THE SEASONAL VARIATION IN STEM AND COARSE ROOT RESPIRATION OF A 20-YEAR-OLD SCOTS PINE (Pinus sylvestris L.)

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ABSTRACT

The gas exchange of a 20-year-old stand of Scots pine was studied during a five-year-period using a measuring system that allowed in situ measurements to be carried out throughout the year; the study was carried out in Central Sweden, as part of the Swedish Coniferous Forest Project (SWECON).

The seasonal changes in stem- and coarse-root respiration rates are presented for one year. Some results of photosynthesis are also given to permit the importance of respiration upon the carbon balance of the tree to be assessed.

The period of net photosynthesis was eight months (April to November). Maximum photosynthetic production occurred in August when the current foliage was fully developed. Net photosynthesis started as soon as the ground thawed and water was available and continued until irradiance in late autumn was too low.

Stem respiration rates were low during late winter and early spring but increased as soon as the air temperature exceeded 0 °C. Although the diurnal course of stem respiration was closely linked to stem temperature, respiration rate at a given temperature was higher during the summer months than at other times of the year.

Coarse-root respiration rates were measured when the ground was not frozen (mid-May to November). Root respiration rate, like stem respiration rate, was mainly determined by temperature but seasonal variation in respiratory activity resulted in a maximum in late September.

INTRODUCTION

To calculate annual carbon balances or to study the relationship between photosynthetic production and growth both the amount of carbon fixed in photosynthesis and the amount lost via respiration must be known. The amount of information from field measurements of stem and root respiration in conifers is especially limited (cf. Linder, 1979). In situ measurements of stem respiration rates in conifers have been made by Johansson (1933), Geurten (1950), Kinerson (1975), Negisi (1975, 1978ab) and Linder and Troeng (1980). Most of these investigations covered a small part of the season only. In a controlled-environment room, Rook and Corson (1978) performed in situ measurements of stem respiration rate on a 7 m Pinus radiata.
Most information on stem and branch respiration rates has been obtained from detached samples. This technique has been questioned more than once, since the cut surfaces might give a wound reaction, resulting in increased respiration (cf. Zelawski, 1960ab).

No information about rates of root respiration is available for trees under field conditions. Our knowledge is restricted to rates measured on potted seedlings or detached root systems under nursery or laboratory conditions (Eidmann, 1943; Eidmann & Schenke, 1967; Keller & Wehrmann, 1963; Negisi, 1966; Keller, 1967; Szaniawski & Adams, 1974).

A few estimates only of the influence of respiration upon the annual carbon balance of a tree are available (Tranquillini, 1979). Since the species, the age of the plant material and the methods used differ, it is difficult to compare the results obtained. Tranquillini and Schütz (1970) estimated the respiratory carbon losses from stem and branches for a 76-year-old trees of *Pinus sylvestris* and *Larix decidua* at the timberline to be 23.1 and 16.9 per cent of the annual net photosynthetic production, and suggested that the carbon losses could be twice as high down in the warmer valleys. For a 15-year-old Scots pine in Central Sweden, the stem and branch respiration accounted for only 3.8 per cent of the annual photosynthetic production (Agren et al., 1980). The available estimates of the importance of root respiration differ as greatly as do those for stem respiration. Eidmann (1962) reported that root respiration in a number of coniferous seedlings accounted for 40–60 per cent of the annual photosynthetic production, while Tranquillini (1959) estimated the respiratory carbon losses from roots to be 7.3 per cent for seedlings of *Pinus sylvestris* growing at the timberline.

One of the aims of the Swedish Coniferous Forest Project (SWECON) is the construction of simulation models for predicting the primary production of a forest dominated by Scots pine. To achieve this, a better understanding of the processes and factors regulating growth was needed. The present study was carried out as an integrated part of the project, to increase the understanding of the dynamics of primary production in Scots pine.

The present paper presents some results on the annual course of stem and coarse-root respiration in a 20-year-old Scots pine tree. The results are compiled into an estimated annual carbon budget for the tree.

