Tree Physiology 12, 281–290
© 1993 *Heron Publishing—Victoria, Canada*

Rapid response of large, drought-stressed beech trees to irrigation

JAN ČERMÁK[1], RAINER MATYSSEK[2] and JIRÍ KUČERA[1]

[1] *Institute of Forest Ecology, Faculty of Forestry, University of Agriculture, 64400 Brno-Sobesice, Czechoslovakia*

[2] *Swiss Federal Research Institute for Forests, Snow and Landscape, CH-8903 Birmensdorf ZH, Switzerland*

Received February 25, 1992

Summary

Large, declining beech (*Fagus sylvatica* L.) trees (diameter at breast height = 50 cm), growing on heavy clay soils in the highlands near Zurich, Switzerland, were amply irrigated in late summer. During irrigation, the xylem sap flow rate, Q_{wt}, was measured by the stem-tissue heat balance method with internal heating and sensing. Only a gradual and slight increase in Q_{wt} in response to irrigation was observed in the control trees, whereas Q_{wt} in the declining trees, whose transpiration rates were only 2–20% those of the control trees, increased 2–5 times within minutes. This suggests, that severe local drought was the major factor limiting tree growth at the site. The extent of the response permits estimation of the supply-limited (soil water) and demand-limited (tree structure) components of stress. Drought caused a decline in Q_{wt} in the trees with short crowns and limited root systems that had originally been growing in dense canopies and had become suddenly exposed to full illumination as a result of a severe wind storm and thinning. Trees with deep, narrow, dense crowns, growing in more open places and adapted over a long period to high irradiance remained healthy during drought. Prolonged, periodic water shortage reduced the amount of foliage up to 90% but during drought stimulated the growth of fine roots in the surface and upper soil layers. The stem conductive systems of the declining trees were still partially functional.

Introduction

It remains controversial how well trees suffering from severe, chronic drought, as indicated by inhibition of leaf production and expansion and premature leaf loss, are able to make use of a sudden increase in soil water. Studies on the response of trees to changes in environmental conditions have demonstrated that trees are sensitive to both a decrease (Kramer and Kozlowski 1979, Čermák et al. 1980, Rychnovská et al. 1980, Čermák 1984, Čermák and Kučera 1990*a*, 1990*b*, 1990*c*, Čermák 1991) and an increase (Kozlowski 1984, Čermák and Kučera 1990*d*) in water supply. However, there is little information on the response of large, water-stressed trees in forest stands to a rapid increase in soil water. If the conducting systems are largely intact, there may be a substantial increase in the rate of stem sap flow within minutes. However, if most of the conductive vessels have been blocked by cavitation in water columns under high tension, the recovery of sap flow may take days or weeks. We investigated how quickly large beech trees displaying visible symptoms of drought increased their rate of stem sap flow following irrigation.

Materials and methods

Four large, 115-year-old beech (*Fagus sylvatica* L.) trees, two healthy controls and two declining trees (Table 1), were studied in a mixed forest located at an altitude of 585 m in the highlands 20 km east of Winterthur near Zurich, Switzerland (Long. 8°47′ and Lat. 47°30′). The stand consisted of 25.9% European beech (*Fagus sylvatica* L.), 12.6% Norway spruce (*Picea abies* (L.) Karst.), 15.5% white fir (*Abies alba* L.), 45.2% Scots pine (*Pinus sylvestris* L.) and 0.8% European ash (*Fraxinus excelsior* L). The 115-year-old beech trees had a mean height of 33.5 m, a mean diameter at breast height (dbh) of 39.5 cm and a mean timber volume of 1.94 m^3. The site was characterized as *Galio-odorati-Fagetum typicum*, var. *Primula* and *Pulmonaria* on brown forest soil with a high clay content (W. Keller, personal communication). Most of the ground was covered by dense understory vegetation, 0.1–1 m in height.

