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Long-Distance Water Transport in Aquatic Plants[1]

Ole Pedersen*

Freshwater Biological Laboratory, University of Copenhagen, Helsingørsgade 51, DK-3400 Hillerød, Denmark

Acropetal mass flow of water is demonstrated in two submerged angiosperms, *Lobelia dortmanna* L. and *Sparganium emersum* Rehman by means of guttation measurements. Transpiration is absent in truly submerged plants, but the presence of guttation verifies that long-distance water transport takes place. Use of tritiated water showed that the water current arises from the roots, and the main flow of water is channeled to the youngest leaves. This was confirmed by measurement of guttation, which showed the highest rates in young leaves. Guttation rates were 10-fold larger in the youngest leaf of *S. emersum* (2.1 μL leaf^{-1} h^{-1}) compared with the youngest leaf of *L. dortmanna* (0.2 μL leaf^{-1} h^{-1}). This is probably due to profound species differences in the hydraulic conductance (2.7×10^{-17} m^4 Pa^{-1} s^{-1} for *S. emersum* and 1.4×10^{-19} m^4 Pa^{-1} s^{-1} for *L. dortmanna*). Estimates derived from the modified Hagen-Poiseuille equation showed that the maximum flow velocity in xylem vessels was 23 to 84 cm h^{-1}, and the required root pressure to drive the flow was small compared to that commonly found in terrestrial plants. In *S. emersum* long-distance transport of water was shown to be dependent on energy conversion in the roots. The leaves ceased to guttate when the roots were cooled to 4°C from the acclimatization level at 15°C, whereas the guttation was stimulated when the temperature was increased to 25°C. Also, the guttation rate decreased significantly when vanadate was added to the root medium. The observed water transport is probably a general phenomenon in submerged plants, where it can act as a translocation system for nutrients taken up from the rich root medium and thereby assure maximum growth.

It has remained a mystery how rooted plants growing under water distribute nutrients derived from the sediments to the green shoots commonly constituting more than 80% of plant biomass. Mass transport is clearly needed to sustain the extensive growth in apical shoots occurring up to 3 m above the sediment, which often provides the predominant nutrient source (Barko and Smart, 1981; Barko et al., 1991). The transport mechanism should also be adjustable to ensure that nutrients taken up by roots are channeled to tissue in active growth. Water transport is the most likely mass transport mechanism, but for more than 100 years it has been questioned whether truly submerged plants possess acropetal water transport (Unger, 1862; Sauvageau, 1891; Hochreutiner, 1896; Pond, 1905; Thoday and Sykes, 1909; Thut, 1932). Transpiration from leaf surfaces obviously cannot generate the same flow as in terrestrial plants. Major textbooks have treated water transport in submerged plants superficially because of lack of interpretable data, and not much knowledge has been gained since the turn of the century (Gessner, 1956; Sculthorpe, 1967; Hutchinson, 1975; Raven, 1984).

Dyes, gravimetric methods, and conventional potometers have traditionally been applied by aquatic plant physiologists to the study of water transport in aquatic plants (Unger, 1862; Sauvageau, 1891; Hochreutiner, 1896; Thoday and Sykes, 1909; Wilson, 1947; Vardar, 1950; Höhn and Ax, 1961). Recently, however, Pedersen and Sand-Jensen (1993) demonstrated acropetal water transport in eight of nine investigated species by the use of tritiated water ([^{3}H]HO). They found rates sufficiently fast to ensure nutrient supply from roots to shoots at maximum growth rates, and the examined species mainly channeled the water flow to young leaves in active growth. The interpretation of quantitative experiments with [^{3}H]HO in two-compartment systems is, however, open to critique because water moves fairly easy in the apoplast inside and outside the endodermis, and these experiments call for verification by nontracer methods. Nondestructive methods that allow repeated measurement on the same individual with only minor manipulation of the growth environment would be most preferable.

Von Minden (1899) described guttation (exudation of mainly xylem components through special leaf structures termed hydathodes) in a variety of submerged and amphibious plants, and Pedersen and Sand-Jensen (1993) confirmed this observation in *Littorella uniflora* (L.) Aschers., *Lobelia dortmanna* L., and *Sparganium emersum* Rehman. Determination of guttation rates provides a suitable conservative estimate of the acropetal water transport, but it is confined to species and leaves with functional hydathodes. The distribution to leaves at different locations and of different ages can be determined and the guttation product analyzed. Another major advantage is that guttation can be measured without transferring the plants from their natural sediment to a chamber system. Thus, root hairs are not disrupted and ionic composition, osmotic pressure in the pore water, and chemical gradients around the roots are maintained. All aspects are highly dependent on osmotic gradients in the root and on root pressure, which is thought to be the main driving force for guttation and acropetal water transport in submerged plants (Wilson, 1947; Gessner, 1956; Höhn and Ax, 1961; Sculthorpe, 1967; Pedersen and Sand-Jensen, 1993).