A more detailed description of the research programme on gas exchange carried out within SWECON can be found in Linder and Troeng (1980).
MATERIALS AND METHODS

The measurements were performed in a 20-year-old stand of Scots pine (*Pinus sylvestris* L.) at the Jädraås Research Site of SWECO in Central Sweden (60°48'N.; 16°30'E.; alt. 180 m). Detailed descriptions of the stand and the site are given by Flower-Ellis *et al.* (1976) and Axelsson and Bräkenhielm (1980).

The studies of gas exchange within the stand were carried out using an open gas exchange system with 16 temperature-controlled assimilation chambers. Carbon dioxide was measured by infra-red gas analysis (UNOR 2, Maihak, Hamburg, FRG) and water vapour concentration by dew-point meters (Walz Mess- und Regeltechnik, Eltersdorf, FRG). Each of the 16 sample lines was analysed at least every 45 minutes throughout the year, except during short periods when the system had to be repaired. The system was described in detail by Linder *et al.* (1980).

The results presented in this report were obtained from a single representative tree on an untreated plot during 1978. The tree was harvested in the late spring 1980, and some of the structural data are compiled in Table 1.

TABLE 1.
Structural data for the tree on which the measurements were performed. The tree was harvested in late April, 1980 and the root system was excavated one month later. The tree was 20 years old and had 12 live whorls.

<table>
<thead>
<tr>
<th></th>
<th>Weight g</th>
<th>Area dm²</th>
<th>Length m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stem</td>
<td>4364</td>
<td>77.4</td>
<td>5.0</td>
</tr>
<tr>
<td>Branches (needle bearing)</td>
<td>1603</td>
<td>22.7</td>
<td></td>
</tr>
<tr>
<td>Branches (without needles)</td>
<td>1163</td>
<td>19.3</td>
<td></td>
</tr>
<tr>
<td>Needles</td>
<td>3160</td>
<td>917.2</td>
<td></td>
</tr>
<tr>
<td>Taproot</td>
<td>394</td>
<td>7.3</td>
<td>0.6</td>
</tr>
<tr>
<td>Coarse roots &gt; 5 mm</td>
<td>794</td>
<td>71.2</td>
<td>21.5</td>
</tr>
<tr>
<td>Coarse roots 2-5 mm</td>
<td>161</td>
<td>73.3</td>
<td>83.3</td>
</tr>
</tbody>
</table>

Needle area was measured by a leaf-area meter (LI-3000, Lambda Instrument Co. Inc., Nebraska, U.S.A.) and the area of the stem and the branches was calculated using the length and the diameter in the middle of each internode. The
weights were determined after drying to constant weight at 85 °C.

The root system of the tree was excavated as soon as the soil had thawed in mid-May. The roots were excavated by hand and followed down to a diameter between 1-2 mm. The area of the coarse roots was determined by measuring the diameter every 50 cm along the roots. For roots less than 5 mm in diameter, the total length was measured and the projected surface area was determined using the leaf-area meter. From the area and length an average diameter was derived and used for calculating the total area of finer roots (2-5 mm).

Stem respiration rate was measured on a nine-year-old stem internode that increased in surface area from 3.8 to 4.4 dm² during 1978. Coarse-root respiration rate was measured on a root 20 cm away from the stump. The area of the root was at the end of the season 0.8 dm². Stem respiration was measured throughout the year (January November) and coarse-root respiration during the period when the ground was not frozen (mid-May November).

The chambers used for the measurements of stem and coarse-root respiration rate were split PVC tubes with top and base-plates of 8 mm thick PVC. The stem chamber was 230 mm long with an inside diameter of 104 mm and the root chamber was 150 mm long and with an inside diameter of 52 mm. The two halves were screwed together around the stem or root with seals of foam-rubber. The stem chamber was surrounded by a radiation shield of white-painted aluminium. Air, stem, and root temperature was recorded using thermocouples. For further details concerning the chambers and the measuring system see Lind 'er et al. (1980).

The radial changes of the stem were measured by a strain gauge transducer (Hellkvist et al., 1975) placed in the middle of the living crown.

