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Characteristics of Biomass Productivity and Related Growth Parameters in Napiergrass (*Pennisetum purpureum* Schumach.)

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ABSTRACT

Napiergrass (*Pennisetum purpureum* Schumach.) is a tropical grass. It is well known among the herbaceous plants as a plant with very high biomass productivity. One of the features in biomass productivity is a significantly higher leaf area. In addition, the form of light-interception changes according to the growth stage. These synergistic effects largely contribute to a higher biomass production. On the other hand, napiergrass has a unique water transport system, which is likely to support lower root weight. This article mainly reviews knowledge of biomass productivity and related growth parameters, particularly water transport, in napiergrass.

Keywords: crop growth rate, hydraulic resistance, leaf area, light-interception, root, water storage, water transport

CONTENTS

INTRODUCTION

Napiergrass, *Pennisetum purpureum* Schumach. (Poaceae), introduced from Africa, is an enormous (3-4 m in height in various tropical and temperate areas), sugarcane-like grass (**Fig. 1**), and is also known as elephantgrass because elephants willingly eat it. Napiergrass has a high biomass yield surpassing most tropical grasses (Skerman and Riveros 1990; Humphreys 1994). High biomass yield has mainly been recorded in the high biomass-yielding cultivar 'Merkeron', which is the eyespot (*Aureobasidium zeae*) immune F_1 hybrid between outstanding tall selection, No. 1 and a very leafy dwarf, No. 208 (Burton 1990). The highest yield encountered was 82 t ha^{-1} yr^{-1} of dry matter (DM) yield in Puerto Rico (Vicent-Chandler *et al*. 1959) and more than 50 DM t ha^{-1} yr^{-1} was recorded in tropical and temperate areas (Watkins and Lewy-van Severen 1951; Duke 1981; Kitamura *et al*. 1982; Mislevy *et al*. 1986). Napiergrass is used mainly as forage for livestock in the wet tropics. Forage quality is high and maintains for longer periods than most warm-season grasses, particularly the leaf blades of 'Mott', a dwarf napiergrass, which is made up more than 70% of harvested DM until autumn (Hanna and Monson 1988; Woodard and Prine 1991). Because napiergrass is persistence to frequent defoliation by management factors such as the application of manure and/or fertilizer, it plays a role as the major livestock feed in smallholder dairy production systems in Kenya (Potter 1987; Orodho 1990).

Napiergrass is regarded not only as livestock but also as an important source of biomass energy and a non-wood source as pulp for paper fabrication and lignin for construction materials (Ferraris and Stewart 1979; Ito *et al*. 1990; Woodard *et al*. 1991; Jewell *et al*. 1993; Shank 1993a, 1993b). Because high biomass yield is the important factor for an energy crop, research with napiergrass has also dealt with biological and thermal processes that produce liquid or gaseous fuel and its effective storage method (Ito *et al*. 1990; Woodard *et al*. 1991; Jewell *et al*. 1993; Shank 1993a,

Fig. 1 Napier grass growing at Kyushu University, Fukuoka, Japan, in summer.

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Invited Mini-Review

Table 1 Growth parameters between napiergrass and maize.

Growth parameters	**unit**	**Napiergrass**	**Maize**	**Sample**
Plant height	(m)	3.0	2.8	Field-grown plants at vegetative stage
Leaf area index	(m^2 m^{-2})	13.3	7.8	(Matsuda *et al*. 1991)
Light extinction coefficient		0.37	0.47	
Stem density	(Stem no. m^{-2})	25	8.0	
Leaf area	(m^2 $tiller^{-1}$)	0.5	1.0	
Plant dry weight	(g $plant^{-1}$)	359.9	221.0	Pot-grown plants at vegetative stage
Top / root ratio	(g g^{-1})	3.4	1.4	(Nagasuga and Kubota 2006)
Plant leaf area	($\times 10^{-2}$ m^2)	163.6	71.6	
Leaf area	($\times 10^{-2}$ m^2 $tiller^{-1}$)	8.6		
Tiller no.		18.3	1.0	
Leaf area ratio	($\times 10^{-4}$ m^2 g^{-1})	4.7	3.3	
Leaf area per root dry weight	($\times 10^{-4}$ m^2 g^{-1})	20.6	8.0	
Leaf area (LA)	($\times 10^{-2}$ m^2 $tiller^{-1}$)	20.2	48.2	Pot-grown plants at early vegetative stage
Stem cross-sectional area (SA)	($\times 10^{-4}$ m^2 $tiller^{-2)}$	1.0	2.2	(Nagasuga and Kubota 2005)
LA/SA	($\times 10^{2}$ m^2 $tiller^{-2}$)	20	22.3	
Stem length	(cm)	47	56	

