Gas Exchange in Three Populations of Norway Spruce1)

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Introduction

Measurements of CO_2 exchange in trees have demonstrated genetic variations in net and total photosynthesis, dark respiration, and photorespiration, as discussed in the literature (Ferrell, 1970). Such measurements can also be used to help in selecting rapidly growing genotypes, especially in clonal material, as demonstrated by Huber and Polster (1955). Measurements of photosynthesis and respiration over short time intervals do not, however, always give results that correlate well with yield data. This conclusion has been made on the basis of physiological considerations (Decker, 1955) as well as of actual comparisons between growth and CO_2 exchange parameters (Brix, 1967; Sweet and Wareing, 1968; Luukkanen, 1973).

One way of overcoming the difficulties in analyzing complex processes such as net photosynthesis is to partition the process into smaller fractions and to study them separately. Different subprocesses that have received much attention recently are, for instance, dark respiration, and, particularly photorespiration. Decker (1957, 1970) has suggested that photorespiration is a major factor affecting the variation in photosynthetic performance within a species. In poplars, variation in photorespiration seems to be correlated with net photosynthesis at least under certain conditions, and the CO_2 compensation point seems to follow this variation (Luukiianen and Kozlowski, 1972). As emphasized by Ferrell (1970), correlations between photosynthesis and other related processes should be studied under varying conditions and over longer periods of time in order to obtain a better understanding of the relationships between CO_2 exchange and growth. Growth models, already applied to the environmental variation (e.g. Ledig, 1969; Hari and Luukiianen, 1973, 1974) of CO_2 exchange in trees may finally make possible the application of photosynthesis and respiration measurements to selection and breeding in practice.

Apart from clonal material, natural populations of trees have also been included in CO_2 exchange studies. In Scots pine relatively small differences were found by Gordon and Gatherum (1968) among provenances ranging from 42° to 66° latitude. In this material the photosynthetic efficiency and growth of the seedlings were mostly negatively correlated. Furthermore, photoperiodic responses also seemed to interact with the variation of photosynthetic performance with latitude.

Two Polish populations of Scots pine, classifield as ecotypes, had different photosynthetic efficiencies, and the variation seemed to depend on the time of measurement during the growing season (Zelawski et al., 1969). Experimental conditions were also found to affect the variation of CO_2 exchange among provenances of Pinus strobus (Bourdeau, 1963).

Several workers have attempted to relate differences in photosynthesis to other than CO_2 exchange processes. In particular relations with the water balance have been studied. In Pseudotsuga menziesii variations in stomatal responses to water stress correlate with ecotypic differences in CO_2 exchange, as discussed by Ferrell (1970). In poplar clones similar relationships have been investigated and found to be present (Luukkanen and Kozlowski, 1972). These relationships have also been studied in Polish populations of Scots pine, but no clear correlations were found (Zelawski et al., 1969).

In the present study a first attempt was made to estimate the variation of main CO_2 exchange parameters within and among populations of Norway spruce in Finland. The relationships among various CO_2 exchange characteristics have also been analyzed and discussed.

Materials and Methods

The study material consisted of seedling Norway spruce (Picea abies (L.) Karst.) derived from open-pollinated parent trees in three stands. One of the stands was located in Southern Finland (A: Loppi, 60° 20' N., 24° 25' E., elevation 120 m), and two of them were situated near the spruce timberline in Lapland (B: Laanila, 68° 26' N., 27° 23' E., elevation 200 m; and C: Pallasjärvi, 68° 03' N., 24° 05' E., elevation 410 m). In each stand, seven random trees were selected and six seedlings were analyzed from each half-sib family. The seedlings were grown during the first growing season in two separate nurseries (A in Southern Finland, B and C in Lapland). During the second growing season, in 1972, all seedlings, transplanted in individual cardboard containers about half liter in volume and randomized into six replications, were grown in a growth chamber under the following conditions: fluorescent light irradiance about 10 Wm^{-2}, daylength 16 hours, day temperature 25 to 30° C, night temperature about 20° C. The seedlings were watered frequently and supplied with nutrient solution once every week. All measurements were made after the shoot growth of the current year was completed (within four weeks, beginning on July 12, 1972), so as to assure as comparable stages of development as possible in different sources of material.

