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# Internal gas transport in *Typha latifolia* L. and *Typha angustifolia* L. 2. Convective throughflow pathways and ecological significance

Troels Tornbjerg, Malene Bendix, Hans Brix\*

Department of Plant Ecology, Institute of Biological Sciences, University of Aarhus, Nordlandsvej 68, DK-8240 Risskov, Denmark

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## Abstract

The gas flow pathways within *Typha latifolia* L. and *Typha angustifolia* L. were evaluated by studying the internal pressurization and convective flow through individual leaves and the internal resistances to gas flow within the plants. Air enters the middle-aged leaves against a small pressure gradient by humidity-induced pressurization, is convected down the lacunae of the leaves to the rhizome, and from there is vented back to the atmosphere, through old or damaged leaves or through horizontal rhizomes to other shoots. A model was developed to analyze the gas flow pattern within the plants under different conditions. The analysis showed that the throughflow pattern is dynamic: leaves can be influx leaves under a certain set of conditions and efflux leaves under different conditions. The specific internal resistance to gas flow was generally low in leaves (less than  $1 \text{ Pa s mm}^{-2}$ ) and rhizomes ( $3 \text{ Pa s mm}^{-2}$ ), and somewhat higher in junctions between leaves and rhizome ( $5\text{--}14 \text{ Pa s mm}^{-2}$ ). *T. angustifolia* generally produced a greater leaf area specific convective flow rate (up to  $31 \mu\text{l min}^{-1} \text{ cm}^{-2}$ ) than *T. latifolia* (up to  $11 \mu\text{l min}^{-1} \text{ cm}^{-2}$ ). This greater ventilation capacity of *T. angustifolia* may be significant for its ability to grow in deeper water, and may contribute to the explanation of the depth distribution of the two species.

## 1. Introduction

Most vascular aquatic macrophytes have a lacunar system of intercellular air spaces that acts as a gas transport pathway, aerating underground organs and ox-

\* Corresponding author.

idizing the rhizosphere (Armstrong, 1979, 1982). The internal gas transport in the lacunae can occur by molecular diffusion or by non-throughflow and throughflow convection (Brix, 1993). Oxygen supplied by molecular diffusion exceeds that of non-throughflow convection in almost any situation, while oxygen supplied by throughflow convection may exceed that of molecular diffusion multiple times (Armstrong and Armstrong, 1990; Armstrong et al., 1991). Therefore, species with a convective throughflow mechanism may have a competitive advantage over species relying exclusively on diffusive gas transport, allowing them to inhabit deeper waters and more reduced sediments.

The two commonly occurring cattails in northern Europe (*Typha latifolia* L. and *Typha angustifolia* L.) differ in their distribution in relation to water depth. *T. latifolia* dominates the inner upper littoral zone while *T. angustifolia* dominates the outer upper littoral zone (Grace and Wetzel, 1982; Weisner, 1993). The two species differ in morphology in that *T. angustifolia* has taller and narrower leaves and taller and thinner shoots than *T. latifolia*. It has been suggested that *T. angustifolia* is able to grow in deeper water because of its lower leaf production costs and larger rhizome storage compared with that of *T. latifolia* (Grace and Wetzel, 1982). However, studies by Weisner (1993) suggest that *T. angustifolia* is competitively superior to *T. latifolia* at all water depths, and that the zonation is caused by the ability of *T. latifolia* to expand fast shortly after establishment.

The ability of plants to transport oxygen through the shoots to the below-ground parts when growing in water may influence their depth tolerance. The zonation within the littoral zone of some emergent macrophytes growing in Australia suggests that species producing a significant convective gas flow through their rhizomes are able to grow in deeper water than species without or with only a low convective gas flow (Brix et al., 1992). Supply of oxygen to the root system was concluded to be the limiting factor for the natural depth zonation of *Zizania latifolia* (Griseb.) Stapf and *Phragmites australis* (Cav.) Trin. ex Steud., the former being restricted to deep water and the latter to more shallow water (Yamasaki, 1984). Furthermore, studies have indicated that the narrow-leaved *Typha domingensis* Pers. grows in deeper water and may have a greater capacity to aerate its roots and rhizosphere than *T. latifolia* (Grace, 1988, 1989).

It has been recently documented that *T. latifolia* and *T. angustifolia* produce static pressure differentials up to 570 Pa owing to humidity-induced diffusion (Bendix et al., 1994). This internal pressurization produces gas flows up to 8 cm<sup>3</sup> min<sup>-1</sup> out of cut rhizomes. No information is available as yet on how the gas transport occurs within intact plants of the two species. In this study an attempt is made to clarify the gas flow pattern within the plants by analyzing the pressurization potential of individual leaves, the gas flow pathways, and the internal resistances to gas flow within the plants. The findings are discussed in relation to the natural depth distribution of the two species.

## 2. Materials and methods

### 2.1. Plant material

In February 1992 rhizomes (approximately 50 cm long) of *T. angustifolia* and *T. latifolia* were collected and propagated in a greenhouse as described earlier (Bendix et al., 1994). After 3 months the shoots of both species were almost 2 m high, and non-flowering specimens of each species were selected for the experiments.

