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Short note

Effect of the root temperature on growth parameters of various European tree species

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Summary — European forest tree species have been investigated regarding the reaction of growth of shoots, roots and leaves during an incubation of the root system at various temperatures ranging from 5 to 35 °C for 4 months. Species-specific differences in the reaction to root temperatures could be demonstrated. Growth optima (total dry mass increment) ranged from about 15 °C (*Picea abies*, *Larix decidua*, *Pseudotsuga menziesii*, *Betula verrucosa*) to 25 °C (*Quercus robur*, *Carpinus betulus*) and up to 30 °C (*Pinus nigra*). Chilling of the root system of *Juglans regia* down to 2 °C resulted in a rapid and long-lasting decrease of net photosynthesis, but only in a moderate decrease of stomatal conductance and transpiration. Respiration was stimulated after some days. The ecological consequences of different optima for root temperatures among various species are discussed regarding their natural distribution and their reactions to increasing temperatures caused by the greenhouse effect.

root temperature / shoot growth / *Quercus robur* / *Larix decidua* / *Picea abies* / *Betula verrucosa* / *Pseudotsuga menziesii* / *Carpinus betulus* / *Pinus nigra* / *Acer pseudoplatanus*

Résumé — Effets de la température racinaire sur la croissance de diverses espèces ligneuses européennes. Les effets d'une incubation du système racinaire à différentes températures (5 à 35 °C) pendant 4 mois, sur la croissance aérienne de plusieurs espèces ligneuses forestières européennes, ont été analysés. D'importantes différences interspécifiques ont été mises en évidence dans cette réponse. Les optima thermiques de croissance en biomasse totale allaient de 15 °C (*Picea abies*, *Larix decidua*, *Pseudotsuga menziesii*, *Betula verrucosa*) à 25 °C (*Quercus robur*, *Carpinus betulus*), voire 30 °C (*Pinus nigra*). Un refroidissement des racines de *Juglans regia* à 2 °C a résulté dans une diminution rapide et durable de l'assimilation nette de CO₂, mais seulement d'une baisse limitée de conductance stomatique et de transpiration. La respiration était stimulée après quelques jours. Les conséquences écologiques de ces différences des optima thermiques sont discutées en regard de la distribution des espèces et de leurs réactions à des accroissements de température dus à l'effet de serre.

température racinaire / croissance aérienne / *Quercus robur* / *Larix decidua* / *Picea abies* / *Betula verrucosa* / *Pseudotsuga menziesii* / *Carpinus betulus* / *Pinus nigra* / *Acer pseudoplatanus*

INTRODUCTION

Soil temperature is an important and sometimes underestimated factor for growth and vitality of trees because it governs the root activity and by this evidently other vital functions of a tree (Havranek, 1972; Levitt, 1972; Heninger and White, 1974; Martin et al, 1989). Unfortunately, only few direct comparable indications about optima of root temperatures for various tree species exist in the literature. Many investigations have been performed to optimize seedling growth in nurseries.

According to Vapaavuori et al (1992), shoot growth in *Pinus sylvestris* and *Picea abies* is maximal at 12 °C root temperature. Lower or higher temperatures decreased the accumulation of the shoot fresh weight. In contrast, Graves et al (1989a) indicated an optimal temperature for seedling growth of 24 °C for *Ailanthus altissima*, about 30 °C for *Acer rubrum* (Graves, 1989b) and about 34 °C for *Gleditsia triacanthos inermis* (Graves, 1988). The authors discuss the results as indicators for the usefulness and tolerance of trees as ornamentals to be planted in inner city areas, where elevated soil temperatures above 30 °C are normal in summer time (Garves, 1988). Heninger and White (1974) found optima for *Picea glauca* at 19 °C, *Pinus banksiana* had a maximum at 27 °C, *Pseudotsuga menziesii* between 15 and 27 °C, and *Betula papyrifera* between 19 and 31 °C.