The infra-red gas analyzer apparatus employed was a closed measurement system and consisted of a Beckman 15A analyzer, a Hartmann & Braun T multipoint recorder, a water-jacketed plexiglass assimilation chamber and auxiliary equipment for adjusting air flow (0.9 1 min^{-1}) and temperature. Desired temperatures were achieved using a Therrnomix II pump and heater which circulated tap water through the water jacket of the chamber and also maintained it to within ±1° C of the desired temperature. Excess water was removed from the air stream by cooling it in an ice bath before the CO_2 measurement. The air was rehumidified in a water flask before it re-entered the assimilation chamber in which the air was maintained at near 80% relative humidity. The temperature was monitored by thermocouples placed inside the chamber. The chamber volume was 1140 ml and the total volume of the system 1890 ml.

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Five high pressure mercury vapour lamps (Philips) were used as light sources when making photosynthesis and photorespiration measurements. The irradiance at the chamber bottom was 27 Wm^{-2}. The spectral distribution of this light source and other details of the methods are given by PELKONEN (1973).

Net photosynthesis was determined at four temperatures, 13, 18, 23, and 28° C, by measuring the time required to lower the concentration of CO_2 from 300 to 275 ppm and by converting these values to mg CO_2 per g dry weight of needles and hour. Dark respiration was measured by the analogous method using the range 275 to 287 ppm CO_2.

The CO_2 compensation points were determined at 20° C, by allowing the CO_2 concentration in the air passing a seedling to reach equilibrium. The CO_2 concentration was recorded when no changes were detected over a time period of 15 minutes. In order to accelerate this measurement, the CO_2 concentration was lowered to near compensation point using a bypass to a flask containing NaOH solution.

Photorespiration was calculated from measured values of photosynthesis at the given CO_2 concentration and the CO_2 compensation points, by the modified extrapolation method (DECKER, 1957; FORRESTER *et al.*, 1966 a, 1966 b; TREGUNNA *et al.*, 1966; BRIX, 1967; ZELAWSKI, 1967; LUUKKANEN and KOZLOWSKI, 1972). The method is based on the assumption that there is a linear response of photosynthesis to CO_2 concentration, the slope of the response curve being called the "carboxylation efficiency". Values of photorespiration were obtained by multiplying carboxylation efficiency by the value of the CO_2 compensation point in ppm (FORRESTER *et al.*, 1966 a). Total photosynthesis was calculated by adding together the values of net photosynthesis and photorespiration.

The amounts of chlorophyll in the needles were determined from 25 mg samples of fresh needles. The pigment was extracted at 4° C in a glass piston homogenizer using 80% cold acetone to which some $MgCO_3$ had been added. After centrifugation, the absorbances were measured at 663 and 645 nm. The MACKINNEY-ARNON equations suggested by ŠESTÁK (1971) were used to obtain the amounts of chlorophyll *a*, chlorophyll *b*, and total chlorophyll in the samples.

Results

Photosynthetic Capacity. Seedlings from the southern stand (A) had a photosynthetic capacity, or photosynthetic rate per seedling, about four times as large as the seedlings from Northern Finnish stands B and C *(Fig. 1)*. This difference was due to the considerably greater size of the southern seedlings. *Fig. 1* shows also the means and standard deviations of the shoot growth in the different families. An analysis of variance confirmed that the difference between the two northern stands was not statistically significant as far as photosynthetic capacity, plant size or growth were concerned.

Variations in photosynthetic capacity within stands (among families) are demonstrated in *Fig. 1* for each stand separately. Differences in plant size referred to above explained much of the variation in photosynthetic capacity. In one northern stand (B) the variation among families was highly significant ($P < 0.01$). Analyses of variance did not show clear differences among families in the remaining stands, but a separate closer examination of them (a t-test) also revealed some significant differences ($P < 0.05$) among the means.

Photosynthetic Efficiency. On an average, seedlings from one northern stand (C) had the highest and seedlings from the southern stand (A) the smallest photosynthetic efficiency, or photosynthetic rate per unit of needle dry weight *(Fig. 2)*.