RESULTS

Diurnal variations

The course of stem respiration rate during the day followed the fluctuations in stem temperature closely (Figure 1). If stem respiration rate was related to air temperature instead, a hysteresis loop was obtained caused by inertia in the warming and cooling of the stem. However, there was no such relationship between the diurnal changes in stem radius and temperature. The diurnal shrinkage and swelling of the stem made it impossible to distinguish within-day growth from swelling (Figure 1B). With the onset of transpiration in the morning, the stem radius decreased, and no pronounced recovery was observed.
until transpiration ceased in the evenings (Figure 2). It was not even possible to separate radial growth from swelling during rainy days unless there was a long spell of rain.

The diurnal course of coarse-root respiration rate followed soil temperature in a similar manner as stem respiration followed stem temperature.

**FIGURE 1.** The diurnal course of (A): stem temperature (solid line), water concentration deficit (broken line) and (B): stem respiration rate (solid line), radial change (broken line) during a week in July.

**FIGURE 2.** The average diurnal course in stem radius during a week in July in relation to transpiration rate. The transpiration rate was calculated from stomatal conductance and the ambient water concentration deficit (cf. Linder & Troeng, 1980).
The seasonal variation in stem respiration rate largely followed the seasonal variation in air temperature (Figure 3). The highest rates of respiration were found during the period of stem growth (mid-May to August). Throughout the period to November, the Q_{10} of respiration was close to 2 (Figure 3C). The two high Q_{10} values in April and May are erroneous, caused by a very rapid rate of change in the respiration rate so that it was not possible to obtain a correct ten-day average value of the Q_{10}. It was considered meaningless to calculate Q_{10} for the winter months when the stem was frozen most of the time.

![Figure 3](image)

**FIGURE 3.** The seasonal variation in (A): Maximum-, mean-, and minimum temperature; (B): Stem respiration rate, and (C): Q_{10} of stem respiration from April to November 1978. The presented values are mean values for ten-day-periods.

The respiration rate at a certain temperature also changed over the season (Figure 4). The decline in respiration rate at the end of May and beginning of June coincided with a spell of dry and warm weather but it is not possible from the present investigation to determine which factor that caused the drop in respiration rate.

The relationship between respiration rate and stem temperature, throughout the season, was an exponential function with a Q_{10} close to 2, as shown in Figure 4. However, if the relationship is calculated from the average rates of respiration and average temperatures over ten-day periods, a linear relationship is obtained when the mean temperature is above 0 °C (Figure 5).
FIGURE 4. The change in response of stem respiration to stem temperature during 1978. All samples have been divided into ten-day periods and thereafter assorted into temperature classes. The values presented are the average in each class. Broken lines indicate that the temperatures in question were not represented during that period. The enclosed stem area increased during the period of measurement from 3.8 to 4.4 dm$^2$. Number of samples 8898.

FIGURE 5. The relationship between daily mean air temperature and daily respiration rate from January to November 1978. The values are the averages per ten-day period.

Coarse-root respiration rate increased during the summer, the maximum rates occurring in late September when stem respiration rate had started to decrease (Figure 6). The peak rate expressed per unit surface area at 10 °C was higher for the root (2.5 mg CO$_2$ dm$^{-2}$ h$^{-1}$) than for the stem (1.75 mg CO$_2$ dm$^{-2}$ h$^{-1}$).
The seasonal changes in stem and root respiration were similar but the increase in root respiration occurred one month later in spring, and the decline in the autumn was also delayed by one month (Figure 7). The highest rates of respiration were found in the period June to August for the stem and during July to September for the coarse root. The total annual respiratory loss for the stem was 8.5 g CO$_2$ dm$^{-2}$ and for the root 7.9 g CO$_2$ dm$^{-2}$.

FIGURE 7. The seasonal course in photosynthesis (solid line), stem respiration (broken line), and coarse-root respiration (dotted line) of a 20-year-old Scots pine. The presented values were based upon the structure given in Table 1. Root respiration during the winter months was calculated using records of soil temperature. For absolute values see Table 2.
Annua\textsuperscript{al} carbon budget

The amount of information available was insufficient to allow a detailed carbon budget to be drawn up, so some simplifications and estimates were made.

