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SAFETY AND EFFICIENCY OF XYLEM WATER TRANSPORT IN TWO CASHEW (*Anacardium occidentale* L.) STRAINS AT THE SEEDLING STAGE

*Efisiensi dan Keamanan Transportasi Air Dua Strain Jambu Mete (*Anacardium occidentale L.*) pada Stadia Pembibitan*

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ABSTRACT

As cashew trees are grown by transplanting seedlings, the seedling often suffers from drought damaged due to prolonged dry season. Previous study found that the ability to maintain water transport in xylem related to drought resistant character. To determine whether there was trade-off between the ability to maintain water transport in xylem and an efficiency of water transport, differences in xylem vulnerability to dysfunction, hydraulic conductance, and the relationship to xylem vessel diameter were examined in two cashew strains. The xylem vulnerability to dysfunction was evaluated by the applied pressure which induced 50% loss of stem hydraulic conductivity (P_{50}). The hydraulic conductance on root, stem, and leaf were determined with High Pressure Flow Meter (HPFM). Variations in the P_{50} values were found between A3-1 and Pangkep, whereas the values were 1.75 and 0.50 MPa, respectively. However, since there was no difference in the hydraulic conductance and the vessel diameter, the trade-off between the ability to maintain water transport in xylem and an efficiency of water transport did not occur in cashew. It was suggested that good combination of efficiency and safety of water transport enables A3-1 to strongly uptake soil water either in dry or wet season resulting in good adaptation to drought prone environment, and the P_{50} value would be suitable parameter for evaluating drought tolerance of cashew at the seedling stage.

Key words: cashew strain, vessel, xylem dysfunction, hydraulic conductance, drought

ABSTRAK

Pengembangan jambu mete secara transplanting sering diikuti cekaman kekeringan pada bibit akibat musim kering yang berkepanjangan. Studi awal memperlihatkan bahwa kemampuan xylem mempertahankan fungsi transportasi air merupakan karakter pertahanan penting terhadap cekaman kekeringan. Untuk mengetahui apakah terjadi kompensasi antara kemampuan pertahanan fungsi xylem dan tingkat efisiensi transportasi airnya dilakukan pengujian pada aspek kepekaan fungsi xylem, hantaran hidraulik, dan ukuran vesselnya. Kepekaan fungsi xylem ditentukan dari nilai tekanan udara yang menyebabkan kehilangan 50% *hydraulic conductance* (P_{50}). Nilai *hydraulic conductance* pada akar, batang, dan daun ditentukan dengan menggunakan metode *High Pressure Flow Meter* (HPFM). Hasil pengujian menunjukkan terdapat perbedaan nilai P_{50} diantara dua strain jambu mete yang diuji, yakni secara berturut-turut 1,75 dan 0,50 MPa pada strain A3-1 dan Pangkep. Karena tidak disertai perbedaan pada *hydraulic conductance* dan ukuran vesselnya, maka disimpulkan tidak ditemukan nilai adanya mekanisme kompensasi antara kemampuan pertahanan fungsi xylem dan tingkat efisiensi pengangkutan air. Hal ini memungkinkan A3-1 tetap dapat menyerap air tanah secara cukup, baik pada musim kering maupun musim basah, dan mampu beradaptasi dengan baik di daerah rawan kekeringan. Dan nilai P_{50} dapat dijadikan sebagai parameter representatif untuk evaluasi toleransi bibit jambu mete terhadap cekaman kekeringan.

Kata kunci: strain jambu mete, vessel, fungsi xylem, *hydraulic conductance*, cekaman kekeringan

INTRODUCTION

Since the cashew seedlings transplanted to fields, they have faced with fluctuation of soil-water availability following wet and dry seasons. Considering the availability of soil water, cashew seedlings should maintain water continuity in the xylem to ensure transport of water in the xylem vascular during drought season (PITONO *et al.*, 2002). On the other hand, they must also effectively transport water during the short wet season in order to promote their optimal growth. Exploring this character is crucial for constructing cashew development strategy in drought prone area, especially in choosing plant materials. The previous experiments revealed that there was genotypic variability in the xylem vulnerability to dysfunction among cashew strains (PITONO *et al.*, 2002), however, whether there was a trade-off between the safety and efficiency of water transport in cashew seedlings had been poorly understood.