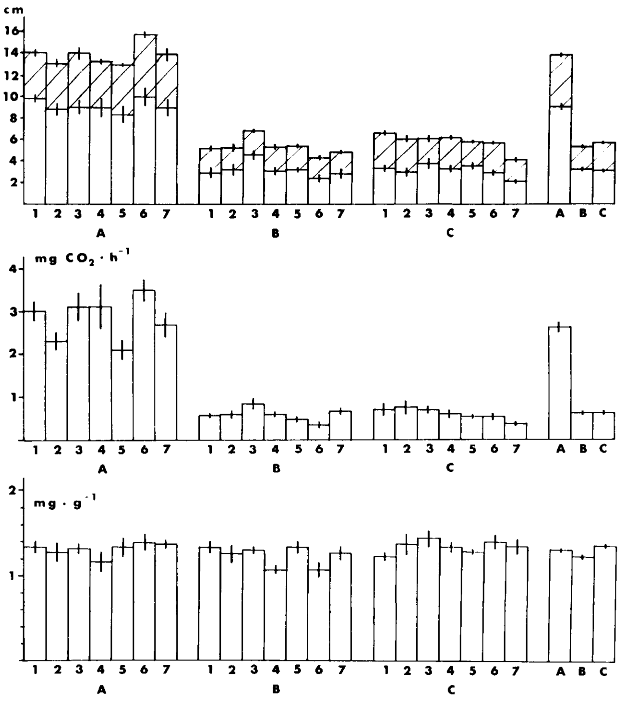

Fig. 1. — Means of shoot growth during two years (above), photosynthetic capacity at 18° C (middle), and chlorophyll *a* amounts (below) in each of seven families of three spruce stands and the stand averages. Standard deviations are indicated by vertical bars. *Above:* Shaded columns show the shoot growth during the second and open columns that during the first growing season, whole columns show the seedling height. *Middle:* Photosynthetic capacity is expressed per unit time and whole seedling. *Below:* Amounts of chlorophyll *a* per g of fresh weight are indicated.

The difference in the mean photosynthetic efficiency between Northern and Southern Finnish stands was significant ($P < 0.05$) at all temperatures, but stands B and C, both from Northern Finland, did not differ from each other at any temperature. At 13° C, or the lowest tempera-

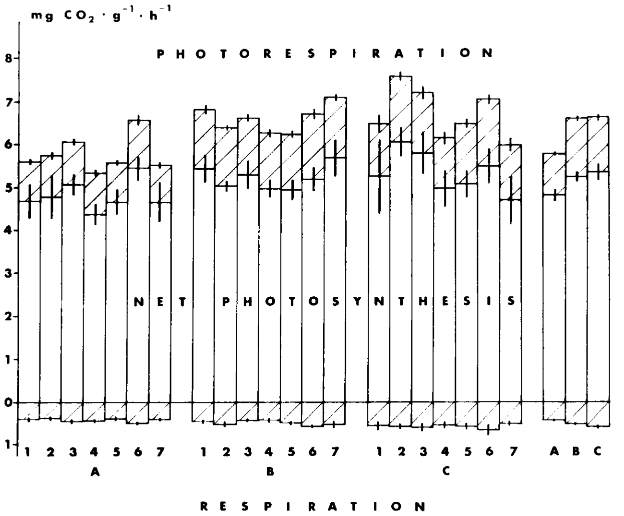

Fig. 2. — Means of photorespiration (at 20° C, shaded columns, above), net photosynthesis (at 18° C, open columns), and dark respiration (at 20° C, shaded columns, below) in each of seven families of three spruce stands, and the stand averages. Standard deviations are indicated by vertical bars. All rates are expressed per unit of dry weight of needles.

ture used during the experiments, the variation among the stands was most conspicuous.

In all the stands, the net photosynthetic efficiency reached its highest value at 18° C. The overall average in the complete material was 5.14 mg g^{-1} h^{-1} (dry weight) at this temperature. *Fig. 2* demonstrates the variation in family means of this parameter within each stand respectively.

An examination of different families within the stands showed that the only significant ($P < 0.05$) differences in photosynthetic efficiency among families were to be found in the Southern Finnish population (A) at 23° C. In general, the variation among families of any particular stand was greatest at 18° C, the temperature at which maximum photosynthetic efficiency was reached. As regards different stands, the smallest variation was found in stand B of Northern Finland. In this stand the range of variation among families was very small, in contrast to the variation of photosynthetic capacity. However, the significance of the variation of photosynthetic efficiency among families was not much lower in this stand compared with C. This result indicated that in stand B, the variation within families was relatively smaller than in the remaining stands.