The purpose of this study was to (a) determine the origin of the water taking part in the acropetal water transport, (b) quantify the rates of acropetal water transport by means of guttation measurements and demonstrate to which leaves the water is channeled, and (c) demonstrate whether the water

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* Fax 45-48-24-14-76.

transport is an active process depending on energy conversion in the roots.

MATERIALS AND METHODS

Plant Material

Two species of submerged aquatic angiosperms (*Lobelia dortmanna* L. and *Sparganium emersum* Rehman, the submersed form) were chosen for experiments. The two species are similar in growth form, i.e. the stem makes up only a small fraction of the total length of the plant (root plus stem plus leaves), the leaves are continuously set in a rosette from an apical stem meristem, and leaves expand from a basal leaf meristem and have one (*S. emersum*) or a group (*L. dortmanna*) of hydathodes at the leaf tip. The number of leaves per mature plant is relatively constant because the older leaves are shed when new leaves emerge. However, there are some profound differences in growth form that were utilized in this survey. The average leaf length of *S. emersum* is 50 cm (up to 2 m above the sediment), and the total number of leaves per plant is four to seven (Moeslund et al., 1990). In contrast, *L. dortmanna* has up to 20 leaves per plant, and the average leaf length is only 5 cm (Moeslund et al., 1990). Leaf position and age are referred to in the following order: in *S. emersum*, leaf Nos. 0 to 4, where leaf 0 is the youngest leaf still wrapped in the sheath of leaf 1 and leaf 4 is the oldest; in *L. dortmanna*, leaf Nos. 1 to 17, where leaf 1 is the youngest and leaf 17 is the oldest.

L. dortmanna was collected from an oligotrophic soft-water lake (Skånes Värsjö), rooted in large blocks (40 × 40 × 20 cm deep) of natural sediment, and grown submerged in 10 cm of water with an alkalinity of 0.1 meq L^{-1}. *S. emersum* was collected from a eutrophic, hard-water stream (Havelse Å) and grown in natural sediment in plastic pots submerged in a 50-cm deep aquarium with alkaline tap water (5.0 meq L^{-1}), representing ground water derived from the same catchment area. Both species were held at 15°C and 250 μmol of photons m^{-2} s^{-1} from fluorescent light tubes in a 16-h light/8-h dark cycle.

Tracer Studies

[^{3}H]HO was used as a qualitative tracer to determine the origin of the water translocated and described the distribution pattern of the acropetal water transport within *S. emersum*. [^{3}H]HO (yielding a pore water concentration of 3.7 MBq mL^{-1}) was injected into numerous sediment sites (about 1 cm apart) in pots containing *S. emersum* in active growth. The sediment surface was sealed with water-free lanolin, and the plants were transferred to a large water-filled aquarium, thereby minimizing the importance of possible leakage of [^{3}H]HO from the root compartment. After 4 d of incubation the leaves were harvested, cut into pieces (<0.25 cm^2), and left for 1 week in 2 mL of deionized water in capped vials for equilibration of [^{3}H]HO. Equilibration was facilitated by freezing and thawing the samples twice per d. The specific activity was measured in subsamples on a liquid scintillation counter (LKB Wallac 1219 Rackbeta) using Aqualyte scintillation cocktail. Subsequent analysis of [^{3}H]HO after 2 weeks showed no significant change in specific activity.

Collection of Guttation Product

The two species were manipulated to allow collection of guttation droplets from the hydathodes at the leaf tips. However, species differences in leaf lengths required slightly different experimental setups. For *L. dortmanna* the water level was reduced to just below the tips of the shortest leaves, and the large plastic trays containing the rooted plants were covered with gas-tight, transparent polyvinyl chloride, leaving a small 5-cm gas space between the water surface and the cover. This gas space soon became saturated with water vapor, allowing guttation droplets to emerge from the hydathodes. Droplets were collected on leaves of different ages at 2- to 6-h intervals, varying according to plant activity. Collection was made with small glass capillaries (1 cm long) stretched to a tip diameter of 50 to 100 μm, which were weighed on an electrobalance (Cahn 29, accuracy 0.01 μL of water) before and after collection.