Considering the Hagen-Poiseulle law, water transport in xylem vessel is directly determined by the pressure gradient and vessel diameter if the xylem vessel continuous from root to leaves; however, the xylem conduits usually consist of many vessels and water should pass between the pair of vessel via pit membranes (SIMPSON, 1982; TYREE *et al*., 1994). Many factors are considered to determine the efficiency of water transport in vascular system such as vessel volume, the permeability of pit membranes to water movement, vessel density, etc. (TYREE *et al*., 1994; ZIMMERMANN, 1983; MAYR *et al*., 2003). On the other hand, the xylem vulnerability to dysfunction in plants is directly determined by air permeability in vessel wall and pit membranes and indirectly related to vessel size, and this mechanism is called cavitation (TYREE and DIXON, 1986; SPERRY and TYREE, 1988, 1990; TYREE *et al*., 1994). Moreover, drought-stress promotes air entry into water-filled xylem conduit through pit membranes and induces xylem dysfunction in water transport (SPERRY and TYREE, 1988; SCHULTZ and MATTHEWS, 1988; TYREE and SPERRY, 1989). Excessive cavitation is unfavorable to plant function as it decreases the hydraulic conductance of the xylem and threatens the supply of water to the leaves. If plant is fail to prevent excess cavitation, it would progressively spread to fill the entire xylem and the plant could die of dehydration (MCDOWELL *et al*., 2008). Moreover, the vulnerability of xylem to dysfunction depends on the balance between embolism formation and its possible repair (LOVISOLO *et al*., 2008; JOHNSON *et al*., 2009; DOMEC *et al*., 2006).

The trade-off between efficiency of water transport and xylem vulnerability might occur only if the increase in vessel volume enhance the air permeability in vessel wall and pit membranes (TYREE *et al*., 1994). This phenomenon was found in conifer, in which the overall high hydraulic safety of conifer xylem and its low efficiency indicate a trade-off between these hydraulic aspects (TYREE *et al.*, 1994). On the other hand, another study on a leader shoot xylem of Norway spruce found there was no trade-off safety and efficiency of hydraulic properties (MAYR *et al*., 2003). So that, the variances of hydraulic properties are approved among plant species and it is not clearly yet understood in cashew.

In this study, the experiment was conducted to evaluate the relationship between xylem vulnerability to dysfunction and plant hydraulic conductance between two cashew strains, A3-1 and Pangkep, in order to clarify whether there was trade-off between the safety and efficiency of their water transport at the seedling stage.

MATERIAL AND METHODS

Experimental Design

This experiment was carried out in a vinyl house of field station of Department of Agriculture, Okayama University, Japan from June to September 2004. The study was performed on two cashew strains A3-1 and Pangkep, in which the previous study (PITONO *et al*., 2002) approved that A3-1 was more resistant in xylem to dysfunction than Pangkep. The experimental design was comprised of sixteen replicates per strain in a completely randomized design, with five plants per replicate.

Plant Materials

Initially, the seeds were immersed in 28^{o}C water for 24 hours, and then incubated for a week on the moist sand in a growing chamber in which air temperature was 29^{o}C during day and night periods. When the radicle emerged, the germinated seeds were planted to 4.3 l pots in a vinyl house. The pots were each filled with approximately 5.5 kg field soil. Then synthetic compound fertilizer ($N:P_2O_5:K_2O$ = 10:10:10) was incorporated into the soil at the rate of 16.5 g per pot. The plants were well watered throughout the experiment. All primary branches were removed at the branch base and only the main stems were grown. The plant of each strain similar in appearances were selected a week before the hydraulic measurements. The stem length was determined from the soil surface to the bud tip of main stem, and the stem diameter with bark was measured at 2 cm above the soil surface.

