

Carbon gain and wood production in trees of deciduous beech (Fagus silvatica) and trees of evergreen spruce (Picea excelsa).

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Introduction

It is well known in forest management that coniferous trees have a higher timber production than broad leaved deciduous tree species. Pinus sylvestris, Picea excelsa or Pseudotsuga douglassii produce about 10, 12 or 18 m³ wood per hectar and year respectively, whereas the comparative figures are 5, 8, or 10 m³ of wood per hectar and year for Fagus silvatica, Quercus petraea or Fraxinus excelsior (Bonnemann und Röhrig, 1972). This difference in wood production contrasts the performance of photosynthesis in conifers and broad leaved trees. Larcher (1971) showed that the maximal rate of net photosynthesis in conifers reaches 4 - 5 mg CO₂ g⁻¹h⁻¹ and it is thus much lower than the maximal rate of net photosynthesis in broad leaved trees, which ranges between 10 and 12 mg CO₂ g⁻¹h⁻¹. These differences are not quite as large on a unit area basis, but since the carbon relations of a plant strongly depend on the carbon returns per unit

carbon investment, in the following photosynthesis will be discussed on a unit dry weight basis. The ecological question is, which processes make conifers more productive than broad leaved trees in terms of wood yield despite a lower photosynthetic rate.

The following processes will be examined:

1. It was suggested repeatedly that evergreen conifers have the advantage to start net photosynthesis early in spring and to carry on until late autumn. This would result in a higher photosynthetic gain per unit foliage.
2. For the general geographic distribution of spruce and beech one could hypothesize that both species are adapted to a different degree to the climatic conditions of a habitat, which could lead to large differences in daily CO₂ uptake.
3. The translocation, distribution and turnover of carbohydrate could have principle differences in both tree types, which could result in differences of wood yield.

Methods

Experiments were performed as part of the "Solling-Projekt der Deutschen Forschungsgemeinschaft" in the years 1969 to 1972 in the Solling area northwest of Göttingen. It is a montane climate with a distinct cold winter and a temperate summer season of about 6 to 7 months. 1000 mm of rainfall show a summer and a winter maximum. A 120 year old stand of Fagus

silvatica (26 m high) and a 89 year old stand of Picea excelsa (25,5 m high) were chosen for measurements. CO₂ exchange was monitored continually with 3 temperature and humidity controlled cuvettes for 9 months in beech and with 5 cuvettes for 12 months in spruce. Additionally leaf biomass was estimated. Wood production was assessed by other groups of this interdisciplinary project (Ellenberg, 1971). For details of results and measurements see Schulze, 1970 and Schulze et al., 1977 a and b, Fuchs et al., 1977.

Results

1. The photosynthetic gain of Fagus silvatica

Fig. 1 shows the seasonal change of the light dependence of the CO₂ exchange of sun and shade leaves at optimal temperatures and high air humidity. In sun leaves the photosynthetic rates at light saturation increased rapidly in early summer. Almost constant rates were reached in June and July. Already in early August the light saturated CO₂ uptake decreased. Leaf fall was in October. The seasonal development was different in shade leaves. The light saturated CO₂ uptake increased at a slower rate than in the sun leaves, but highest rates were reached in August at a time when the rate of CO₂ uptake in sun leaves decreased already. Leaf fall was later in the shade than in the sun leaves. The maximal rates of CO₂ uptake per unit leaf dry weight were higher in shade than in sun leaves (Tab. 1).

In order to quantify the performance of the photosynthetic capacity in respect to the ambient climatic conditions

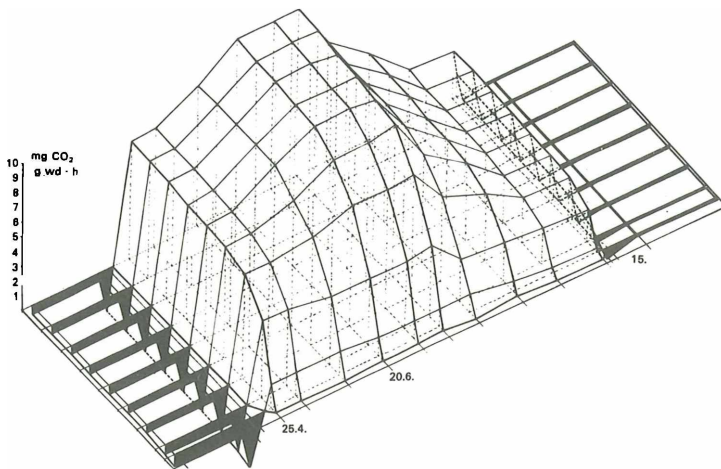


Fig. 1 a: The annual change of the light dependence of CO₂ exchange in the sun crown of *Fagus silvatica* at temperatures of 16 - 22°C and a relative humidity of 80 - 100%. X-axis date, y-axis light intensity, z-axis CO₂ exchange. The dark shaded areas present bud respiration.

