Note

Photosynthesis and Transpiration of an Emergent Plant *Zizania latifolia*

Takayoshi TSUCHIYA, Atsushi SHINOZUKA and Isao IKUSIMA

Abstract

Photosynthesis and transpiration were measured for a stand of the emergent plant, *Zizania latifolia* (GRISEB.) TURCZ. at a sheltered shore of the Hitachi-Tone River, Japan. Net photosynthetic rate per unit leaf area at light saturation was $12 \mu \text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, which is in the lower range for emergent plants. The daily course of net photosynthesis and transpiration had no midday depression, *i. e.* the maximum was recorded around noon. Vapor pressure difference did not regulate leaf conductance at photosynthetic photon flux densities saturating net photosynthesis.

Key Words: emergent plant, photosynthesis, transpiration, *Zizania latifolia*

1. Introduction

The emergent vegetation is one of the sites showing the highest primary production in the world (WESTLAKE, 1982). We reported a high productivity of *Zizania latifolia* (GRISEB.) TURCZ. along the shore of the Hitachi-Tone River, Japan (TSUCHIYA *et al.*, 1993) with its large allocation of biomass production to foliage structure.

High resource availability may also have allowed high productivity. Carbon availability from the air is higher of several magnitudes than from water (MADSEN and SAND-JENSEN, 1991). Having aerial leaves as well as terrestrial plants is highly advantageous to carbon uptake. In comparison with carbon, however, water tends to be less available to aerial leaves. ISHIHARA and SAITOH (1987) reported that stomatal closure associated with midday depression of photosynthesis was partly due to water deficiency, even for *Oryza sativa* L. grown under irrigation. Midday depression was also reported for some wild emergent plants (PEARCY *et al.*, 1974; SALE *et al.*, 1985; SALE and ORR, 1986), though it was related to increased leaf temperature. In contrast, JONES (1987) re-

ported that a C_4 emergent plant, *Cyperus papyrus* L. did not show midday depression in spite of the presence of stomatal regulation dependent on the vapor pressure difference between the intercellular spaces in the leaf and the atmosphere (VPD). Diurnal change in leaf conductance as it relates to photosynthesis and transpiration is still unknown for many other emergent plants.

Z. latifolia is closely related to *O. sativa*, both of which develop a relatively poor root system in muddy sediments compared with their thick foliage above the water surface. The objectives of the present study are (1) to measure diurnal change in the photosynthesis and transpiration of *Z. latifolia* and (2) to clarify whether its stomata are closed at midday.

2. Materials and methods

The study site is located on a relatively sheltered shore of the Hitachi-Tone River near its confluence with the Tone River. Emergent vegetation extends along the shore to a width of about 10 m and a water depth of 1 m. The vegetation is dominated by *Z. latifolia* with a low coverage of *Phragmites australis* (CAV.) TRIN. ex. STEUDEL. Further details of the study

site were described previously (TSUCHIYA *et al.*, 1993).

Z. latifolia has stomata on both abaxial and adaxial sides of the leaf lamina. Gas exchange was measured using a portable porometer with a chamber for leaves having stomata on both abaxial and adaxial sides (Koito KIP-8501, Yokohama, Japan). Leaf temperature, air temperature and photosynthetic photon flux density (PFD) were obtained simultaneously. Net photosynthesis, transpiration, leaf conductance and VPD were obtained according to ISHIKAWA *et al.* (1990).

In a preliminary study we found that net photosynthesis and transpiration did not differ significantly based on location within a leaf lamina, which usually reaches a length of more than 1 m. In contrast, leaf age affected photosynthesis. We measured the highest net photosynthesis on the second to fourth youngest leaves out of a total of six leaves per a shoot, whereas transpiration was not significantly different except for the oldest leaves which showed higher rates and greater leaf conductance.

