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<https://doi.org/10.5109/24439>

出版情報：九州大学大学院農学研究院紀要. 46 (2), pp.267-274, 2002-02-28. 九州大学農学部
バージョン：
権利関係：



Specific Difference in Water Transport Regulation in Two High-Productive C₄ Crops, Napiergrass, *Pennisetum purpureum* Schumach. and Maize, *Zea mays* L., Grown in Different Light Intensities.

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(Received October 26, 2001 and accepted November 20, 2001)

The specific difference in water transport regulation in a plant was investigated by the plant excision diagnosis (PED) using two C₄ plant species, napiergrass, *Pennisetum purpureum* Schumach. and maize, *Zea Mays* L. Under the full sunlight condition, the water transport to a leaf in napiergrass was regulated by the stem node connected to the leaf, whereas in maize the stem base functioned as a strong regulator of the water transport from roots to the stem and leaves. Unlike this evidence, the water transport in shade-grown napiergrass was regulated at the stem base, not at the individual stem nodes, and such a regulating position or organ was not identified in maize grown in shade. As compared with maize, napiergrass is likely capable of doing a fine regulation of water transport according to the different growth conditions. Napiergrass is possible to perform a large production through a more efficient water distribution and utilization in a plant.

INTRODUCTION

Napiergrass is a tropical origin C₄ plant and known as a species marking the highest record of biomass production among the herbaceous plants grown in the world. The growth or production system of this species is characterized by the high leaf area index, the high efficiency of light penetration in the canopy (Ito and Inanaga, 1988a; Ito *et al.*, 1988b; Ito *et al.*, 1989; Matsuda *et al.*, 1991), the extremely high ratio of shoot/root weight (Matsuda *et al.*, 1991) and the relatively high photosynthetic ability in leaves grown at lower strata in the canopy (Ito and Inanaga, 1988c; Nada *et al.*, 1994). By integrating these characters, this species constructs a canopy structure of highly light utilization in photosynthesis, with the resultant large production (Kubota *et al.*, 1994).

We have also observed that napiergrass keeps a high T/R ratio and relatively high activity in leaf photosynthesis in plants grown under the water deficit soil conditions. This may suggest that napiergrass has efficient water transporting and controlling functions. We have so far studied on the relationship between the production system of napiergrass and the water use efficiency. In a previous paper (Nagasuga *et al.*, 1998), in order to clarify the feature of water utilization of napiergrass, we applied the plant

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excision diagnosis (PED) and had a suggestion that the transport of water from a stem to leaves was strongly restricted and adjusted by the individual stem nodes.

A further experimental approach to the production and water utilization system of napiergrass is considered to be important not only in understanding the specific physiological and ecological feature in this species, but also in accumulating the fundamental information for the genetic improvement towards higher photosynthetic production and water saving production of crops. In this study, to identify the specific feature of napiergrass in contrast with maize, we compared the water transport situations in both species grown under different light environments.

MATERIALS AND METHOD

1. Materials

Napiergrass, *Pennisetum purpureum* Schmach. var. merkeron, and Maize, *Zea mays* L. var. gold dent KD772, were grown in pots and a field in the experimental farm of Agricultural Faculty, Kyushu University in 1999 and 2000.

2. The growth condition and experimental treatments

2-1 The field growth condition

Shoots sprouted from the over-wintered napiergrass stocks were transplanted and grown with a spacing of 150 cm × 50 cm (1.3 hills m⁻²) in the field of sandy soil in 2000. As the basic fertilization, N, P₂O₅ and K₂O were applied 25, 10 and 10 kg per 10 a, respectively, and additionally fowl compost and plant oil cake each were used 1500 kg per 10 a. Furthermore, slaked lime was applied 400 kg per 10 a as the soil conditioner.

Maize plants were grown with a spacing of 70 cm × 30 cm (4.8 hills m⁻²) in a field adjacent to the napiergrass field. The three seeds per hill were sown on July 5 in 2000, and thereafter at the fifth leaf emergence stage plants were thinned to one plant per hill. The fertilizer application level and method were the same as those in the napiergrass field.

2-2 The growth in pots

Young shoots of napiergrass grown at the 7–8th leaf emergence stage were separated from the parent stocks. The shoots were transplanted in 18L pots filled with sandy soil and grown during the summer seasons in 1999 and 2000. As the basal fertilization, N, P₂O₅ and K₂O were applied 3 g, 2 g and 2 g per pot, respectively. At the time of transplanting, the two thirds of each leaf of a shoot was removed to prevent the growth damage caused by water loss.

