Whole-plant CO$_2$ exchange of seedlings of two *Pinus sylvestris* L. provenances grown under simulated photoperiodic conditions of 50° and 60°N

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Summary. Seedlings of Scots pine (*Pinus sylvestris* L.) from Russia (59°58'N) and Poland (53°34'N) were grown for 4 months in controlled environment chambers, simulating the photoperiod conditions of 50° and 60°N. The Russian population grown at 50°N showed earlier height growth cessation than the Polish population. Photoperiodic conditions of 60°N increased proportional allocation of dry mass to shoots and lowered allocation to roots in the Russian population, which also had greater allocation to roots than the Polish population in both treatments. Total non-structural carbohydrate concentrations in roots and secondary needles of both populations were significantly higher at the end of the 4 month growing season at 50° compared to 60°N. Net photosynthesis rates were similar for both provenances and both treatments. The rate of transpiration was higher and water-use efficiency lower for plants grown in long-day conditions of 60°N. The mean respiration rate of roots ranged between 30 and 36 nmol CO$_2$ · g$^{-1}$ dry mass · s$^{-1}$ and was 2–4 times higher than values observed for needles. Root respiration rates were greater in the Polish than the Russian population. Despite this, the greater allocation to root dry mass of the Russian population resulted in greater root respiratory cost as a proportion of daily carbon gain. Overall, root respiration accounted for between 18 to 34% of the total daily net carbon assimilation of these populations. Root and total respiration as a proportion of net daily carbon assimilation were greater at 50° than 60°N. Mean net integrated CO$_2$ gains were 2.2–2.5 mmol CO$_2$ · day$^{-1}$ for seedlings from Russia compared to 3 mmol CO$_2$ · day$^{-1}$ for Poland.

Key words: Scots pine – Photoperiod – Growth cessation – Water-use efficiency – Carbon gain

Introduction

The dependence of Scots pine (*Pinus sylvestris*) seedling growth on photoperiod was known from the early 1930s (Bogdanov 1931) and later (Wareing 1950a, b 1951; Wassink and Wiersma 1955; Downs and Borthwick 1956; Vaartaja 1959; Koski and Sievänen 1984). The influence of photoperiod can be especially important for plants grown from seeds transferred long distances from the place of origin. Results of provenance experiments with Scots pine showed a significant differentiation in growth among populations with respect to long distance transfer of plants. It was found that northern populations, from 57–67°N, are sensitive to transfer to the south, as evident in reduced height growth and above ground volume production compared to their native latitude (Giertych 1979; Giertych and Oleksyn 1981). At the same time, populations originating from the central part of the species range in Europe, from 54–57°N, grow as well or better at the northern latitudes as local provenances. The nature of these growth differences is not fully understood.

Most of the controlled experiments in this field have been performed with fixed day/night photoperiod and temperature regimes, which deviate far from the natural variation of daylength and temperature at any given latitude. Under such conditions it is not possible to judge whether growth or other changes are due to photoperiod or are a result of differences in temperature or quantum flux density over the experimental period or other factors (Oden and Dunberg 1984). In contrast to previous studies our treatments tracked the natural changes in day and night length over the course of the growing season. Also, diurnal variation in incident light was introduced to simulate light changes over the course of the day. At the same time daily integrated light levels were balanced among the treatments in order to eliminate the possible confounding effect of unequal quantum flux due to differences in daylengths.

Relatively little is known concerning photosynthesis, respiration and/or whole plant carbon balance of woody plants under different photoperiods. The weakest link in such estimations is, in general, insufficient information
concerning root respiration (Linder and Troeng 1981). The present study was undertaken in order to determine the effects of photoperiodic regime on needle photosynthesis, water-use efficiency and transpiration; root; and needle respiration; and whole-plant carbon gain of two provenances of Scots pine originating from northern and central parts of the species' European range.

Materials and methods

Plant material and growth conditions. In early January 1990, seeds of two Scots pine (Pinus sylvestris L.) provenances originating from the Forest District of Konddezskoe, Russia (59°58'N, 33°30'E) and Milomlyn, Poland (53°34'N, 20°00'E), were sown in 0.35 l pots filled with an 80:20% sand/forest soil (v:v) mixture. Growth responses alone of 22 additional provenances not used in this study were presented elsewhere (Oleksyn et al. 1992). The seeds were soaked overnight in distilled water before sowing. Eight pots with 12 seeds of each population were sown. The pots were watered daily with a modified half-strength Hogland's solution. Two weeks after sowing all pots were treated with a metasal fungicide (Ridomil 2LE, Ciba-Geigy) in order to prevent damping-off.