These data point to the fact that in tree species (or even in progenies, see Gur et al, 1976), specific root temperature optima seem to exist, which are of great importance for stress tolerance at various sites and perhaps at elevated air (and soil) temperatures resulting from the greenhouse effect. Because little is known about forest trees in Central Europe in this respect, we investigated eight European tree species regarding the growth reaction in dependence from various soil temperatures rang-

ing from 5 to 35 °C during a period of 4 months from sprouting to full leaf and shoot extension.

METHODS

One-year-old seedlings of *Quercus robur* (L), *Larix decidua* (Mill), *Picea abies* (Karst), *Pinus nigra* (Am) and *Pseudotsuga menziesii* (Mirb) obtained from a local nursery were potted during the autumn in plastic vessels with a bottom hole, fitting into another plastic vessel, which allowed a drainage and the addition of water to a level of 3 cm. A coarse sand as substrate was used. The plants were overwintered in a greenhouse at +2–6 °C, and transferred during February to a specially equipped greenhouse with a rather constant air temperature of 18–20 °C (mean value 19 °C).

The double pots were inserted into special water-bath containers with constant temperatures of 5, 10, 15, 20, 25, 30 and 35 °C. Ten replicates for each species and each temperature were used. In a second series, the same procedure was used with plants of *Carpinus betulus*, *Betula verrucosa* and *Acer pseudoplatanus*, which were stored at +3 °C in a dark container. Because not enough water-bath containers were available at that time, we only tested the temperatures of 5, 15, 25 and 35 °C.

The plants were cultivated in a greenhouse of the BBA Braunschweig under normal daylight conditions (February–July) without additional light, and under the normal photoperiod. Pots were fertilized twice with a complex fertilizer (WOPIL) and watered daily by hand, bringing the water level in the external vessel to the label at 3 cm. The course of height growth increment was measured every 2 weeks, and on 15 June 1994 the plants of the first series were harvested, those of the second series 4 weeks later. Leaf areas and dry weights of roots, shoots and leaves (needles) were determined (48 h oven-dried at 80 °C).

The mean dry weights of 20 plants of each species were determined before starting the incubation in the water bath (at the beginning of the growth period) and later subtracted from the mean weight of the plants after the end of the cultivation period. Therefore, only the growth increment is indicated.

Seedlings of *Juglans regia* (6 months old, cultivated in a greenhouse in Kleinmachnow) were incubated with their root system in pots with a substrate moisture level of 80% of field capacity, covered with plastic bags to avoid overflooding and anaerobic conditions, and in 2 °C cold water up to 15 days. Control plants were cultivated at normal soil and air temperatures in a greenhouse ranging from 15 to 25 °C. After 24 h, 7 and 12 days, net photosynthesis, stomata conductance, transpiration and dark respiration were measured with a LICOR 6200 of six plants each (treated and untreated) in two replicate series beginning at 0900 hours to avoid a noon depression. The temperature was 18, 19, 20 and 25 °C, the relative humidity (RH) 45, 45, 40 and 29.9% and PFD of 1 450, 1 446, 1 577 and 1 021, respectively, in the photosynthetic active range.

The mean values of the plants with a chilled root system were related to those of the control and expressed as percentage in order to demonstrate the effect of low root temperatures (+2 °C) on physiological processes in the leaves.

For statistical analyses we used the *F*-test, and thereafter the *t*-test to evaluate the significance of differences of mean values (between two variants). The results are indicated by the symbols: 0 = no difference; * (*P* = 0.05); ** (*P* = 0.01); *** (*P* = 0.001).

RESULTS

The most reliable value for the overall productivity is the increment of the total dry mass. It represents photosynthetic efficiency minus losses by respiration. Figures 1 and 2 demonstrate that dry matter accumulation was strongly influenced by the root temperatures after a growth period of about 4 months.

The eight tree species exhibited clear differences in their reaction to the various root temperatures. *P abies*, *L decidua*, *B verrucosa*, *Ps menziesii* and probably *A pseudo-platanus* have optima for the total growth near or below 15 °C, *Q robur* and *C betulus* at 25 °C and *P nigra* at 30 °C.