### 2.2. Internal pressurization and convective gas flow

Experiments were carried out in a constant temperature ( $27 \pm 2^\circ\text{C}$ ) room with a relative air humidity of 31–44%. The plants were irradiated by a high-pressure sodium lamp (Osram, NAV-T, 400 W) placed at a distance of 0.5 m and giving a photon irradiance at the leaves of 200–300  $\mu\text{mol m}^{-2} \text{s}^{-1}$  PAR. Internal static pressurization ( $\Delta P_s$ ) and convective gas flow rate were recorded by a datalogger as described earlier (Bendix et al., 1994). Pressure and flow were stabilized within 5 min after mounting the rhizome or leaf on silicone tubes, and data sampled during the following ten minutes were used for further data processing. After  $\Delta P_s$  and convective gas flow rates produced by the intact plant had been measured, the oldest leaf was cut off at the base. The basal end of the cut leaf lamina was connected to silicone tubes by means of a flexible sealing compound (Terostat 9), and pressurization and gas flow of this single leaf were measured. The pressurization and gas flow from the plant with the oldest leaf cut off were then measured again. This procedure was repeated with all the remaining leaves, until pressurization and convective gas flow of all leaves and the entire plant with successively fewer leaves had been measured.

### 2.3. Leaf surface area, porosity and anatomy

The surface area of the parts of the leaves which were exposed to the atmosphere and thereby potentially pressurizing were measured using a rolling band leaf area measurer (LI-COR, Portable area meter, Model LI-3000, Lambda Instruments Corporation, USA).

For measurement of porosity (% of internal gas volume), the excised leaves were cut into 10 cm long pieces, weighed, sealed at both ends with silicone grease, and their total volume measured by submerging the piece of leaf into a narrow measuring cylinder and recording the volume of water displaced. Assuming that the specific weight of the plant tissue itself was  $1 \text{ g cm}^{-3}$ , the porosity was calculated from the ratio of tissue fresh weight and volume. The porosities of the rhizome, the short bundle of excised leaf bases and the junctions between leaves and rhizome were estimated by the same technique.

Anatomical studies were carried out as described by Bendix et al. (1994).

#### 2.4. Internal resistance to gas flow

The internal resistance to gas flow within the leaf sections, the rhizome, the short bundle of leaf bases and the junctions between leaves and rhizome was measured by connecting the material between a cylinder of compressed atmospheric air and a gas flow meter (Top-Track, Model 822-1, Sierra Instruments, Inc., Carmel Valley, CA; capacity  $0\text{--}10\text{ cm}^3\text{ min}^{-1}$ ) with a pressure transducer in parallel (P-Sensor, type PU-25, capacity 2500 Pa, Burster Präzisionsmesstechnik, Gernsbach, Germany). By applying a pressure from the gas cylinder, corresponding values of pressure and flow were recorded. During measurements the tissues were submerged in water to ensure there were no gas-leaks and that joints were gas-tight. The specific internal resistance to gas flow,  $R_s$  ( $\text{Pa s mm}^{-2}$ ) was calculated by the following formula

$$R_s = PA(FL)^{-1} \quad (1)$$

$P$  being the applied pressure (Pa),  $F$  the flow rate ( $\text{mm}^3\text{ s}^{-1}$ ),  $A$  the mean cross sectional area of the plant section ( $\text{mm}^2$ ), and  $L$  the length of the section (mm) (Brix et al., 1992).

The effect of leaf-age on the internal resistance to flow in the junction between leaves and rhizome was evaluated by connecting silicone tubes to the rhizome and every leaf of a plant, with the leaves cut off 0.5 m above the junction between leaves and rhizome. A pressure was applied from a small air pump (Rena 301) to one of the leaves, and the flow from the rhizome or from other leaves was recorded. The internal resistance to gas flow,  $R_i$  ( $\text{Pa s mm}^{-3}$ ) was calculated as follows

$$R_i = PF^{-1} \quad (2)$$

$P$  being the applied pressure (Pa) and  $F$  the recorded flow rate ( $\text{mm}^3\text{ s}^{-1}$ ). Note that the unit of  $R_i$  ( $\text{Pa s mm}^{-3}$ ) deviates from the unit of the specific internal resistance to gas flow,  $R_s$  ( $\text{Pa s mm}^{-2}$ ). Unlike values of  $R_i$ , values of  $R_s$  are directly comparable, because  $R_s$  takes account of the cross sectional area and the length of the flow route. As all leaves were cut to the same length in this experiment, values of  $R_i$  can be compared, bearing in mind that the younger leaves had smaller cross sectional areas than the older.