Parts of the stand were damaged by wind in 1981–82, and were heavily thinned the next year, so that about 50% of the trees were removed. Heavy machinery compressed the soil along skid trails during logging operations. However, some parts of the stand remained untouched. Beech, but not the other species, showed all the phases of tree decline in 1990, from healthy, fully leafed trees, to declining trees with leaves reduced in size and number, to dead trees. Healthy trees grew in untouched parts of the stand in the more open sites and had deep, narrow, regular crowns, whereas declining trees, which had been growing in dense parts of the stand until 1981–82, had short, irregular crowns. Ground vegetation always grew close to the stems of the dead trees and sometimes those of healthy trees as well, if not suppressed by the shade. However, vegetation was always absent within a circle about 5 m in diameter around the declining trees.

Table 1. Dendrometrical characteristics of sample trees of beech (*Fagus sylvatica* L.) selected for irrigation and measurement of sap flow rate.

Parameter	Control tree		Declining tree	
	No. 1	No. 2	No. 3	No. 4
Diameter at breast height, cm	54	48	44	51
Basal area, m^2	0.229	0.181	0.152	0.204
Tree height, m	35	36	37	33
Timber volume, m^3	4.22	3.40	2.91	3.54
Crown ground plan area, m^2	22	13	36	42
Estimated leaf loss, %	<10[1]	<10[1]	80	90
Bare area around tree stems, m^2	0	7[2]	18	13
Irrigated area around tree stems, m^2	19	10[3]	18	13
Irrigation water applied, liters	3000	2000	3500	3500
Irrigation water applied, mm	158	200	194	269

[1] Partial leaf loss in late summer.

[2] Due to soil compression along a skid trail.

[3] Only northern side of the tree was irrigated.

The xylem sap flow rate, Q_{wt}, was measured 3.7 m above the ground on opposite sides (south–north) of the stems of the sample trees for 20 days in August, applying the compensating stem tissue heat balance, with internal, direct electric heating and sensing (Čermák et al. 1973, Kučera et al. 1977, Čermák and Kučera 1981, Čermák et al. 1982). Potential evaporation, E_p, was calculated according to Türc (1961).

Trees were irrigated experimentally on days of almost cloudless weather with tap water. The water temperature was 20 °C and the soil temperature at 5 cm was 18 °C. Three or four times a day, 500 l (50 mm) of water was applied with sprinklers over a period of 20 min. Water was applied on either the north or south side of the sample trees. To facilitate water penetration around Tree 2, 20 holes of diameter 10 cm were drilled 50 cm deep in the compressed soil on the north-side of the tree.

Results and discussion

Soil water content and root density

Soil water reached field capacity in the spring and then decreased gradually until late summer. The soil density was 1.3–1.5 g cm^{-3} near both the control and declining trees (Table 2). Near some declining trees the soil density was 4% less, causing a significant difference in the availability of water on the clay soil (Scheffer and Schachtshabel 1976). Very few fibrous roots were found in the upper horizons (0–60 cm) of the soil around healthy trees. Around the declining trees there was a dense network of fibrous roots in the uppermost soil horizon (0–5 cm) and at the soil surface just below the litter. Such roots were present only within the circles of bare soil around the stems.

Transpiration under drought and its response to irrigation

Before irrigation, the xylem sap flow rate, Q_{wt}, was high in both of the healthy control trees, although it was slightly lower in Tree 2 than in Tree 1. The soil around Tree 2

Table 2. Soil density and water content in representative parts of the stand.

Sampling location	Soil depth (cm)	Density of dry soil (g cm^{-3})	Soil water water (% by volume)
Beneath the herb layer and less dense canopy of the forest stand	5–15	1.11	34.9
	30–40	1.52	36.0
	60–70	1.44	42.4
At a distance of 1–2 m from the control beech trees	10–20	1.33	15.4
	30–40	1.48	19.0
	70–80	1.47	28.4
At a distance of 1–2 m from the declining beech trees	5–15	1.19	16.4
	30–40	1.43	20.7
	60–70	1.52	26.4

had a slightly lower water content and a higher density than that around Tree 1 because it was closer to a skid trail. The Q_{wt} of declining trees was low, ranging from 2 to 20% that of healthy trees (Table 3). A much greater difference in the Q_{wt} on opposite sides of stems was found in declining trees than in control trees.