1993b). Many studies have been conducted about the utility of napiergrass as forage and energy resource, however, there is little information about biomass productivity itself. Napiergrass shows high biomass yield and persistence both to frequent defoliation and to various environmental stress conditions. The information about the mechanisms of these factors is useful for cultivating and breeding not only napiergrass but also other plants. In this article, the features of napiergrass with a focus on biology, high biomass productivity and related features are reviewed.

BIOLOGY

Napiergrass is a robust, perennial bunch that reaches a height of 3-4 m. This is composed of 20-90 clumps (**Table 1**) up to 1-2 m tall of coarse stems (about 2.5 cm thick near the base) and erected large leaves (1.2 m long and 2.5 cm wide). Panicle length is bristly with a bottle-brush shape and can be 10 to 33 cm long.

This species is widely distributed throughout tropical and temperate regions of the world since napiergrass grows well at high temperatures (25 to 40°C). It can grow in a wide range of soils, performing best in fertile and well-drained soils, and can tolerate short, moderate drought because of its deep root system (it reaches more than 1m depth; Skerman and Riveros 1990). Napiergrass cannot tolerate flooding, waterlogging and low temperature (minimum temperature for survival is the range from –0.9-4°C), and light frosts can kill its herbage (Inanaga *et al*. 1990). However, underground parts can remain alive if the soil is not frozen (Ito and Inanaga 1988a).

Napiergrass reproduces sexually, and yields small-sized seed that are quantitatively poor – rarely more than 1-2 kg/ha pure germinating seed – and do not germinate well (Diz and Shank 1993; Humphreys 1994). Because of low seed production, planting is conducting typically by placing stem cuttings and crown divisions horizontally in shallow furrows (Sollenberger *et al*. 1990). Stem cuttings are from the plant established in the previous year and crown divisions are seedlings with 7-8 leaves sprouted from over-wintered stocks. These are planted in the depth of 5-10 cm at early summer season (Ito and Inanaga 1988a). This vegetative propagation has restricted a widespread use, especially in developed countries where labor is more expensive (Schank and Diz 1991). Problems with seed propagation are solved partially through hybridization with pear millet, *P. glaucum* L. R. Br., and further selection (Diz and Schank 1993; Diz *et al*. 1994, 1995). Pear millet is an annual, high quality, diploid grass (2n = 2x =14) which is grown as a grain and forage crop. Napiergrass is a tetraploid (2n = 4x =28). The F_1 hybrids (triploid: 2n = 3x =21) are completely sterile due to their unbalanced chromosome number, which causes irregularities during meiosis (Khan and Rahman 1963; Muldoon and Pearson 1979). One of the commercial methods is to produce triploid seed by seeding a cytoplasmic male-sterile pear millet line between rows of perennial napiergrass (pollen source; Powell and Burton 1966). However, this would only be possible in areas which are frost free until late December (USA), due to the late flowering of napiergrass (Powell and Burton 1966). Another approach involves doubling the chromosome number of the triploid hybrid, which then restores fertility (Hanna 1981). The amphiploids (hexaploids: 2n= 6x = 42) obtained usually showed a high degree of regular meiosis, and their progeny had a wide range of pollen and seed fertility (Diz and Schank 1993).

HIGH BIOMASS PRODUCTIVITY

Vigorous biomass productivity of napiergrass is maintained during the summer season, and this leads to high biomass yield, particularly total DM yield (Ito and Inanaga 1988a; Matsuda 1991). Generally, an increase in the rate of crop DM (crop growth rate, CGR) is determined by synergistic effects composed of total leaf area and net assimilation rate (NAR). Napiergrass has a higher leaf area, leaf photosynthesis and efficient form for light interception, and these contribute to the maintenance of high CGR.