#### 2.5. Gas flow pattern

A series of equations was used to describe the gas flow pattern within an intact plant. The equations are based on measured static internal pressurization ( $\Delta P_s$ ) and recorded gas flow rates ( $F_s$ ) of individual leaves of different age. During a short time interval ( $\Delta t$ ) the volume of air that flows into or out of a leaf ( $iF_t$ ) can be calculated as

$$iF_t = (\Delta P_s - \Delta P_{t-\Delta t}) \Delta P_s^{-1} F_s \Delta t \quad (3)$$

where  $\Delta P_{t-\Delta t}$  is the pressure differential at  $t=t-\Delta t$ . The pressure differential at time  $t$  ( $\Delta P_t$ ) can be calculated from

$$\Delta P_t = \Delta P_{t-\Delta t} + (iF_t - oF_{t-\Delta t}) V^{-1} P_{\text{atm}} \quad (4)$$

where  $oF_{t-\Delta t}$  is the outflow from the leaf into the rhizome at  $t=t-\Delta t$ ,  $V$  is the internal gas volume of the leaf, and  $P_{\text{atm}}$  the atmospheric pressure, nominally set to 101.325 kPa. The outflow of air from the leaf to the rhizome ( $oF_t$ ) is calculated from

$$oF_t = (\Delta P_t - \Delta P_{\text{Rh}(t-\Delta t)}) R_J^{-1} \Delta t \quad (5)$$

where  $\Delta P_{\text{Rh}(t-\Delta t)}$  is the pressure build-up in the rhizome at  $t=t-\Delta t$ , and  $R_J$  is the internal resistance to gasflow in the junction between the leaf and the rhizome ( $\text{Pa s mm}^{-3}$ ). The pressure differential in the rhizome ( $\Delta P_{\text{Rh}(t)}$ ) can be calculated from the following formula

$$\Delta P_{\text{Rh}(t)} = \Delta P_{\text{Rh}(t-\Delta t)} + (iF_{\text{Rh}(t)} - oF_{\text{Rh}(t-\Delta t)}) V_{\text{Rh}}^{-1} P_{\text{atm}} \quad (6)$$

where  $iF_{\text{Rh}(t)}$  is the total flow from the leaves into the rhizome,  $oF_{\text{Rh}(t-\Delta t)}$  is the outflow from the rhizome at  $t=t-\Delta t$  and  $V_{\text{Rh}}$  is the internal gas volume of the rhizome. The total flow into the rhizome ( $iF_{\text{Rh}(t)}$ ) and the flow out of the rhizome ( $oF_{\text{Rh}(t)}$ ) are found from the following formulas

$$iF_{\text{Rh}(t)} = \Sigma oF_t \quad (7)$$

$$oF_{\text{Rh}(t)} = \Delta P_{\text{Rh}(t)} R_{\text{Rh}}^{-1} \Delta t \quad (8)$$

where  $\Sigma oF_t$  is the net sum of the outflow from all leaves, and  $R_{\text{Rh}}$  the resistance to gas flow out of the rhizome ( $\text{Pa s mm}^{-3}$ ).

This set of equations was solved numerically in steps of 0.002 s using the Euler method and a standard PC spreadsheet. At steady state, when  $iF_t = oF_t$  and  $\Delta P_t$  is constant ( $\Delta P_t = \Delta P_{t-\Delta t}$ ), leaves that are capable of maintaining higher pressures than the rhizome ( $\Delta P_t > \Delta P_{\text{Rh}(t)}$ ) will have positive gas flow rates ( $iF_t > 0$ ) and be influx leaves, and leaves with lower pressures than the rhizome will have negative flow rates and be efflux leaves. The basic features of the gas flow model are illustrated in Fig. 1.

### 3. Results

#### 3.1. Pressurization and gas flow

The static pressure differentials and gas flow rates of individual leaves are shown for representative specimens of the two *Typha* species in Fig. 2. Individual leaves of single plants showed different pressurization capacity dependent on leaf age. Static pressure differentials were generally lowest in the youngest and the older leaves (Fig. 2). The static pressure differentials ( $\Delta P_s$ ) of individual leaves of the two species were within the same range (300–800 Pa). However, the specific gas

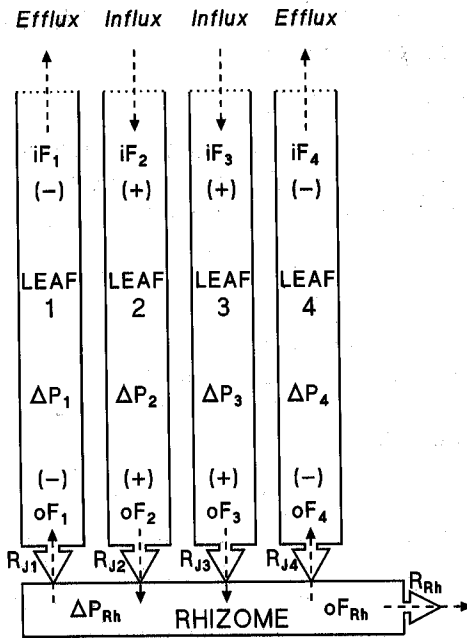


Fig. 1. Sketch showing the basic features of the gas flow model. The model plant is shown with only four leaves for simplicity.  $iF$  is the volume of air flowing into or out of a leaf.  $oF$  is the volume of air flowing out of the leaf into the rhizome. + and - designate the direction of the flow indicated by arrows.  $\Delta P$  and  $\Delta P_{Rh}$  are the pressure build-up in the leaves and the rhizome, respectively.  $R_j$  is the internal resistance to gas flow in the junction between the leaf and the rhizome, and  $R_{Rh}$  is the internal resistance to gas flow out of the rhizome. Leaves 2 and 3 that are capable of maintaining higher pressures than the rhizome ( $\Delta P > \Delta P_{Rh}$ ) will have positive gas flow rates ( $iF > 0$ ) and be influx leaves. Leaves 1 and 4 with  $\Delta P < \Delta P_{Rh}$  will have negative flow rates ( $iF < 0$ ) and be efflux leaves. See description in the text for further details.

flow rate (flow per leaf surface area) was three times higher for *T. angustifolia* compared with *T. latifolia* (Fig. 2).

