Häsler (1982) in *Pinus montana (= P. mugo)* on two similar sites. This can partly be explained by the fact that the trees in the present experiment had been growing on the different sites for eight years, whereas those in the study on mountain pine were potted plants, just brought to the sites a few weeks before the measurements. Furthermore, the basic difference in the growth pattern of evergreen and deciduous trees must be considered.

With regard to climatic factors, soil temperature and leaf-air water vapour pressure difference displayed particularly great differences. It has been repeatedly demonstrated that air humidity affects photosynthesis in larches (Richards, 1981, in *Larix lyallii*; Matyssek, 1981, in *Larix decidua* and *Larix leptolepis*). As Havranek (1972) has shown, however, low soil temperatures may also influence photosynthesis in larches negatively. More attention should be paid to this factor in future.

The light dependence curves of photosynthesis (Figure 9) show clearly that trees growing near the alpine timberline seldom experience optimum conditions. This finding is supported not only by the low maximum values for the tree on the N-facing slope but also, and more strongly, by the mean curves of light dependence under natural conditions. The fact that there is only a slight difference between the curves with and without limiting

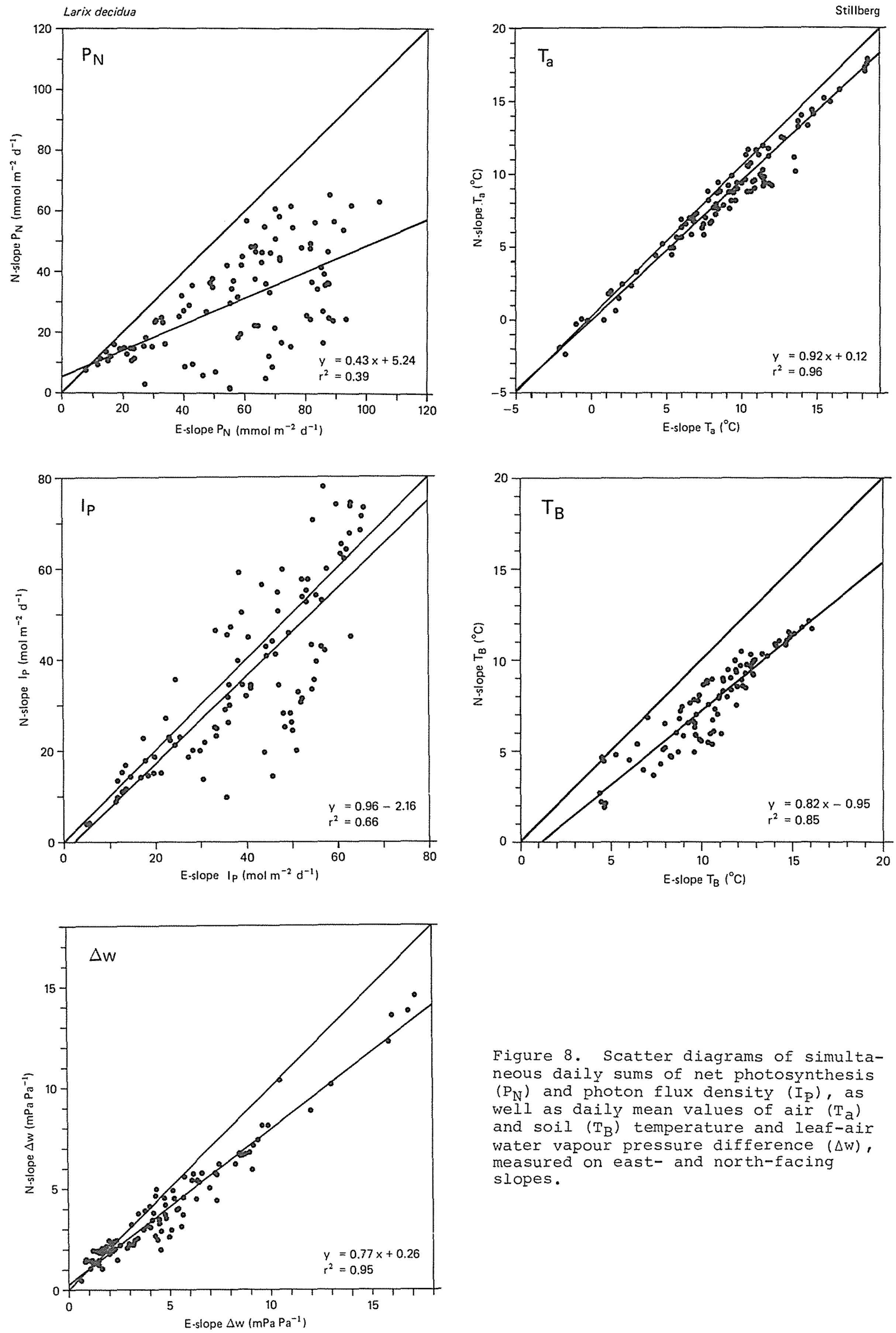

Figure 8. Scatter diagrams of simultaneous daily sums of net photosynthesis (P_N) and photon flux density (I_P), as well as daily mean values of air (T_a) and soil (T_B) temperature and leaf-air water vapour pressure difference (Δw), measured on east- and north-facing slopes.

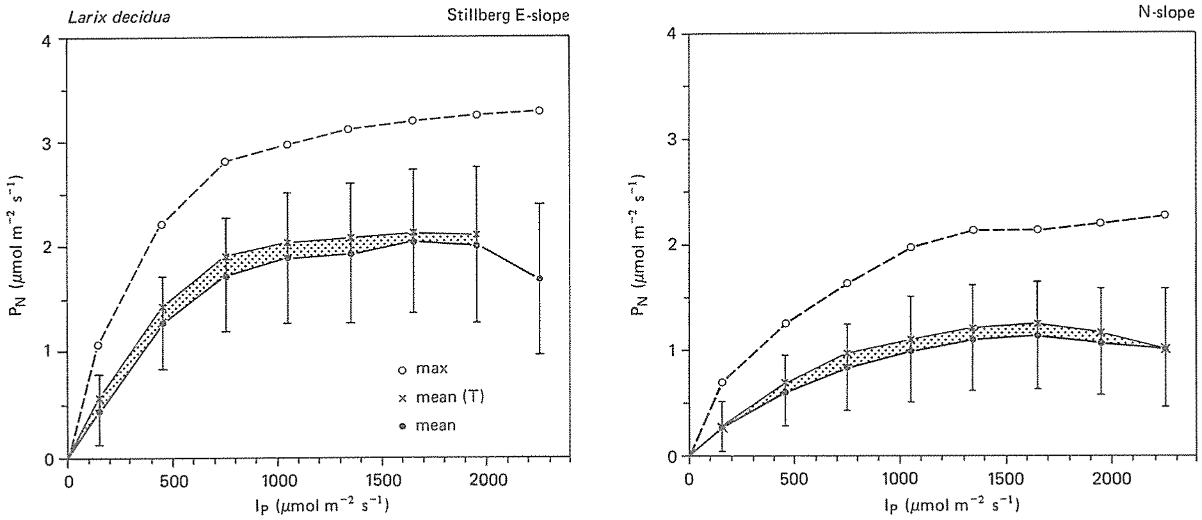

Figure 9. Net photosynthesis in relation to photon flux density. Mean values including all natural weather conditions (mean), mean values with temperature at optimum levels (mean(T)) and maximum response (max).

