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ORIGINAL ARTICLE

Tomomi Matsui · Takayoshi Tsuchiya

Root aerobic respiration and growth characteristics of three *Typha* species in response to hypoxia

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Abstract The responses of root aerobic respiration to hypoxia in three common *Typha* species were examined. *Typha latifolia* L., *T. orientalis* Presl, and *T. angustifolia* L. were hydroponically cultivated under both aerobic and hypoxic growth conditions to measure root oxygen consumption rates. Hypoxia significantly enhanced the root aerobic respiration capacity of the two deep-water species, *T. orientalis* and *T. angustifolia*, while it did not affect that of the shallow-water species, *T. latifolia*. *T. angustifolia* increased its root porosity and root mass ratio, while *T. latifolia* increased its root diameter under the hypoxic growth conditions. The relative growth rates in biomass of *T. orientalis* and *T. angustifolia* were 59 and 39% higher, respectively, under the hypoxic growth conditions than under the aerobic growth conditions. In contrast, that of *T. latifolia* did not differ between the two conditions. In *T. orientalis* and *T. angustifolia*, enhanced root aerobic respiration rates under the hypoxic growth conditions would have increased the nutrient uptake, and thus higher relative growth rates were obtained. For the deep-water species, *T. orientalis* and *T. angustifolia*, the root aerobic respiration capacity was enhanced, probably in order to maintain the generation of respiratory energy under hypoxia.

Keywords Anoxia tolerance · Root oxygen consumption · *Typha angustifolia* · *Typha latifolia* · *Typha orientalis*

Introduction

Wetland plants usually root in waterlogged soil, where the oxygen concentration around the root tissue is nearly zero, due to the substantial consumption of oxygen in chemical and biological oxidation processes (Teal and Kanwisher 1966; DeLanune et al. 1990; Lorenzen et al. 1998). The roots thus always experience oxygen deficiency and anoxic stress (Jackson and Armstrong 1999). Wetland plants widely differ in their abilities to tolerate the anoxic stress, which induces zonal distribution based on water depth (Yamasaki 1984; Grace 1989; Brix et al. 1992; Weisner et al. 1993). Elucidating the differences in morphological and physiological strategies to overcome anoxia in wetland plants would thus greatly help us to understand wetland ecosystems more precisely.

When deprived of oxygen, in flooding, plant cells convert from aerobic to anaerobic metabolism. Anaerobic metabolism is considered to be an adaptation to anoxia since it allows ATP production to continue, although usually at a much lower rate than under aerobic respiration (Cronk and Fennessy 2001). In wetland plants, oxygen is soon re-introduced by elongation of stems or petioles to reach the water surface or by development of other oxygen-carrying structures; subsequently, the plant cells convert to aerobic respiration (Cronk and Fennessy 2001). Even beyond critical situations where they are inundated, many wetland plants develop aerenchymatous lacunae that serve as a pathway for oxygen transport from aboveground parts to underground parts in order to overcome the anoxic problem (Teal and Kanwisher 1966; Armstrong 1972; Justin and Armstrong 1987). Oxygen in leaves can move downward by diffusion with low resistance through the lacunae to support aerobic respiration of the roots. Some species have another mechanism to transport a massive amount of oxygen to their underground parts. They supply oxygen by through-flow convection driven by pressure differentials (Dacey 1980, 1981; Armstrong and Armstrong 1990; Brix et al. 1992; Grosse 1996). In addition to their own respiratory consumption, the oxygen molecules are partly released to surrounding soils and form an oxidative layer around the root surfaces,

T. Matsui (✉) · T. Tsuchiya
Graduate School of Science and Technology,
Chiba University, Yayoi-cho, Inage-ku,
Chiba 263-8522, Japan
E-mail: matsui@graduate.chiba-u.jp

which prevents excessive plant absorption of toxic reduced substrates such as Fe^{2+}, Mn^{2+} and sulphide (Armstrong 1967; Mendelssohn and Postek 1982; Sorrell and Dromgoole 1987; Armstrong et al. 1992; Sorrell and Armstrong 1994).