Entire plants with successively fewer leaves produced higher pressures and gas flows from the remaining leaves when the oldest leaves were removed (Fig. 3). Removing the two oldest leaves of the specimen of *T. angustifolia* increased  $\Delta P_s$  and the gas flow rate (Fig. 3a). The pressurization increased successively when the six oldest leaves of the specimen of *T. latifolia* were removed, whereas maximum gas flow rates were recorded after removing the two oldest leaves (Fig. 3b).

### 3.2. Porosity and internal resistance to gas flow

Overall porosity of the leaves varied from 66.5 to 72.5% for *T. angustifolia* and 62.0 to 74.3% for *T. latifolia*. Generally, the porosity in older leaves was higher than in younger leaves. The porosity increased from the leaf apex towards the leaf

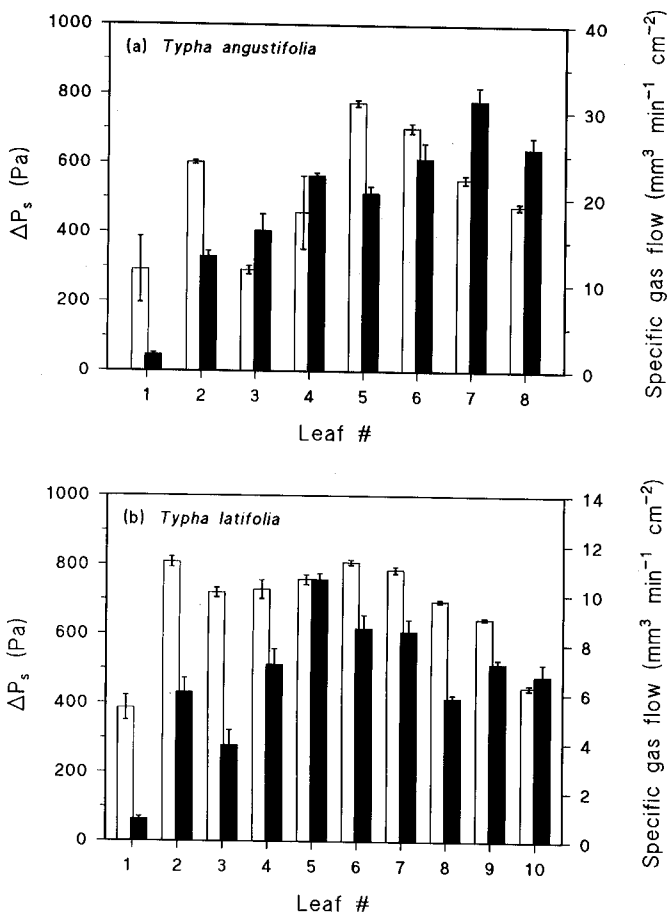


Fig. 2. Static internal pressurization,  $\Delta P_s$  (Pa; open bars) and area specific gas flow rate ( $\text{mm}^3 \text{min}^{-1} \text{cm}^{-2}$ ; solid bars) for excised leaves of (a) *T. angustifolia* and (b) *T. latifolia*. Leaves are numbered according to age, Leaf 1 being the youngest. Vertical bars indicate  $\pm 1$  s.d. ( $n=10$ ). During the experiments the relative humidity was 31–44% and the air temperature 25.2–28.5°C. It should be noted that the scale of the axes differ.

base, but decreased in the youngest leaves towards the basal part containing the meristematic tissue.

The specific internal resistance to gas flow ( $R_s$ ) decreased from the leaf apex (16–51 Pa s  $\text{mm}^{-2}$ ) towards the leaf base (less than 0.1 Pa s  $\text{mm}^{-2}$ ). No flow was registered through some of the apical pieces of leaves, in spite of an applied pressure of more than 600 Pa. When a higher pressure was applied, gas leaked out of the joints between the piece of leaf and the silicone tubes.

The internal resistance to gas flow ( $R_i$ ) was much higher in young leaves than in older (Table 1).  $R_i$  was low (3.5–4.0 Pa s  $\text{mm}^{-3}$ ) in older leaves (Nos. 5–8), increased to 47 Pa s  $\text{mm}^{-3}$  in Leaf 3 and was infinite in the two youngest leaves