At an early growth stage (until 8 weeks after transplanting), NAR is the main contributor to high CGR of napiergrass. A small leaf area of young plants allows each leaf to receive sunlight easily. Therefore, NAR and CGR generally depend on leaf photosynthetic capacity at an early growth stage. Napiergrass maintains a high CGR and NAR for a longer time than maize (Matsuda 1991). It has C_4 leaf photosynthesis and this high capacity is maintained in the lower leaves (Ito and Inanaga 1988b; Nada *et al*. 1991). A rapid increase in CGR of napiergrass at an early growth stage would depend on high NAR resulting from high C_4 leaf photosynthesis and maintenance of photosynthetic capacity.

The main contributor to high biomass yield changes from NAR to leaf area index (LAI) as the plant grows. A higher leaf area of napiergrass is caused by vigorous leaf production (Ito and Inanaga 1988a, 1988b; Ito *et al*. 1988). LAI (leaf area per unit cultivated area) increases linearly and can reach 12-15 m^2 m^{-2} by vigorous tillering (until middle vegetative stage), enlargement of individual leaves through leaf elongation and an increase in leaf number (**Table 1**). Leaf production is accelerated by high temperature, and this leads to a small difference in DM yield among the possible cultivation areas in central Japan even though leaf production and DM yield of plants grown in northern areas are restricted by low temperatures at an early vegetative stage (Ito and Inanaga 1988b; Ito *et al*. 1988). The application of fertilizer also increases DM yield by vigorous leaf production. Miyagi (1981) investigated the effect of nitrogen fertilizer on yield and found that yield increased remarkably by applying nitrogen fertilizer up to 60 kg 10 a^{-1} on calcareous soil and that this was associated with an increase in LAI through enlargement and quantitative enrichment of leaves. These newly expanded leaves also contributed to a remarkable increase in DM both at an early growth stage and to recovery from low temperature condition (Ito and Inanaga 1988c).

However, excessive leaf production often causes mutual shading, as a result, a decline in total DM. Therefore, it is often found that high yielding rice cultivars have not only a high leaf area but also a useful form for light interception (Saitoh *et al.* 1990; Takeda *et al.* 1984). Napiergrass changes its form for light interception as the plant grows. A wide range of stem inclination (20°-90°) is observed at an early growth stage, thereafter all stems elongate erectly and vigorously; as a result, stem inclination concentrates at a high angle (from 70°-90°; Kubota *et al.* 1994). In addition, a longer stem with robust base and erect leaves fluctuates flexibly by natural wind. Synergistic effects of these factors lead to the decline in the light extinction coefficient (K) of the canopy from 1.1 to 0.3 and allow sunlight to penetrate to lower leaves in the canopy throughout the growth stage (Ito and Inanaga 1988a; Matsuda *et al.* 1991; Kubota *et al.* 1994). Avoidance of mutual shading is involved in high utilization of sunlight energy for efficient DM production in napiergrass. While, the increase in respiration with plant growth is not so high in napiergrass. Because of senescence of elongated internodes, respiration in the stem decreases remarkably with plant growth (Ito *et al.* 1992). In addition, dry matter distribution to the root, which conducts respiration only, is significantly lower (Matsuda *et al.* 1991; Nagasuga *et al.* 1998). DM yield of plants generally depends on the cumulative amount of assimilates, which occupy more than 90% of DM yield, composed of the difference between plant photosynthesis (producing assimilates) and respiration (consuming assimilates). A small increase in respiration contributes to high biomass yield of napiergrass through the restriction of the loss of assimilates by respiration (Ito *et al.* 1992).