In addition to oxygen supply to roots and radial oxygen loss from root surfaces to surrounding soils, root respiration is also an important physiological process that helps to ameliorate the ill effects of flooding. It is well known as an aspect of the homeostasis of respiration that some plants have the ability to maintain similar respiratory rates (measured at the growth temperature), even when grown at different temperatures (Lambers et al. 1998; Kurimoto et al. 2004). In addition to responding to temperature differences, respiration homeostasis can also operate in response to differences in the growth oxygen conditions: the root respiration rate of the flooding-tolerant *Carex pseudocyperus* L. increased when it was grown in a hypoxic solution compared with an aerated solution (Moog and Brüggemann 1998), while there was no apparent difference in root respiration rate for the flooding-sensitive *C. extensa* Goodenough (Moog and Brüggemann 1998) or for various species of terrestrial herbs (Mark et al. 2001). Increased root respiration in hypoxia could be the case among many flooding-tolerant plants although it has been little demonstrated. In order to obtain a deeper insight into the mechanisms for overcoming hypoxic stresses, more precise information on acclimation in root respiration is required.

A hypothesis was made that plant species growing in deep-water regions, which are more likely to be flooding-tolerant species, increase their root aerobic respiration capacity to a greater extent than species growing in shallow-water regions, in order to maintain the generation of respiratory energy under hypoxia. To confirm this, we conducted an experiment using three *Typha* species differing in distribution with regard to water depth: *Typha latifolia* L., distributed in shallow-water regions, and *T. orientalis* Presl and *T. angustifolia* L., distributed in deep-water regions. *T. latifolia* and *T. angustifolia* are distributed throughout the world and the difference in their habitat based on water-depth gradient has been well demonstrated (Grace and Wetzel 1982; Grace 1988, 1989). For *T. orientalis*, however, there have only been a few studies, probably because its distribution is restricted to eastern parts of Asia and Oceania. Sorrell et al. (2000) reported that *T. orientalis* was distributed in areas of up to 150 cm in water depth. A similar distribution pattern was observed at the Ushigafuchi Pond in Tokyo, Japan, where the three *Typha* species co-occur along the water depth gradient (T. Matsui, in preparation).

Typha species are macrophytes possessing an efficient convective through-flow mechanism (Brix et al. 1992). Many investigations have been made on the differences in their abilities to supply oxygen to roots, and these have proved that *T. orientalis* and *T. angustifolia* are superior in their capability for through-flow convection to *T. latifolia* (Brix et al. 1992; Bendix et al. 1994; Tornbjerg et al. 1994; White and Ganf 1998; Sorrell et al. 2000; Sorrell and Brix 2003). Here, we compare the responses among the three *Typha* species to rhizosphere hypoxia, particularly in root aerobic respiration rate, as well as in growth characteristics and root morphology.

Materials and methods

Plant materials and experimental design

Seeds of *Typha* species were collected from fallow fields in Chiba City, Japan, in November 2002. The following April, the seeds were sown and germinated in sediments in a plastic tray in a greenhouse at Chiba University and watered daily to maintain the sediments in a water-saturated condition. Seedlings grown to 3 cm in shoot height were established in separate pots (540 ml) containing 300 ml of sediments, which were collected from Lake Inba-numa, 20 km north of Chiba City, in March 2003. The plants were cultured for 7 weeks in the open air and watered daily before being used for the greenhouse experiment. Thirty healthy and uniform plants of each species were transplanted to hydroponic chambers. In the greenhouse, the plants were precultured further for 4 weeks under full sunlight at 27–34°C air temperature with 25%-strength Hoagland's solution, which was renewed every 2 days.