After irrigation, the soil water content more than doubled to 32% by volume close to the declining trees, even though some of the water applied (the ground on the north side of Tree 3 sloped away from the tree) drained through the upper soil and away from the treated areas before the dry clay soil swelled.

Xylem sap flow rate increased in all of the beech trees after irrigation, but the extent and the speed of the change differed among them (Figure 1). The slight increase in Q_{wt} in control Tree 1 was not apparent until the next day. Control Tree 2 responded within hours and to a greater extent than Tree 1, reflecting, presumably, the fact that holes had been drilled in the soil around this tree to facilitate penetration of irrigation water (see Table 3).

A pronounced response to irrigation was observed in both declining trees. Within 6 minutes after the start of irrigation to the south-side of Tree 3, Q_{wt} on the south side, but not the north side, of the tree increased abruptly. The rate of change slowed gradually in an exponential pattern after the initial increase, eventually reaching about 1 g s^{-2}. The original value of Q_{wt} doubled within an hour and then stabilized. After the second irrigation an additional abrupt increase in Q_{wt} occurred within the next hour, but the amplitude was smaller than after the first irrigation. No response in Q_{wt} was observed after the third irrigation to the south-side of the tree. No response in Q_{wt} was observed on the north-side of Tree 3 during the three irrigations to the south-side of the tree. The low lateral hydraulic conductivity of the soil presumably impeded the movement of the irrigation water around the tree, because a similar rapid increase in sap flow occurred on the north-side of Tree 3 when it was irrigated on the north side (Figures 2 and 3). The declining Tree 4, which had an extremely low Q_{wt} on both sides of the stem, responded to irrigation on its south side in the same way as Tree 3, although the relative response of Tree 4 was higher than that of Tree 3, because the initial values of Q_{wt} were so low. There was no immediate response of Q_{wt} to irrigation on the north-side of Tree 4, but a small increase was observed late the next day (see Figure 1), suggesting that the superficial fibrous roots on the north side of the tree were dead but that some deeper roots were still able to absorb water. In summary, after irrigation, Q_{wt} increased 2–5 times in declining trees, with the

Table 3. Characteristic values of sap flow rate, Q_{wt}, in large beech trees (*Fagus sylvatica* L.) before and after irrigation.

Parameter	Irrigation	Control tree		Declining tree	
		No 1	No. 2	No. 3	No. 4
Maximum actual Q_{wt} ($kg\ h^{-1}$)	Before	13.9	7.0	3.3	0.5
	After	18.9	13.3	7.6	2.4
	After/before	1.4	1.9	2.3	5.0