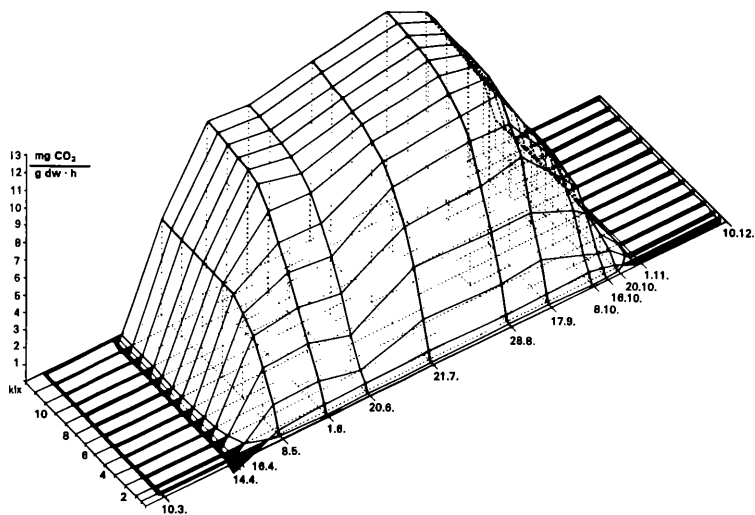


Fig. 1 b: same as figure 1 a but for shade leaves

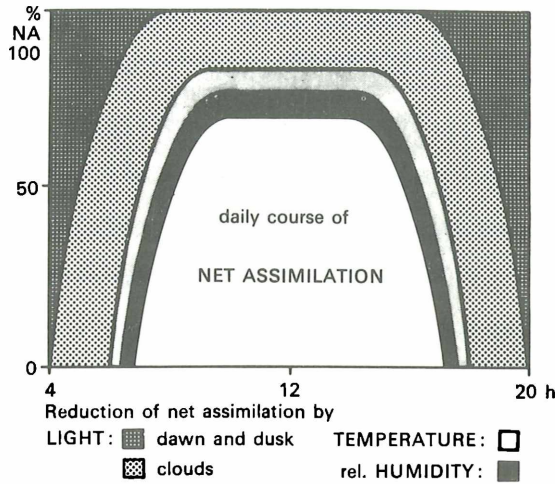


Fig. 2 a: Model of the effect of climatic factors on net assimilation. The maximal primary production (100%) occurs if there is 100% of net assimilation over the entire day. This is reduced by dawn and dusk, clouds, temperature and vapour pressure deficits in the air.

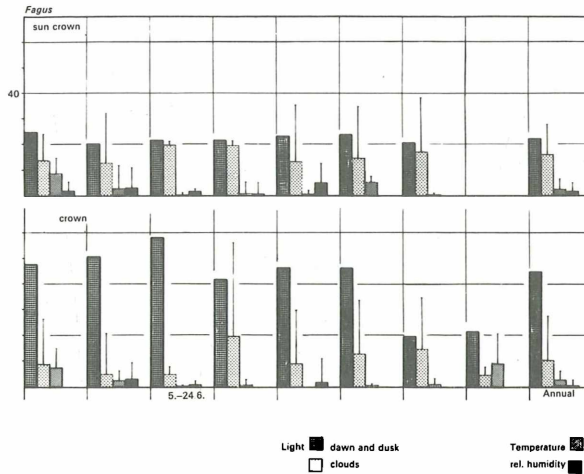


Fig. 2 b: The influence of light, temperature and relative humidity on net assimilation in sun and shade leaves of *Fagus silvatica*. Columns: Mean values of the corresponding time interval, line: Maximal value for a single day within the time interval, abscissa: Time intervals, ordinate: Percentage reduction of maximal net assimilation.