For *S. emersum* the leaf tip was drawn through a slit in floating Styrofoam and covered with a gas-tight, transparent plastic chamber sealed with water-free lanolin, thereby generating a water-saturated atmosphere around the leaf tip. Because of high guttation activity in *S. emersum*, droplets were collected after 1 h of incubation.

The above technique was modified to allow guttation measurements for *S. emersum* in the field. Eppendorf centrifuge tubes (1 mL) were mounted around the leaf tips through a slit in the tube and sealed by water-free lanolin, which created a gas-tight chamber. To facilitate mounting, the water level was reduced by pressing a large plastic cylinder into the sediment around the plants and continuously pumping away the water by a battery-driven submersible pump. After the tubes were in position the cylinder was removed to restore the original water level and flow.

Application of Inhibitors

The influence of root metabolism on acropetal water transport was examined in two experiments with *S. emersum*. To determine the importance of root temperature on guttation, plants were rooted in Styrofoam containers containing a cooling spiral (connected to a thermostat bath) in natural sediment and allowed to grow there for 2 weeks. Root temperature could be manipulated between 2 and 30°C, and the surrounding aquarium water containing the leaves was maintained at 15°C. Guttation was measured as described above. *L. dortmanna* was omitted in these experiments because of the low guttation rate in these plants.

The dependence of water transport on energy-demanding processes was examined by adding vandate to the roots in a two-compartment system. Vandate is regarded as an inhibitor of the root plasmalemma ATPases (Sze, 1984). Experimental plants and controls were transplanted with the shoots in a common shoot compartment, and the roots were planted in individual root chambers (Pedersen and Sand-Jensen, 1993). After the plants had acclimated to 15°C and initial guttation rates were determined, measurements continued in control plants and plants treated with 1 mM VO_4^{3-} added to the root compartment.

Prediction of Flow Velocity and Pressure Gradients

Maximum water velocity within xylem vessels was estimated from the Hagen-Poiseuille equation describing flow conditions in capillaries (Zimmermann, 1983). The minimum pressure (ΔP) required to force the measured amount of water through a single-vessel system of given length (Δl) is

$$\frac{\Delta P\ (\text{Pa})}{\Delta l\ (\text{m})} = Q\ (\text{m}^3\ \text{s}^{-1})\ \frac{8\eta\ (\text{Pa s})}{\pi r^4\ (\text{m}^4)} \qquad (1)$$

where Q is the flow rate, η is the dynamic viscosity, and r is the radius of the vessel. From the knowledge of $\Delta P/\Delta l$, the maximum velocity (v_{max}) in a single-vessel system is given by

$$v_{max}\ (\text{m s}^{-1}) = \frac{\Delta P\ (\text{Pa})}{\Delta l\ (\text{m})}\ \frac{r^2\ (\text{m}^2)}{4\eta\ (\text{Pa s})} \qquad (2)$$

This relationship is valid for a one-vessel system only. Assuming that the apoplast inside the endodermis is one common compartment and the same pressure is exerted on all vessels, the problem can be solved for a multivessel system

$$Q_t\ (\text{m}^3\ \text{s}^{-1}) = \frac{\Delta P\ (\text{Pa})}{\Delta l\ (\text{m})}\ \frac{\pi}{8\eta\ (\text{Pa s})} \sum_i r_i^4(m^4) \qquad (3)$$

Here, Q_t describes the total flow rate (in this case the measured guttation rate) and r_i represents the radius of the ith vessel. Consequently, $v_{max\ i}$ can be estimated when $\Delta P/\Delta l$ derived from Equation 3 is inserted in Equation 2

$$v_{max\ i}\ (\text{m s}^{-1}) = \frac{2Q_t\ (\text{m}^3\ \text{s}^{-1})\ r_i^2(m^2)}{\pi \sum_i r_i^4(\text{m}^4)} \qquad (4)$$

and the result provides a range of V_{max} values in a multivessel system depending on the radius of individual vessels. The v_{max} parameter is useful because it is exactly two times the v_{mean} because of the paraboloid nature of flow in capillaries (Vogel, 1981; Zimmermann, 1983).

Another useful parameter, the hydraulic conductance (K_h), can be derived from the Hagen-Poiseuille law (Gibson et al., 1984). The hydraulic conductance is given by the following relation

$$K_h\ (\text{m}^4\ \text{Pa}^{-1}\ \text{s}^{-1}) = Q_t\ (\text{m}^3\ \text{s}^{-1})\ \frac{\Delta l\ (\text{m})}{\Delta P\ (\text{Pa})} \qquad (5)$$

and from Equation 3 we obtain

$$K_h\ (\text{m}^4\ \text{Pa}^{-1}\ \text{s}^{-1}) = \pi\ \frac{\sum_i r_i^4(m^4)}{8\eta\ (Pa\ s)} \qquad (6)$$

Leaf tips of *S. emersum* were fixed and embedded in glycolmethacrylate (O'Brien and McCully 1981) after the guttation rates had been established. The material was cut on an automicrotome, stained with toluidine blue, and photomicrographed (Polyvar, Reichert-Jung), and the diameter of the xylem vessels was established from the photomicrographs.