Maize (one plant pot⁻¹) was grown in 15L pots filled with sandy soil containing 2.5 g of N and 1.6 g each of P₂O₅ and K₂O.

2-3 Light treatments

Both species grown in pots for about 44 days after the transplanting of napiergrass or the shoot emergence of maize were subjected to the shade (30% of the natural sunlight) and full sunlight conditions for 17 days. These materials were used for examination by PED, and the specific difference in water transport situation was compared in relation to

the light conditions.

3. The investigation method

3-1 Dry matter production and photosynthetic measurements in pot-grown plants

Both napiergrass and maize grown for 67 days in pots were sampled to determine the leaf area and dry matter weight of plants. The leaf area was measured with an automatic area meter (AAM-8, Hayashidenko, Japan). Maximum rates of photosynthesis and transpiration in the top leaves of both species were measured with a portable photosynthesis-transpiration meter (SPB-H4, ADC, UK) in a photosynthetically saturating light intensity of $1800 \mu\text{molm}^{-2} \text{s}^{-1}$ in the summer of 2000.

3-2 The plant excision diagnosis (PED)

Using the upper 3rd–4th leaves of pot-grown napiergrass and maize, the responses in leaf photosynthetic rate (P_n) and transpiration rate (Tr) shown directly after the plant excision treatment were monitored with a portable photosynthesis-transpiration meter in a light intensity of 900 to $1200 \mu\text{molm}^{-2} \text{s}^{-1}$ in the mid August in 1999. The excised positions in a plant are shown in Fig. 1. According to the procedure reported in a previous paper (Nagasuga *et al.*, 1998), both species were excised at the stem base (Fig. 1, A) first, and then the upper end of a node (Fig. 1, B). Based on the responding pattern in P_n and Tr shown after the excisions, the water transport situation in a plant was diagnosed.

3-3 The diurnal changes in parameters related to transpiration

Using the top leaves of both species grown in the field, the diurnal changes in Tr ,

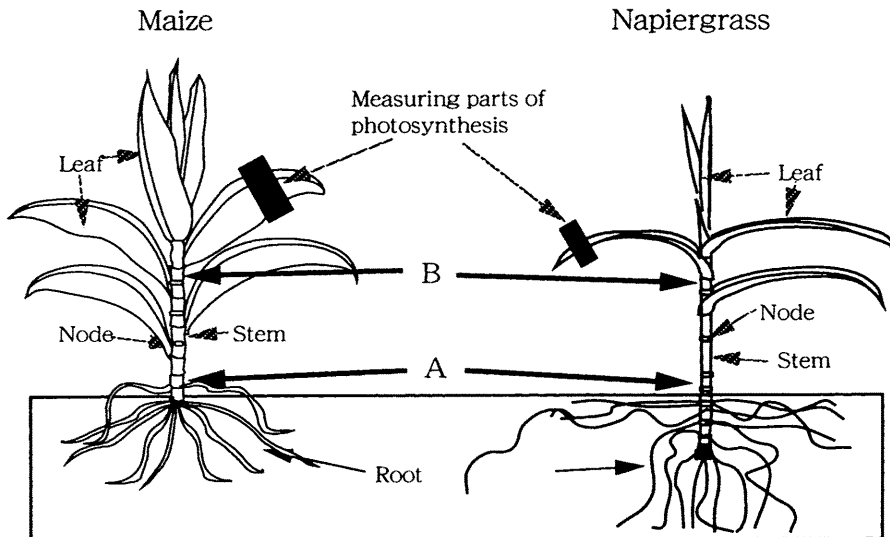


Fig. 1. Excised positions of napiergrass and maize plants in PED. A and B represent the excised positions, stem base and the upper end of stem node, respectively.

stomatal conductance (Gs) and leaf water potential (LWP) were measured with a super-porometer (L-1600, Licor, USA) and psychrometer (L-51, Wescor, USA).

RESULTS AND DISCUSSION

It has been well known that napiergrass constructs a highly effective photosynthetic production system in the canopy as cited above. The field-grown napiergrass likely always keeps a high T/R ratio, and wilting phenomena are not frequently found in the leaves. This fact suggests that this species may have a better regulating function for the water utilization and transport as well as the high photosynthetic potential. In the previous paper, by the use of PED for napiergrass we suggested that the water flow in this species was strictly controlled at individual nodes of the stem, and also predicted that this function was changeable with the growth stage and growth environments. In this paper, PED was employed for both maize and napiergrass, and the diagnostic results obtained were compared between both species to deepen the understanding of the specific feature of water transport regulation.