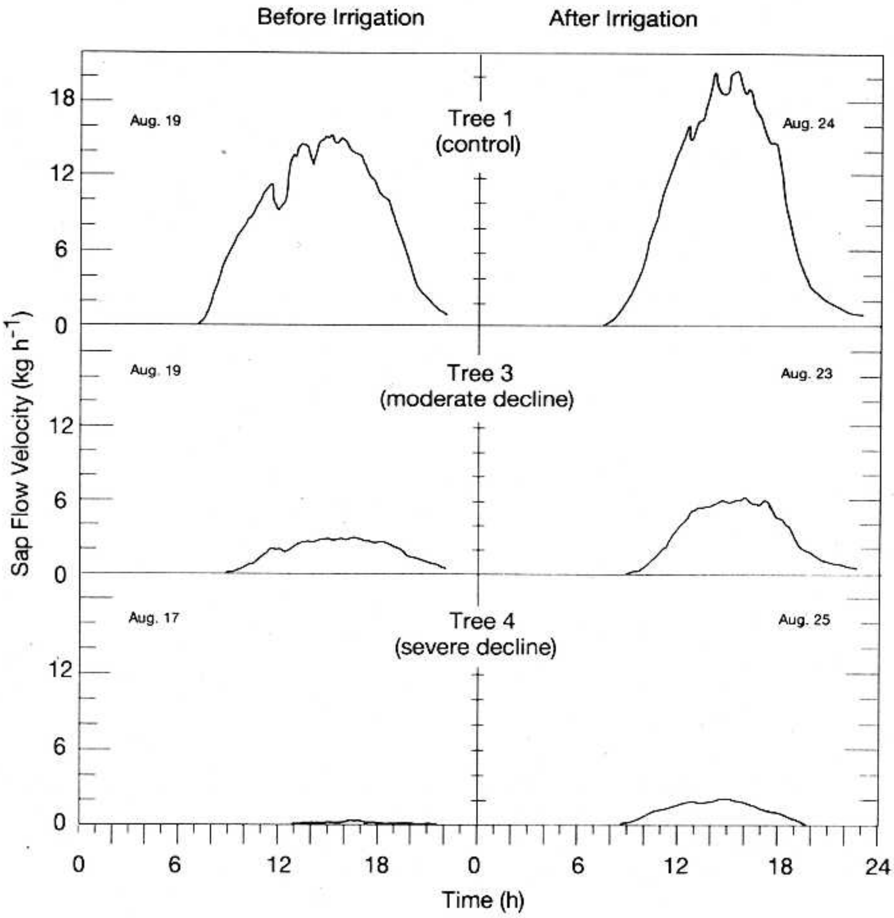

Figure 1. Diurnal courses of xylem sap flow rate in healthy (control) and declining beech (*Fagus sylvatica* L.) trees before and after irrigation with a total of 150 mm of irrigation water. Xylem sap flow rate was measured at 3.7 m above ground during late summer when potential evaporation was close to 3.5 mm day^{-1}

more injured Tree 4 showing a relatively greater increase than Tree 3 (see Table 3).

Tree conductive systems and the relative importance of limiting factors

After the first two irrigations, Q_{wt} increased rapidly in the declining trees and then gradually reached a stable plateau. By the third irrigation, the maximum capacity for water transport of the conductive xylem was reached and the attached foliage determined the demand of the whole tree for water. If it is assumed that the water transport capacity of the stem is adjusted throughout the season to account for leaf loss, then the lower sap flow rates obtained after irrigation of declining trees compared with those of healthy trees might be a result of both loss of foliage and cavitation. If the extent of cavitation is small, the declining tree will still be able to respond quickly to an ample supply of water. Irrigation permitted estimation of the

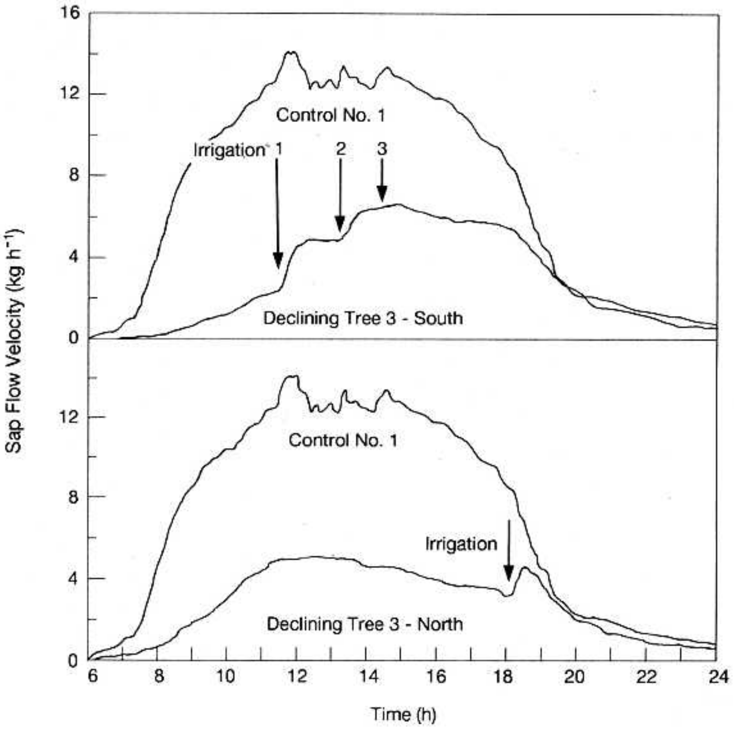

Figure 2. Diurnal course of xylem sap flow rate in healthy (Tree 1) and declining (Tree 3) beech (*Fagus sylvatica* L.) trees before and after several consecutive 20-min irrigations, each of 50 mm, on the north and south sides of declining Tree 3. Xylem sap flow rate was measured at 3.7 m above ground during late summer when potential evaporation was close to 3.5 mm day^{-1}.