The vessel diameter was also measured on leaves of *L. dortmanna*. Here, it was not possible to measure the diameter of xylem vessels in material used for guttation measurements. Instead, the dimensions were measured on fresh leaves of the same size and age on hand-cut sections stained with Calcofluor white M2R (Sigma) and analyzed by means of epifluorescence microscopy.

RESULTS

Source of Transported Water

After 4 d of incubation, [^{3}H]HO, derived from the sediment pore water, was found in all leaves of *S. emersum* (Fig. 1). However, [^{3}H]HO was incorporated mainly into the youngest leaves still in active growth. Leaf 0, so termed because it is hidden within the leaf sheath of leaf 1, attained a specific activity of 84% relative to the specific activity of the root medium, whereas leaf 4 accumulated no more than 4% (Fig. 1).

Leaf Position and Guttation Rates

Monocotyledons usually have a parallel leaf venation, and most species with hydathodes have only one hydathode located where the vascular bundles converge at the leaf tip (Salisbury and Ross, 1992). *S. emersum* has this anatomy (O. Pedersen, unpublished data), and only one drop of guttate emerged at a time. Leaves of dicotyledons often have a netlike venation, and hydathodes, if present, appear along the outermost edge of the leaf (Metcalf and Chalk, 1979). *L. dortmanna* has three to nine hydathodes at the leaf tip (Tswett, 1907), and more than one drop of guttate appeared during incubation.

Guttation rates were strongly dependent on leaf location and leaf age. In *S. emersum*, the youngest leaf (leaf 1) guttated 2.13 μL h^{-1}, leaf 2 guttated 0.30 μL h^{-1}, and leaf 3 rarely guttated water, yielding an average of only 0.006 μL h^{-1} (Fig. 2). Leaf 4 and older leaves never showed guttation. Similar guttation rates were obtained from field populations of *S.*

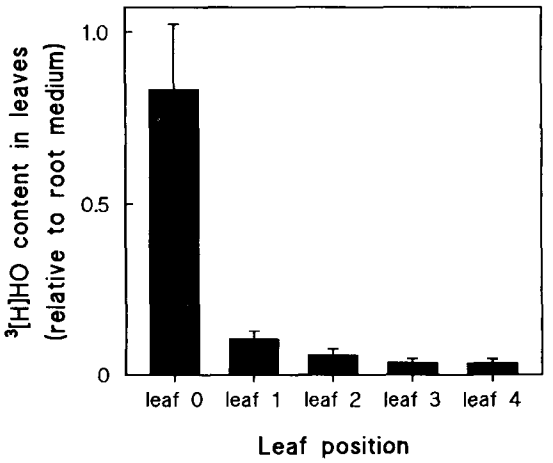

Figure 1. Internal distribution of [^{3}H]HO in leaves of different ages (leaf 0 youngest) of *S. emersum*. Values are shown as the relative specific activities of the whole leaf water pool (cell water plus apoplast water) to that in the root medium where [^{3}H]HO was initially added 4 d before (means ± SE, n = 5).