The tree structure used was the structure as found at the harvest in spring 1980 (Table 1). The photosynthetic production was calculated for each-age class of needles separately, using data from two assimilation chambers that had been on the tree throughout 1978 (Troeng & Linder, unpubl.). To account for the decrease in photosynthetic efficiency with increasing needle age the relationships given by Linder and Troeng (1980) were used.

The amounts of stem and coarse-root respiration was estimated from the results presented in this report using the area of stem and coarse roots, respectively.

Needle and current-shoot production was set equal to the production during 1979, as determined in the harvest. Total root production was estimated as suggested by Agren et al. (1980), using the production figures given by Persson (1978), where the amount of root belonging to the tree was calculated in relation to the basal area of the tree at 10 cm height (78.5 cm\textsuperscript{2}).

After harvest, the growth of the stem section enclosed for measurements of respiration rate was determined for each year by cutting off one growth-ring at a time with a scalpel. During 1978 the growth of the section in the chamber was 29.2 g dw (14.6 g C), and during the same year the total respiratory carbon loss was 37.4 g CO\textsubscript{2} (10.2 g C); for each gram of carbon respired there was an increase of 1.43 g C in the stem biomass. This relation was used to obtain an estimate of total stem growth (256 g C). Branch respiration was estimated by assuming that the respiratory carbon loss, expressed per unit surface area, was 50 per cent of that of the stem (cf. Agren et al., 1980). Branch growth was then estimated in the same way as for the stem.

The amount of coarse-root (> 2 mm) respiration was calculated from chamber measurements and the measured surface area assuming that both coarse-root fractions had the same respiration rate per unit surface area.

The production of fine roots (0-2 mm) was estimated according to Agren et al. (1980) to be 2443 g C and the production of coarse-roots (> 2 mm) to be 120 g C.

A theoretical estimate of the cost of biomass production in Scots pine (Axelsson & Agren, 1976) using the information from Penning de Vries (1974) gave a respiration cost in carbon units of 28 per cent. Using this figure for the fine-root fraction, a 'growth respiration' of 684 g C was obtained. If the
same relationship was used for the stem section on which the respiration measurements were performed, a ratio between maintenance and growth respiration of 1.5 was obtained. Assuming this ratio to be valid for the fine-root fraction, this gives a maintenance cost of 1026 g C during the year. However, the fine roots have a high turnover rate and the value should therefore be divided by 7 (Persson, 1978), giving a total fine-root respiration of 831 g C yr\(^{-1}\)

The various components in the estimated carbon budget are presented in Table 2 both in absolute values, and as a percentage of the annual photosynthetic production.

**TABLE 2**
An estimated annual carbon budget for a 20-year-old Scots pine. The calculation was based upon the structure of the tree when harvested in spring 1980 (Table 1) and upon gas exchange measurements from 1978. The dry weight of the biomass was converted into carbon assuming a 50 per cent carbon content of the biomass (cf. Larcher, 1969).

<table>
<thead>
<tr>
<th>Component</th>
<th>g Carbon</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PHOTOSYNTHESIS</strong></td>
<td>4976</td>
<td></td>
</tr>
<tr>
<td><strong>RESPIRATION</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stem</td>
<td>179</td>
<td>3.6</td>
</tr>
<tr>
<td>Coarse-roots &gt; 5 mm</td>
<td>169</td>
<td>3.4</td>
</tr>
<tr>
<td>Coarse-roots 2-5 mm</td>
<td>157</td>
<td>3.2</td>
</tr>
<tr>
<td>Fine roots</td>
<td>831</td>
<td>16.7</td>
</tr>
<tr>
<td>Branches</td>
<td>68</td>
<td>1.4</td>
</tr>
<tr>
<td><strong>GROWTH</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Needles</td>
<td>580</td>
<td>11.7</td>
</tr>
<tr>
<td>Current shoots</td>
<td>158</td>
<td>3.2</td>
</tr>
<tr>
<td>Stem</td>
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</tr>
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<td>Branches</td>
<td>97</td>
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<tr>
<td>Coarse roots</td>
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<td>2443</td>
<td>49.1</td>
</tr>
<tr>
<td></td>
<td>5058</td>
<td>101.7</td>
</tr>
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</table>