Leaf area, dry matter weight, Pn, Tr and the related parameter values were compared between both species grown in pots (Table 1). A large difference was detected in the area of single leaf blade between napiergrass and maize, but there was not a significantly difference in total leaf area of a plant between both species. Also no significant specific differences were found in Pn and Tr per unit leaf area or per plant, and in dry matter

Table 1. Photosynthetic rate (Pn), transpiration rate (Tr), one leaf area (LA), photosynthetic rate of one leaf (LPn), transpiration rate of one leaf (LTr), total leaf area of a plant (TLA), photosynthetic rate of a plant (PPn), transpiration rate of a plant (PTr) and total dry matter weight (TDW) in napiergrass and maize at the vegetative stage (66th day after planting).

| Parameters | A. napiergrass | (A/B) | B. maize | |
|--|-----------------|--------|-----------------|-------|
| Pn ($\mu\text{mol m}^{-2}\text{s}^{-1}$) | 23.0 \pm 1.71 | (1.16) | 19.7 \pm 4.02 | N. S. |
| Tr ($\text{mmol m}^{-2}\text{s}^{-1}$) | 3.99 \pm 0.35 | (1.22) | 3.28 \pm 0.35 | N. S. |
| LA ($\times 10^{-3}\text{m}^2$) | 0.84 \pm 0.24 | (0.29) | 2.90 \pm 0.03 | *** |
| LPn ($\mu\text{mol s}^{-1}$) | 0.19 \pm 0.05 | (0.33) | 0.57 \pm 0.12 | * |
| LTr ($\times 10^{-3}\text{mmol s}^{-1}$) | 3.19 \pm 0.78 | (0.34) | 9.49 \pm 0.97 | ** |
| TLA (m^2) | 0.39 \pm 0.11 | (0.85) | 0.46 \pm 0.01 | N. S. |
| PPn ($\mu\text{mol s}^{-1}$) | 8.69 \pm 1.67 | (0.95) | 9.16 \pm 1.90 | N. S. |
| PTr (mmol s^{-1}) | 1.52 \pm 0.33 | (1.00) | 1.52 \pm 0.16 | N. S. |
| TDW (g) | 243 \pm 51.8 | (1.00) | 243 \pm 5.05 | N. S. |

Values in () represent relative values of napiergrass to those of maize. *, **, ***, statistically different at 5%, 1%, 0.1%: N. S.; not significantly different. Each value was calculated as follows;

LA=TLA / total living leaf numbers in a plant

LPn=LA \times Pn

LTr=LA \times Tr

PPn=TLA \times Pn

PTr=TLA \times Tr

weight of plant. Judging from these findings, both species are thought to be in a roughly similar and good growth situation during the summer experimental season.

PEDs were conducted along the water flow from the stem base to an upper stem node using napiergrass and maize grown in pots under the full sunlight. The responses of Pn and Tr to the plant excision treatment were monitored and the specific difference was compared (Fig. 2). The variations in Pn and Tr observed by the excision treatment were already confirmed to indicate the water flow situation in a plant (Nagasuga *et al.*, 1998). The rapid increase in the two parameter values after the excision treatment were observed in both species as shown in Fig. 2, and this reaction was variable with the excised position in a plant and different with species. In napiergrass no change was found in Pn and Tr after the stem base excision, but a rapid increase appeared in a leaf when excised at the upper end of the stem node connected to the leaf. Different from this, in maize the increase in Pn and Tr was observed by the stem base excision.

These facts suggest that the water transport from roots to leaves in napiergrass is regulated individually by the stem node having each leaf. In other words, the water regulation in napiergrass is made at the lower stream region in water flow through plant. While in maize, all the leaves on a stem were primarily regulated by the stem base (the upper stream region). Like this, as compared with maize, napiergrass is capable of conducting a more fine and effective regulation for water transport and distribution through a plant.