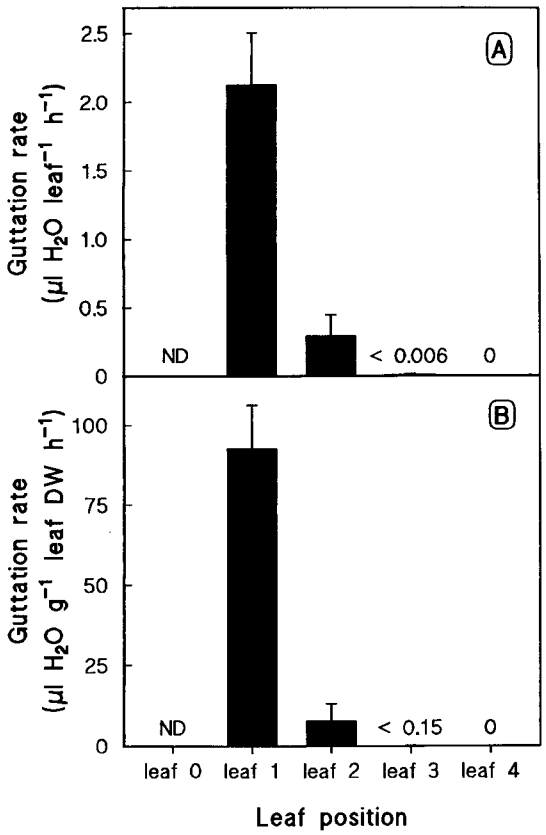

Figure 2. Guttation rates (A) and guttation normalized to leaf dry weight (DW) (B) in *S. emersum* leaves of different ages. Guttation rates were not determined (ND) in leaf 0 because of its protected position within the sheath of leaf 1. Values are means ± SE of nine plants.

emersum. Relative proportions of guttation among leaves 1, 2, and 3 were 1.0:0.141:0.003. When normalized to unit dry weight, the relative properties were 1.0:0.085:0.002 and thus lower for leaves 2 and 3 because leaf 1 is smaller than the older leaves. Guttation rates, scaled to the water content of the leaf, provide an estimate of water turnover rate. We probably have to acknowledge, however, that only a small fraction of the leaf water pool is engaged in acropetal water transport. *S. emersum* showed a turnover rate of 0.6% h^{-1} for leaf 1 and <0.1% h^{-1} for older leaves on the basis of leaf water.

L. dortmanna displayed a decline in guttation rate with leaf age, except that leaf 1 was not the most active leaf (Fig. 3). However, guttation rates normalized to leaf dry weight or leaf water content declined steadily with leaf age because leaf 1 weighs much less than older fully developed leaves. The turnover of the leaf water pool in leaf 1 was 10.8% h^{-1} compared to 0.6% h^{-1} for *S. emersum*. When normalized to leaf dry weight, *L. dortmanna* also showed much higher maximum rates (755 µL g^{-1} dry weight h^{-1}) than did *S. emersum* (93 µL g^{-1} dry weight h^{-1}).

According to Equation 3 the flow rate (Q_t) is inversely proportional to the length of the transport route. In principle, the observed skewed distribution of guttation rates could be explained by the increase in leaf length with age and position, thereby providing greater resistance to water transport. Plotting the guttation rate versus leaf length examines whether this can actually be the case for the two investigated species. Figure 4A shows that leaf length is a possible mechanism for regulation of the guttation rate in *S. emersum*, whereas this cannot be so for *L. dortmanna* (Fig. 4B).

Control of Acropetal Water Transport

Temperature around the roots of *S. emersum* had a profound impact on the guttation rate. Guttation stopped at 4°C in plants acclimated to 15°C (Fig. 5), and lowering the temperature from 15 to 10°C reduced the guttation rate 5-fold. The temperature response was reversible, and after the roots were cooled to 4°C, the guttation rate resumed the initial level when the temperature was returned to 15°C (Fig. 5). Guttation was stimulated when temperature was elevated from 15 to 25°C. An estimate of Q_{10} for guttation in *S. emersum* provided very different values, depending on whether the temperature was lowered or raised from the level of acclimatization at 15°C. Q_{10} was estimated as 8.2 when the temperature was lowered from 15 to 10°C and 1.4 when raised from 15 to 25°C. Correction for change in viscosity of the water with temperature was made prior to Q_{10} estimation (Vogel, 1981; Douglas et al., 1983).

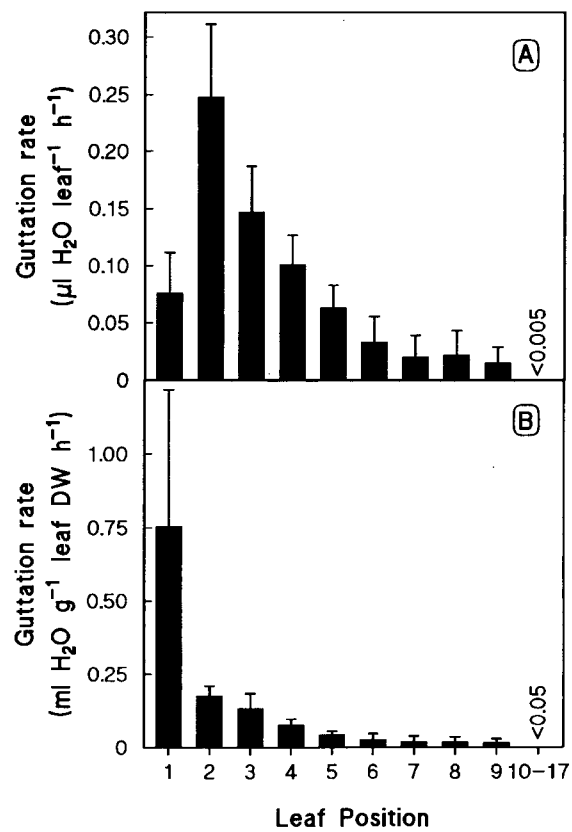

Figure 3. Guttation rates (A) and guttation normalized to leaf dry weight (DW) (B) in *L. dortmanna* leaves of different age. Values are means ± SE of 10 plants.