We prepared two growth conditions: aerobic (0.19 mmol $O_2\ l^{-1}$) and hypoxic (0.02 mmol $O_2\ l^{-1}$). For each species, four plants were randomly selected and transplanted to a hydroponic tank of each growth condition after measuring their fresh weight. In order to estimate their initial dry weight, the fresh weights of another ten plants were recorded, and they were then oven-dried for 72 h at 80°C to obtain the dry weight. To maintain the nutrient solution at aerobic (0.19 mmol $O_2\ l^{-1}$) and hypoxic (0.02 mmol $O_2\ l^{-1}$) conditions, atmospheric air and oxygen-free nitrogen gas, respectively, were continuously introduced. The oxygen concentration of the nutrient solution was monitored by a Clark-type oxygen electrode sensor (HDO-110; Denki Kagaku Keiki, Tokyo) throughout the experimental period. The solution was circulated by a pump throughout the experimental period and renewed every day in order to maintain a stable nutrient condition. The shoot heights and numbers of leaves of all the plants were measured every 6 days. The experiment was run for 40 days.

At the end of the experiment, the roots were used for measurements of root aerobic respiration rate and root morphology, as described below. After the measurements, the dry weights of roots and the remaining aboveground parts were measured after oven-drying for 72 h at 80°C.

Root aerobic respiration

The detached root was submerged in a 200-ml flask filled with oxygen-saturated water in the dark. The ambient water temperature was maintained at 20°C throughout the measurements. The decrease in dissolved oxygen concentration was continuously monitored until it reached 0.003 mmol O_2 l^{-1} measured by a Clark-type oxygen electrode sensor (UD-101E; Central Science, Tokyo) mounted through the central hole of the rubber stopper of the flask. The water was vigorously stirred by a Teflon-coated magnetic stir bar at the bottom of the flask. The procedure was repeated 3 times for each plant sample. The root oxygen consumption rate (nmol O_2 g^{-1} root dry weight s^{-1}) was estimated as the decrease in the amount of dissolved oxygen in the flask.

Root porosity and diameter

After the respiration measurement, the porosity of root (POR) in percent was determined by the pycnometer method (Jensen et al. 1969). An approximately 0.2-g segment of undamaged root was employed for the measurement. First, a 25-ml pycnometer was filled with water and weighed (*p*). The root sample was gently blotted dry on filter paper and weighed (*r*). The root sample was submerged in the water in the pycnometer and weighed (pr). The root sample was retrieved from the pycnometer and ground into a paste with a pestle and mortar. The resultant whole ground sample was returned to the pycnometer with water and weighed (pgr). The POR was calculated as follows:

$$\mathrm{POR} = \frac{100(\mathrm{pgr} - \mathrm{pr})}{(r + p - \mathrm{pr})}. \qquad (1)$$

The diameter was measured at the root base with a vernier caliper. Three replicates in each plant were examined.

Relative growth rate and biomass allocation

The relative growth rate (RGR) in plant dry weight was calculated as follows:

$$\mathrm{RGR} = \frac{\log(W_\mathrm{f} - W_\mathrm{i})}{\Delta t}, \qquad (2)$$

where W_i and W_f are the total dry weights at the beginning and end of the experiment, respectively, and Δt is the experimental period (40 days). The root mass ratio (RMR) was obtained as the root dry weight divided by the total plant dry weight.

Results

Root aerobic respiration

Regardless of plant species, the aerobic respiration rate of roots decreased with a decrease in the dissolved oxygen concentration in the water phase (Fig. 1). The long-term response of root aerobic respiration to hypoxia, however, differed among the species. The root aerobic respiration rate of *T. latifolia* did not differ between the two growth conditions. In contrast, *T. orientalis* and *T. angustifolia* grown under the hypoxic growth condition exhibited significantly higher root aerobic respiration capacities than those grown under the aerobic growth condition (Table 1). The difference was more substantial in *T. angustifolia* than in *T. orientalis*.

