

[Short Report]

Effects of Shading on Hydraulic Resistance and Morphological Traits of Internode and Node of Napiergrass (*Pennisetum purpureum* Schumach.)

Kiyoshi Nagasuga and Fumitake Kubota

(Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University, Fukuoka 812-8581, Japan)

Key words : Cross-sectional area, Hydraulic resistance, Internode, Internode length, Napiergrass, Shade.

Napiergrass (*Pennisetum purpureum* Schumach.) is a tropical C₄ grass with significantly higher biomass productivity. In addition, this plant adapts to changes in environmental conditions well. For example, shading increased leaf area and decreased both total dry weight and the ratio of dry matter distribution to root (Nagasuga, 2005). However, in the subsequent full-sunlight condition after shading, napiergrass maintained a high leaf area and recovered both total dry weight and the ratio of dry matter distribution to root without leaf wilting (Nagasuga, 2005). Generally, shaded plants showed leaf wilting and did not grow so well under subsequent full-sunlight conditions (Elias, 1983; Chiariello et al., 1987; Schultz and Matthews, 1997). Nobel (1983) suggested that these were associated with water shortage. In woody plants, shading increased leaf area (transpiring area) and hydraulic resistance of plant organs (Schultz and Matthews, 1993, 1997; Cochard et al., 1999), and these caused an imbalance between water uptake and transpiration. As a result, water shortage occurred under subsequent full-sunlight conditions (Schultz and Matthews, 1997). Napiergrass showed vigorous biomass production without water shortage when light intensity changed (Nagasuga, 2005; Nagasuga and Kubota, 2006). This suggests that adaptation of the water transport system to change in light intensity condition contribute to high biomass production of this plant.

The response of water transport to light intensity condition was examined previously by measuring total hydraulic resistance (R) of napiergrass shoots under various light conditions (Nagasuga and Kubota, 2006). R is the water potential gradient per water flow in the plant, and this is a useful indicator to understand the feature of water transport. It was found that 1) a 6-d exposure to full sunlight after long shading decreased R of the shoot to the value between those of the plants

grown under full-sunlight and shade conditions, and 2) these changes mainly depended on those of stem (Nagasuga and Kubota, 2006). A similar result was found in *Fagus sylvatica* L., which avoided leaf wilting under full-sunlight conditions after shading. This temperate woody plant also decreased hydraulic resistance of branch by thinning, which is the same as full sunlight exposure after long shading (Lemoine et al., 2002). These results suggested that the flexibility of R of stem was a powerful factor that kept leaf growth and biomass production under the variable light intensity condition.

The grass stem is composed of internode and node, and their structures (Dong et al., 1997; Shane et al., 2000) and hydraulic resistance (Meinzer et al., 1992; Nagasuga et al., 2000; Nagasuga and Kubota, 2005) are quite different. In sugarcane, for example, internode is composed of an orderly arrangement of vascular bundles and this hydraulic resistance is low (Meinzer et al., 1992). On the other hand, the node shows a more complicated arrangement of vascular bundles (Dong et al., 1997; Shane et al., 2000), and significantly higher hydraulic resistance (Meinzer et al., 1992). However, which organs contribute mainly to water transport and adaptation to a change in environmental condition, particularly light intensity, in grass stems, remains to be clarified.

In this study, we examined the hydraulic and morphological responses of internode and node to various light treatments to understand which organ mainly controlled water transport in the stems of napiergrass.

Materials and Methods

1. Plant material and growing conditions

Napiergrass, *P. purpureum* var. merkeron, was grown in pots at the experimental farm of Kyushu University

(latitude 33.4°N, longitude 130.2°E) in 2002. On July 4, young shoots sprouted from the parent stocks were transplanted into 18-L pots filled with sandy soil. From 28 d after transplanting, one-third of the experimental plants were grown under full-sunlight conditions for 30 d (control, C plants), one-third under shading (30% of full sunlight using shade cloth) for 30 d (S plants), and one-third under shading for 24 d followed by full sunlight for 6 d (SF plants). Details were as reported previously (Nagasuga and Kubota, 2006).