The maximum of the development of the leaf area is in *Quercus* at 20 °C, similar to *Tilia cordata*, which has a maximal growth increment at this root temperature (Lyr and Garbe, 1995).

Turner and Jarvis (1975), Graves et al (1989a), Lippu and Puttonen (1989), Fos-

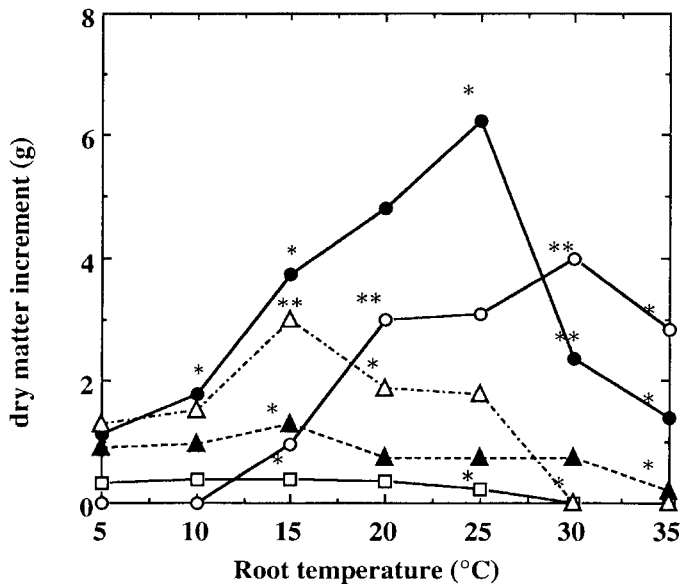


Fig 1. Effect of root temperatures from 5 to 35 °C on the growth (total dry matter accumulation in g) of *Q robur* (●), *P nigra* (○), *L decidua* (Δ), *Ps menziesii* (▲), and *P abies* (□) after a growth period of 17 weeks in a greenhouse with air temperatures of 18–20 °C. The degree of significance of the difference between the values is indicated by *, ** and *** (see Methods).

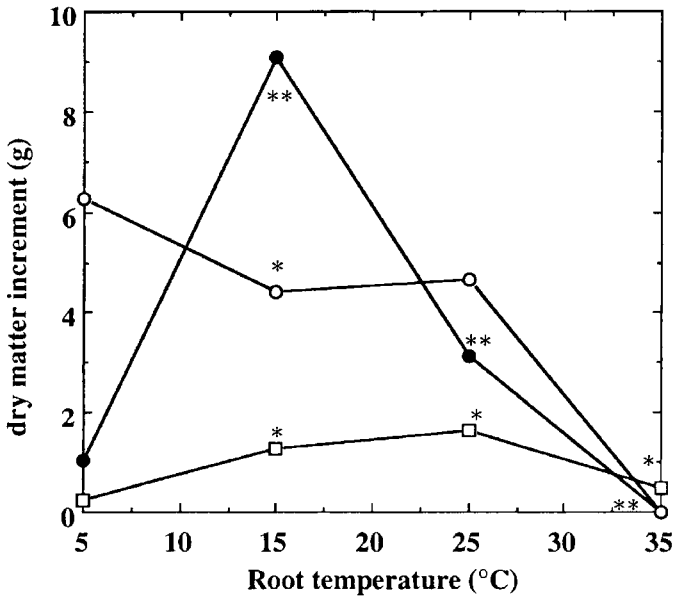


Fig 2. Effect of root temperatures from 5 to 35 °C on the growth (total dry matter accumulation in g) of *B. verrucosa* (●), *A. pseudoplatanus* (○) and *C. betulus* (□) after a growth period of 17 weeks in a greenhouse with air temperatures of 18–20 °C. The degree of significance of the difference between the values is indicated by *, ** and *** (see Methods).

ter et al (1991) and Vapaavuori et al (1992) indicated that net photosynthesis can be influenced by root temperatures. Temperatures lower or higher than the optimum decrease carbon dioxide assimilation by probably different routes.