CO$_2$ Compensation Points and Photorespiration. Only one temperature, 20° C, was used in these measurements. Northern seedlings had highly significantly ($P < 0.001$) higher compensation points than the southern ones. An average over the whole material was 56.9 ppm, the higher stand means being 61.2 ppm (B) and 60.0 ppm (C), and the lowest 49.4 ppm (A).

Within stands, the CO$_2$ compensation points differed significantly ($P < 0.05$) among families in one northern stand (B). Photorespiration *(Fig. 2)* largely followed the variation pattern that was found in the case of the CO$_2$ compensation points and photosynthetic efficiency. The highest rates of photorespiration (per unit of needle dry weight) occurred in northern stands. On an average, photorespiration was nearly 20% of the total photosynthesis, or about 1 mg g^{-1} h^{-1} at 20° C. Family averages of photorespiration ranged from 0.89 mg in family No. 7 in the southern stand (A) to about 1.5 mg g^{-1} h^{-1} in most of the northern families (c. f. *Fig. 2*).

Dark Respiration. Average dark respiration (which, as in the case of photorespiration, was measured at 20° C and expressed as mg CO$_2$ per unit of time and needle dry weight only) amounted to 0.48 mg g^{-1} h^{-1} in the complete material. This corresponded to somewhat less than 10% of the total photosynthesis at this temperature *(Fig. 2)*. Similarly to photosynthetic efficiency, compensation points and photorespiration, the dark respiration also reached the lowest values in the Southern Finnish progenies (A). The difference in dark respiration between northern and southern populations was highly significant ($P < 0.01$). In two stands, one from Southern (A) and another from Northern (B) Finland, dark respiration also varied significantly ($P < 0.05$) among families within each respective stand. In the third population (C), differences in dark respiration among families remained small, which in part resulted from the fact that the variation within families was relatively larger in this than in any other stand.

Chlorophyll Amounts. Highest amounts of chlorophyll *a* were found in one northern stand (B) which significantly ($P < 0.05$) differed from the other northern stand (C) in this respect. Seedlings from stand B also had significantly ($P < 0.05$) lower amounts of chlorophyll *b* and total chlorophyll than those of the two remaining stands. The average amounts of total chlorophyll in each family as well as the stand means and their standard deviations are also shown in *Fig. 1.*

Relationships Between CO$_2$ Exchange Parameters. Seedlings with a high photosynthetic rate per unit of foliage also had a high photorespiration rate per unit of foliage. Other highly significant ($P < 0.001$) correlations were also found between CO$_2$ exchange parameters, but these were, however, probably caused by the differences among stands rather than by actual cause-and-effect relationships.

Table 1 shows a summary of the ratios between parameters of CO$_2$ exchange, including photosynthetic rate per unit of foliage, photorespiration, and dark respiration. Only measurements at 18° C are included in this table, which shows the stand means. The Southern Finnish families (A) had higher photosynthesis/photorespiration ratios than the Northern Finnish families B and C. This difference was also highly significant ($P < 0.001$). The photorespiration/dark respiration ratios, on the other hand, were lower ($P < 0.01$) in the Southern Finnish families (A) as compared with stands B and C. The ratios of photosynthesis to dark respiration did not show any statistically significant variation. As regards the differences in ratios within the stands, in one northern stand (C) the photosynthesis/photorespiration ratio varied highly significantly ($P < 0.01$) among families of that stand. Significant ($P < 0.05$) varia-

Table 1. — Average ratios between some CO$_2$ exchange parameters in three stands and the means over all stands[1]).

Stand	Ratio					
	Photosynthesis/ Photorespiration		Photosynthesis/ Dark respiration		Photorespiration/ Dark respiration	
	Mean	F-value	Mean	F-value	Mean	F-value
Southern Finland						
A (Loppi)	5.02	0.45	11.2	0.57	2.34	0.62
Northern Finland						
B (Laanila)	3.84	1.87	11.1	1.51	2.89	0.59
C (Pallasjärvi)	3.94	3.46**	11.5	0.55	2.91	0.55
Mean	4.27	69.76***	11.4	0.31	2.72	6.84**

[1]) Degrees of freedom for the F-value: 6 and 35 within a stand, 2 and 123 in the whole material, respectively.