2. Hydraulic resistance

Total hydraulic resistance (R) of internode and node were measured at the end of the experiment with the pressure-flow meter (Nagasuga et al., 2000). First, we sampled the plants completely filled with water early in the morning for measurement (Nagasuga and Kubota, 2006). Next, the stem segment was cut with a razor blade and connected to the coupling of the pressure-flow meter under water. In this study, the stem segment was composed of the node with the fifth or sixth highest expanded leaf and the internode attached below it. This was the growing stem during the light treatment. Finally, water pressurized with N_2 gas was injected into the bottom of the internode, and steady-state flow rate and applied water pressure were measured with the pressure-flow meter. R ($MPa \text{ s mol}^{-1}$) was calculated as follows:

$$R = \Delta P / q,$$

where ΔP is applied water pressure and q is water flow rate through the pathway. The variable q was measured at three different P values (from 0.05 MPa to 0.3 MPa above atmosphere), and R was calculated as the slope of the P versus q relationship. After measuring the total hydraulic resistance of the stem segment, we excised the node to estimate the total hydraulic resistance of internode. The total hydraulic resistance of node was calculated as the difference in R between the stem segment and internode. Hydraulic resistances per internode length (length-specific hydraulic resistance, r), per cross-sectional area of internode (cross-sectional-area-specific hydraulic resistance, R^S), and per both length and cross-sectional-area (specific hydraulic resistance, R^{SP}) were calculated as reported previously (Nagasuga and Kubota, 2006). The cross-sectional area of internode was calculated as $\pi \times (\text{diameter of internode}/2)^2$, and diameter was measured at the bottom of internode.

Results and Discussion

Napiergrass had a higher R of stem (Nagasuga and Kubota, 2005), and the response of R of shoot to light treatment depended on that of stem through the changes in stem length and its cross-sectional area (Nagasuga and Kubota, 2006). In this study, we focused on the effect of light treatment on R of stem in relation to those of internode and node.

The entire length of the stem segment in S and SF plants was greater than that in C plants (Fig. 1A). S plants had the greatest internode length (mean=81.9 mm), followed by SF plants (69.1 mm) and C plants (61.5 mm; Fig. 1A). The node length in S plants was shorter than that in C plants and similar to that in SF plants (Fig. 1A). These results indicated that the change in entire length of stem segment in response to light treatment depended on that of internode. On the other hand, the cross-sectional area of both internode and node decreased due to shading, with the values of SF plants being intermediate between those of C and S plants (Fig. 1B).

Total hydraulic resistance (R) of stem segment was significantly higher in S and SF plants than in C plants (Fig. 2). A similar result was found in internode: S plants had a significantly higher R of internode than C plants, and SF plants showed intermediate values between them (Fig. 2). These indicated that change in R of stem segment also depended on that of internode. Normalization of R by both length and cross-sectional area of internode (R^{SP}) eliminated the difference among the treatments (Table 1). However, r and R^S ,

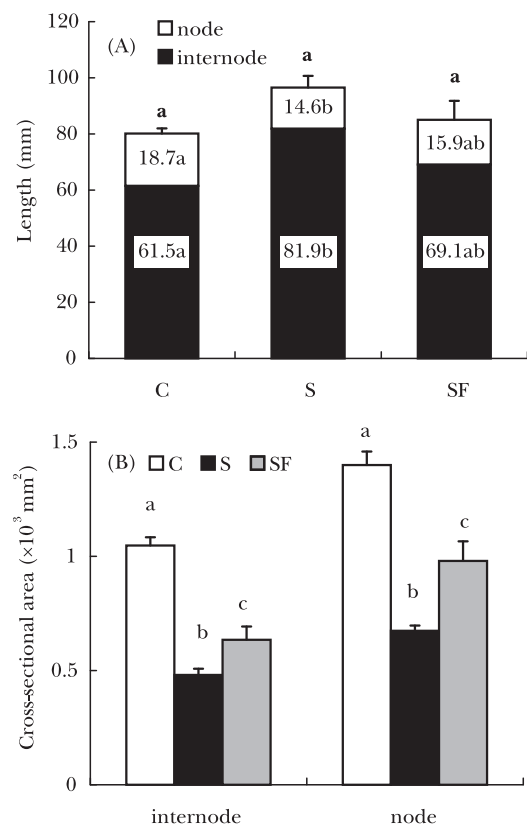


Fig. 1. Entire length of stem segment, composed of an internode and a node (A), and cross-sectional area of internode and node (B) in control (C), shaded (S), and partially shaded (SF) napiergrass plants (see text for treatment details). Data are means \pm SE ($n=5-7$). Different letters on or inside the bars indicate that the means are different among the treatments at 5% level by Fisher's LSD test.

Table 1. Total hydraulic resistance (R), length-specific hydraulic resistance (r), cross-sectional-area-specific hydraulic resistance (R^S), and specific hydraulic resistance (R^{SP}) of internode in control (C), shaded (S), and partially shaded (SF) napiergrass plants (see text for treatment details).

