

Whole-plant CO₂ exchange of seedlings of two *Pinus sylvestris* L. provenances grown under simulated photoperiodic conditions of 50° and 60°N

J. Oleksyn¹, M. G. Tjoelker², and P. B. Reich²

¹ Polish Academy of Sciences, Institute of Dendrology, Parkowa 5, PL-62-035 Kornik, Poland

² University of Minnesota, Department of Forest Resources, St. Paul, MN 55108, USA

Received November 5, 1991/Accepted April 16, 1992

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 CO₂ · 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 CO₂ gains were 2.2–2.5 mmol CO₂ · day⁻¹ for seedlings from Russia compared to 3 mmol CO₂ · 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 1950 a, b 1951; Was-sink 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, stem 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 Kondezhskoe, 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 metalaxyl fungicide (Ridomil 2E, 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 $286 \pm 21 \mu\text{mol m}^{-2}\text{s}^{-1}$, 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 $570 \mu\text{mol m}^{-2}\text{s}^{-1}$ PPFD under the chamber conditions described earlier, using the Parkinson leaf chamber PLC-B (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 CO_2 assimilation rates (A) in $\text{nmol g}^{-1}\text{s}^{-1}$ and transpiration rates (E) in $\mu\text{mol g}^{-1}\text{s}^{-1}$. After gas exchange measurements the plant components were oven-dried at 65°C and weighed. For each photoperiod treatment

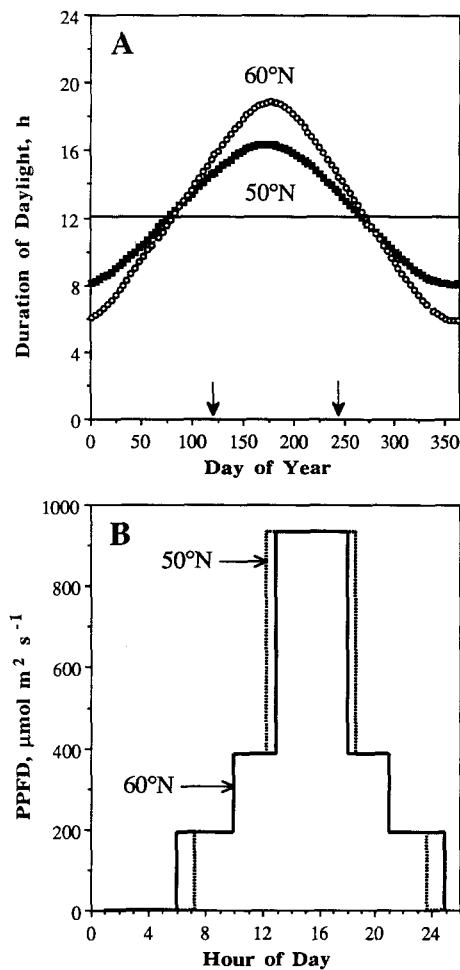


Fig. 1. A Daylength (sunrise to sunset) at 50° and 60°N latitude as a function of time of year. Arrows indicate the period experimentally simulated. B Typical diurnal cycle of irradiance in the 50° and 60°N photoperiods modified to equalize the total integrated quantum flux among the treatments. June 21, the longest day of the year is shown

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 (240th 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 photoperiod (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 Q_{10} of 2 (Ting 1982). All calculations were performed on a plant basis and ANOVA was performed ($n = 5$ 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.

Table 1. Dry mass components (g) of 1-year-old Scots pine seedlings grown under photoperiod conditions of 50° and 60° N. Leaf-weight ratio is total needle dry mass/total plant dry mass. Means (SE) are shown ($n = 5$)