CHARACTERISTICS OF WATER TRANSPORT

Continuous water supply to the leaves is necessary for full photosynthetic capacity. Higher plants transpire between 100 and 1000 water molecules per molecule of assimilated carbon (Maseda and Fernández 2006). Transpiration increases with the increase in leaf area. Leaf area increases vigorously with plant growth and this is involved in an imbalance between water loss by transpiration and water absorption from the soil, as a result, mild water shortage is often found in mature plants even grown in good soil water condition (Huck *et al.* 1983; Ishihara and Saito 1987; Hirasawa and Ishihara 1991). Reduction in water use causes stomatal closure or a decline in leaf area, both of which reduce biomass productivity (Brodribb and Feild 2000; Salleo *et al.* 2000; Davis *et al.* 2002; Sperry *et al.* 2002). Therefore, higher photosynthesis (Sperry 2000; Tyree 2003) and faster leaf expansion (Nardini and Salleo 2002) have often been found in plants with a higher capacity of water supply between life forms (Brodribb *et al.* 2005), species (Brodribb and Field 2000; Sack *et al.* 2003), and genotypes (Sangsing *et al.* 2004).

Napiergrass has a high leaf area and quantitatively poor root system (**Tables 1, 3**). Quantitatively, an imbalance between them causes water shortage, however napiergrass keeps transpiration as high as that of maize with rich root system under various soil water conditions (Nagasuga *et al.* 2002; Nagasuga and Kubota 2006) and is resistant to drought (Duke 1978). These results indicate that napiergrass has a unique and effective water transport system. One of the features in water transport of napiergrass is high resistance to water flow within a plant. Napiergrass shows a high hydraulic resistance (the reciprocal of hydraulic conductance) of shoots, and significantly higher hydraulic resistance is found in the stem, particularly nodal stems in the direction of the leaf (**Table 2**). In addition, hydraulic response to environmental factors is so flexible (Nagasuga *et al.* 1998, 2002; Nagasuga and Kubota 2006b). For example, hydraulic resistance of the shoot and stem increases largely by long periods of shading and decreases quickly within a few days under subsequent full sunlight condition (**Table 3**). High hydraulic resistance is not so useful for conducting much water to the leaves, however this contributes to the avoidance of catastrophic xylem failure when high tension in xylem conduits cavitates the water column under severe soil drought condition (Tyree and Ewers 1991).

Table 2 Hydraulic resistance[a] of napiergrass and maize.

Sample	Napiergrass	Maize
Shoot	21.9	4.8
Leaves	6.9	1.2
Stem	15.0	3.6
Stem components		
Node (leaf direction)	45.2	15.9
(stem apex direction)	2.1	4.5
Internode	0.3	0.4

a: $\times 10^{-2}$ MPa s $mmol^{-1}$
The plants with 10 leaves grown in field condition were sampled for measurements. Values of the node with 5th or 6th leaf and the internode attached below it are shown as those of stem components. Based on Nagasuga and Kubota (2005).

Table 3 Hydraulic resistance[a] of napiergrass.

Sample	Treatment	Value
Shoot	Control	10.5
	Shade	17.4
	SF	12.1
Leaves	Control	4.0
	Shade	4.4
	SF	4.9
Stem	Control	6.7
	Shade	12.3
	SF	8.1

a: $\times 10^{-2}$ MPa s $mmol^{-1}$
The plants with 10 leaves grown in the pots were sampled for measurements. Control and shade plants are grown under full sunlight condition and shading (30% of full sunlight) for 30 d after transplanting, respectively. SF plants are grown under full sunlight for 24 d and shading for 6d after transplanting. Based on Nagasuga and Kubota (2006b).

Low water-conducting capacity of napiergrass may be supported by a bunchy stem and water storage. Water-conducting capacity of the stem is composed from two factors: hydraulic resistance and the ratio of the leaf area to stem cross-sectional area. In woody plants, low water-conducting capacity resulting from high hydraulic resistance is partly supported by low ratio of the leaf area to stem cross-sectional area (Tyree and Ewers 1991). Although LAI is significantly higher, enrichment of tillers decreases leaf area both per tiller and per stem cross-sectional area of napiergrass, which are as low as those of maize with a higher hydraulic conductance (**Table 1**). This indicates that quantitative water-conducting capacity is not so low when compared with qualitative values. In addition, napiergrass has a high water storage capacity, and an estimated 8% of daily transpiration is supplemented maximally by the water stored in the plant (Nagasuga 2004). This is as high as that of smaller trees (Goldstein *et al.* 1998). Water storage is useful for minimizing temporal imbalances between water supply and demand in the sites of evapo-transpiration (Tyree and Yang 1990; Holbrook 1995; Nardini and Salleo 2000; Meinzer *et al.* 2001). Water storage of napiergrass is mainly conducted in the stem (**Fig. 2**). Napiergrass stems have high water storage (Nagasuga 2004) and flexible hydraulic resistance to changing light intensity and soil water conditions (Nagasuga *et al.* 1998, 2002; Nagasuga and Kubota 2006b). The leaves die easily by water shortage, but the stem persists under severe soil water stress and produces leaves quickly just after the recovery of soil water stress (Nagasuga and Kubota 2006a). Although water absorption and water conductance to the leaves are not so high in napiergrass, water transport