daily courses of CO₂ uptake were measured throughout the year and estimates were made, which factors diminished the photosynthetic capacity during the course of a day (Fig. 2). A simplified model of production was used assuming that maximal photosynthetic production was possible if optimal conditions of light and humidity were present from dawn to dusk, similar to conditions in climate rooms. Under natural conditions, this maximal rate is not reached because of low light in the morning and in the afternoon even on a sunny day. Furthermore cloud cover and non-optimal temperatures and humidities reduce the maximal photosynthesis. Fig. 2 shows that low light at dawn and dusk reduced the hypothetical maximal production of sun leaves by about 20%. Cloud cover was the next important factor. Underoptimal conditions of light reduced maximal photosynthesis by about 40% during the day. The effect of non-optimal light is even more pronounced in the shade crown. Non-optimal temperatures were present in spring and autumn only. Also water vapour deficit of the air had a measurable effect in young leaves and in late summer only. The additive treatment of estimating the effect of single climatic factors is theoretically not quite correct, but it is justified in the present case where one factor is predominantly limiting, namely light, and all the other factors, namely temperature and humidity are close to the optimum.

The daily courses of net photosynthesis result in the seasonal carbon gain. Fig. 3 shows that sun leaves had a higher daily carbon gain than shade leaves in early

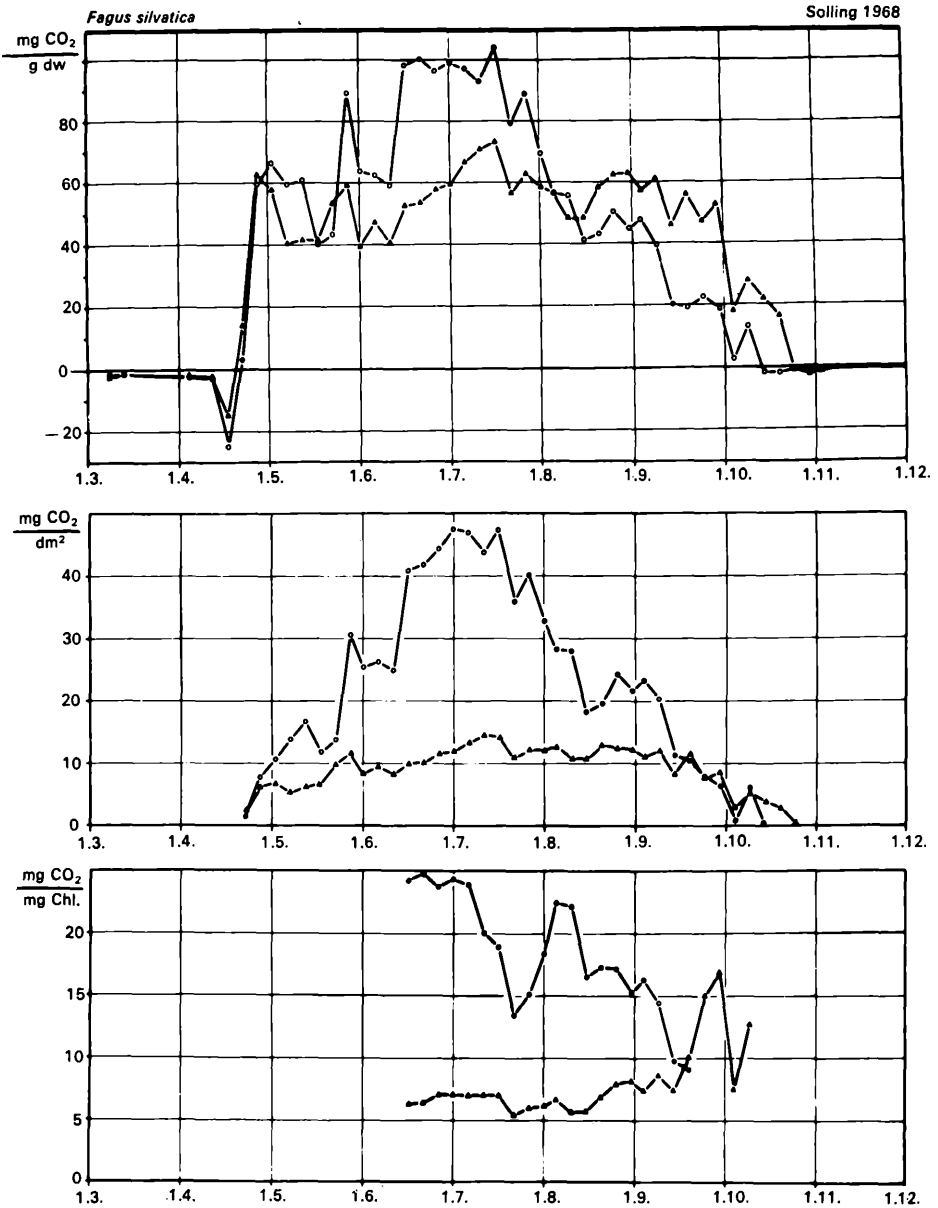


Fig. 3 The daily balance of net assimilation during the year under natural conditions (mean values over 5 days from sunrise to sunset) for sun and shade leaves of *Fagus silvatica* based on dry weight. Abscissa: Date, ordinate: CO₂ exchange.

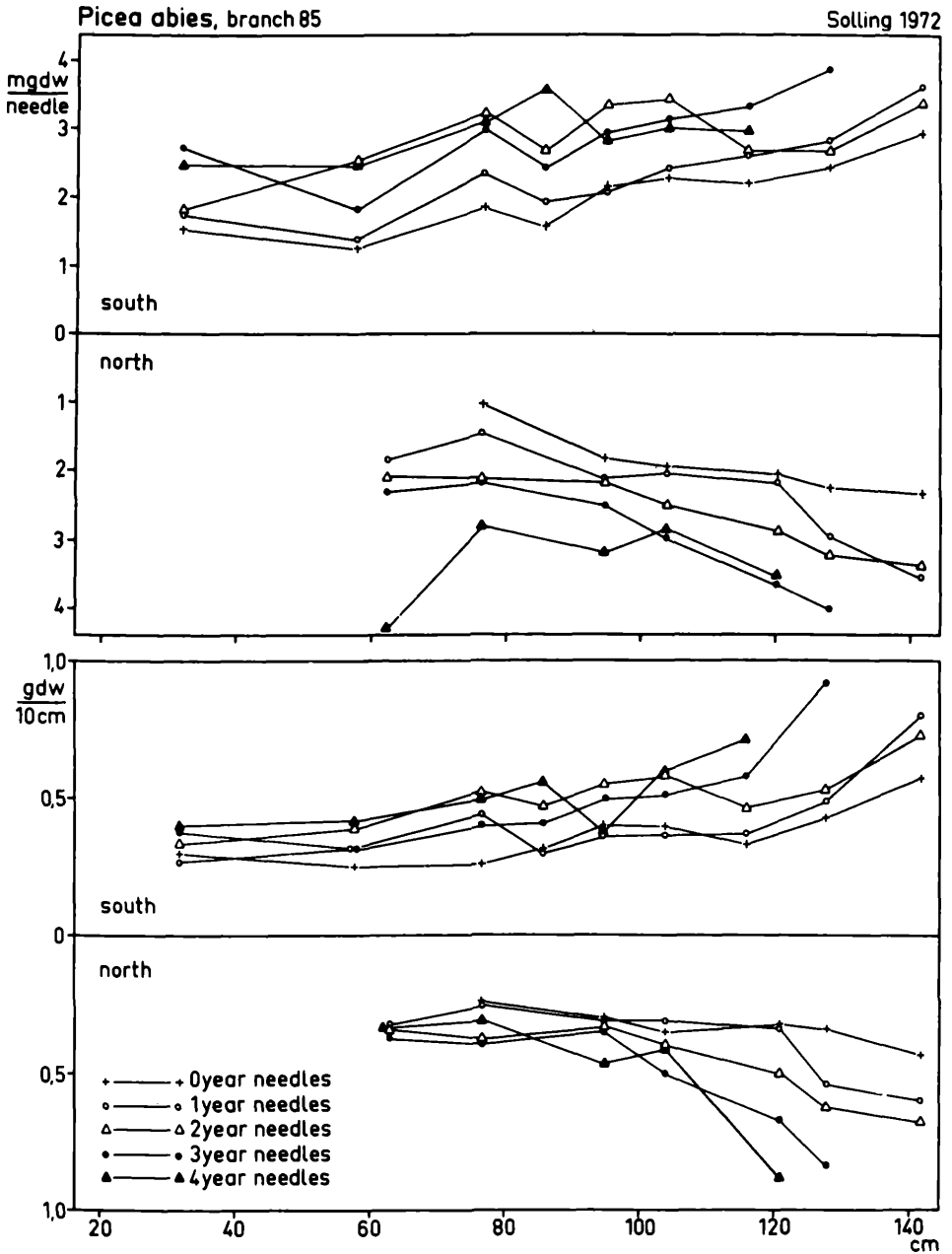


Fig. 4 The change of dry weight per needle (top) and of needle biomass per 10 cm of twig length along the axis of a main branch in the lower sun crown. Determinations were made on every 7th lateral twig.

summer. But shade leaves reached highest rates in autumn and on a seasonal basis the carbon gain of sun and shade leaves was very similar on a unit dry weight basis (Tab. 1).