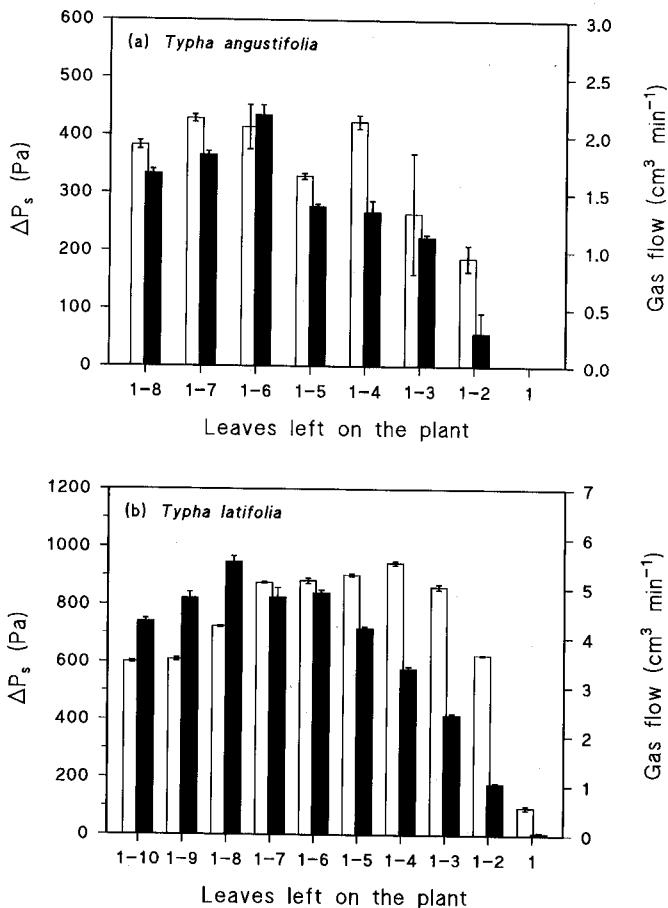


Fig. 3. Static internal pressurization,  $\Delta P_s$  (Pa; open bars) and convective gas flow rates through the cut rhizome ( $\text{cm}^3 \text{min}^{-1}$ ; solid bars) for entire plants with successively fewer leaves; (a) *T. angustifolia* and (b) *T. latifolia*. Leaves 1–8 and 1–10 indicate that all leaves were still on the plant, while Leaf 1 indicates that only the youngest leaf was left on the plant. Leaves are numbered according to age. Vertical bars indicate  $\pm 1$  s.d. ( $n=10$ ). During the experiments the relative humidity was 31–44% and the air temperature 25.2–28.5°C. It should be noted that the scales of the axes differ.

(Nos. 1 and 2).  $R_i$  was 3.0–3.5 Pa s  $\text{mm}^{-3}$  between the older leaves (Nos. 5–8), but 60–115 Pa s  $\text{mm}^{-3}$  between Leaf 3 and the older leaves.

Overall, the porosity and the specific internal resistance to gas flow ( $R_s$ ) within different plant parts of the two *Typha* species were similar (Table 2). An exception was the junctions between leaves and rhizome, which had higher porosity and, surprisingly, higher internal resistance in *T. latifolia* than in *T. angustifolia*. The mean cross sectional areas of leaves and rhizomes were higher for *T. latifolia* than for *T. angustifolia*.



Table 1  
Internal resistance to gas flow ( $R_i$ ; Mean  $\pm$  SD,  $n=10$ ) within a specimen of *T. latifolia* measured between different plant parts. All leaves were cut to a length of approximately 0.5 m and are numbered in accordance with their age, Leaf 1 being the youngest. ( $\rightarrow$  indicates the direction of the flow.)

Flow direction between plant parts	$R_i$ (Pa s mm <sup>-3</sup> )
Leaf 1 $\rightarrow$ Rhizome	$\infty^a$
Leaf 2 $\rightarrow$ Rhizome	$\infty^a$
Leaf 3 $\rightarrow$ Rhizome	47 $\pm$ 15
Leaf 4 $\rightarrow$ Rhizome	N.D.
Leaf 5 $\rightarrow$ Rhizome	4.0 $\pm$ 1.1
Leaf 6 $\rightarrow$ Rhizome	3.5 $\pm$ 1.0
Leaf 7 $\rightarrow$ Rhizome	N.D.
Leaf 8 $\rightarrow$ Rhizome	3.5 $\pm$ 1.0
Leaf 3 $\rightarrow$ Leaf 5	111 $\pm$ 41
Leaf 3 $\rightarrow$ Leaf 6	115 $\pm$ 37
Leaf 3 $\rightarrow$ Leaf 8	60 $\pm$ 19
Leaf 5 $\rightarrow$ Leaf 6	3.1 $\pm$ 1.1
Leaf 5 $\rightarrow$ Leaf 8	3.5 $\pm$ 0.9
Leaf 6 $\rightarrow$ Leaf 8	3.0 $\pm$ 0.7
Leaf 8 $\rightarrow$ Leaf 6	3.0 $\pm$ 0.8

<sup>a</sup> No flow registered in spite of an applied pressure of > 600 Pa. The internal resistance to gas flow is infinite.

N.D., not determined.

