

Change in Hydraulic Resistance and Shoot Morphology of Napiergrass (*Pennisetum purpureum* Schumach.) under Shaded Condition

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Abstract : Acclimation to light condition is associated with change in water transport system in napiergrass. In this study, the effects of shading on shoot hydraulic resistance and morphology of napiergrass (*Pennisetum purpureum* Schumach.) were investigated. In the plants under shading (to 30% of full sunlight) for 30 days (S plants), total hydraulic resistance of a shoot (R_{shoot}) increased from that of full sunlight (control). In the plants grown under shade condition for 24 d followed by full sunlight conditions for 6 d (SF), the R_{shoot} value was intermediate between that of control and S plants. A similar response to shading was found in total hydraulic resistance of a stem (R_{stem}), which accounted for more than 60% of R_{shoot} , but the total hydraulic resistance of the leaves was not significantly affected by shading. Leaf length, leaf area and stem length were larger, but the stem cross-sectional area (SA) was smaller in S and SF plants than in the control plants. SF plants showed similar leaf length, leaf area and stem length to those in S plants, but the SA in SF plants was slightly larger. Normalization of R_{stem} by SA and stem length decreased the difference among the treatments, indicating the increase of R_{shoot} and R_{stem} under shading resulted from the decrease of SA and the increase of stem length.

Key words : Hydraulic resistance, Napiergrass, Shading, Specific hydraulic resistance, Stem cross-sectional area, Stem length.

Napiergrass (*Pennisetum purpureum* Schumach.) is a tropical herbaceous plant with especially high dry-matter productivity (Ito and Inanaga, 1988a, b; Matsuda et al., 1991; Kubota et al., 1994) and high ability to acclimate to environmental conditions (Ito and Inanaga, 1988a, b). This strong acclimation ability of napiergrass means that the dry matter production recovers quickly from inhibition caused by environmental stress when returned to favorable conditions. Ito and Inanaga (1988a) reported that napiergrass showed high dry-matter yield in eastern Japan, an area with a temperate climate, as in a tropical area, although dry-matter production was strictly restricted by low temperature during the early growth stage. The dry matter increase restricted in the early stage was quickly recovered by an increase in leaf number and leaf area under subsequent high temperature conditions. Therefore, these authors suggested that high yield in napiergrass should be attributed not only to high dry matter productivity but also to high acclimation to growth temperature condition during plant growth (Ito and Inanaga, 1988a, b).

Light intensity strongly affects dry matter production

through the regulation of the water transport system. In shade-acclimated plants, hydraulic resistance of plant organs was large because xylem cross-sectional area and average conduit diameter per unit xylem cross-sectional area was small, but the ratio of leaf area (transpiring area) to stem cross-sectional area (water conducting area) was large (Schultz and Matthews, 1993) and root weight remained small (Nagasuga, 2005). Under full sunlight condition, these characteristics caused an imbalance between water uptake and transpiration, resulting in leaf wilting and the inhibition of extension growth (Elias, 1983; Chiariello et al., 1987; Schultz and Matthews, 1997). Therefore, to maintain high biomass production, crop plants must be able to acclimate to changes in light condition, such as early summer following the rainy season in Japan (Hirasawa et al., 1998).

In a previous study on napiergrass, substantial fluctuation of total dry matter weight was observed in responses to shade treatment (Nagasuga, 2005). Total dry-matter weight largely decreased under the shade conditions, but fully recovered under subsequent full-sunlight condition. Leaf area remained large under the shade conditions due to increased allocation of

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Abbreviations: L, stem length; LA, leaf area; P , applied water pressure; q , water flow rate through the pathway; R^L , leaf area specific hydraulic resistance; R_{leaf} , total hydraulic resistance of the leaves; R_{shoot} , total hydraulic resistance of a shoot; $R_{\text{stem}}^{\text{sp}}$, specific hydraulic resistance of a stem; $R_{\text{stem}}^{\text{s}}$, stem cross-sectional area-specific hydraulic resistance of a stem; R_{stem} , total hydraulic resistance of a stem; r_{stem} , stem length-specific hydraulic resistance of a stem; SA, stem cross-sectional area.

Table 1. Leaf length, leaf area, stem length and stem cross-sectional area (SA) in napiergrass.