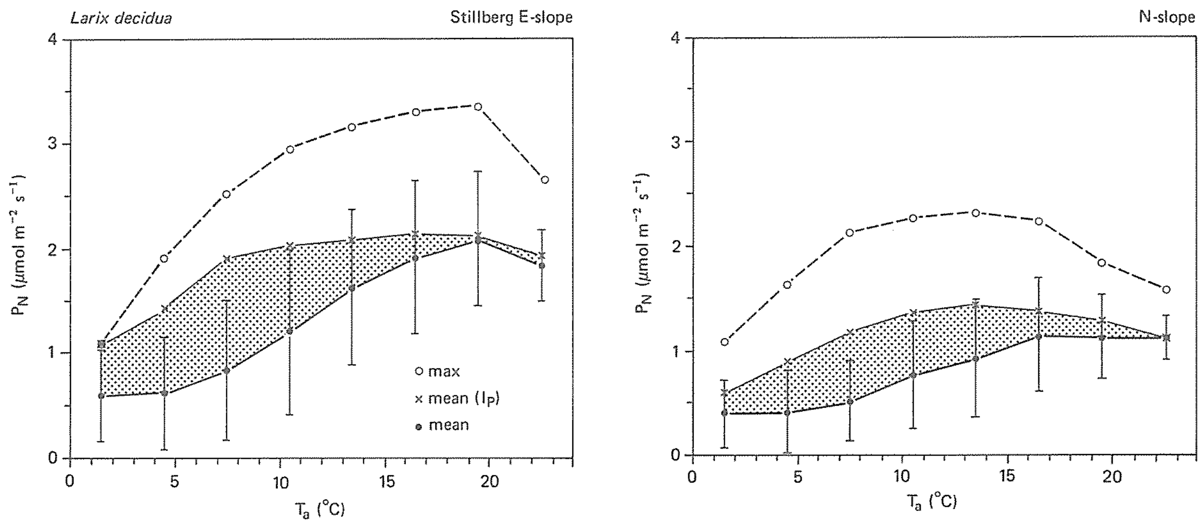

Figure 10. Net photosynthesis in relation to air temperature. Mean values including all natural weather conditions (mean), mean values with photon flux density at optimum levels (mean(I_P)) and maximum response (max).

air temperatures indicates that air temperature need hardly be regarded as a decisive factor. Larches seem to do well at rather low temperatures, attaining quite high rates of photosynthesis even at 10°C (Figure 10). The sole indication that more favourable site conditions could contribute to a higher air temperature optimum of photosynthesis than was recorded for the larch on the shady slope, is the curve of maximum net photosynthesis against air temperature for the larch on the sunny slope. To what extent plant adaptation was involved must for the moment remain undecided. Havranek (1972) reports that larches are able to adapt relatively quickly, at least to changes in soil temperature. It must also be mentioned that Gowin *et al.* (1980) have demonstrated that the chlorophyll content of larch needles is positively correlated with temperature.

Air humidity does not seem to have any great effect on net photosynthesis either (Figure 11). However, the curves of maximum values do show that a considerable reduction on CO_2 uptake may occur at high leaf-air water vapour pressure differences (above 10 mPa Pa^{-1}). This threshold agrees well with that found by Matyssek (1981). Nevertheless, net photosynthesis does increase on average with drier air, which shows that other factors are more important.

If the time factor is considered in connection with CO_2 uptake, the difference

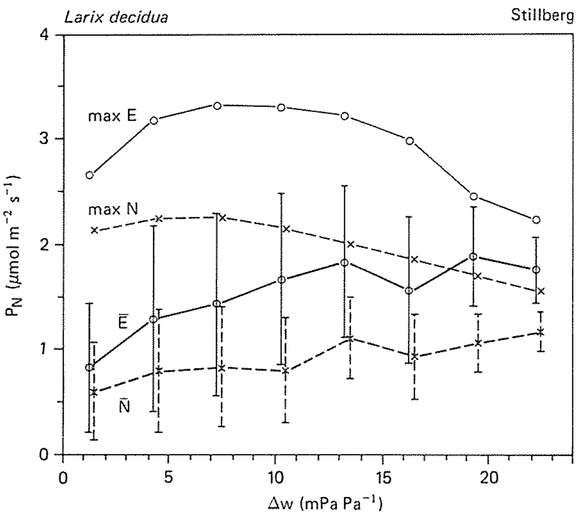

Figure 11. Net photosynthesis in relation to leaf-air water vapour pressure difference. Mean values with standard deviation for east (——) and north (---) facing slopes are shown with maximum values from east (max. E) and north (max. N) slopes.