	R	r	R^S	R^{SP}
	($\times 10^{-3}$ MPa s mol $^{-1}$)	(MPa s mol $^{-1}$ mm $^{-1}$)	(MPa s mm 2 mol $^{-1}$)	($\times 10^{-2}$ MPa s mm mol $^{-1}$)
C	2.11 \pm 0.39a	0.034 \pm 0.006a	2.16 \pm 0.35a	3.49 \pm 0.53a
S	9.65 \pm 2.07b	0.120 \pm 0.027b	6.53 \pm 1.44b	5.88 \pm 1.55a
SF	5.03 \pm 0.49a	0.076 \pm 0.01ab	3.10 \pm 0.26a	4.54 \pm 0.20a

Data are means \pm SE ($n=5-7$). Different letters within each column indicate significant differences ($P<0.05$) among treatments (Fisher's LSD test).

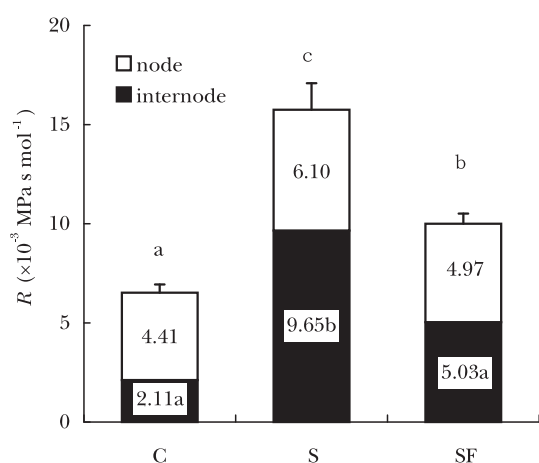


Fig. 2. Total hydraulic resistance (R) of the stem segment, internode, and node in control (C), shaded (S), and partially shaded (SF) napiergrass plants (see text for treatment details). Data are means \pm SE ($n=5-7$). Different letters on or inside the bars indicate that the means are significantly different among the treatments at 5% level by Fisher's LSD test.

which represent R normalized by length and cross-sectional area only, showed significant differences among the treatments (Table 1). Changes in R of internode would be associated with both length and cross-sectional area of internode.

In grapevine, shading decreased the hydraulic resistance of the internode through the decline in xylem area (Schultz and Matthew, 1993). Similarly, the hydraulic resistance of the branch changed in response to light treatment and this was associated with the change in xylem area (Lemoine et al., 2002). In this study, we did not examine the xylem area.

However, the cross-sectional area of internode changed in response to light treatment and the number of vascular bundles did not differ with the treatment (data not shown). Changes in cross-sectional area might be associated with the xylem area.

In conclusion, changes in hydraulic resistance of the stem segment in response to light treatment depended on the change in the internode through the changes in length and cross-sectional area.

Acknowledgements

We thank Dr. Okada, Dr. Murai-Hatano and the members of the National Agricultural Research Center for Tohoku Region for valuable suggestions.

References

- Chiariello, N.R. et al. 1987. *Funct. Ecol.* 1 : 3-11.
 Cochard, H. et al. 1999. *Plant Cell Environ.* 22 : 101-108.
 Dong, Z. et al. 1997. *Ann. Bot.* 80 : 147-158.
 Elias, P. 1983. *Biol. Plant.* 25 : 68-74.
 Lemoine, D. et al. 2002. *Ann. Sci. For.* 59 : 761-766.
 Meinzer, F.C. et al. 1992. *Plant Cell Environ.* 15 : 471-477.
 Nagasuga, K. et al. 2000. *Biotronics* 29 : 71-78.
 Nagasuga, K. 2005. *Bull. Inst. Trop. Agr. Kyushu Univ.* 28 : 15-20.
 Nagasuga, K. and Kubota, F. 2005. *Jpn. J. Crop Sci.* 74 : 179-184*.
 Nagasuga, K. and Kubota, F. 2006. *Plant Prod. Sci.* 9 : 364-368.
 Nobel, P.S. 1983. *Biophysical Plant Physiology and Ecology*. W. H. Freeman and Co., New York. 1-608.
 Schultz, H.R. and Matthews, M.A. 1993. *Planta* 190 : 393-406.
 Schultz, H.R. and Matthews, M.A. 1997. *Oecologia* 110 : 312-319.
 Shane, M.W. et al. 2000. *Ann. Bot.* 86: 245-258.

*In Japanese with English summary.