Parameter	Provenance				ANOVA Effects		
	Kondezhskoe, Russia		Milomlyn, Poland		$P > F$		
	60° N	50° N	60° N	50° N	Prov	Trt	Prov × Trt
Primary needles	0.21 (0.02)	0.16 (0.04)	0.23 (0.04)	0.36 (0.05)	0.02	0.34	0.04
Secondary needles	0.64 (0.17)	0.68 (0.13)	0.55 (0.09)	0.74 (0.13)	0.91	0.40	0.58
Stem	0.17 (0.03)	0.16 (0.04)	0.11 (0.02)	0.16 (0.03)	0.29	0.55	0.36
Root	0.54 (0.09)	0.73 (0.15)	0.36 (0.06)	0.50 (0.08)	0.06	0.13	0.81
Total plant	1.56 (0.28)	1.73 (0.36)	1.26 (0.18)	1.75 (0.28)	0.62	0.26	0.57
Root : shoot	0.55 (0.06)	0.73 (0.02)	0.40 (0.02)	0.40 (0.03)	0.0001	0.03	0.02
Leaf weight ratio	0.54 (0.03)	0.49 (0.00)	0.62 (0.01)	0.63 (0.01)	0.0001	0.14	0.09

Prov, provenance

Trt, treatment

Sugar analysis. Total nonstructural carbohydrate (TNC) concentrations were determined for roots and secondary needles using a modification of the methods described by Hassig and Dickson (1979) and Hansen and Møller (1975). Sugars were extracted from oven-dried dry tissue in methanol-chloroform-water. Starch in the tissue residual was then gelled and converted to glucose with amyloglucosidase. Sugar concentrations were determined colorimetrically.

Results

There was no significant impact of photoperiod on root, needle, stem or total dry mass in either provenance (Table 1). Total dry mass did not differ significantly between the two provenances, but the Russian population had 32% greater root dry mass ($P = 0.06$) and 56% less primary needle mass ($P = 0.02$) than the Polish population. The population from Russia was also characterized by higher