relative importance of the factors limiting the xylem sap flow rate. Before irrigation, Q_{wt} was limited by long-term effects, including permanent changes in the structure of the conducting xylem of the roots, stem and leaves, as well as by the short-term effect, i.e., the varying supply of soil water. Irrigation relieved the supply-limited portion of the stress, so that the value of Q_{wt} after irrigation reflected only the changed structural properties of the tree that affect water demand in the long-term (see Table 3). However, it is possible that long-term irrigation of the declining trees might result in *de novo* regeneration of xylem, roots and leaves leading eventually to full recovery (Stout 1959).

The high Q_{wt} observed and the small increase in Q_{wt} in response to irrigation of the control trees indicated that these trees were subject only to mild water stress. The increase in Q_{wt} in the declining trees in response to irrigation indicates that the primary cause of decline was local drought. In contrast to the control trees, the Q_{wt} in declining trees was also partially inhibited by the demand-limited components of water stress, i.e., by the consequences of chronic drought on tree structure. When water was applied to the dense surface network of fibrous roots at the soil surface, it was quickly absorbed, indicating that survival of these trees was related to their

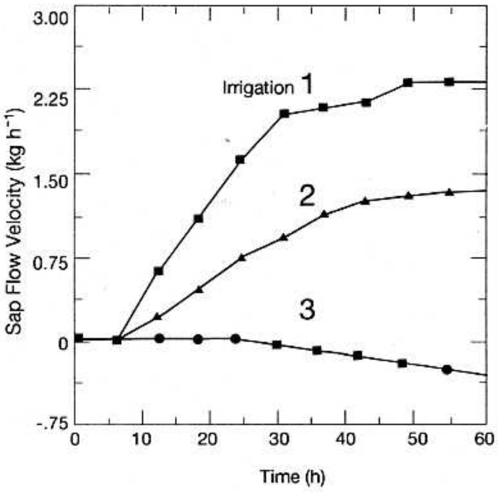

Figure 3. Effect of irrigation on xylem sap flow rate in a declining beech (*Fagus sylvatica* L.) tree with a dbh of about 50 cm. Xylem sap flow rate was measured at 3.7 m above ground during three consecutive 20-min irrigations, each of 50 mm. The data from Figure 2 have been compiled so that the start of each irrigation is on the *y*-axis.

ability to utilize effectively the small amount of water available (Table 1). Drought evidently led to the death of the major deep-rooting system and to its replacement by a dense network of fibrous roots at the soil surface.

Xylem sap moves at a velocity of only several meters per hour (Zimmermann and Brown 1971, Jones 1983). This means that sap could have moved a maximum of 60 cm in the 6-min response time, indicating that water passing the measuring point 3.7 m above ground could not have been the water applied to the ground. We conclude, therefore, that the declining trees possessed some functional conducting xylem in the stems, i.e., 13–42% of the vessels had continuous water columns. Because the appearance of emboli follows drought stress closely (Zimmermann 1983, Tyree and Sperry 1989), it is surprising that trees can resist drought for several years. The driving force for the sudden increase in water flow in response to irrigation was the gradient of water potential, $-\Delta\Psi = -\Psi_{\text{leaves}} - (-\Psi_{\text{soil}})$, which increased greatly when the soil water tension (Ψ_{soil}) was released after irrigation, even though the high tension in the leaves (Ψ_{leaves}) remained constant (it cannot change significantly within a few minutes under stable fine weather).