	Leaf length (m)	Leaf area (m ²)	Stem length (m)	SA (mm ²)
C	0.86 ± 0.03 a	0.240 ± 0.010 a	0.72 ± 0.07 a	1342 ± 104 a
S	1.25 ± 0.03 b	0.326 ± 0.034 ab	1.03 ± 0.08 b	800 ± 59 b
SF	1.17 ± 0.05 b	0.374 ± 0.029 b	1.08 ± 0.05 b	1010 ± 134 b

C, S and SF means plants grown under full sunlight for 30 d (control plants), under shade for 30 d (S plants), and under shade for 24 d followed by full sunlight for 6 d (SF plants). Values are means ± SE (n = 5-7). Different letters within columns indicate significant differences (P<0.05) among treatments (Fisher's LSD).

dry matter to the leaves at the expense of the roots. Although significantly lighter root weight and large leaf area were maintained over the experimental period, leaf wilting was not observed under the full sunlight conditions directly after shading. These findings suggest that the acclimation to changed light condition may be associated with maintenance of leaf water status and leaf area after shading and, in particular with the recovery of water transport capacity.

Total hydraulic resistance of a shoot (R_{shoot}) is one of the factors regulating water transport to the leaves, and it is affected by morphological traits, such as leaf length and stem cross-sectional area (SA). Hydraulic resistance of plant organs and morphological traits change in response to light treatment (Schultz and Matthews, 1993), particularly in the plants that acclimated to light intensity condition well (Cochard et al., 1999). Napiergrass may also adapt to light treatment related the modification of R_{shoot} and these morphological traits. In this study, we examined (i) whether R_{shoot} and morphological traits in napiergrass changed in response to shade conditions and to subsequent full sunlight, and (ii) which morphological traits were related to change in R_{shoot} . To assess hydraulic adaptation to change of light intensity, we compared hydraulic resistances of plants grown under full sunlight for 30 d, under shade for 30 d, and under shade for 24 d followed by full sunlight for 6d.

Materials and Method

1. Plant material and growth condition

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 with 7 or 8 leaf were separated from the parent stocks and transplanted individually into 18 L pots filled with sandy soil. At transplanting, two-thirds in length of each leaf was cut to prevent damage due to water loss. As the basal fertilization, 3 g of N (ammonium-N), 2 g of P₂O₅ and 2 g of K₂O were applied to each pot. From 28 d after transplanting, one-third of the experimental plants (n = 8) were grown under full sunlight conditions for 30 d (control plants), one-third were grown under shade conditions (shaded to 30% of full sunlight using shade cloth)

Table 2. Hydraulic resistance (R) and leaf area specific hydraulic resistance (R^L) in napiergrass.

		R	R^L
		(MPa s mol ⁻¹)	(± 10 ⁻³ MPa s m ² mol ⁻¹)
Shoot	C	0.124 ± 0.014 a	29.5 ± 3.4 a
	S	0.176 ± 0.011 a	57.1 ± 6.4 b
	SF	0.153 ± 0.016 a	57.8 ± 3.3 b
Leaf	C	0.046 ± 0.012 a	10.8 ± 2.7 a
	S	0.039 ± 0.010 a	13.3 ± 3.6 a
	SF	0.046 ± 0.008 a	20.2 ± 2.9 a
Stem	C	0.078 ± 0.007 a	18.7 ± 1.9 a
	S	0.137 ± 0.017 b	44.3 ± 3.2 b
	SF	0.104 ± 0.017 ab	37.6 ± 6.2 b

Values are means ± SE (n = 5-7). Different letters within columns indicate significant differences (P<0.05) among treatments (Fisher's LSD).

for 30 d (S plants), and one-third were grown under shading for 24 d followed by full sunlight for 6 d (SF plants).