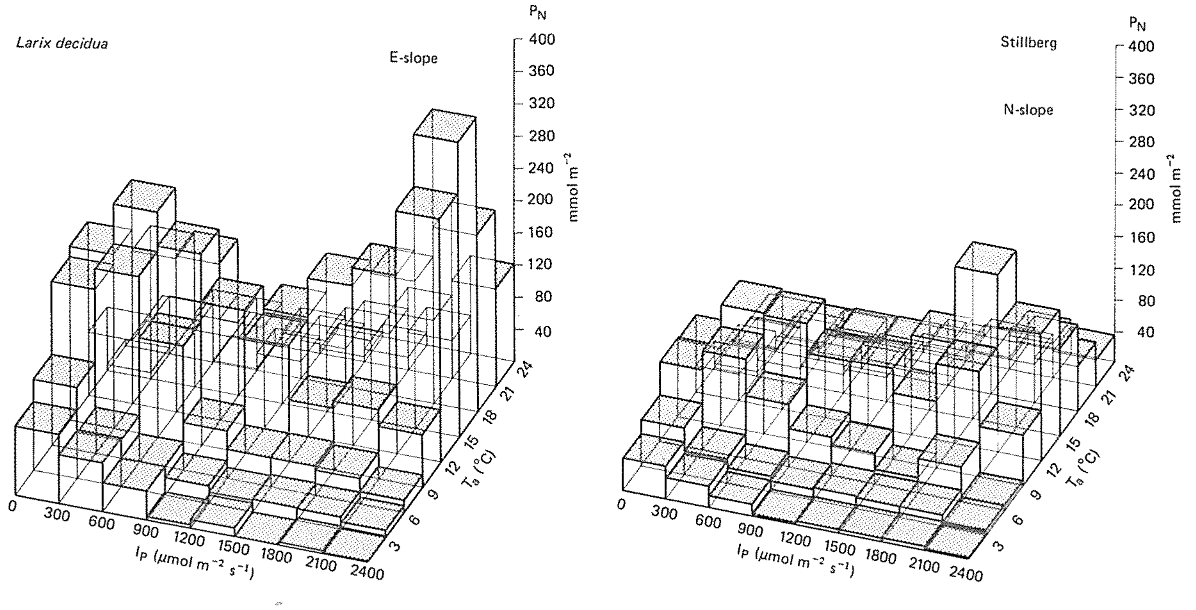

Figure 12. Sums of CO_2 uptake at different levels of photon flux density and temperature on neighbouring east- and north-facing slopes, measured under natural conditions between 26th June and 4th October 1983.

between the plants on the two sites is particularly evident (Figure 12). Moser (1973), Fuchs *et al.* (1977) and Häsler (1982) have shown that large quantities of CO_2 are absorbed even when light is limiting. The different distribution recorded in the present study, and in particular the second maximum of CO_2 uptake at higher light intensities and high air temperatures, may be due to the extremely warm conditions in July, which even on the N-facing slope resulted in temperatures seldom experienced on the neighbouring E-facing slope.

In conclusion it may be said that the results show how important it is to employ extensive series of measurements covering several years in analyses and possibly also in model calculations. Depending on the time of year, events such as frosts or sudden warm periods may have a decisive effect on photosynthesis and consequently on tree growth. As Larcher (1969) has shown, the time factor is crucial. Even including this factor, however, it is obviously very difficult to explain the marked differences in net photosynthesis in the larches on the two sites solely on the basis of climatic conditions. Other factors, in particular soil moisture and nutrient supply probably deserve more attention. Furthermore, increased importance should be ascribed to the cumulative effects of years of exposure to adverse conditions, in particular just the type of extreme conditions obtaining on a N-facing slope at the alpine timberline encountered in the present study.

ACKNOWLEDGEMENTS

I thank Dr. H. Turner for supporting the work and for supplying the mean data shown in Figure 1, Mrs. Dr. D. Häsler-Küng for critical reading and Mrs. M. Sieber for the careful translation of the manuscript.

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