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DISCUSSION

The prospect of obtaining an indirect measure of radial growth from measurements of stem respiration was pointed out by Johansson (1933), who divided the total respiration into 'dormant' and 'productive' respiration, terms that we now refer to as 'maintenance' and 'growth' respiration. However, until we can find a technique to 'correct' our measurements for the diurnal shrinkage and swelling of the stem, it will not be possible to study stem growth with a high resolution in time. Even if it was possible to correct for water-induced changes in stem radius, other problems affect attempts to obtain an indirect measure of growth. The first problem is that the amount of living cells is not constant during the season, hence it is not possible to subtract the maintenance respiration without estimating the amount of living biomass at any point in time. The second problem is that volume and density do not increase in parallel, and the wall thickness differs between early wood and late wood (cf. Zumer, 1969ab).

The seasonal changes in stem respiration rate were in accordance with earlier reports (Johansson, 1933; Tranquillini & Schütz, 1970; Linder & Troeng, 1980). The observed decrease in stem respiration rate during the warm and dry spell in early summer could have been caused by water stress (Negisi, 1975). However, during the same period a decrease in the carbohydrate reserves of the needles was observed by Ericsson (1980). This suggests that there may have been a shortage of carbohydrates in the stem caused by favourable conditions for cambial growth at the same time as the photosynthetic production was reduced by supra-optimal temperatures.

The increase in respiration rate during early summer can not only be explained by the 'growth respiration' but must to some extent also be an effect of increased maintenance respiration caused by the increase in respiring biomass and an acclimation to the prevailing temperature (cf. Rook, 1969). The decrease in respiration rate in the autumn may be explained in a similar way as a result of a decrease in living biomass and further acclimation to lower temperatures.

The linear relationship found between mean temperature and mean respiration rate was earlier reported for Norway spruce by Johansson (1933) using weekly means of temperature and stem respiration rates. A relationship such as the one shown in Figure 5 would be very useful when trying to predict the amount of stem respiration during the season, since once the relationship had been established, temperature records only would be needed for the prediction.
However, more data must be analysed to test whether the relationship is the same from year to year.

If the seasonal course of coarse-root respiration rate to some extent reflects growth, the radial growth of coarse roots occurred mainly when the aboveground growth had stopped and the supply of assimilates was high (cf. Figure 6 and 7). The late start of radial growth in coarse-roots is in agreement with the findings of Ladefoged (1952), Head (1968) and Wargo (1979) and an autumn peak in root respiration rates was reported for *Larix decidua* by Tranquillini (1979). The relatively high value for annual coarse-root respiration (7.9 g C dm\(^{-2}\)) can to some extent be explained by a higher loss during the winter months, as compared with the stem (17.8 and 9.3 per cent respectively), and by relatively warm soil during the autumn months. Inspection of the harvested root system suggested that the root section that had been enclosed in the respiration chamber from mid-May to November had grown somewhat more in diameter during 1978 than had other coarse-roots. The increase in radial growth could have been an effect of 'exposure' and reduction of pressure (cf. Fayle, 1968). An overestimation of coarse-root respiration may therefore have been introduced in the carbon budget (Table 2).

In spite of the estimates made in calculating the carbon budget, the budget balanced surprisingly well (Table 2). However, even large errors in most of the estimates would not change the main features of the budget which are similar to that presented by Agren *et al.* (1980) for a five year younger tree from the same site. It should be noted that the site in question is extremely poor and dry which can be one explanation for the high cost of growth and maintenance of the root system.

It is apparent that much more information is needed before we can understand and predict the dynamics of primary production of trees growing under natural conditions; especially important is a better understanding of the dynamics of root production.

ACKNOWLEDGEMENTS

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REFERENCES