We tested the effect of a root chilling with seedlings of *J. regia*, a sensitive species adapted to a warmer climate, which was expected to give a strong reaction. Net photosynthesis, stomatal conductance, transpiration and dark respiration were measured on fully expanded leaves of six seedlings growing under normal greenhouse conditions in May. The values obtained from normal grown controls were related to those where the root system was cooled down to about 2 °C. As figure 3 demonstrates, the chilling of the root system caused a rapid decrease of photosynthesis within 24 h, which stayed depressed up to 12 days. Stomata conductance reacted only moderately with a tendency for normalization. Transpiration was hardly influenced. Respiration showed, at the beginning of the

experiment, a strong depression and later on a strong stimulation. The significance of the differences to the control plants is indicated by the symbols 0, *, **, *** (see Methods).

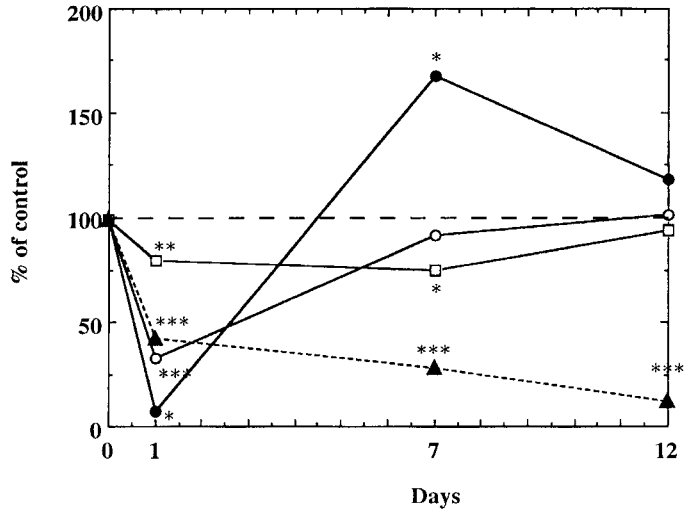
These data demonstrate a strong and rapid influence of the root activity on the activity of leaf processes.

DISCUSSION

As our results indicate, there exist distinct differences for optimal root temperatures in the eight tree species investigated. In previous experiments, we found optimal growth in *P. sylvestris* at 10–15 °C, in *Fagus sylvatica* and *T. cordata* at 20 °C compared with *Q. robur* at 25 °C (Lyr and Garbe, 1995).

Figures 1 and 2 demonstrate that *P. abies* had an optimal root temperature at about 15 °C. The same was true for *L. decidua* and *Ps. menziesii*. The values for *A. pseudoplatanus* are not so clear because of the strong growth at 5 °C. But the optimum seemed to

Fig 3. Effect of chilling of the root system of *J regia* on the leaf activity (▲ = net photosynthesis, O = stomata conductance, □ = transpiration, ● = respiration). Values are expressed in % of those of unchilled control plants (= 100%).



be below 15 °C. In contrast, *C betulus* seemed to have its optimum at 25 °C, similar to *Q robur*, whereas *P nigra* grew best at 30 °C and had a poor growth at 5 and 10 °C.

The data also indicate that there are different tolerance amplitudes regarding the root temperature. The investigated tree species may be classified according to the scheme in table I.

In our investigations only the root temperatures have been varied, whereas shoot temperatures were normal and equal (18–20 °C) for all variants. Therefore, photosynthesis and shoot growth were not directly impaired. It might be that the optimal values of root temperatures measured by our method are not restricted to the root system, but may be a specific feature of all

Table I. Classification of the investigated tree species (including the data obtained by Lyr and Garbe, 1995) according to their temperature demand for optimal growth and their temperature tolerance.

Temperature optimum	Tolerance range		
	Broad (30 °C)	Medium (25 °C)	Narrow (20 °C)
Low (10–15 °C)	<i>P abies</i> <i>Ps menziesii</i>	<i>P sylvestris</i> <i>L decidua</i>	<i>B verrucosa</i> <i>A pseudoplatanus</i>
Medium (20 °C)		<i>F sylvatica</i> <i>T cordata</i>	
High (25 °C)	<i>Q robur</i> <i>C betulus</i>		
Very high (30 °C)			<i>P nigra</i>

organs of a tree species. This needs further investigation. The causes of the growth influencing effect of root temperatures seems to be different at sub- and supraoptimal temperatures. Suboptimal temperatures cause a lowered root activity (low respiration, slow metabolism and low biosynthetic capacity).