2. The photosynthetic gain in Picea excelsa

The investigations in spruce were complicated by the fact that in this species there is not only a difference between sun and shade crown, but also a significant differentiation of needles with age. The oldest needles were 12 years old and on average needles reached 5 years. Fig. 4 shows a 4-fold change of needle dry weight from the base to the tip of a 2 m long main branch. Furthermore dry weight increases with needle age. A 1.5 to 2 m long branch in the lower sun crown carries a total length of 90 - 130 m lateral side branches. Fig. 5 shows for 1 year old needles the distribution of needle weights within the crown. The heaviest needles were found on the tips of the branches and in the upper sun crown, whereas the largest accumulation of needle weight occurred in the inner portions of the lower sun crown. Thus, needle position and needle age are important parameters.

Current year needles show a seasonal course of the light dependence of net photosynthesis which is similar to that of beech (Fig. 6 a). Bud break is not only later than in beech, but CO₂ uptake also decreases by November. The seasonal change of maximal rates of net photosynthesis was different in 1 year old needles (Fig. 6 b). The rates were generally lower than in the current year needles (Tab. 1)

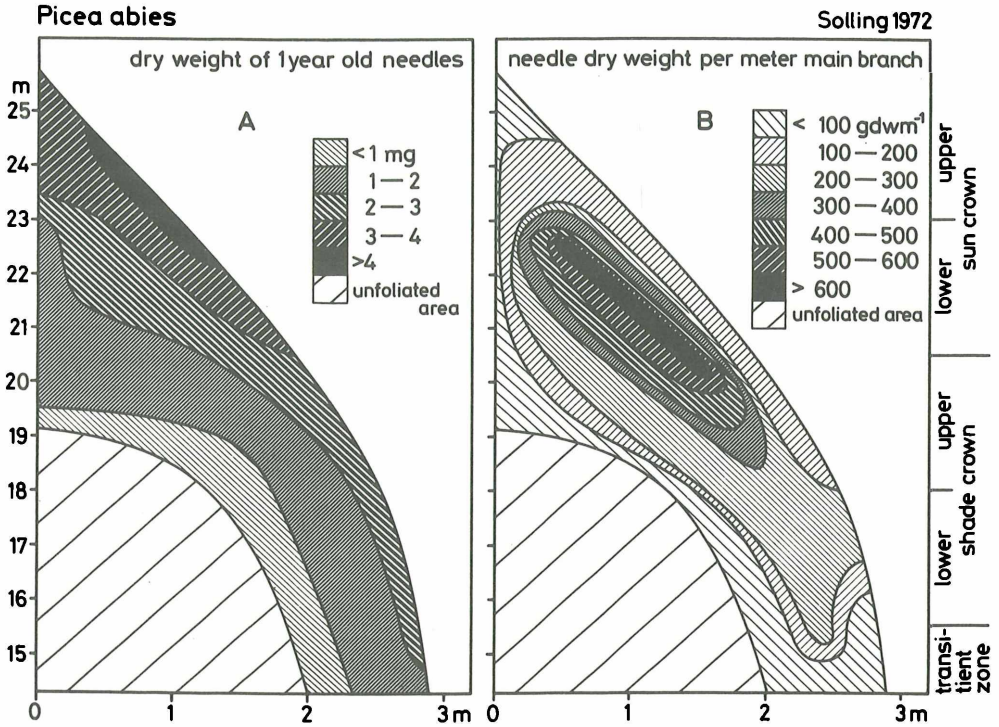


Fig. 5 a: Distributions of regions of similar dry weight per needle in the tree crown.

Fig. 5 b: Distributions of regions of similar needle biomass per meter of branch in the cross section of the tree crown.

and there was very little change during the time from April to September. The maximal rates in beech were about three times higher than of spruce and contrast the findings for wood yield (Tab. 1).