An explanation of the history of the experimental stand

Originally, the trees growing in the more open, better illuminated parts of the stand developed deep, dense crowns, whose large surface (high LAI) increased the interception of water, thus decreasing the supply of soil water due to precipitation beneath the crowns. The high demand for water of such exposed crowns led to the development of large, extensive root systems, especially external to the crown ground plan areas, which also stabilized the trees mechanically.

Trees growing in what had originally been dense, shaded parts of the stand had only short crowns with a low LAI, so that interception of precipitation was low. Because of their erect branches and smooth bark, stem flow in beech trees is high (Larcher 1976). This combination of factors presumably accounts for the dense development of superficial roots near the base of these trees.

After the sudden opening of the stand, such root systems would not have been well adapted to take advantage of the increased water availability on the site. The ability of the trees to use the available water would have been limited also by the low hydraulic conductivity of the clay soil and the limited amount of physiologically accessible water (Scheffer and Schachtshabel 1976). Utilization of soil water in the immediate vicinity of the tree stems, where root density was highest appears to have caused severe local drought, which eliminated the ground vegetation around the base the trees. A drought-induced increase in root length (Riedacker 1976, Linder and Axelsson 1982, Schulze and Chapin 1987, Mooney and Winner 1988) could have led to the development of a dense network of thin roots close to the soil surface, permitting the trees to utilize water from precipitation or condensation more effectively. However, drought also caused a reduction in foliage mass by decreasing leaf production and leaf size and hastening the onset of leaf fall. This must have led to a gradual decrease in carbon gain, then a reduction in root and foliage production, and finally to the decline of the trees. When the trees died, the lack of competition for water around the stems and the change in light regime permitted the recovery of ground vegetation around the dead stems.

Conclusions

Large, water-stressed beech trees can respond to irrigation within minutes, even after several years of chronic drought. The supply-limited and demand-limited components of water stress (i.e., a shortage of soil water and a damaged conducting system) were estimated. We conclude that the conducting systems of beech trees are relatively resistant and remain largely undamaged, i.e., not all vessels are blocked by cavitation and not all roots stop absorbing water until the trees lose more then 90% of their foliage. However, leaf loss and tree decline may proceed rapidly on clay soils that have limited hydraulic conductivity, because of severe local drought stress in trees with poorly developed root systems.

The relatively resistant conductive systems of beech trees may help them to survive in the short term, but the extent of changes in tree structure and other irreversible changes due to drought do not allow the trees to survive in the long term. The successful management of beech trees on heavy clay soils should include progessive thinning to allow the trees to adapt their structure for long-term mechanical stability and a high water demand.

Acknowledgment

The authors thank Dr. W. Keller for the information on site characteristics and D. Tarjan, M. Walsel,

U. Buhlmann and Dr. E. Bednárová for soil sampling and estimation of water content.

References

Čermák, J. 1991. Transpiration of trees and its importance in forest ecology. Assoc. Prof. Thesis, Univ. Agric., Brno.

Čermák, J. and J. Kucera, J. 1981. The compensation of natural temperature gradient in the measuring point during the sap flow rate determination in trees. Biol. Plant. 23:469–471.

Čermák, J. and J. Kucera. 1990*a*. Scaling up transpiration data between trees, stands and watersheds. Silva Carel. 15:101–120.

Čermák, J. and J. Kucera. 1990*b*. Changes in transpiration of healthy mature trees due to environmental conditions and of those with damaged water conductive system. *In* Verification of Hypotheses and Possibilities of Recovery of Forest Ecosystems. Eds. E. Klimo and J. Materna. Proc. Cs. MAB Natl. Comm./IUFRO Internat. Workshop, Beskydy Mt., Agric. Univ. Brno, Czechoslovakia, pp 275–286.

Čermák, J. and J. Kucera. 1990*c*. Extremely fast changes of xylem water flow rate in mature trees, caused by atmospheric, soil and mechanical factors. *In* Methodologies to Assess the Impacts of Climatic Changes on Vegetation: Analysis of Water Transport in Plants and Cavitation of Xylem Conduits. Eds. A. Raschi and M. Borghetti. Proc. CEC Int. Workshop, Firenze, Italy.