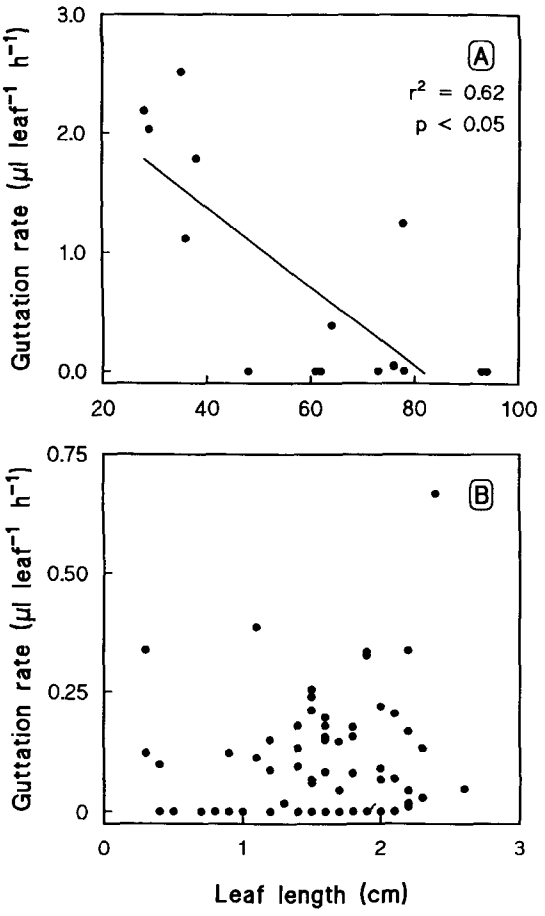

Figure 4. Guttation rates versus leaf length in *S. emersum* (A) and *L. dortmanna* (B).

Application of vanadate to the root medium of *S. emersum* reduced the guttation rate significantly (Fig. 6). During the time course of the experiment, control plants increased guttation to 86% of the initial rates, whereas plants with inhibitor decreased guttation rate to only 10% of the controls. The increase in guttation rate of control plants is probably due to acclimatization of the plants to the composition of the root medium, and the same relative increase would probably have occurred in the other plants had they not been inhibited by vanadate.

Prediction of Flow Velocity and Pressure Gradients

The flow rate is almost 10-fold higher for *S. emersum* than for *L. dortmanna*, but the median maximum flow velocity is highest in *L. dortmanna* (Table I). Note from the Hagen-Poiseuille equation that v_{max} equals $2v_{mean}$ because of the paraboloid flow front for nonturbulent flow in capillaries. *S. emersum* also has 5 times more xylem vessels of the double median diameter and a much longer transport distance for water in the long (35 cm) leaves. Accordingly, hydraulic conductance is almost 100-fold larger in *S. emersum* than *L. dortmanna*, and the root pressure needed to drive the transport is lower in *S. emersum* than in *L. dortmanna*.

DISCUSSION

Water release through apical leaf pores by guttation provides the most direct proof that acropetal water transport really takes place in aquatic plants. The hydathodes are probably important for flow regulation because most submerged plants do not develop stomata (Sculthorpe, 1967), which serve to regulate gas and water exchange in terrestrial plants (Salisbury and Ross, 1992).

The variable guttation rate among leaves of different ages is probably attributable to age-dependent changes in hydraulic conductance. Such changes can, in principle, occur at any point along the length of water transport from the root to the leaf tip, but change in water conductivity of the hydathode provides a simple and appropriate regulation mechanism. If the hydathodes simply clog when the leaves become mature, the water flow will stop. The water follows