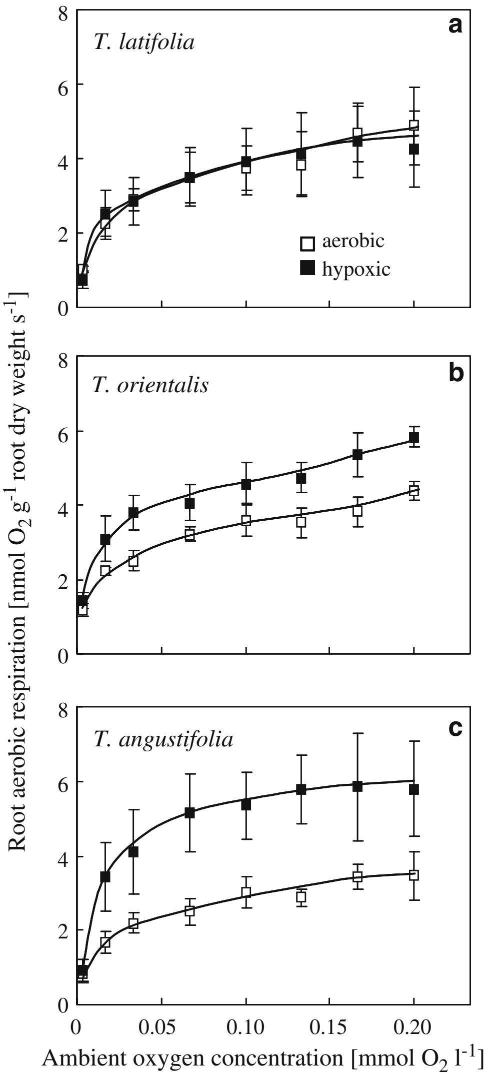

Fig. 1 Oxygen dependence of root aerobic respiration rate of *Typha latifolia* (**a**), *T. orientalis* (**b**) and *T. angustifolia* (**c**) grown under the aerobic (*open square*; 0.19 mmol O_2 l^{-1}) and hypoxic (*filled square*; 0.02 mmol O_2 l^{-1}) growth conditions in hydroponic culture. *Error bars* indicate ±1 SE ($n = 4$)

Root porosity and diameter

The root systems exhibited a compact and dense form under the hypoxic growth condition, irrespective of species. However, the responses of the root anatomy to rhizosphere hypoxia differed among the species

Table 1 Two-way ANOVA testing the effects of growth condition (aerobic or hypoxic) and ambient oxygen level on root aerobic respiration rate of three *Typha* species. Values in the table are the probability of a greater *F* value (*P* level). $P < 0.05$ given in *bold*

Source of variance	df	*T. latifolia*	*T. orientalis*	*T. angustifolia*
Growth condition	1	0.8777	**0.0000**	**0.0000**
O_2 level	7	**0.0003**	**0.0000**	**0.0000**
Growth condition×O_2 level	7	0.9988	0.8020	0.2675
Error	48			

Table 2 Growth, biomass allocation and root morphology of *Typha latifolia*, *T. orientalis* and *T. angustifolia* grown under the aerobic and hypoxic growth conditions in 40 days of hydroponic culture [mean ± 1 SE ($n = 4$)]. Means within columns followed by *different letters* are significantly different ($P < 0.05$) according to Tukey's test, after testing for heterogeneity of variances

	Relative growth rate (mg g^{-1} day^{-1})	Root mass ratio (g g^{-1})	Root porosity (%)	Root diameter at root base (mm)
T. latifolia				
Aerobic	15.2 ± 1.5 ab	0.517 ± 0.012 a	35.6 ± 1.7 a	1.15 ± 0.06 a
Hypoxic	19.9 ± 0.7 ac	0.570 ± 0.024 a	34.3 ± 1.6 a	1.35 ± 0.05 b
T. orientalis				
Aerobic	12.1 ± 3.1 b	0.431 ± 0.010 bd	35.1 ± 2.5 a	1.07 ± 0.05 a
Hypoxic	19.3 ± 1.7 ac	0.463 ± 0.015 bd	32.8 ± 2.7 a	1.10 ± 0.07 a
T. angustifolia				
Aerobic	15.3 ± 1.6 ab	0.338 ± 0.017 c	26.7 ± 2.1 b	1.07 ± 0.06 a
Hypoxic	21.2 ± 2.0 c	0.421 ± 0.022 d	32.4 ± 1.7 a	1.13 ± 0.07 a

(Table 2). *T. latifolia* and *T. orientalis*, having high POR, were not affected by the growth conditions, while *T. angustifolia* increased its POR under the hypoxic growth condition ($P < 0.05$). For root base diameter, a difference was only observed for *T. latifolia*: the hypoxic growth condition afforded significantly thicker roots ($P < 0.05$).