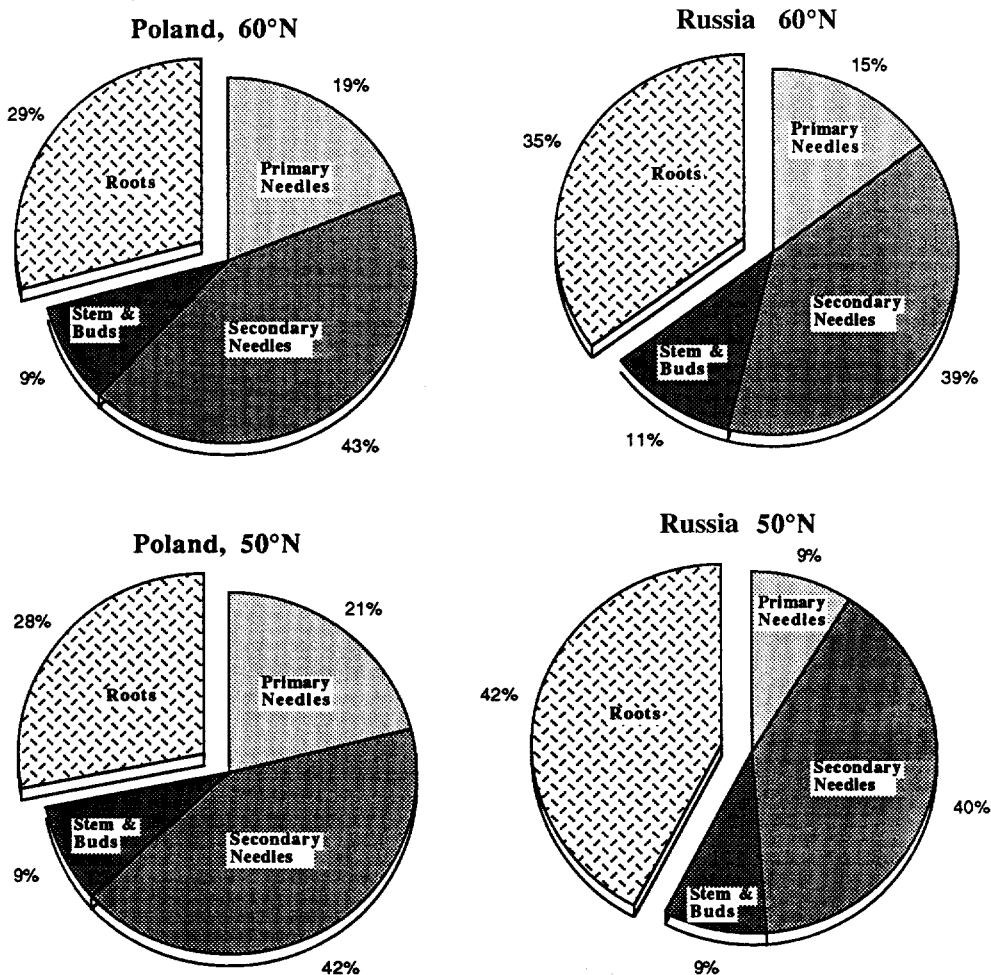


Fig. 2. Proportional allocation of dry mass (%) in 1-year-old Scots pine seedlings grown under the photoperiodic conditions of 50° and 60° N. Photoperiod, population and photoperiod * population interactions were statistically significant ($P < 0.05$) for all parameters except allocation to the secondary needles

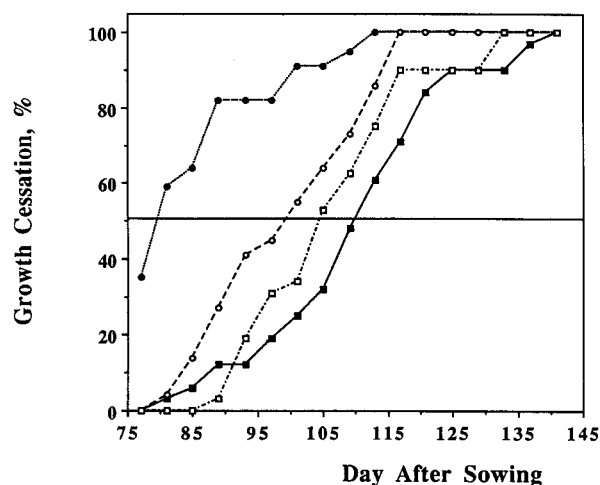


Fig. 3. Time course (days after sowing) of height growth cessation as a percent of total number of seedlings grown under the photoperiods of 50° and 60° N latitude. ● Russia, 50° N; ■ Poland, 50° N; ○ Russia, 60° N; □ Poland, 60° N

proportional allocation of dry mass to roots ($P = 0.01$) and lower allocation to needles ($P = 0.01$) than the Polish population (Fig. 2). The Russian population also had greater proportional allocation to roots at the photoperiodic conditions of 50° than at 60° N (Fig. 2).

The two populations differed in length of height growth period, measured as the number of days from sowing to 50% budset (Fig. 3). Seedlings from Russia at the short-day conditions of 50° N set bud 19 days earlier than those at the long-day conditions of 60° N. There were minimal effects of photoperiod on growth cessation for the Polish population.

Total non-structural carbohydrate concentrations in needles and roots were significantly higher at 50° than at 60° N (Fig. 4, Table 2). However, there were no substantial differences in TNC or sugar concentration between the studied populations (Table 2).

The rates of CO₂ assimilation did not differ significantly between provenances, photoperiodic treatments or different needle types (Table 3). Primary needles, at the end of the growing season, showed rates of photosynthesis similar to secondary needles. However, CO₂ dark respiration rates for primary needles were in all cases lower than those of the younger, secondary needles. For dark respiration rates of primary needles, significant effects of both population and photoperiod were found; whereas, for secondary needles only populations differed significantly (Table 3).

The populations did not differ in the rate of transpiration, and photoperiod treatment affected them significantly (Table 3). In all cases, the rates of transpiration were higher for seedlings grown under the long-day photoperiod. As a result water-use efficiency was significantly lower for the photoperiod conditions of 60° than for 50° N (Table 3).

Rates of root respiration were similar for both photoperiod treatments. Mean root respiration was 12–17% lower for the Russian provenance than for the Polish provenance (Table 3). Differences between provenances in root and stem respiration rates were statistically significant (Table