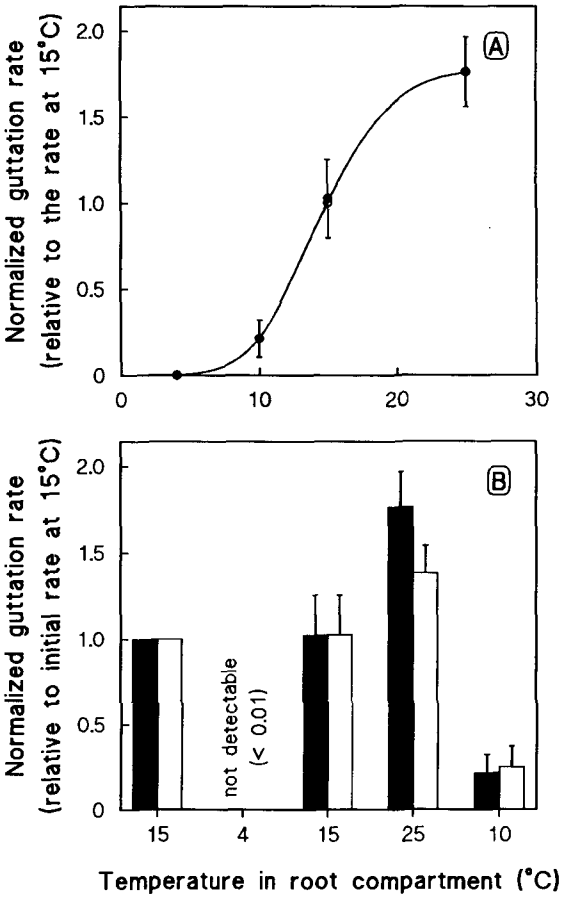

Figure 5. Temperature dependence of the guttation rate in *S. emersum* shown relative to the initial rate at 15°C (A) (not corrected for change in viscosity). All plants were exposed to the four experimental temperatures. B, Guttation rates in chronological order. After roots were cooled to 4°C, guttation resumed the initial rate when the temperature was returned to 15°C. Values are means ± SE of measurements on leaf 1 in five plants. Solid bars represent observed rates, and open bars are rates corrected for change in viscosity of the water in the range of temperature tested (the viscosity at 15°C is set as basis for this correction).

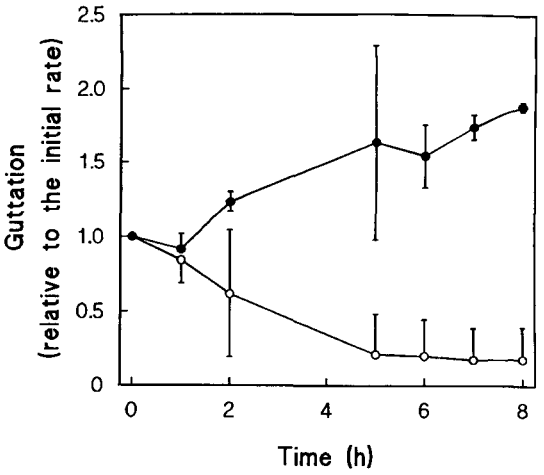

Figure 6. Time response of the guttation rate in *S. emersum* following addition of vanadate to the root medium. Guttation rates relative to the initial rate are shown for control plants (●) and inhibited plants (○). Values are means ± SE of measurements on leaf 1 in three plants.

the route showing least resistance to flow, and the youngest leaves with fully opened hydathodes are flushed more intensively. There have been few investigations of hydathodes in aquatic plants. However, there are suggestions of an age-dependent blockage by gum substances of the hydathodes in *L. dortmanna* (Von Minden, 1899) and *Ranunculus fluitans* Lam. (Wilson, 1947; Mortlock, 1952). Also, occlusion of the hydathodes in older strawberry leaves has been reported (Takeda et al., 1991). Removal of waxes blocking the hydathodes in nonguttating strawberry leaves initiated guttation, suggesting that the main resistance to water flow was the wax deposit and other substances excreted through the hydathodes. Thus, an age-dependent occlusion of the hydathodes may result in this uneven pattern of guttation rates observed between leaves of different ages.

The difference in leaf length with age is another possible explanation for the observed uneven guttation pattern. It is implicit in Equation 3 that the longer the transport distance the lower the rate of discharge because of the increased flow resistance. If this was the sole mechanism in operation, leaf guttation rate should decline with leaf length but never stop completely. *L. dortmanna* continued to release water in old leaves but did not show a positive relationship between leaf length and guttation rate. However, this relation was found in *S. emersum* which, on the other hand, stopped guttating in old leaves. In both species leaves stop expanding when mature, and older leaves (leaves 2–5 and 4–20 for *S. emersum* and *L. dortmanna*, respectively) are approximately the same length, which cannot explain the gradual reduction in guttation rates. Although guttation was never observed in leaf 4 and older leaves of *S. emersum*, the tracer experiments showed that some water was supplied to these leaves. Thus, the reduced guttation rate with leaf length observed for *S. emersum* may be due to increasing hydraulic resistance with leaf length or to clogging of hydathodes in older, longer leaves.