Fig. 3 shows the diurnal changes in Gs and LWP of field-grown napiergrass and maize at the vegetative growth stage. There was a specific difference in Gs; the Gs of napier-

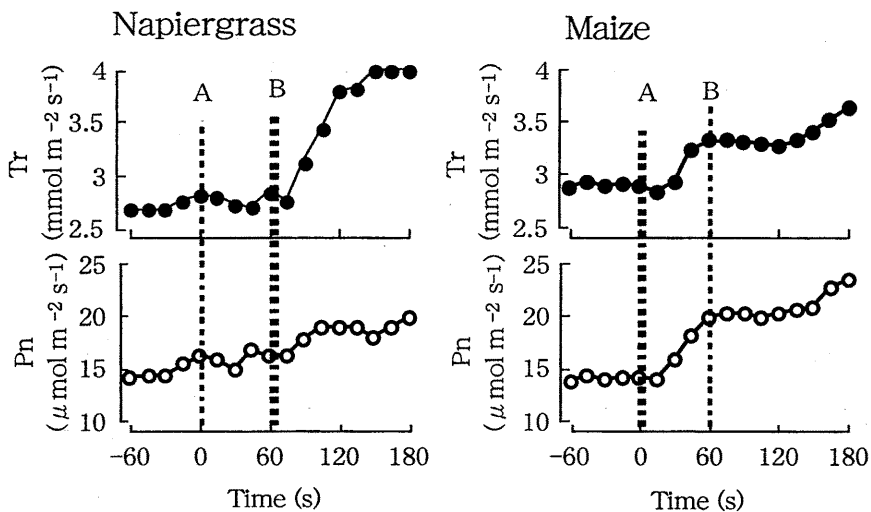


Fig. 2. Changes in photosynthetic rate (Pn) and transpiration rate (Tr) after plant excisions of napiergrass and maize. Plant excisions were made twice at the times of dotted lines. Measuremental light intensity was $900\sim 1200\mu\text{mol m}^{-2}\text{s}^{-1}$. A and B represent the excised positions, stem base and the upper end of stem node, respectively.

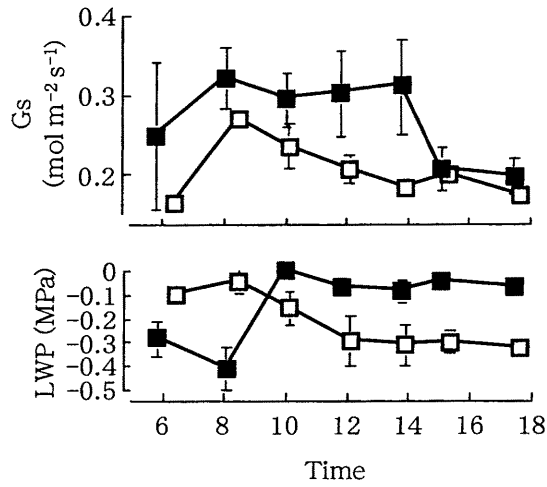


Fig. 3. Diurnal changes in stomatal conductance (Gs) and leaf water potential (LWP) in napiergrass and maize.
 ■ Napiergrass □ Maize

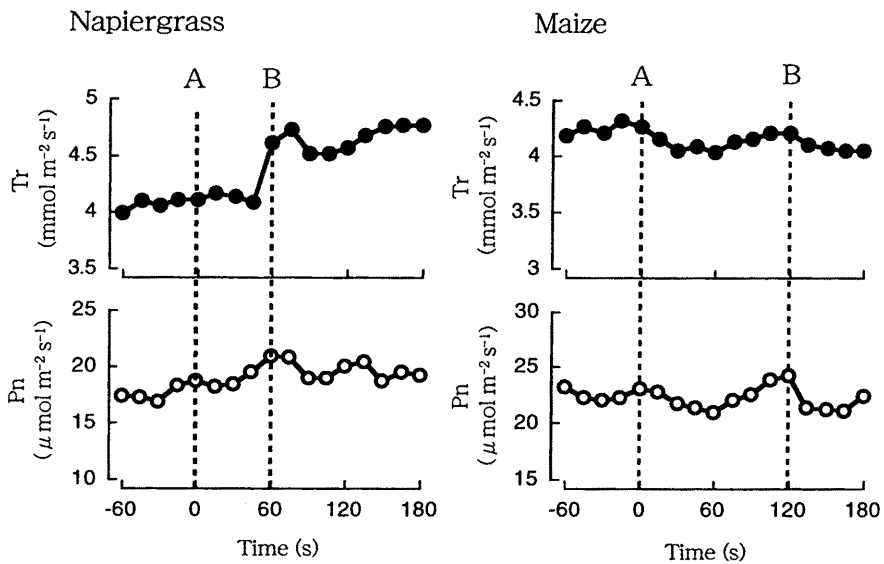


Fig. 4. Changes in photosynthetic rate (Pn) and transpiration rate (Tr) after plant excisions in napiergrass and maize grown under the shade condition. Plant excisions were made twice at the times of dotted lines. Measuremental light intensity was $900\sim 1200\mu\text{mol m}^{-2} \text{s}^{-1}$. A and B represent the excised positions, stem base and the upper end of stem node, respectively.