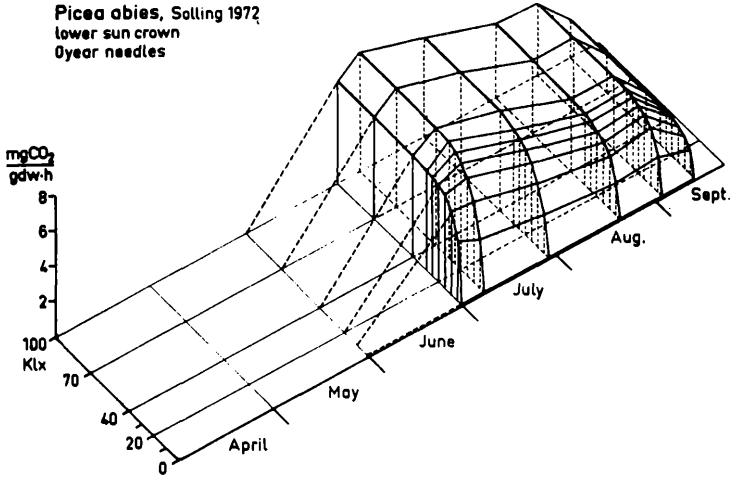


Fig. 6 a: Seasonal change of light dependent rates of net photosynthesis in current year old needles of the lower sun crown at an air temperature of 9 - 13°C and a vapour deficit between needle and air of 0 - 15 mg H₂O l⁻¹