Several authors point to the fact that low temperatures decrease water penetration into the roots due to an increased plasma and water viscosity (Running and Reid, 1980; Lippu and Puttonen, 1989). This should be the causal effect for a decreased photosynthesis and transpiration. However, this seems to be true only for temperatures below 7 °C or less (Havranek, 1972). Evidently other factors are involved.

It seems that the main cause of slow growth at suboptimal temperatures is a reduced hormone supply by the root (cytokinines and gibberellines), perhaps combined with an elevated production of abscisic acid (ABA). Leaves of oak and beech are small and dark green at temperatures of 5–15 °C (Lyr and Garbe, 1995), which does not seem to be caused by a deficit in water or mineral nutrition. Chilling of the root system in *P sylvestris* resulted in a decrease of the level of IAA and an increase of ABA (Menjailo et al, 1980).

This would explain the reduced shoot and leaf growth as well as a decreased photosynthesis. At low root temperatures (and high photosynthetic activity at temperatures near 20 °C) an accumulation of carbohydrates in leaves and shoots is to be expected as a consequence of a reduced sink capacity of the root, which inhibits photosynthesis by feedback mechanisms (Delucia, 1986). We observed the same effect during root anaerobiosis in *F sylvatica* and *T cordata*, where a strong increase of starch (and soluble sugars) in the leaves and shoots was measured as long as root growth was suppressed by overflowing (results to be published).

This would best explain the effects measured in *J regia* by cooling down the root system to 2 °C. The rapid decrease in photosynthesis compared to the control plants is probably caused by an overproduction of ABA, which also resulted in a decrease of stomatal conductance. However, the long-lasting depression of photosynthesis is more likely caused by an elevated level of sugars in the leaves, which cannot be expelled because the roots have no sink capacity by their lowered metabolism. This would explain why stomata conductance and transpiration were normal after a short time. This does not favor the hypothesis of root resistance as limiting factor, because then photosynthesis, stomata conductance and transpiration should react with equal tendency.

At high temperatures (30 and 35 °C) *P abies*, *P sylvestris*, *L decidua* and *Ps menziesii* did not survive the experimental growth period. After sprouting many shoots died and were partly replaced by new ones (*Larix*), which later on also died. Therefore, the gain of dry matter accumulation was zero.

Only *Q robur*, *C betulus* and *P nigra* tolerated temperatures above 25 °C and still had a considerable growth increment at 35 °C. Evidently they are more adapted to a warm summer climate than the other species.

The main reason for poor growth or death at supraoptimal temperatures seems to be the strongly increased root respiration, which according to Gur et al (1972), can even result in an anaerobiosis and the production of ethanol, or more disastrous, of acetaldehyde. Additionally, a decrease in cytokinin synthesis occurs (decreased biosynthetic capacity). Therefore, differences of temperature-dependent root respiration in various trees are of ecological significance (Lawrence and Oechel, 1983).

Although a constant root temperature is an artificial condition compared with field

conditions, it demonstrates specific differences regarding a specific (root?) temperature requirement. Whether this reflects a general temperature demand remains an open question. Trees of northern origins are physiologically more adapted to lower or moderate temperatures during the vegetation period. This can be one factor (beside frost resistance, drought tolerance and photoperiodical behavior) for the natural distribution of a species. Probably in a more detailed analysis even differences in progenies could be detected (Gur et al, 1976).

With increasing global temperatures caused by the greenhouse effect, tree species with a low temperature demand for optimal growth will suffer more than others. This can result in a shift of some tree species areas to the north.

At many sites, soil temperatures are presently still below the optimal values. Therefore, increasing temperatures can induce an increased growth in many species, which was observed in recent years in many European countries, but was mainly attributed to an increased nitrogen supply from the atmosphere.

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