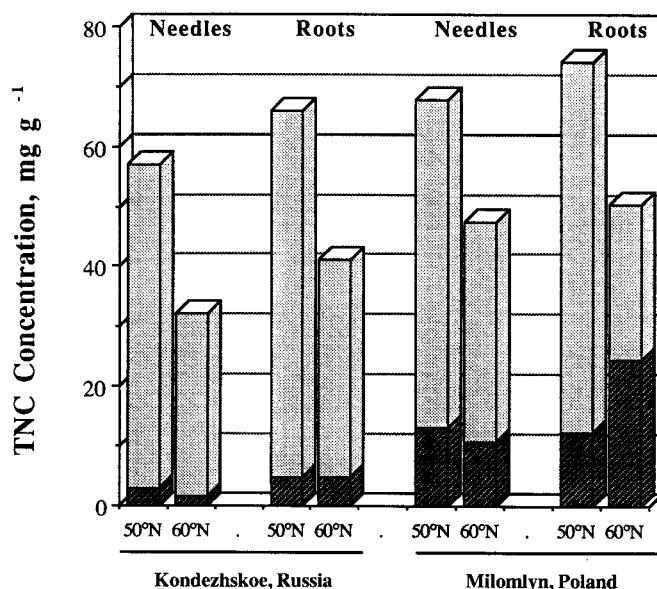


Fig. 4. Starch (hatched columns), sugar (dotted columns), and total non-structural carbohydrate (TNC) concentrations in roots and secondary needles of Scots pine provenances grown under the photoperiod conditions of 50° and 60° N latitude

Table 2. Summary of ANOVA for starch, sugar and total nonstructural carbohydrate (TNC) concentration in secondary needles and roots of 1-year-old Scots pine seedlings grown under photoperiod conditions of 50° and 60° N

Parameter	Provenance		Treatment		Interaction Prov * Trt	
	F	P>F	F	P>F	F	P>F
Needles						
Starch	3.33	0.09	0.11	0.75	0.01	0.92
Sugar	0.32	0.58	13.12	0.01	0.23	0.64
TNC	1.88	0.19	5.49	0.03	0.05	0.82
Roots						
Starch	0.73	0.41	6.18	0.02	5.95	0.03
Sugar	1.08	0.31	33.46	0.01	1.40	0.25
TNC	0.27	0.61	27.25	0.01	2.87	0.11

3). Stem respiration showed a significant interaction between population and photoperiod. The population from Poland had the highest mean rate at the photoperiodic conditions of 60° N, whereas those from Russia at 50° N (Table 3).

The results of integrated whole-plant carbon gain for 24 h are shown in Table 4. Mean net carbon gain ranged from 2.2 mmol CO₂ · day⁻¹ for provenance Kondezhskoe at 50° N to 3.1 mmol CO₂ · day⁻¹ for provenance Milomlyn at 50° N. For both provenances the integrated daily root respiration was 26–31% higher for 50° N than for 60° N, but due to the relatively high plant-to-plant variation, these differences were marginally significant at $P = 0.12$ (Table 4).

The daily net carbon gain was slightly lower ($P = 0.15$) for the provenance from Russia than for the one from Poland. Daily respiratory costs as a proportion of total

Table 3. CO₂ and H₂O gas exchange values of 1-year-old Scots pine seedlings grown at the photoperiodic conditions of 50° and 60° N. Means (SE) are shown (*n* = 5). Respiration was measured at 25° C

Parameter	Provenance				ANOVA Effects <i>P>F</i>		
	Kondezhskoe, Russia		Milomlyn, Poland		Prov	Trt	Prov × Trt
	60° N	50° N	60° N	50° N			
CO ₂ assimilation rate (nmol · g ⁻¹ · s ⁻¹)							
Primary needles	96 (3.7)	88 (11.0)	100 (8.4)	97 (17.0)	0.56	0.62	0.82
Secondary needles	87 (11.0)	96 (6.2)	102 (5.6)	88 (6.9)	0.70	0.67	0.15
Transpiration rate (μmol · g ⁻¹ · s ⁻¹)							
Primary needles	56 (4.7)	35 (3.2)	53 (5.0)	33 (6.3)	0.64	0.001	0.96
Secondary needles	44 (7.6)	34 (5.6)	53 (1.8)	36 (6.4)	0.38	0.03	0.61
Water-use efficiency (mmol CO ₂ · mol H ₂ O ⁻¹)							
Primary needles	2.8 (0.21)	4.3 (0.45)	3.2 (0.33)	5.1 (0.52)	0.15	0.001	0.57
Secondary needles	3.3 (0.29)	4.9 (0.51)	2.9 (0.26)	4.1 (0.41)	0.14	0.002	0.57
Dark respiration rate (nmol · g ⁻¹ · s ⁻¹)							
Primary needles	10 (0.6)	13 (1.6)	8 (0.7)	10 (1.0)	0.02	0.03	0.89
Secondary needles	16 (1.5)	14 (1.0)	20 (1.9)	18 (1.1)	0.009	0.18	0.67
Stem respiration rate (nmol · g ⁻¹ · s ⁻¹)							
	17 (1.5)	23 (1.4)	25 (3.0)	21 (1.1)	0.12	0.63	0.02
Root respiration rate (nmol · g ⁻¹ · s ⁻¹)							
	30 (1.0)	31 (0.8)	36 (2.3)	35 (1.4)	0.003	0.70	0.46