grass held a high value until about 14:00 whereas that of maize showed a decreasing tendency with time from morning to evening. The value of LWP kept high until the late afternoon in napiergrass. As already mentioned, the water transport from stem to individual leaves in napiergrass was regulated by the individual stem nodes. It may be considered that such a nodal function allows the water condition in each leaf of napiergrass to be adequately sustained through a day, and thereby the Gs and LWP of this species remained higher for a longer time.

In order to examine the water transport in both species in relation to sunlight environments, the post-excision responses of Pn and Tr in plants grown in the shaded and unshaded conditions were investigated. Fig. 4 shows the responses of Pn and Tr to the plant excision treatment. In shade-grown maize, the pre-excision values of Pn and Tr were high, and the post-excision increases in both parameter values were not detected. This may predict that the water transport regulation does not function in a shade-grown maize which contains water sufficiently inside. Contrary to this, in shade-grown napiergrass both parameters showed a rapid increase after the stem base was excised. In napiergrass, the water transport regulation was kept even under the shade condition,

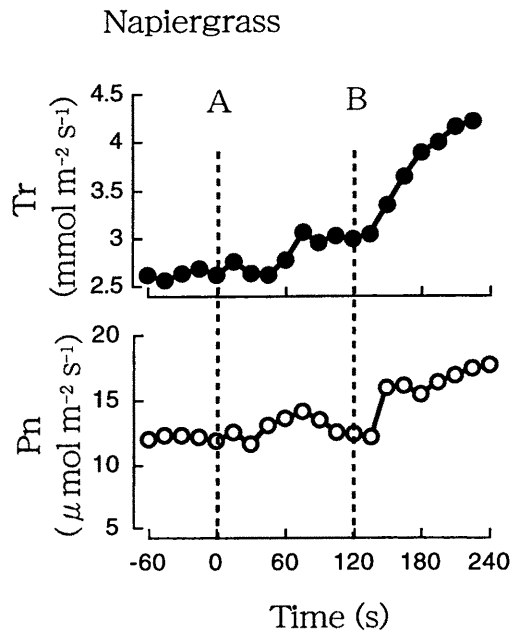


Fig. 5. Changes in photosynthetic rate (Pn) and transpiration rate (Tr) after plant excisions in shade-grown napiergrass that was replaced in the full sunlight condition for 4 hours after the cessation of shade treatment. Measuremental light intensity was $900\sim 1200\mu\text{mol m}^{-2}\text{s}^{-1}$. Plant excisions were made twice at the times of dotted lines. A and B represent the excised positions, stem base and the upper end of stem node, respectively.

though the regulating position moved from the upper node down to the stem base. When the shade-grown napiergrass was replaced under the full sunlight condition to promote transpiration, the water transport regulating position was returned from the stem base to the upper stem node again within four hours (Fig. 5). The shift of the regulating position with light is an interesting phenomenon unique to napiergrass, and from this it may be suggested that this species is able to have a wide adaptability to light and water environments.

In general, plants grown under insufficient light intensities are featured by a taller canopy, higher T/R ratio and increased leaf area, and frequently became highly sensitive to droughts, high temperatures and high solar radiation. Shultz and Matthews (1997) reported that in a shade-grown *P. auritum* plant the function of evaporation regulation was deteriorated, and the cavitation (air foam accumulation in vessels) occurred more frequently when the shade-grown plant was replaced in a strong solar radiation and/or in the air of high vapor pressure deficits. Similarly to this, the functional depression in water transport regulation in both napiergrass and maize plants grown under the shade condition in our experiment, but napiergrass was able to keep a function of water transport regulation under such a growth condition. The flexible change in the stem node function may cause napiergrass to show a wide adaptation to different light or water environments, and this is regarded as one of the main causes of realizing a large biomass production and effective water saving production in this species.

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