Significance levels: ** $P < 0.01$
*** $P < 0.001$

tion was also found in a separate t-test among families of stand B when the photosynthesis/photorespiration or photosynthesis/dark respiration ratios were concerned, and in the Southern Finnish stand (A) when the photorespiration/dark respiration ratio was studied.

Discussion

According to the present study, the CO$_2$ metabolism was distinctly different in spruce seedlings from Northern and Southern Finnish populations. However, the different pretreatments of seedlings from northern and southern stands has to be kept in mind when these results are studied. A variation among progenies of individual trees within a stand was also established, although the small number of experimental plants (seven trees per stand and six half-sibs per parent tree) rendered statistical evidence of the variation often difficult. Higher rates of photosynthetic rate per unit of foliage in northern populations, as found in the present work, is in accordance with earlier investigations. Similar results have been obtained in Scots pine (Gordon and Gatherum, 1968) and in *Betula pubescens* (Vaarama, 1970) in Finland.

Half-sib families differed in various ways within a stand when different populations were analyzed. For instance, in one northern stand (B) the photosynthetic rate per unit of foliage varied much less among families than in any of the two remaining stands. Stand C, although geographically closer to B, much resembled the Southern Finnish stand (A), as far as photosynthetic efficiency was concerned.

The smaller size of seedlings in northern populations has been suggested as a cause of higher photosynthetic rate per unit of foliage in these plants as compared with seedlings of southern origin and grown in comparable condition (Gordon and Gatherum, 1968). This may account for the variations in photosynthetic efficiency which have been found especially in laboratory experiments, often conducted at relatively low light intensities. In the present study, part of the observed variation in photosynthesis may be explained by plant size, since a slight inverse relationship was found between photosynthetic rate per unit of foliage and the dry weight of needles.

In the present study, the CO$_2$ compensation points and rates of photorespiration also clearly differed between southern and northern populations. High compensation points in northern trees may in part be a result of differences in the response of CO$_2$ exchange to temperature in different geographic origins of trees. In Douglas-fir, for instance, photorespiration has been found to double when the temperature increased from 20 to 28^0 C (Brix, 1967). In poplar clones the increase in photorespiration varied from 60 to 260% over a temperature increase from 20 to 30^0 C among six different clones; the average increase among clones was 120% (Luukkanen, 1971). On the other hand, no clear differences were found in the present study as regards optimum temperatures for net photosynthesis between northern and southern spruces.

Rates of dark respiration were higher in northern spruce seedlings than in the material of southern origin. Similar results have been earlier obtained by Schmidt (1961) as well as by Pisek and Winkler (1959) in spruce.

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Summary

The CO$_2$ exchange of half-sib progenies from two Northern Finnish and one Southern Finnish stand of Norway spruce was investigated using two-year old seedlings and a closed IRGA system. Rates of photosynthesis, dark respiration, and photorespiration, as expressed per unit of needle dry weight, as well as the CO$_2$ compensation points were higher in Northern Finnish than in Southern Finnish spruce seedlings. More distinct differences were found in rates of photosynthesis and photorespiration than in rates of dark respiration.

The size of northern spruce seedlings was, despite higher photosynthetic rate per unit of foliage in these plants, considerably smaller than that of southern spruce seedlings. This also accounted for the higher photosynthetic rate per seedling of southern spruces. The size and hence photosynthetic rate per seedling varied significantly among families of one northern stand. The variation of photosynthetic rate per unit of foliage among families was largest at 18^0 C (the temperature of maximum net photosynthesis rates), and, among stands, in the Southern Finnish population. However, one Northern Finnish stand resembled much the Southern Finnish population in this respect and differed clearly from the other northern stand.

The CO$_2$ compensation points differed significantly between Northern and Southern Finnish populations of spruce and also among families of one Northern Finnish stand. At 20^0 C, photorespiration amounted to about 20% of total photosynthesis, as compared to less than 10% for the ratio of dark respiration to total photosynthesis at this temperature. Dark respiration varied significantly among families in the Southern Finnish and in one Northern Finnish stand.

Variables that described plant size generally correlated inversely with photosynthetic or dark respiration rate per unit of needle dry weight. Amounts of chlorophyll appeared to exhibit a positive relationship with photosynthetic rate per unit of foliage and a negative one with dark respiration, but neither of these correlations proved to be statistically significant.

Key words: Photosynthesis, photorespiration, dark respiration, CO$_2$ compensation point, Norway spruce, half-sib families.

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