Čermák, J. and J. Kucera. 1990*d*. Water uptake in healthy and ill trees, under drought and hypoxia and non-invasive assessment of the effective size of root systems. *In* Above and Belowground Interactions in Forest Trees in Acidified Soils. Ed. H. Persson. Proc. COST 612 Workshop, Simlangsdalen, Sweden, pp 185–195.

Čermák, J., M. Deml and M. Penka 1973. A new method of sap-flow rate determination in trees. Biol. Plant. 15:171–178.

Čermák, J., J. Huzulák and M. Penka. 1980. Water potential and sap flow rate in adult trees with moist and dry soil as used for the assessment of the root system depth. Biol. Plant. 22:34–41.

Čermák, J., J. Jenik, J. Kučera and V. Zidek. 1984. Xylem water flow in a crack willow tree (*Salix fragilis* L.) in relation to diurnal changes of environment. Oecologia 64:145–151.

Čermák, J., J. Úlehla, J. Kučera and M. Penka. 1982. Sap flow rate and transpiration dynamics in the full-grown oak (*Quercus robur* L.) in floodplain forest exposed to seasonal floods as related to potential evapotranspiration and tree dimensions. Biol. Plant. 24:446–460.

Jones, H.G. 1983. Plants and microclimate. Cambridge University Press, Cambridge, 323 p.

Kozlowski, T.T. 1984. Responses of woody plants to flooding. *In* Flooding and Plant Growth. Ed. T.T. Kozlowski. Academic Press, New York, pp 129–163.

Kramer, P.J. and T.T. Kozlowski. 1979. Physiology of woody plants. Academic Press, New York.

Kučera, J., J. Čermák and M. Penka. 1977. Improved thermal method of continual recording the transpiration flow rate dynamics. Biol. Plant. 19:413–420.

Larcher, W. 1976. Okologie der Pflanzen. UTB Ulmer-Verlag, 320 p.

Linder, S. and B. Axelsson. 1982. Changes in carbon uptake and allocation patterns as a result of irrigation and fertilization in a young *Pinus sylvestris* stand. *In* Carbon Uptake and Allocation in Subalpine Ecosystems as a Key to Management. Ed. R.H. Waring. Univ. Oregon, Corvallis, Oregon, pp 38–44.

Mooney, H.A. and W.E. Winner. 1988. Carbon gain, allocation and growth as affected by atmospheric pollutants. *In* Air Pollution and Plant Metabolism. Eds. S. Schulte-Hostede, N.M. Darral, L.W. Blank and A.R. Wellburn. Elsevier, London and New York, pp 272–287.

Riedacker, A. 1976. Rhythmes de croissance et de régénération des racines des végétaux ligneux. Ann. Sci. For. 33:109–138.

Rychnovská, M., J. Čermák and P. Šmíd. 1980. Water output in a stand of *Phragmites communis* Trin. A comparison of three methods. Acta Sci. Nat. (Brno) 14:1–27.

Scheffer, F. and P. Schachtschabel. 1976. Lehrbuch der Bodenkunde. Enke-Verlag, Stuttgart, 394 p.

Schulze, E.-D. and F.S. Chapin, III. 1987. Plant specialization to environments of different source availability. Ecol. Studies 61:120–148.

Stout, B.B. 1959. Supplemental irrigation of 75-year-old hardwoods. Black Rock Forest Papers No.25.

Türc, L. 1961. Évaluation des besoins en eau d'irrigation, évapotranspiration potentielle. Ann. Agron. 12:13–49.

Tyree, M.T. and J.S. Sperry. 1989. Vulnerability of xylem to cavitation and embolism. Ann. Rev. Plant Physiol. Mol. Biol. 40:19–38.

Zimmermann, M.H. 1983. Xylem structure and the ascent of sap. Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 144 p.

Zimmermann, M.H. and C.L. Brown. 1971. Trees—structure and function. Springer-Verlag, Berlin, Heidelberg, New York, 336 p.