The acropetal water transport in *S. emersum* and *L. dortmanna* is clearly an active process confined to the roots. The flow is stopped by cooling the root compartment to 4°C, which indicates that the water transport is dependent on root metabolism and also that the driving force is restricted to the roots. These findings are supported by the reduced flow following addition of vanadate to the root compartment. Guttation is not stopped completely by adding vanadate, perhaps because not all of the ATPases are inhibited (Sze, 1984) or only part of the guttation phenomenon is directly dependent on energy conversion in the roots. Zholkevich (1992) suggested that root pressure results from an osmotic

Table I. *Estimates of flow velocities inside the xylem vessels, pressure gradients, root pressure, and hydraulic conductance in S. emersum and L. dortmanna*

Estimates are based on guttation rates and the modified Hagen-Poiseuille equation and must be viewed as conservative because capillaries are assumed to be ideal and continuous (Zimmermann, 1983; Gibson et al., 1984). The dynamic viscosity (η) is 1.14×10^{-3} Pa s at 15°C (Douglas et al., 1983), and the length of the water transport route (Δl) is set to 0.35 and 0.05 m for *S. emersum* and *L. dortmanna*, respectively. Median values and ranges in parentheses are shown apart from the mean guttation rate.

	S. emersum	*L. dortmanna*
Guttation rate (Q, μL h^{-1})	2.13 (0.43–3.66)	0.25 (0.02–0.67)
Vessel dimensions (r, μm)	6.3 (2.5–15.3)	3.2 (1.6–9.6)
Number of vessels (n)	55.5 (32–100)	11.0 (7–12)
Maximum flow velocity ($2v_{mean} = v_{max}$, cm h^{-1})	23 (2–223)	84 (16–334)
Pressure gradient (ΔP, kPa m^{-1})	3.4 (3.0–22.3)	159.0 (8.7–198.1)
Root pressure (P_{min}, kPa)	1.1 (1.0–7.4)	7.5 (0.4–9.9)
Hydraulic conductance (K_h, m^4 Pa^{-1} s^{-1})	2.7×10^{-17} (9.8×10^{-18}–7.4×10^{-17})	1.4×10^{-19} (1.1×10^{-19}–2.5×10^{-18})

as well as a metabolic component, the latter being very sensitive to the energy status of the root cells and sensitive to inhibition by 2,4-dinitrophenol and cytochalasin B. The osmotic component depends on energy input only over longer time spans. Accordingly, root pressure resulting in an acropetal water current, thought to be unimportant for most terrestrial plants as a mechanism of long-distance transport of water (Salisbury and Ross, 1992), can apparently be of great importance in aquatic angiosperms, where it is able to serve as a bulk transport system.

The predicted values of flow velocity and pressure gradients must be considered conservative estimates because an ideal capillary structure is assumed when the Hagen-Poiseuille equation is applied (Zimmermann, 1983; Gibson et al., 1984). Often, the xylem vessels are supposed to be less than 50 to 70% effective mainly because of discontinuous vessels and spiral thickenings in the cell walls (Zimmermann, 1983). The calculated minimum root pressure for the two species needed to support the measured guttation rates is much smaller than the root pressures of 200 to 300 kPa reported for herbaceous plants (Stocking, 1956). Even though an effectiveness of 50% is assumed, only 2 to 15 kPa are required to drive the observed flow rates in the two aquatic plants. The flow velocities listed in Table I are less than 1 m h^{-1}. This is clearly at the low end of reported flow velocities in xylem vessels for terrestrial plants (Salisbury and Ross, 1992), but those values arise from true transpiration currents. Root pressure must be considered a weaker force than evaporation from the leaf surface. Although more detailed anatomical studies (pore area and overlay frequency of tracheids [Gibson et al., 1984]) are required to evaluate precise estimates of flow velocities and pressure gradients, the measured parameters are useful for comparison of the general hydraulic architecture of the two species investigated. Especially significant is the hydraulic conductance per unit length (K_h), which is 100 times higher in *S. emersum* than in *L. dortmanna*, reflecting the 10-fold greater water transport capacity.

In summary, the present measurements of guttation from leaf tips of two submerged plants show that they possess an acropetal mass transport system for water that (a) works even when transpiration is absent, (b) is channeled to sites of active growth and should assure nutrient and hormone supply from roots, (c) results in estimated maximum water transport velocities of 23 to 84 cm h^{-1}, and (d) is dependent on energy conversion in the roots.

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