Four pots of each population were placed in two controlled environmental growth chambers (Conviron Model E-15, Winnipeg, Manitoba, Canada.) Germination occurred under a 16/8 h day/night photoperiod, with a photosynthetic photon flux density (PPFD) at plant level of 286 ± 21 μmol m⁻² s⁻¹, as provided by two 1000 W metal halide and two 1000 W sodium lamps (GTE Sylvania). Throughout the entire experiment air temperature in the chambers was maintained at 20/17°C and relative humidity at 60/70% day/night. In order to randomize any possible chamber effects, all pots were rotated within each chamber and photoperiod treatments were alternated between the chambers every 4 days.

Following completion of germination at 22 days after sowing, two photoperiod treatment regimes were initiated. Based on the daylengths (sunrise to sunset) of the Smithsonian Meteorological Tables (List 1958), the chambers were programmed to simulate the natural daylength changes over the course of a growing season (May 1 to September 1) at 50° and 60°N latitude (Fig. 1A). The light treatments were reprogrammed at 4 day intervals to track the changing daylength. In addition to the latitudinal daylength regimes, a diurnal light treatment was introduced and modified, so that the maximum instantaneous and total daily integrated quantum flux was the same among the two photoperiod treatments (Fig. 1B).

Gas exchange and growth measurements. Gas exchange rates were measured using a portable infra-red gas analyzer (Analytical Development Corporation, Hoddesdon, UK) operated in the differential mode. Photosynthetic measurements were made at the end of the 4 month growing season, separately on freshly detached primary and secondary needles at 570 μmol m⁻² s⁻¹ PPFD under the chamber conditions described earlier, using the Parkinson leaf chamber PLC-C (Analytical Development Corporation, Hoddesdon, UK). Previous measurements revealed no difference in photosynthetic rate between attached and freshly detached needles. Fully expanded primary and secondary needles were sampled. Foliage in the cuvette was arranged to prevent self-shading. The following day the plants were harvested. The soil/sand medium was washed from the roots with water and the plants were separated into primary and secondary needles, roots, and shoots with buds. Dark respiration of needles was taken under room conditions (relative humidity 50%, 25°C), using the Parkinson leaf chamber PLC-C covered with a black cloth. Respiration was measured on the entire intact root system, gently blotted to remove excess water before measurement. Root respiration rate was recorded following an equilibrium period (approximately 8 min) in the cuvette. Gas exchange rates were calculated on a dry mass basis using modified equations of von Caemmerer and Farquhar (1981), resulting in CO₂ assimilation rates (A) in mmol g⁻¹ s⁻¹ and transpiration rates (E) in μmol g⁻¹ s⁻¹. After gas exchange measurements the plant components were oven-dried at 65°C and weighed. For each photoperiod treatment and population, five randomly selected plants were used in gas exchange measurements. Dry mass growth in both provenances in response to photoperiod was the same for the seedlings used in this study as for a larger sample presented elsewhere (Oleksyn et al. 1992). For all variables, differences between treatments and populations were tested by ANOVA. The experimental design was completely randomized.

An integrated carbon exchange budget was estimated for the day on which the measurements were taken (240 h day of year). Net photosynthetic and dark respiration rates of primary and secondary needles were multiplied by the component dry masses and summed over the respective day of the cycle (15.2 h for 60°N; 13.5 h for 50°N) and night period (8.8 h for 60°N; 10.5 h for 50°N). Dark respiration rates of stem and roots were multiplied by the tissue dry mass and summed over the period of 24 h. The dark respiration values were adjusted to the day and night time temperatures, using a Q₁₀ of 2 (Ting 1982). All calculations were performed on a plant basis and ANOVA was performed (α = 5 per treatment and population group).

When each population first showed signs of shoot growth cessation with the development of terminal buds, the number of plants with buds were counted every 4 days until all individuals set bud. According to Wareing (1950a) height growth in Scots pine ceases with the formation of a terminal resting bud, which remains present throughout the period of dormancy.