Table 4. Integrated daily (24 h) carbon gain of 1-year-old Scots pine seedlings grown under the photoperiodic conditions of 50° and 60° N. Means (SE) are shown (*n* = 5). Respiration rates were adjusted to day and night temperatures

CO ₂ exchange (mmol · day ⁻¹)	Provenance				ANOVA Effects <i>P>F</i>		
	Kondezhskoe, Russia		Milomlyn, Poland		Prov	Trt	Prov × Trt
	60° N	50° N	60° N	50° N			
CO ₂ assimilation							
Primary needles	1.12 (0.14)	0.77 (0.30)	1.20 (0.10)	1.55 (0.22)	0.05	0.99	0.10
Secondary needles	2.73 (0.40)	3.28 (0.76)	2.97 (0.38)	3.14 (0.54)	0.93	0.52	0.73
Total assimilation	3.85 (0.47)	4.04 (1.05)	4.17 (0.42)	4.69 (0.63)	0.50	0.61	0.82
Dark respiration							
Primary needles	-0.04 (0.00)	-0.05 (0.01)	-0.04 (0.01)	-0.08 (0.02)	0.16	0.03	0.07
Secondary needles	-0.19 (0.04)	-0.22 (0.05)	-0.21 (0.04)	-0.32 (0.05)	0.22	0.19	0.42
Stem respiration	-0.16 (0.02)	-0.21 (0.05)	-0.17 (0.04)	-0.19 (0.03)	0.90	0.41	0.67
Root respiration	-0.93 (0.16)	-1.34 (0.31)	-0.77 (0.14)	-1.04 (0.19)	0.29	0.12	0.75
Total respiration	-1.32 (0.21)	-1.81 (0.29)	-1.19 (0.21)	-1.64 (0.29)	0.60	0.14	0.94
Net carbon gain	2.52 (0.35)	2.23 (0.65)	2.98 (0.10)	3.05 (0.40)	0.15	0.81	0.68

Table 5. Daily respiratory CO₂ loss as percent of daily net assimilation for 1-year-old Scots pine seedlings grown under the photoperiodic conditions of 50° and 60° N. Means (SE) are shown (*n* = 5)

Component	Provenance				ANOVA Effects <i>P>F</i>		
	Kondezhskoe, Russia		Milomlyn, Poland		Prov	Trt	Prov × Trt
	60° N	50° N	60° N	50° N			
Primary needles	1 (0.1)	1 (0.1)	1 (0.2)	2 (0.3)	0.33	0.01	0.02
Secondary needles	5 (0.7)	6 (0.6)	5 (0.5)	6 (0.6)	0.42	0.06	0.49
Stem + buds	4 (0.2)	6 (0.5)	4 (0.6)	4 (0.3)	0.07	0.15	0.18
Roots	25 (3.4)	34 (2.0)	18 (1.7)	22 (3.9)	0.01	0.01	0.26
Total respiratory loss	35 (3.9)	47 (3.0)	28 (2.6)	34 (3.5)	0.01	0.01	0.43

daily net assimilation were significantly lower ($P = 0.01$) for plants growing at 60°N (Table 5). Total respiration costs as a proportion of net assimilation were also significantly higher ($P = 0.01$) in the Russian population than for the population from Poland.

Discussion

The populations differed significantly in response to long- and short-day photoperiod conditions in terms of growth cessation. Population Kondezhskoe, originating from the northern part of the species range in Russia, showed an earlier bud-set at 50°N than in 60°N , whereas the length of the height growth season for the Polish provenance of Milomlyn from the central part of the species range was not sensitive to photoperiod (Fig. 3).