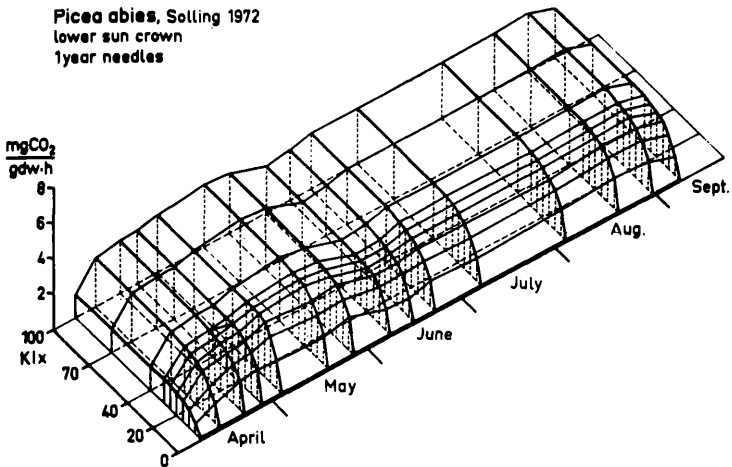


Fig. 6 b: same as figure 6 a but for 1-year-old needles

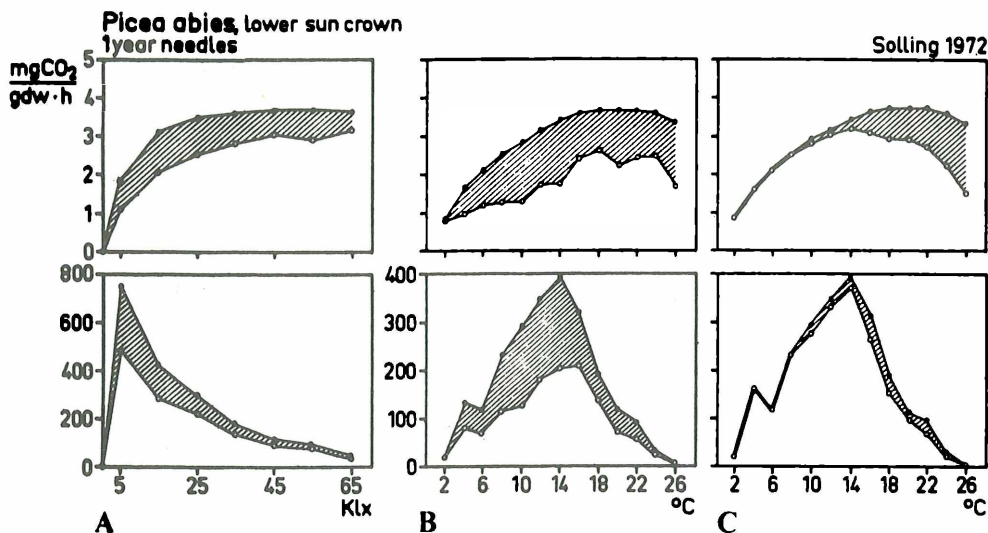


Fig. 7 A: The rate of CO₂ uptake as related to light intensity with temperature and humidity at optimal levels (●) and under naturally variable climate (○). Top: CO₂ rates per h. These were calculated for the naturally variable climate from the measured sums of CO₂ uptake and the absolute time span during which the different light conditions occur. Bottom: Total sums of CO₂ uptake. These are the additive sums of field measurements for the natural variable climate. They were calculated for the optimal conditions from the light dependency curves and the total duration of time at which these conditions occurred. The sensitivity of the light dependent photosynthetic capacity of non-optimal conditions of temperature and humidity at the various light intensities is indicated by the shaded area. B: same as A but for temperature being variable at optimal (●) and natural (○) conditions of light and humidity. C: same as A but for temperature being variable but at light saturation and only for humidity being either optimal (●) or naturally changing (○).

A different approach was used in order to characterize the effect of non-optimal climatic conditions on net photosynthesis (Fig. 7). The response curve for one factor being variable with all other factors being optimal was compared with the same response curve but all the other factors change in a natural manner. The effect of underoptimal light and humidity conditions, for instance, becomes obvious from the comparison of the temperature response curve at light saturation and high humidity and the temperature response curve as it is derived from naturally changing light and temperature conditions. Non-optimal conditions of light reduce the maximal rate of net photosynthesis by about 40% during the course of a day. Thus in spruce light is also the dominant factor determining the daily course of CO₂ uptake. There are no significant differences in adaptation of photosynthesis which could explain the differences in wood yield of beech and spruce.

The daily carbon gain (Fig. 8) is determined by the photosynthetic capacity as well as by the length of the daylight. 1-year-old needles show highest daily carbon gain in mid-summer. Because of reduced daylight the daytime carbon gain is strongly reduced in April and October although the rates of maximal photosynthesis were quite high in these months. There is very little carbon exchange during the winter months. Tab. 1 shows that the daily and seasonal carbon gain per needle dry weight do not explain the differences in wood yield of spruce and beech. Despite a longer season of positive daily carbon gain (260 days in spruce versus

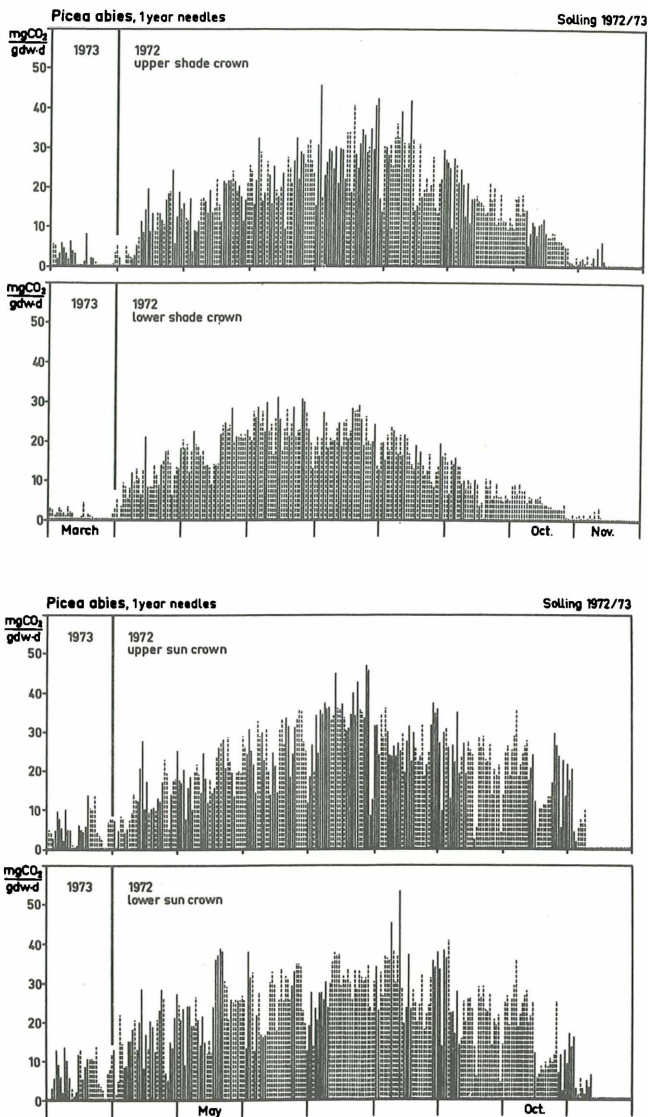


Fig. 8: The annual change of daytime sums of net photosynthesis of 1-year-old needles in different crown heights from April 1972 until March 1973. Drawn lines: Measured days; dashed lines: Calculated values from stepwise multiple regressions.