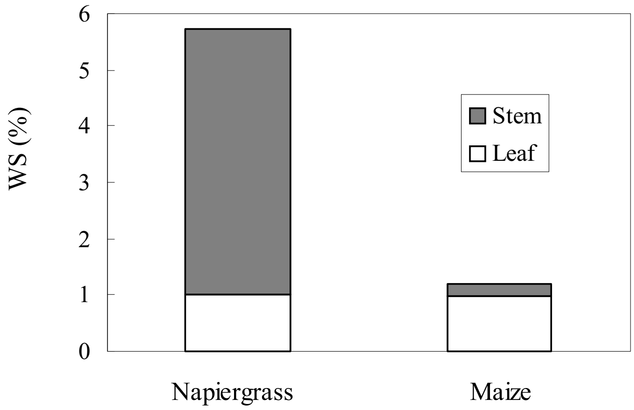

Fig. 2 Water storage in the leaves and stems of napiergrass and maize grown in pots. Water storage is shown as an indicator for the contribution of water storage within a plant to total plant transpiration in the daytime (Daily PTr), and is calculated as Water storage = ΔWC / Daily PTr × 100. ΔWC, water content depression by transpiration during the daytime.

system in the stem has a hydraulically buffering effect composed of high hydraulic resistance and water storage and can avoid critical water shortage under various soil water conditions. Higher biomass productivity of napiergrass is conducted through hydraulic safety, and not through the enrichment of water supply.

CONCLUSION

The main aim of this article is to critically examine the literature on high biomass yielding mechanisms of napiergrass with a focus on biology, biomass productivity and water transport. Although there is little work, the mechanisms of higher biomass productivity and a unique water transport of napiergrass are gradually becoming clear. The former is composed of three factors: (i) a larger leaf area by vigorous tillering, leaf enlargement and enrichment; (ii) an efficient form for light interception by higher plant length, erect leaves and changes in stem inclination and (iii) high capacity and maintenance of leaf photosynthesis. The latter is associated with a regulation of water flow within the plant, tiller enrichment and water storage. The root system is quantitatively poor, however this extends into the soil deeply and widely (Skerman and Riveros 1990). This may contribute to a high biomass yield from the steady acquisition of water and nutrient resources in the soil. The next step will be to examine the hydraulic relationship among plant organs and its contribution to biomass productivity. This would be useful information for understanding the framework of high biomass yield and acclimation of napiergrass to various environmental conditions, and would contribute to the improvement of biomass productivity and wider adaptability of other plants.

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JAPANESE ABSTRACT

ネピアグラスは熱帯アフリカ原産の飼料作物であり、極めて優れたバイオマス生産能力を有することで知られている。ネピアグラスの高バイオマス生産メカニズムを明確にすることが出来れば、その情報は、本植物の栽培管理技術の更なる改善を目指す上で有益であるばかりでなく、育種技術を利用してその他の植物の生産性の改善を図る上でも貴重な基礎的知見となる。ネピアグラスの高バイオマス生産に関与する主な要因として、高い葉面積と生育に伴う群落受光態勢の変化がこれまでに報告されている。また、ネピアグラスは、少ない根量の下でも水ストレスを受けることなく旺盛な生育を示すことから、植物体内での水の輸送機構にも高バイオマス生産を実現させる重要なポイントがあるものと考えられる。本論文では、上記の点に注目してネピアグラスのバイオマス生産特性を解析した研究に焦点を当てる。