In order to eliminate the factor of leaf age, therefore, we selected 12 leaves of the second to fourth leaf orders out of 4 shoots within a 1m × 1m quadrat at the center of the *Z. latifolia* stand. Diurnal changes in photosynthesis and transpiration were measured hourly from 9:00 to 18:00 (solar time) on 3 August 1990, one of the hottest and driest days of the year. For the 8 to 12 leaves selected, the assimilation chamber was placed at the center or somewhat higher where the surface inclination was nearly horizontal.

3. Results

On the measurement day there were few clouds in the sky except between 9:30 and 10:30 a.m. Maximum PFD above the leaf canopy was about $2 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at noon. Since our random selection also included leaves shaded by other overlying leaves, the PFDs measured on the leaf surface varied widely from 10 to 100 % of full sunlight (Fig. 1A). Air temperature varied from 29 to 35°C during the day, its

peak being later than that of PFD and VPD (Fig. 1B). Leaf temperature of *Z. latifolia* did not exceed air temperature by more than 1°C, indicating that an unrestrained transpiration rate from the lamina surface cooled the leaf. VPD in the ambient air was about $15 \text{ mmol} \cdot \text{mol}^{-1}$ at midday (Fig. 1C).

Daily changes in photosynthetic rate coincided roughly with those in PFD and VPD. Maximum net photosynthesis was on a high plateau, $10\text{--}14 \text{ } \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, from 11:00 till 16:00 (Fig. 1D) because of the saturating PFDs. Relationship of PFD and net photosynthesis did not differ from morning to afternoon (Fig. 2A). Maximum rates of transpiration and leaf conductance occurred slightly later than those of photosynthesis (Fig. 1). Maximum transpiration was $3 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ when leaf conductance was about $0.25 \text{ } \mu\text{mol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Transpiration tended to be saturated by higher PFD in the afternoon than in the morning (Fig. 2B), presumably because of higher VPD. Midday depression of photosynthesis and transpiration was not observed.

Leaf conductance was dependent on PFD and their relation also did not differ from morning to afternoon (Fig. 3A). Values of leaf conductance obtained at above light saturation (about $1 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in PFD) were plotted against the prevailing VPD in order to eliminate the effect of PFD on leaf conductance (Fig. 3B) In contrast to PFD, VPD did not affect leaf conductance in a surplus of PFD.

4. Discussion

Water use efficiency, calculated as photosynthesis divided by transpiration, of *Z. latifolia* was only about $3 \text{ mmol CO}_2 \cdot \text{mol}^{-1} \text{ H}_2\text{O}$ relatively constant during midday. This value is similar to that of a C_3 emergent plant, *Typha latifolia* L., ($2.8\text{--}4.9 \text{ mmol} \cdot \text{mol}^{-1}$, McNAUGHTON, 1973), and lower than a C_4 emergent plant, *Cyperus papyrus* ($6.5 \text{ mmol} \cdot \text{mol}^{-1}$, JONES, 1987) or terrestrial plants (5 to $8 \text{ mmol} \cdot \text{mol}^{-1}$, YOSHIE, 1986). Therefore, in addition to its relatively low net photosynthetic rate, *Z. latifolia* must be considered a C_3 plant, though there have been no anatomical or physiological reports to verify

Fig. 1. Diurnal changes in (A) PFD on leaf surface, (B) air temperature, (C) ambient air VPD, (D) net photosynthetic rate, (E) transpiration rate, and (F) leaf conductance of *Z. latifolia* leaves. Measured on 3 August 1990.

Fig. 2. PFD dependence of (A) net photosynthesis and (B) transpiration of *Z. latifolia* in the morning (open circles) and afternoon (solid circles). Data are the same as in Fig. 1.

Fig. 3. Leaf conductance of *Z. latifolia* in relation to (A) PFD and (B) VPD. Data at PFDs higher than $1 \text{ mmol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ are shown in the right figure. Symbols are the same as in Fig. 2.

this. Lower water use efficiency is not an adaptive disadvantage for aquatic plants insofar as water deficiency does not occur in their leaves. High transpiration results in a lowering of leaf temperature which reduces respiration, thus maintaining high net photosynthesis (PEARCY *et al.*, 1974).