176 days in beech) the annual carbon gain per unit dry weight remains lower in spruce than in beech.

3. The carbon balance of spruce and beech

Tab. 1 summarizes the carbon balance of spruce and beech.

It is obvious that both species invest about the same amount of carbohydrates into new foliage each year, although the growth of new needles appears to be even slightly less in spruce than in beech. However, because of the longevity of the needles the total foliar biomass is 5 to 6 times larger in spruce than in beech. Despite a lower carbon gain per needle dry weight, the resulting annual CO₂ gain of the stand is considerably larger in spruce than in beech. This is based on the large needle biomass which results from the longevity and the accumulation of foliage over years. Calculated over the total life span, a needle has a carbon gain which is 2 - 3 times larger than that of a deciduous leaf.

Estimates of the carbon allocation were made. Although beech and spruce allocate about the same proportion of the total carbon gain into new timber, the absolute amount is higher for spruce than for beech because of the larger annual carbon gain of the total stand.

Discussion

The natural vegetation of mid Europe is primarily dominated by broad leaved trees such as Fagus, Quercus, Acer, Tilia, Fraxinus and others. The ecological problem is, why the

Tab. 1: CO₂ assimilation and carbon balance of *Fagus sylvatica* and *Picea excelsa*

	<i>Fagus sylvatica</i>		<i>Picea excelsa</i>			
	sun	shade	sun ^{0Yr} shade	sun ^{1Yr} shade	sun ^{2Yr} shade	sun ^{2Yr} shade
Maximum rate of CO ₂ uptake (mg CO ₂ g ⁻¹ h ⁻¹)	12.4	14.2	4.8	6.5	3.6	4.0
Maximum daily sums of CO ₂ uptake (mg CO ₂ g ⁻¹ d ⁻¹)	122	94	73	50	40	31
Seasonal CO ₂ uptake (g CO ₂ g ⁻¹ a ⁻¹)	9.8	9.2	4.5	2.8	5.2	3.2
Days of positive CO ₂ uptake (d a ⁻¹)	176				260	
Current year leaf growth (t ha ⁻¹ a ⁻¹)	2.93				2.47	
Total leaf biomass (t ha ⁻¹)	2.93				17.90	
Annual gain of CO ₂ uptake (tC ha ⁻¹ a ⁻¹)	8.6=100%				14.9=100%	
./. Leaf, bud respiration	1.7	20%			3.0	20%
./. Leaf turnover	1.9	22%			1.8	12%
./. aboveground wood growth	2.1	24%			3.1	21%
./. Wood respiration, belowground growth	2.9	34%			7.0	47%

species which has the higher biomass production, namely spruce, is not competitive in the natural vegetation. Certainly other factors than productivity per se determine the natural vegetation and there are certainly numerous factors where the broad leaved trees are favoured. Fagus for instance is more shade tolerant than spruce and regenerates under a crown cover. Thus it will succeed during succession. Furthermore other abiotic factors limit the distribution of conifers in oceanic climates, such as snow and wind damage. Fungus attack strongly reduces the life span of spruce in humid areas and on soils with high nutrient status. On the other hand, if conditions are less favourable, as in the boreal or alpine climate then conifers succeed. One may hypothesize that this is based on the more economic carbon turnover which becomes of significance for succession under extreme conditions. Certainly conifers need many years to accumulate the necessary foliage biomass before they reach highest productivity. This is not the case in broad leaved trees, but it is a common observation that broad leaved trees, such as Betula and Alnus may form an early successional stage after clear felling even in the boreal climate. They are succeeded by conifers in a later successional stage. These hypotheses of the significance of evergreen and deciduous growth form have not been sufficiently studied in respect to plant geography.

Summary

Spruce has a larger annual productivity of wood than beech despite lower photosynthetic rates per needle dry weight. Due to the longevity of the needles spruce invests slightly less carbohydrates into new foliage than beech each year but it accumulates a larger total amount of foliage over many years which results in a larger annual total carbon gain per stand. This in turn is the basis for a higher wood growth.

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