Xylem Vulnerability to Dysfunction

The xylem vulnerability to dysfunction was determined in the selected plants at 80 days after planting (DAP) as previously described (PITONO *et al.*, 2002). Briefly, the stem was cut 2 cm above the soil surface, and the stem segment approximately 18 cm in length was inserted into a cylindrical pressure chamber with the ends of the segment protruded from both ends of chamber. The distal end of segment was flushed with water at the pressure of 0.2 MPa for 10 minutes. Then an initial conductivity (k_m) was determined by inducing water flow through the segment by applying a gravitational pressure of 5.39 kPa to one end and the water efflux from the other end was measured. The flow rate was measured every minute with a digital balance (Sartorius BP221S, with resolution of 0.1 mg) and if the variations in three successive measurements were less than 3%, the values was recorded. Hydraulic conductivity was defined as the mass flow rate of the water through the segment (kg s^{-1}) divided by the pressure gradient (MPa m^{-1}). After determination of k_m, the air pressure in the chamber was raised to 0.25 MPa for 10 minutes, and then the chamber pressure was reduced to zero and the conductivity of the segment was measured again. This process was conducted repeatedly by applying gradually higher air pressures (by 0.25 MPa increment) until less than 5% of the k_m remained. The percent loss of conductivity (PLC) was calculated as follow :

$$PLC = (k_m - k_i)/k_m x100\%,$$

where k_i was conductivity after i^{th} pressurization.

Then the values of applied pressure which induced 50% loss of stem hydraulic conductivity (P_{50}) were determined from the graphic of relationship between applied pressure (P_x) and percentage of loss of conductivity (PLC).

Hydraulic Conductance

The hydraulic conductance in the root, shoot, leaf, and whole plant were measured on the selected plants for each strain using a High Pressure Flow Meter (HPFM) as described by TSUDA and TYREE (1997; 2000). The stem was cut about 2 cm above the soil surface and the shoot was immediately immersed in the water. The root stump was connected to the HPFM with a water-tight seal. The root conductance was determined from the values of water flow into root (F) and applied pressure (P) that measured every 3 seconds while the applied pressure gradually increased at the constant rate of 3-7 kPa s^{-1}. The root conductance (k_{root}) was calculated as the slope of the plot of F versus P: k_{root} = dF/dP. The stem base was connected to HPFM and then perfused with water at a pressure of c.a. 0.5 MPa for up to 15 minutes until the flow rate of shoot conductance became stable. The shoot conductance (k_{shoot}) was measured by a transient measurement. The stem conductance (k_{stem}) was measured in similar way after removing leaves. Plant conductance (k_{plant}) and leaf conductance (k_{leaf}) were calculated as follows:

$$k_{plant} = 1/k_{shoot} + 1/k_{root}$$
$$k_{leaf} = 1/k_{shoot} - 1/k_{stem}$$

Vessel Diameter

Vessel diameter was determined on the stem segments used in the xylem vulnerability to dysfunction measurements. A transverse section at the center of each segment was mounted on a microscope slide. A photo image of the xylem vessels was captured on the light microscope (10x), which was equipped with a digital camera (Fujix digital camera HC-300i) that linked to PC-based Adobe Photoshop 5.0. The transectional area of individual vessels was determined along several xylem arrays at two opposite radial sectors on PC-based Sion Image. The vessel diameter (d) was calculated as follow:

$d = 2\sqrt{(A/\pi)}$, where A is the vessel area.

Number of Samples and Statistics

The xylem vulnerability to dysfunction and vessel diameter measurements were done on the same thirty stem samples of each strain (A3-1 and Pangkep). However, the hydraulic conductance (k_{plant}, k_{shoot}, k_{leaf}, and k_{root}), stem length, stem diameter, and dry biomass were determined on the same of the other thirty samples of each strain. Values are given as mean ± standard error. Differences were tested with Student's t-test (5% probability level) after checking for normal distribution and variance of the data.

RESULTS

The shoot dry mass in Pangkep strain was slightly higher than in A3-1 one, however, the significant difference was not detected (Figure 1). The leaf growth was relatively similar between the two strains without significant differences in the leaf dry weight. The difference in shoot dry weight was clearly detected in stem only where the stem dry weight was higher in Pangkep than in A3-1. The large growth of stem in Pangkep was also indicated by the higher values in length and diameter of stem compared to A3-1 (Figure 2).