The relative insensitivity of Polish races of Scots pine to long-range transfer has been described in the literature. Plants from this region tolerate long-range transfers, growing well, for example, in Sweden and Canada in the north (Giertych 1979, 1980; Giertych and Oleksyn 1981). At the same time, populations from the northern part of the European range of this species exhibit poor growth after long-distance transfer to more southern latitudes. Until now, no physiological explanation has been provided to explain these observed differences. Based on our data, we propose that the good early growth of Polish races of Scots pine at northern conditions relative to native provenances can be attributed to their lower allocation of dry mass to roots (Fig. 2), insensitivity to photoperiod in terms of growth cessation (Fig. 3), and favourably smaller proportional respiratory CO_2 loss (Table 5).

In general, higher dry mass allocation to roots under short-day photoperiod conditions was found in populations with shorter height growth periods (Oleksyn et al. 1992). Formation of a terminal bud at the end of the height growth period is associated with a switch of dry matter accumulation from the shoot to the root (Ledig et al. 1970). Roots of Scots pine never enter into a stage of true dormancy but during unfavorable conditions, their active elongation may stop. For instance as was shown by Dormling (1986), root growth will temporarily cease when soil temperature is below 0°C . Overall, the higher allocation of dry matter to roots, which is characteristic of Scots pine populations from northern parts of the species range (Oleksyn et al. 1992) could be one of the factors contributing to their slower above-ground growth, due to the impact of allocation on whole-plant growth rate (Reich et al. 1992).

There have been several attempts to evaluate the influence of genetic factors upon CO_2 exchange in Scots pine (Zelawski and Goral 1966; Gatherum et al. 1967; Oleksyn and Bialobok 1986). However, separation of genetics from various environmental and intrinsic factors is difficult, especially in field studies. We did not find any significant effect of photoperiod or seed source on the CO_2 assimilation rate of the seedlings (Table 3). Net CO_2 exchange measurements were performed for both provenances after bud set, when terminal leader elongation had ceased and the plants were at a similar stage of development. These

results are consistent with those of Al-Shahine (1969), who found no differences in CO_2 exchange rates of Polish and Turkish Scots pine provenances when these plants were at the same phenological stage of development as each other. Our results are also similar with those of Bamberg et al. (1967), who found that *Pinus cembra* plants exposed to natural daylengths and to 12 and 8 h photoperiods had similar rates of photosynthesis. However, the populations studied here differed significantly in daily carbon gain of primary needles. The proportional contribution of these needles to the daily assimilation of the northern provenance was lower than for the provenance from Poland, 19–29% versus 29–33% (Table 4). This result is due mainly to differences between populations in allocation of dry mass to primary needles (Table 3), since the rates of CO_2 assimilation do not differ significantly (Table 3). These findings suggest that the stimulating effect of long-day photoperiodic conditions on above-ground productivity of Scots pine (Wareing 1950a, b; Downs and Borthwick 1956; Oleksyn et al. 1992) is due to enhanced needle growth and allocation rather than due to higher rates of photosynthesis.

Statistically significant differences in transpiration rate between photoperiod treatments at 50° and 60°N may possibly reflect changes in needle morphology. Needles from plants growing under long-day conditions in this experiment (Oleksyn et al. 1992), as well as in other studies (Jensen and Gatherum 1965; Denne and Smith 1971; Kriesel and Ciesielska 1982) were longer and thinner than those grown under short-day conditions of 50°N , which were shorter and more xeromorphic. One of the indicators of xeromorphicity can be relative water content in needles. Northern Scots pine provenances from 69 – 57°N when grown at the southern short-day conditions of 43°N showed 37–40% of dry mass content, versus 33–35% for more southern populations (Langlet 1959).

The short-day photoperiod of 50°N resulted in 27% greater mean daily integrated root and total respiration of Scots pine seedlings in comparison with 60°N (Table 4). Seedlings at 50°N also had greater TNC than those at 60°N (Fig. 4), but we know of no data explaining why TNC would be higher in Scots pine under the short-day photoperiod.