2. Hydraulic resistance

Total hydraulic resistance (R) was measured with a homemade pressure-flow meter (Nagasuga et al., 2000) at 58 d after transplanting. Each shoot was cut 5-10 cm above the soil surface and taken to the laboratory. Sufficient water was supplied to eliminate the effect of water shortage on the water pathway, and we used the shoot completely filled with water early in the morning (before 07:00 h) for measurement. The root collar of each shoot was removed with a razor blade and the shoot was connected to the coupling of the pressure-flow meter in water. Water pressurized by N₂ gas was inserted into the shoot. We measured flow rate and applied water pressure under steady-state conditions approximately 15 min after insertion of shoots. After measuring total hydraulic resistance of shoot (R_{shoot}), all leaves attached to the shoot were excised leaving leaf sheaths for estimation of total hydraulic resistance of the stem (R_{stem}). Total hydraulic resistance of the leaves (R_{leaf}) was estimated as ($R_{\text{shoot}} - R_{\text{stem}}$).

Table 3. Hydraulic resistance of stem (R_{stem}), stem length specific (r_{stem}), cross-sectional area of stem specific (R_{stem}^S) and specific ($R_{\text{stem}}^{\text{SP}}$) hydraulic resistance of stem in napiergrass.

	R_{stem} (MPa s mol ⁻¹)	r_{stem} (MPa s mol ⁻¹ mm ⁻¹)	R_{stem}^S ($\times 10^{-3}$ MPa s mm ² mol ⁻¹)	$R_{\text{stem}}^{\text{SP}}$ ($\times 10^{-3}$ MPa s mm mol ⁻¹)
C	0.078 \pm 0.007 a	87.1 \pm 10.1 a	86.2 \pm 5.9 ab	0.113 \pm 0.012 a
S	0.137 \pm 0.017 b	147.6 \pm 27.6 b	98.7 \pm 7.8 a	0.109 \pm 0.016 a
SF	0.104 \pm 0.017 ab	77.2 \pm 15.4 a	70.1 \pm 5.1 b	0.066 \pm 0.006 b

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

R (MPa s mol⁻¹) was calculated as follows:

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

where, ΔP is the change in applied water pressure through the pathway and Δq is the change in water flow rate through the pathway. The variable q was measured at three different P values, and R was calculated as the slope of the q versus P relationship. Leaf area-specific, stem length-specific, stem cross-sectional area-specific and specific hydraulic resistance (R^L , R_{stem} , R_{stem}^S and $R_{\text{stem}}^{\text{SP}}$) were calculated using the following equations:

$$R^L = R \times \text{LA} = \Delta P / (\Delta q / \text{LA})$$

$$r_{\text{stem}} = R / L = (\Delta P / L) / \Delta q$$

$$R_{\text{stem}}^S = R \times \text{SA} = \Delta P / (\Delta q / \text{SA})$$

$$R_{\text{stem}}^{\text{SP}} = R / L \times \text{SA} = (\Delta P / L) / (\Delta q / \text{SA})$$

where, LA is leaf area, L is stem length, and SA is stem cross-sectional area. LA was measured with an automatic area meter (AAM-8, Hayashidennko, Japan), and SA was calculated as $\pi(\text{stem diameter}/2)^2$.

Results and Discussion

Shading increased leaf length, leaf area and stem length to 1.25 m, 0.326 m² and 1.03 m (145%, 136% and 143%, respectively, of the corresponding values for the control plants), and decreased stem cross-sectional area to 800 mm² (60% of the value in the control plants (Table 1). Previous studies showed that the ratio of leaf area (transpiring area) to stem cross-sectional area (water conducting area) was larger and root weight remained low in shade-grown plants (Schultz and Matthews, 1993; Nagasuga, 2005). Furthermore, water-conducting capacity was shown to decrease with a decline of xylem area and diameter of lumens (Schultz and Matthews, 1993). These changes caused an imbalance between water uptake and transpiration, and resulted in leaf wilting under full sunlight after shading (Elias, 1983; Chiariello et al., 1987; Schultz and Matthews, 1997). In napiergrass, however, a quick recovery of plant growth without leaf wilting was observed under full sunlight following a shaded condition (Nagasuga, 2005). In the present study,

leaf area remained high (0.374 m², 155% of the value in the C plants) and cross-sectional area of the stem increased to 1010 mm², (intermediate between those of the control plants (1342 mm²) and S plants (800 mm²) after exposure to full sunlight following shading (SF plants, Table 1).