Table 2  
Mean porosity (%), specific internal resistance to gas flow ( $R_s$ ), and cross sectional areas of different tissues of *T. angustifolia* and *T. latifolia*. Measurements were made on similar loci of the leaves

	Porosity (%)	$R_s$ (Pa s mm <sup>-2</sup> )	Cross sectional area (mm <sup>2</sup> )
<i>T. angustifolia</i>			
Leaves ( $n=8$ )	71	0.6	15
Sheath bundle	47	0.7	–
Junctions	19	5.1	–
Rhizome	50	3.2	82
<i>T. latifolia</i>			
Leaves ( $n=10$ )	70	0.9	33
Sheath bundle	53	1.3	–
Junctions	37	14.2	–
Rhizome	59	3.3	103

### 3.3. Plant morphology and structure of aerenchyma

The most conspicuous morphological difference of the two *Typha* species is the leaf width, which is 4–10 mm for *T. angustifolia* and 10–25 mm for *T. latifolia*. The specimens studied had similar length of leaves (approximately 135 cm), but

the leaf surface area was twofold higher for *T. latifolia* than for *T. angustifolia* because of the difference in leaf width (on average 124 cm<sup>2</sup> per leaf vs. 61 cm<sup>2</sup> per leaf). The number of longitudinal lacunae, running parallel from leaf base to apex, was as high as 15 for *T. angustifolia* and more than 20 for *T. latifolia*. As the structure of the lacunae and the porosity are very similar in the two species, a common description is given here.

The lacunae are continuous from the leaf apex to the junction between the leaf and the rhizome. They are separated longitudinally by partitions and horizontally by thin multi-perforated diaphragms which allow the movement of gases. These diaphragms are found at different levels in adjacent lacunae across the width of the lamina. The diaphragms are one to three cells thick and are composed of stellate parenchyma cells. The pores in the diaphragms increase in size towards the base of the leaf (Fig. 4a, b). The bulk of the leaf is occupied by lysigenous aerenchyma which is less developed in young leaves and near the leaf apex than it is in old leaves and the basal parts of leaves. The internal resistance to gas flow consequently is low in old leaves and in basal parts of leaves.

At the junctions between leaves and rhizome both species have a compact, basal intercalary meristem. The junctions between leaves and rhizome have relatively high internal resistance to gas flow. The lacunae of the leaves are connected to the cortex of the rhizome, but the connection is very compressed. The cortex at

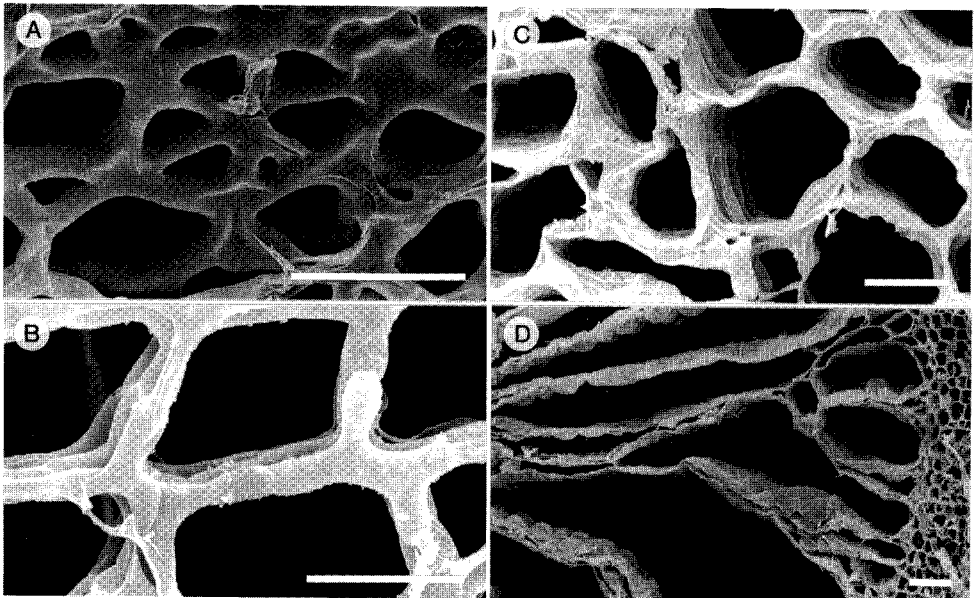


Fig. 4. Scanning electron micrographs of *T. latifolia*. Cross sections of (a) apical part of old leaf showing stellate parenchyma; (b) basal part of old leaf showing stellate parenchyma; (c) rhizome showing cortical lacunae; and (d) adventitious root showing radial lacunae. Scale bars = 100  $\mu$ m.

the junctions between leaves and rhizome consists of dense stellate parenchyma cells.

The cortex of the rhizome consists of stretched stellate parenchyma cells that allow the lacunae of the rhizome to run longitudinally (Fig. 4c). The lacunae of the rhizome are connected to the radial aerenchyma of the adventitious roots that are separated by single layers of cells (Fig. 4d).