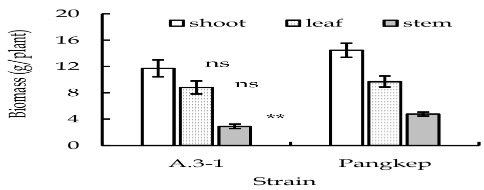

Figure 1. Dry biomass of shoot, leaf, and stem in A3-1 and Pangkep. Values are means ± se of 30 plants. ns and ** indicate no significant and significant differences at P = 0.01

*Gambar 1. Biomas kering tajuk, daun, dan batang pada strain A3-1 dan Pangkep. Nilai adalah rata-rata ± se dari 30 tanaman. Tanda ns dan ** berturut-turut menunjukkan tidak berbeda dan berbeda nyata pada P= 0,01*

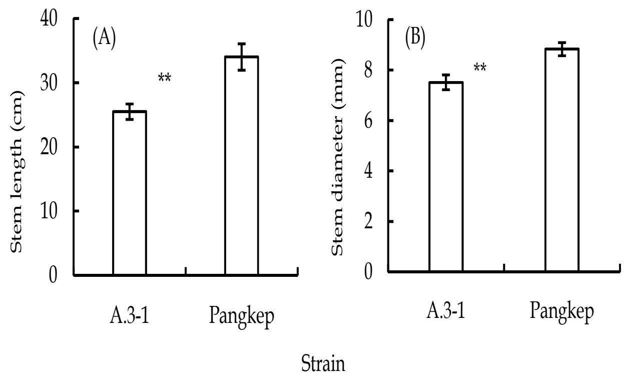

Figure 2. Stem length (A) and stem diameter (B) in strain A3-1 and Pangkep. Values are means ± se of 30 plants ** indicates significant difference at P = 0.01

*Gambar 2. Panjang batang (A) dan diameter batang (B) pada strain A3-1 dan Pangkep. Nilai adalah rata-rata ± se dari 30 tanaman. Tanda ** menunjukkan berbeda nyata pada P= 0,01*

The xylem vulnerability to dysfunction was evaluated using the increase in percentage of loss hydraulic conductivity (PLC) when the positive pressure (P_x) was applied (Figure 3). The PLC increased faster in Pangkep than in A3-1, and their PLC values were significantly different from 0.5 MPa to 1.75 MPa. The xylem was totally dysfunctional with PLC near 100% at 2.0 MPa. The applied pressure that induced 50% loss in conductivity (P_{50}) was significantly different between the strains (Figure 4).

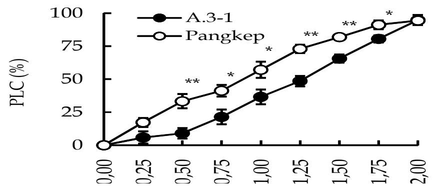

Figure 3. Relationship between applied pressure (P_x) and percent loss of conductivity (PLC) in A3-1 and Pangkep. Values are means ± se of 30 plants. The differences between the strains are significant, indicated by * and ** for P = 0.05 and P = 0.01, respectively

*Gambar 3. Hubungan antara aplikasi tekanan udara (P_x) dan Percent Lost of Conductivity (PLC) pada strain A3-1 dan Pangkep. Nilai adalah rata-rata ± se dari 30 tanaman. Tanda * dan ** berturut-turut menunjukkan berbeda nyata pada P= 0,05 dan P= 0,01*

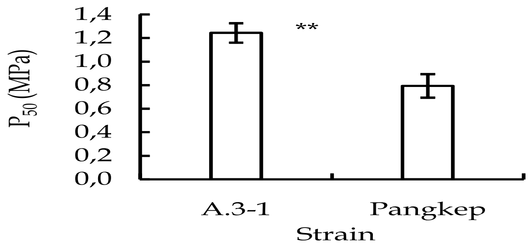

Figure 4. Applied pressure which induced PLC 50% (P_{50}) in strain A3-1 and Pangkep. Values are means + se of 30 plants. ** indicates significant difference at P = 0.01

*Gambar 4. Aplikasi tekanan udara yang menyebabkan PLC 50% (P_{50}) pada strain A3-1 dan Pangkep. Nilai adalah rata-rata ± se dari 30 tanaman. Tanda ** menunjukkan berbeda nyata pada P= 0,01*

The P_{50} values were significantly higher in A3-1 strain than in Pangkep one indicating that A3-1 was less vulnerable in xylem dysfunction. There were no significant differences in the entire hydraulic conductances between the two strains (Table 1). The hydraulic conductance value in the root (k_{root}) was the lowest one with mean values of 20.08 x 10^{-5} kg $MPa^{-1}s^{-1}m^{-2}$ and 14.83 x 10^{-5} kg $MPa^{-1}s^{-1}m^{-2}$ for A3-1 and Pangkep strains, respectively. The hydraulic conductance in the stem (k_{stem}) was the highest and about ten times of the k_{root}.