In general, instantaneous and integrated daily respiration losses were much higher for roots than for leaves. Total daily respiratory losses due to root respiration ranged from 18 to 34% of net CO_2 assimilation (Table 5). Root respiration accounted for roughly two-thirds of the total respiratory costs in both populations in both photoperiods. As with photosynthesis, proportional allocation of dry mass had a greater impact on whole-plant respiratory losses than specific respiration rates. For example, the Russian population had lower root respiration rates than the Polish population, however, its greater allocation to roots resulted in a 40 to 50% greater root respiratory cost as a proportion of total daily carbon gain. In general, respiratory losses due to root respiration vary significantly depending on species, experimental conditions and the methods used for estimation. According to Eidmann (1962) root respiration of conifers is responsible for 40–60% of the losses of annual photosynthetic production. Hagihara and

Hozumi (1981) estimated the annual contribution of roots to respiratory losses by woody organs in a *Chamaecyparis obtusa* plantation at 27%. For Scots pine, Linder and Troeng (1981) estimated this loss at 23% for 20-year-old trees and Ågren et al. (1980) at 6.4% for 14-year-old trees. Ovington (1957), who studied dry matter production of 3- to 55-year-old Scots pine plantations in Britain, found that after the first few years, shoot growth increased at a higher rate than root growth. The same relationship between Scots pine biomass allocation was found in Sweden (Albrektson 1980). This means that proportional respiratory losses due to root respiration will probably decline with increasing age and size.

The results obtained in the present study indicated that provenance can significantly influence the photoperiodic response of Scots pine seedlings. Population variation in productivity is more affected by dry mass allocation and respiratory losses than by net photosynthesis rate. Depending on population and photoperiod, roots can account for up to one-third of the seedlings' daily respiratory losses.

Acknowledgements. This research was partially supported by National Science Foundation grant BSR 885 7129 (to PBR) and by the University of Wisconsin-Madison Department of Forestry and College of Agricultural and Life Sciences.