A previous study showed that water uptake was correlated with xylem cross-sectional area in the stem of woody plants (Goldstein et al., 1998). In addition, the ratio of xylem cross-sectional area to total cross-sectional area in the basal stem was not so different among the plants grown under shade (Shultz and Matthews, 1993) and drought (Lovisolo and Schubert, 1998) conditions. A negative relationship was found between xylem cross-sectional area and hydraulic resistance (Shultz and Matthews, 1993; Lovisolo and Schubert, 1998). These findings suggested that light treatment changed morphology of the stem that modify water-conducting capacity and ultimately stabilize the leaf water status.

R_{shoot} in the S plants was significantly higher (0.176 MPa s mol⁻¹) than that in control plants (0.124 MPa s mol⁻¹), whereas R_{shoot} in the SF plants (0.153 MPa s mol⁻¹) was not as high as that in the S plants (Table 2). R_{shoot} can be divided into R_{leaf} and R_{stem} . R_{stem} accounted for more than 60% of R_{shoot} in all plants, and the response of R_{stem} to light treatment was similar to that of R_{shoot} , although there was no significant difference in both R_{leaf} and R_{leaf}^L among treatments (Table 2). These findings suggested that water-conducting capacity and acclimation of shoot was mostly reflected in the hydraulic characteristics of the stem.

Hydraulic resistance of a stem is generally regulated by stem length and cross-sectional area (Tyree and Ewers, 1991). In this study, normalization of R_{stem} by stem cross-sectional area (R_{stem}^S) decreased the difference in R_{stem} among treatments, although there was still significant difference among treatments (R_{stem} , Table 3). Changes in morphological traits and R_{stem} by light treatment was found in woody plants; shading induced a reduction in stem cross-sectional area and an increase of R_{stem} , which would result in decreased water transport capacity (Schultz and Matthews, 1993, 1997; Cochard et al., 1999). In the SF plants, however,

a 6 d exposure to of full sunlight induced an increase in stem cross-sectional area and a reduction in R_{stem} (Tables 1, 2). Leaf wilting did not occur under full sunlight after shading and it was assumed that root weight would not fully recovered during 6 d under full sunlight conditions. The maintenance of the larger leaf area after the end of shading might be attributed to recovery of the water supply through the reduction of R_{stem} , not to the increase in root weight. SF plant, which had longer and thicker stems than control plants, exhibited R_{stem} as low as those of control plants and significantly lower $R_{\text{stem}}^{\text{SP}}$ (Table 3). These findings indicate that SF plants were superior in both the capacity and the efficiency of water conductance in the stem. In woody plant, $R_{\text{stem}}^{\text{SP}}$ decreased with the increase in conduit diameter (Tyree and Ewers, 1991). Thicker stem included wider diameter (Shultz and Matthews, 1993; Lovisolo and Schubert, 1998), therefore a thicker stem is considered to have a lower $R_{\text{stem}}^{\text{SP}}$. In this study, however, there was no significant difference in $R_{\text{stem}}^{\text{SP}}$ between the control and S plants, which were quite different in stem cross-sectional area (Table 3).

The herbaceous stem consists of complex segments with many nodes and internodes. These elements differed in hydraulic resistance and the composition of vascular bundles, in particular, nodes had significantly higher hydraulic resistance (Sperry, 1986; Meinzer et al., 1992; Nagasuga et al., 2000; Nagasuga and Kubota, 2005) and a more complicated arrangement of vascular bundles (Sperry, 1986) than internodes. In grapevine, shading increased hydraulic resistance in internodes through a reduction of xylem cross-sectional area and average conduit diameter per xylem cross-sectional area (Schultz and Matthews 1993). On the other hand, it was estimated that hydraulic resistance of nodes was decreased by shading in napiergrass (Nagasuga et al., 1998; Nagasuga, 2003). These findings may suggest that internodes and nodes in napiergrass were different in the response of hydraulic resistance to light treatment, which was involved in similarity of $R_{\text{stem}}^{\text{SP}}$ between control and S plants.

In this study on napiergrass, hydraulic characteristics of the stem were affected by light treatment through changes in stem cross-sectional area, and these would allow the maintenance of a large leaf area under shade conditions and a quick recovery of plant growth under full sunlight conditions. In a future study, we will examine the hydraulic characteristics of the stem with respect to hydraulic differences of nodes and internodes.

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*In Japanese with English abstract.