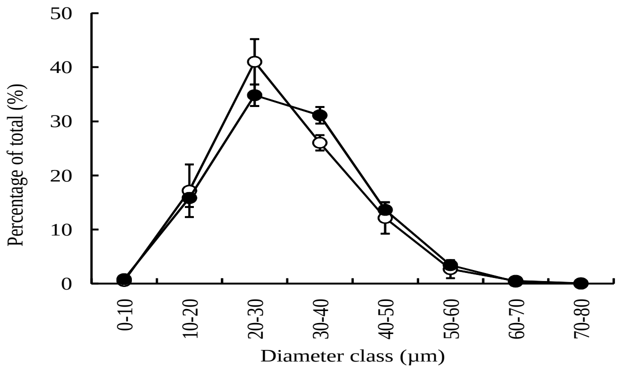

Figure 5. Distribution on of vessel diameter of each diameter class in A3-1 (open symbol) and Pangkep (closed symbol). Values are means + se of 30 plants

Gambar 5. Distribusi diameter vesel pada setiap kelas diameter pada strain A3-1 (simbul terbuka) dan Pangkep (simbul tertutup). Nilai adalah rata-rata ± se dari 30 tanaman

Tabel 1. Hydraulic conductance in root (K_{root}), shoot (K_{shoot}), whole plant (K_{plant}), stem (K_{stem}), and leaf (K_{leaf}) in A3-1 and Pangkep strains for 4 months

Tabel 1. Hantaran hidraulik pada akar (K_{root}), tajuk (K_{shoot}), total tanaman (K_{plant}), batang (K_{stem}), dan daun (K_{leaf}) pada stain A3-1 dan Pangkep pada umur 4 bulan setelah tanam

	Conductance (kg MPa^{-1} s^{-1} m^{-2}) x 10^5		Difference
	A3-1 strain	Pangkep strain	
K_{root}	20.08 ± 2.81	14.83 ± 4.51	Ns
K_{shoot}	27.66 ± 2.12	24.58 ± 3.15	Ns
K_{plant}	11.46 ± 1.26	8.65 ± 1.98	Ns
K_{stem}	125.94 ± 11.06	144.16 ± 13.96	Ns
K_{leaf}	37.15 ± 4.08	31.25 ± 5.21	Ns

Note : Values are means ± se of 30 plants, and ns indicated no significant difference (P<0.05)

Keterangan: Nilai adalah rata-rata ± se dari 30 tanaman, dan tanda Ns menunjukkan tidak berbeda nyata pada P= 0,05

Distribution of vessel diameter in both strains was shown in Figure. 5. The maximum vessel diameter occurred at 70-80 µm in both strains. Mode of vessel distribution in both strains obtained at the same diameter class of 20-30 µm, without significant differences in vessel diameter between them.

DISCUSSIONS

This study analyzed relationship between safety and efficiency xylem water transport in cashew seedling. Safe xylem transport means the xylem has a sufficient protection against conduit blockage, primarily from cavitation and embolism, in which the plants enable to transport water from root to leaf part under shortage soil water conditions. Several evidences approve that a drought-stress causes air entry into water-filled xylem conduit through pit membranes (cavitation) and induces xylem dysfunction in water transport (SPERRY and TYREE, 1988; SCHULTZ and MATTHEWS, 1988; TYREE and SPERRY, 1989). So that, plant's ability to maintain water continuity in xylem could be estimated by xylem tolerance to dysfunction, and tolerant xylem means that more negative water potential is required to induce dysfunction. On the other hand, efficient xylem transport means low flow resistance for a given investment in vascular tissues. And it has long been considered that there is a structural trade-off between these two traits, that efficient xylem comes to be less safety on water transport (TYREE *et al*., 1994; MARTINEZ-VILALTA *et al*., 2002), however, it had not been clarified yet in cashew.