References

- Ågren G, Axelsson B, Flower-Ellis JGK, Linder S, Persson H, Staaf H, Troeng E (1980) Annual carbon budget for a young Scots pine. In: Persson T (ed) Structure and function of northern coniferous forests – a ecosystem study. *Ecol Bull* (Stockholm) 32: 307–313
- Albrektson A (1980) Relations between tree biomass fractions and conventional silvicultural measurements. In: Persson T (ed) Structure and function of northern coniferous forests – a ecosystem study. *Ecol Bull* (Stockholm) 32: 315–327
- Al-Shahine FO (1969) Photosynthesis, respiration and dry matter production of Scots pine (*Pinus sylvestris* L.) seedlings originating from Poland (Nowy Targ) and Turkey (Eskishaher). *Acta Soc Bot Pol* 38: 355–369
- Bamberg S, Schwarz W, Tranquillini W (1967) Influence of daylength on the photosynthetic capacity of stone pine (*Pinus cembra* L.). *Ecology* 48: 264–269
- Bogdanov P (1931) On photoperiodism in woody plants. *Trudy i Issl po Lesn Khoz i Lesn Prom* 10: 21–33 (in Russian with German summary)
- Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and gas exchange of leaves. *Planta* 153: 376–387
- Denne MP, Smith CJ (1971) Daylength effects on growth, tracheid development, and photosynthesis in seedlings of *Picea sitchensis* and *Pinus sylvestris*. *J Exp Bot* 22: 347–361
- Dormling I (1986) Dormancy in Scots pine (*Pinus sylvestris* L.) seedlings. In: Provenances and forest tree breeding for high altitudes. Proceedings of the Frans Kempe Symposium in Umeå 10–11. June 1986, pp 81–98
- Downs RJ, Borthwick HA (1956) Effects of photoperiod on growth of trees. *Bot Gaz* 117: 310–326
- Eidmann FE (1962) Atmung der unterirdischen Organe und Abgaben an die Mykorrhiza. *Int Symp der Baumphysiologen*. Innsbruck, 1961, pp 43–45
- Gatherum GE, Gordon JC, Broerman BFS (1967) Physiological variation in Scots pine seedlings in relation to light intensity and provenance. *Iowa St J Sci* 42: 19–26
- Giertych M (1979) Summary of results on Scots pine (*Pinus sylvestris* L.) height growth in IUFRO provenance experiments. *Silvae Genet* 28: 136–152
- Giertych M (1980) Polish races of Scots pine, Norway spruce and European larch in international provenance experiments. *Arbor Korn* 25: 135–160
- Giertych M, Oleksyn J (1981) Summary of results on Scots pine (*Pinus sylvestris* L.) volume production in Ogievskij's pre-revolutionary Russian provenance experiments. *Silv Genet* 30: 56–74
- Hagihara A, Hozumi K (1981) Respiration consumption by woody organs in a *Chamaecyparis obtusa* plantation. *J Jap For Soc* 63: 156–164
- Hassig BE, Dickson RE (1979) Starch measurement in plant tissue using enzymatic hydrolysis. *Physiol Plant* 47: 151–157
- Hansen J, Møller I (1975) Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. *Ann Biochem* 68: 87–94
- Jensen KF, Gatherum GE (1965) Effects of temperature, photoperiod, and provenance on growth and development of Scots pine seedlings. *For Sci* 11: 189–199
- Koski V, Sievänen R (1984) Timing of growth cessation in relation to the variations in the growing season. In: Tigerstedt PMA, Puttonen P, Koski V (eds) Crop physiology of forest trees. Helsinki University Press, Helsinki, pp 167–193
- Kriesel K, Ciesielska S (1982) The effect of photoperiod on the level of endogenous growth regulators in pine (*Pinus sylvestris* L.) seedlings. *Acta Soc Bot Pol* 51: 59–70
- Langlet O (1959) A cline or not cline – a question of Scots pine. *Silvae Genet* 8: 13–24
- Ledig FT, Boreman FH, Wenger KF (1970) The distribution of dry matter growth between shoots and roots in loblolly pine. *Bot Gaz* 131: 349–359
- Linder S, Troeng E (1981) The seasonal variation in stem and coarse root respiration of a 20-year-old Scots pine (*Pinus sylvestris* L.). In: Tranquillini W (ed) Radial growth in trees. Mitt Forstl Bundes-Veruchsanst Wien, pp 125–139
- List RJ (1958) Smithsonian meteorological tables. *Smithson Misc Collect* 114: 1–527
- Oden P-C, Dunberg A (1984) Abscisic acid in shoots and roots of Scots pine (*Pinus sylvestris* L.) seedlings grown in controlled long-day and short-day environments. *Planta* 161: 148–155
- Oleksyn J, Bialobok S (1986) Net photosynthesis, dark respiration and susceptibility to air pollution of 20 European provenances of Scots pine *Pinus sylvestris* L. *Environ Pollut* 40: 287–302
- Oleksyn J, Tjoelker MG, Reich PB (1992) Growth and biomass partitioning of European populations of *Pinus sylvestris* L. under simulated 50° and 60° N daylengths: evidence for photoperiodic ecotypes. *New Phytol* 120: 561–574
- Ovington JD (1957) Dry-matter production by *Pinus sylvestris* L. *Ann Bot* (London) 21: 287–314
- Reich PB, Walters MB, Ellsworth DS (1992) Leaf lifespan in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* (in press)
- Ting IP (1982) Plant physiology. Addison-Wesley, Reading, MA, pp 180–187
- Vaartaja O (1959) Evidence of photoperiodic ecotypes in trees. *Ecol Monogr* 29: 91–111
- Wareing PF (1950a) Growth studies in woody species. I. Photoperiodism in first-year seedlings of *Pinus sylvestris*. *Physiol Plant* 3: 258–276
- Wareing PF (1950b) Growth studies in woody species. II. Effect of day-length on shoot-growth in *Pinus sylvestris* after the first year. *Physiol Plant* 3: 300–314
- Wareing PF (1951) Growth studies in woody species. III. Further photoperiodic effects in *Pinus sylvestris*. *Physiol Plant* 4: 41–56
- Wassink EC, Wiersma JH (1955) Daylength responses of some forest trees. *Acta Bot Neerl* 4: 657–670
- Zelawski W, Goral I (1966) Seasonal changes in the photosynthesis rate of Scots pine (*Pinus sylvestris* L.) seedlings grown from seed of various provenances. *Acta Soc Bot Pol* 35: 587–598