### 3.4. Gas flow pattern

As the internal resistance to gas flow ( $R_i$ ) was not measured for all plant parts in detail, the resistance within the junctions between leaves and rhizome ( $R_j$ )

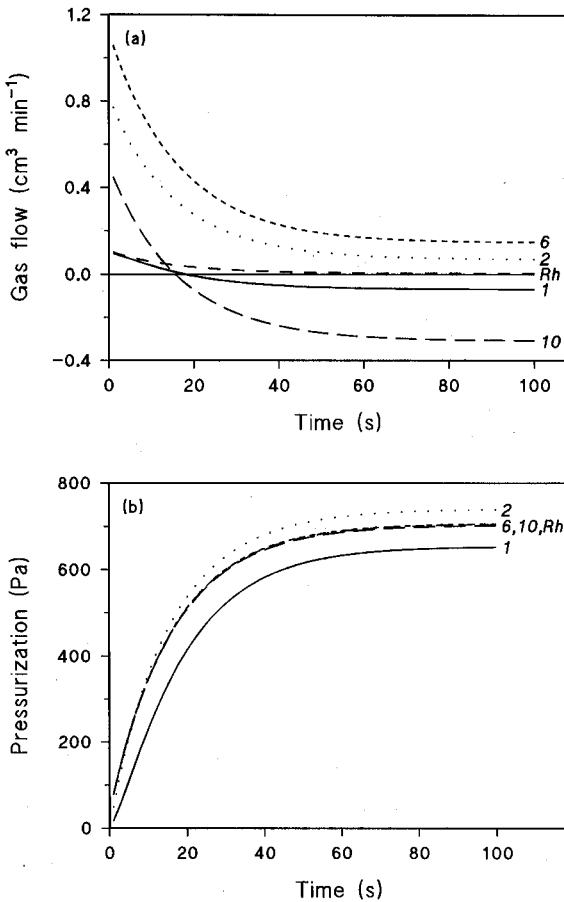


Fig. 5. Calculated time course for (a) convective gas flow rates ( $\text{cm}^3 \text{min}^{-1}$ ) and (b) internal pressure build-up (Pa) of leaves and rhizome of a specimen of *T. latifolia*, with a resistance to gas flow out of the rhizome of  $R_{Rh} = 10000 \text{ Pa s mm}^{-3}$ . Only the results of two influx leaves (Leaves 2 and 6), two efflux leaves (Leaves 1 and 10) and the rhizome (Rh) are shown. Leaves are numbered according to age, Leaf 1 being the youngest. See text for details on method of calculation.

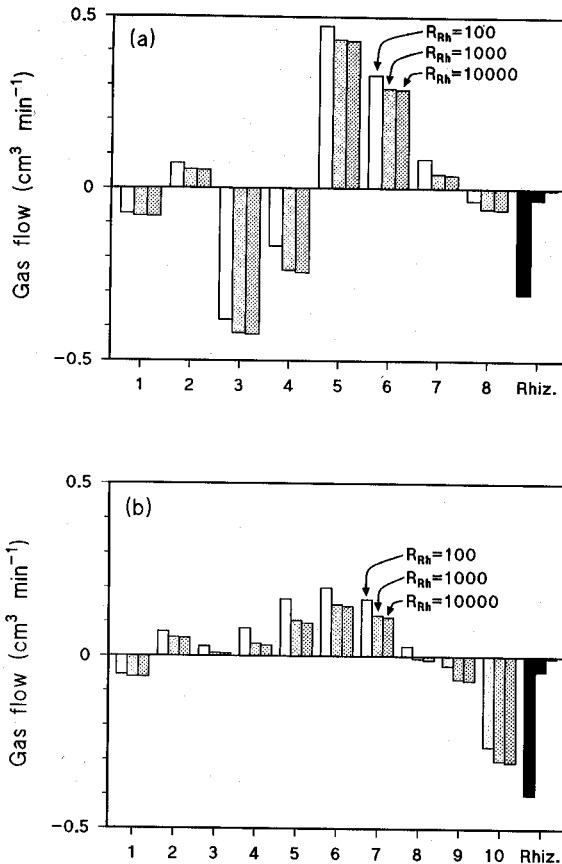


Fig. 6. Calculated steady state rates of convective gas flow ( $\text{cm}^3 \text{min}^{-1}$ ) in and out of leaves and rhizome of specimens of (a) *T. angustifolia* and (b) *T. latifolia*, based on three different values of resistance to gas flow out of the rhizome ( $R_{Rh}$ ;  $\text{Pa s mm}^{-3}$ ). Leaves are numbered according to age, Leaf 1 being the youngest. Positive flow rates represent influx from the atmosphere into the leaves; negative flow rates represent efflux from leaves into the atmosphere. See text for details on method of calculation. It should be noted that Leaf 8 of subfigure (b) changes from being an influx to an efflux leaf, depending on the value of  $R_{Rh}$ .

was estimated on the basis of the results in Table 1 and the porosities of leaf bases in the youngest leaves. The ratio of  $R_j$  between leaves of ascending age was estimated to be: 90:60:30:1:1:1:1:1:1:1. The value of every  $R_j$  was estimated using this ratio and the overall resistance of all junctions between leaves and rhizome being  $8.6 \text{ Pa s mm}^{-3}$  for *T. angustifolia* and  $7.0 \text{ Pa s mm}^{-3}$  for *T. latifolia*, assuming that the  $R_j$  are parallel.

As calculations in the numerical solution procedure proceed, the gas flow rates from the atmosphere into the leaves ( $iF_i$ ) decrease, as the internal pressure differential ( $\Delta P_i$ ) of leaves and rhizome increase towards a steady state after ap-

proximately 100 s (Fig. 5). The gas flow rates in influx leaves remain positive at the steady state, whereas  $iF_i$  of efflux leaves becomes negative (Fig. 5a).