Growth and biomass allocation

The initial plant dry weights were 5.37 ± 0.81 g, 4.55 ± 0.91 g and 5.49 ± 0.36 g (mean ± SD, $n = 8$) for *T. latifolia*, *T. orientalis* and *T. angustifolia*, respectively. During the experimental period, all of the plants of the three *Typha* species examined survived, but their growth responses to rhizosphere hypoxia were different. RGR values for *T. angustifolia* and *T. orientalis* under the hypoxic growth condition were 39% and 59% higher than under the aerobic growth condition, respectively ($P < 0.05$; Table 2). In contrast, the RGR of *T. latifolia* did not differ significantly between the two growth conditions. *T. angustifolia* significantly increased its RMR under the hypoxic growth condition ($P < 0.05$), while the RMRs of *T. latifolia* and *T. orientalis* did not differ between the two growth conditions. Among the three species, *T. latifolia* had the highest RMR ($P < 0.05$). Shoot height was not significantly different between the two growth conditions for any of the species (Table 3). The number of leaves per shoot was highest in *T. orientalis* ($P < 0.05$). *T. latifolia* and *T. angustifolia* did not differ in the number of leaves per shoot between the two growth conditions, while in *T. orientalis* it increased under the hypoxic growth condition ($P < 0.05$).

Discussion

Typha species are plants that inherently grow under anaerobic conditions such as in marshes, swamps and shores of lakes and rivers. The anoxic stress for macrophytes is severe in natural wetlands (DeLaune et al. 1990) compared with the hypoxic growth condition employed in this study (0.02 mmol O_2 l^{-1}). Several investigations that used rather mildly hypoxic cultures (Pearson and Havill 1988; Moog and Janiesch 1990; Mark et al. 2001), such as in this study, have suggested that wetland plants exhibit faster growth under the hypoxic growth condition than under the aerobic growth condition because they possess some morphological and physiological mechanisms to overcome the hypoxic stresses.

The three *Typha* species exhibited different responses of their root aerobic respiration rate to rhizosphere hypoxia. Root aerobic respiration capacities of the deep-water species, *T. orientalis* and *T. angustifolia*, increased when they were grown under the hypoxic growth condition, while the shallow-water species *T. latifolia* was not affected (Fig. 1, Table 1). Moog and Brüggemann (1998) reported for *Carex* species that the root respiration rates of anaerobically precultured intact plants (roots not detached) were higher than those of aerobically precultured plants. The *Carex* species studied may have also had an enhanced root aerobic respiration capacity under hypoxia, as was the case for the *Typha*

Table 3 Shoot heights and numbers of leaves per shoot for *T. latifolia*, *T. orientalis* and *T. angustifolia* grown under the aerobic and hypoxic growth conditions in 40 days of hydroponic culture [mean ± 1 SE ($n=4$)]. Means within columns followed by *different letters* are significantly different ($P<0.05$) according to Tukey's test, after testing for heterogeneity of variances

	Shoot height (cm)		Number of leaves per shoot	
	Initial	Final	Initial	Final
T. latifolia				
Aerobic	64.4 ± 5.6 a	94.9 ± 1.9 a	6.4 ± 0.4 a	9.4 ± 0.4 a
Hypoxic	67.9 ± 2.5 a	92.1 ± 3.3 a	7.0 ± 0.3 a	9.2 ± 0.2 a
T. orientalis				
Aerobic	62.7 ± 4.9 a	91.3 ± 4.7 a	8.8 ± 0.2 b	10.6 ± 0.5 b
Hypoxic	63.4 ± 3.2 a	94.2 ± 2.9 a	9.4 ± 0.2 b	11.6 ± 0.2 c
T. angustifolia				
Aerobic	102.2 ± 2.2 b	127.6 ± 3.1 b	6.8 ± 0.2 a	8.8 ± 0.2 a
Hypoxic	104.9 ± 1.8 b	132.8 ± 6.9 b	7.0 ± 0.3 a	9.2 ± 0.2 a

species in this study, although these authors referred to the possibility that the increase in root respiration rate may be ascribed to an enhanced oxygen supply from shoots derived from altered morphology as a result of hypoxia, such as the development of lacunae (Moog and Brüggemann 1998).