While a C_4 emergent plant, *C. papyrus* was reported having an extremely high photosynthetic rate of up to $35 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (JONES, 1987), C_3 emergent plants have maximum net photosynthetic rates ranging from 10 to $25 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (PEARCY *et al.*, 1974; GLOSER, 1977; SPENCER and BOWES, 1986; ISHIHARA and SAITOH, 1987; JONES, 1988). The maximum net photosynthesis of *Z. latifolia* in the present study falls in the lower range. However, its annual net production is more than $3400 \text{ g dry weight} \cdot \text{m}^{-2}$ (TSUCHIYA *et al.*, 1993), which is the higher range for herbaceous plants in temperate zone (LARCHER, 1984). This may be due to its dense foliage with relatively vertical leaf orientation, which keeps light penetration through the foliage onto the ground surface to only 1% (TSUCHIYA *et al.*, unpublished data). The leaf area index reached $6.0 \text{ m}^2 \cdot \text{m}^{-2}$ in August (TSUCHIYA *et al.*, 1993), close to the mean of values reported for emergent plants (TSUCHIYA, 1991). The relatively low photosynthetic activity may be compensated for by its thick foliage structure with inclined

lamina orientations.

Midday depression of photosynthesis occurs in many terrestrial plants, presumably owing to a decrease in CO_2 concentration, an accumulation of photosynthetate, and a higher afternoon temperature (TENHUNEN *et al.*, 1984; ROESSLER and MONSON, 1985). Similar findings have also been reported for several emergent plants; ISHIHARA and SAITOH (1987) observed a midday depression with an increase in VPD and a decrease in water potential in a cultivated plant, *O. sativa*, when maximum VPD was about $30 \text{ mmol} \cdot \text{mol}^{-1}$. This species has a higher leaf conductance ($0.69 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) than uncultivated aquatic plants ($0.17\text{--}0.35 \text{ mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) (PEARCY *et al.*, 1974; GLOSER, 1977; KÖRNER *et al.*, 1979; SPENCER and BOWES, 1986). This indicates that water deficiency in leaves is more likely to occur in *O. sativa* than in wild aquatic plants. *P. australis* was also reported to show midday depression, owing not to water stress but primarily to high temperature in the afternoon (PEARCY *et al.*, 1974; ONDOK and GLOSER, 1978). *C. papyrus* showed no midday depression of photosynthesis in spite of VPD dependence of stomatal conductance (JONES, 1987). *Z. latifolia* in the present study showed no midday depression. Moreover, its stomata responded little to a change in VPD ranging from 10 to $20 \text{ mmol} \cdot \text{mol}^{-1}$, the same range in which *O. sativa* showed a significant decrease in

net photosynthesis with increasing VPD (ISHIHARA and KUROIDA, 1986). The high productivity of *Z. latifolia* may be partly due to its high water availability together with its well-developed foliage structure.

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摘 要

抽水植物マコモの光合成および蒸散特性

常陸利根川の河岸のマコモ個体群において光合成速度と蒸散速度の日変化を測定した。最大純光合成速度は約 $12 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ であり、抽水植物の値としては低い方であった。光合成速度と蒸散速度はともに真昼に最大値をとり、昼寝現象はみられなかった。光強度が光合成や蒸散を律速しており、大気-葉内飽差は葉コンダクタンスの制限要因とはならなかった。

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(著者：土谷岳令・篠塚篤，千葉大学理学部生物学教室，〒263 千葉市稲毛区弥生町 1-33；生嶋功，千葉大学理学部海洋生態系研究センター，〒263 千葉市稲毛区 弥 生 町 1-33；Takayoshi TSUCHIYA, Atsushi

SHINOZUKA, Department of Biology, Faculty of Science, Chiba University, 1-33 Yayoi-cho, Inage-ku, Chiba 263; Isao IKUSIMA, Marine Ecosystems Research Center, Faculty of Science, Chiba University, 1-33 Yayoi-cho, Inage-ku, Chiba 263)

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