The set of equations was solved numerically for three different values of resistance to gas flow out of the rhizome ( $R_{Rh}=100, 1000$  and  $10\,000\text{ Pa s mm}^{-3}$ ) (Fig. 6). A resistance of  $100\text{ Pa s mm}^{-3}$  simulates a throughflow situation with very good connection to another efflux shoot on the same rhizome; a resistance of  $1000\text{ Pa s mm}^{-3}$  simulates a throughflow situation to a more distant efflux shoot; and a resistance of  $10\,000\text{ Pa s mm}^{-3}$  simulates a non-throughflow situation with just one shoot on the rhizome. These assumptions ignore cases where another shoot on the same rhizome generates a higher pressure than the shoot in question.

The predicted gas flow pathway in the two modelled specimens differs (Fig. 6). The youngest (No. 1), the oldest (No. 8) but also the third and the fourth youngest (No. 3 and No. 4) leaves of the specimen of *T. angustifolia* are efflux leaves for all three values of  $R_{Rh}$  (Fig. 6a). Only the youngest leaf (No. 1) and the two oldest leaves (No. 9 and No. 10) of the specimen of *T. latifolia* are efflux leaves with  $R_{Rh}=100\text{ Pa s mm}^{-3}$ , but for  $R_{Rh}=1000$  and  $10\,000\text{ Pa s mm}^{-3}$ , the youngest leaf (No. 1) and the three oldest leaves (Nos. 8–10) are efflux leaves (Fig. 6b). So, Leaf 8 changes between being an influx and an efflux leaf depending on the possibilities for ventilation through the rhizome. In general, the three to four leaves having the lowest pressurization capacity are efflux leaves.

As the lacunae of all leaves are interconnected, the pressurization capacity of a leaf and the resistance to gas flow out of the rhizome ( $R_{Rh}$ ) determine whether a leaf is an influx or an efflux leaf. Changing the internal resistances to gas flow within the junctions between the leaf and the rhizome to other values ( $1 < R_j < 1000$ ) does not alter the gas flow pattern; only the steady state pressurization and gas flow rates.

#### 4. Discussion

This study documents that the convective gas flow pattern in *T. angustifolia* and *T. latifolia* is similar to that described for *Nuphar lutea* (L.) Sibth. & Sm. (Dacey, 1980, 1981) and other floating-leaved dicotyledons (Grosse et al., 1991). Generally, the leaves of middle age build up higher internal pressures than young and old leaves. This is consistent with leaf development. The ability to pressurize apparently increases with age to a maximum, which is sustained until the leaf starts to senesce. The leaf tissue is initially very tight with a high internal resistance to gas flow. As the leaf matures, the size of the pores in the porous partition within the leaf may increase, and/or the leaf becomes physically damaged and thus lose its pressurization capacity. Consequently, the leaves of middle age are influx leaves, whereas the oldest leaves are efflux leaves. In spite of the low pressurization capacity of the youngest leaves, the efflux from these will be low because of their high internal resistance to gas flow.

Convective throughflow between shoots of the same rhizome system is also

possible. The rhizome systems of *T. angustifolia* and *T. latifolia* are often very extensive and may carry a large number of shoots (Dykyjová et al., 1971; Fiala, 1978). If a rhizome between two adjacent shoots is intact, a throughflow convection of gases is likely, provided that there is difference in the overall pressurization capacity of the two shoots. Even a small pressure differential is able to produce a convective throughflow, because of the highly porous nature of the *Typha* rhizomes. Using Eq. (1) it can be calculated that a pressure differential of 100 Pa between the ends of a 1 m long rhizome having a mean cross sectional area of 100 mm<sup>2</sup> and a specific internal resistance to gas flow of 3.3 Pa s mm<sup>-2</sup> will produce a convective gas flow of 0.18 cm<sup>3</sup> min<sup>-1</sup>. This is a substantial throughflow in spite of a low pressure differential.

Differences in the ability to pressurize their leaves and to convert the pressurization to transport of oxygen to the root system may be part of an explanation for the natural depth distribution of *T. angustifolia* and *T. latifolia* in the littoral zone. Though the leaves of the two species overall have similar pressurization capacities, the area specific gas flow rate is consistently two to three times higher for *T. angustifolia*.

This means that *T. angustifolia* is superior to *T. latifolia* in aerating its roots and rhizosphere and thus may be more tolerant of growing in deep water and on reduced sediments. However, the difference in morphology, biomass allocation pattern, carbohydrate storage in rhizomes and rate of spreading of the two species also influences their relative competitiveness (Grace and Wetzel, 1982; Weisner, 1993). The natural depth distribution of the two species with *T. latifolia* growing in the more shallow littoral zone and *T. angustifolia* on deeper water is a result of depth related competition, with *T. latifolia* being competitively superior in shallow water and *T. angustifolia* in deeper water in the long run. The greater ventilation capacity of *T. angustifolia* may contribute to the explanation of the natural depth distribution of *T. angustifolia* and *T. latifolia*.

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