ATP produced in respiratory pathways in roots is partly used for nutrient uptake to support whole plant growth and maintenance. Poorter et al. (1991) investigated 24 herbaceous plants and proved that 50–70% of the energy produced by root respiration was utilized for nutrient uptake. The rates of nutrient uptakes should be closely correlated with photosynthetic capacity and thus the growth rate of whole plants (Kurimoto et al. 2004), since a large amount of nitrogen is needed for the synthesis of photosynthetic enzymes (Poorter et al. 1990). Indeed, high respiratory activities correlated with high growth rates for the 24 herbaceous plants from a wide range of habitats (Poorter et al. 1990), five boreal tree species (Tjoelker et al. 1999), and three wheat and one rice cultivar (Kurimoto et al. 2004). The increased root respiration rates in *T. orientalis* and *T. angustifolia* under the hypoxic growth condition also might have promoted nutrient uptake for the development of photosynthetic organs and thus finally resulted in the large biomass yield.

Moog and Janiesch (1990) reported that oxygen deficiency affected production of root biomass in three *Carex* species from varying hydrological habitats. The extent of oxygen deficiency in their habitats decreased in the following order: *Carex extensa*, *Carex remota* L. and *Carex pseudocyperus*. *C. extensa* decreased its RMR to reduce respiratory cost versus treated hypoxia. In contrast, *C. remota* and *C. pseudocyperus* increased their RMR and formed a compact, dense root network under hypoxia to oxidize the rhizosphere efficiently. This latter finding agrees with this study, as *T. angustifolia* increased its RMR under the hypoxic growth condition (Table 2), forming a compact, dense root system. An increased RMR results in increased oxygen release from roots to the rhizosphere in as far as the permeability of root surfaces to gases is unchanged. The rhizosphere oxidation will promote efficient conversion from ammonium to nitrate, so that the plants will be able to use sufficient nitrate to support photosynthesis and the growth of the aboveground parts. That *T. latifolia* had the highest RMR among the three *Typha* species can be explained partly by the difference in gas permeability of root surfaces.

Hypoxia also alters the root morphology of some wetland plants. Several flooding-tolerant species form aerenchyma at the onset of waterlogging (Smirnoff and Crawford 1983). *T. angustifolia* experienced an increased POR, and *T. latifolia* experienced an increased root base diameter in this study (Table 2). Justin and Armstrong (1987) examined the responses to flooding of 91 plant species from wetland, intermediate and non-wetland habitats and proved that unaffected high porosities or raised porosities under flooding are a feature of a majority of wetland and intermediate plants. Increased POR and root diameter would lower the resistance to the diffusion of gases in the root and hence promote aeration in roots and root aerobic respiration. *T. orientalis* and *T. latifolia* did not increase their POR in response to hypoxia but exhibited high PORs (ca. 35%) even under the aerated growth condition in this study. This resembles the case of the three juncaceous species and the two cyperaceous species in Justin and Armstrong's study (1987). Chabbi et al. (2000) reported that the POR of *T. domingensis* Pers. under a drained growth condition (22%) increased to 28% under a flooded growth condition. A similar increase in POR was observed in *T. angustifolia* in this study. It is still unclear why different responses of POR and root diameter to hypoxia occur among wetland species such as the three *Typha* species in this study.

This study has proved that the three *Typha* species differ in terms of the response of root aerobic respiration rate to hypoxia, and that the difference was closely correlated with their distribution related to water depth. The deep-water species, *T. orientalis* and *T. angustifolia*, increased their root aerobic respiration rate by adjusting to hypoxia and grew more rapidly. The shallow-water species, *T. latifolia* did not show such root respiratory flexibility but maintained almost the same growth rate between the hypoxic and the aerobic growth conditions, at least for the 40 days of the hydroponic culture. Root thickening and other morphological traits not examined in this study might have sustained substantial root respiration and thus growth in *T. latifolia*.

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