This study evaluated the existing trade-off between efficiency and safety of xylem water transport that corresponded to the values of entire hydraulic conductance and xylem vulnerability to dysfunction in two cashew strains, A3-1 and Pangkep. The results showed that there was a significant difference in xylem vulnerability to dysfunction between the strains, indicated by the values differences of applied pressure which induced 50% loss of stem hydraulic conductivity (P_{50}), in which P_{50} value of A3-1 was significantly higher than that of Pangkep, and it indicated that A3-1 was more resistant to xylem dysfunction than Pangkep strain (Figure. 3 and Figure. 4). Moreover, these results supported the previous evidence that there was genotypic variation in xylem vulnerability in cashew (PITONO *et al*., 2002). Although the xylem vulnerability largely varied between the both strains, there were no significant differences in the whole of hydraulic conductances (Table 1), suggesting that there was clearly no trade-off between the efficiency and safety of water transport in the cashew strains. And these results added new evidence of no trade-off safety and efficiency on the xylem hydraulic properties on the woody plant species, as it previously approved in the leader shoots of Norway *spruce* (MAYR *et al*., 2003) and in woody *Rosaceae* (WHELLER *et al*., 2005)

The efficiency of water transport is mainly determined by the vessel volume, whereas the xylem vulnerability is not directly related to the vessel size but to the air permeability in vessel wall and pit membrane (TYREE and DIXON, 1986; SPERRY and TYREE, 1988, 1990; TYREE and SPERRY, 1989; TYREE *et al*., 1994; SPERRY and SAILENDRA, 1994) and associated with inter-vessel wall thickness in case of *Prunus* genotypes (COCHARD *et al*., 2008). These results showed that even the vessel diameter was similar between the both strains, the xylem of A3-1 was more resistant to dysfunction than Pangkep, suggesting that characteristic of vessel wall and pit membrane was more permeable in Pangkep than in A3-1. Another study in woody *Rosaceae* showed that the total area of pits in a vessel rather than individual pit structure that is most important in setting a safety and efficiency of water transport in xylem vessel (WHELLER *et al*., 2005).

This study was focused to observe xylem vulnerability on the stem tissue for evaluating the safety and efficiency of the water transport in cashew seedling with considering the stem xylem properties was most crucial for water transportation in cashew seedling. In addition, there are variations on the characteristic of xylem vulnerability among the part of plant tissues. Several previous studies have been able to show that petioles and leaves from various plant species were more vulnerable to xylem dysfunction due to xylem cavitation than stems (SCULTZ, 2003; CHOAT *et al*., 2010; ALSINA *et al*., 2007). So that, it remains challenge to explore more architecture properties of xylem tissues in cashew.

The results approved that a good combination between efficiency and safety of xylem water transport was found in A3-1 strain. Since several evidences show that there are large variations in xylem tolerance among plant species (TYREE *et al.*, 1994) and within species (NEUFELD *et al*., 1992; WILLIGEN and PAMMENTER, 1997), and plants with tolerant xylem to dysfunction tend to adapt well to drought environments (SPERRY and POCKMAN, 1993; WILLIGEN and PAMMENTER, 1997). It implies that A3-1 strain strongly enables to uptake soil water either in dry or wet season, resulting in good adaptation to drought prone environment. Also, the relatively low shoot growth might be more advantage for A3-1 strain to achieve the minimum required water for maintenance of normal metabolic activity under shortage of soil water. However, we should be more careful in controlling a micro climate at the cashew nursery. Previous experiment (PITONO *et al*., 2004) indicated that shading nursery induced increase of spindly growth and vessel diameter that corresponded to decrease in the safe xylem water transport. More proportion of carbohydrate allocation to develop a root tissue might be another strategy of cashew seedling to improve its capacity in exploring much soil water and properly be evaluated in further study.

CONCLUSIONS

There was genotypic difference in xylem vulnerability to dysfunction between the strains A3-1 and Pangkep, while A3-1 showed more resistant to xylem dysfunction than Pangkep, even the whole hydraulic conductance was similar between them. These results suggested that no trade-off between safety and efficiency of xylem water transport in the cashew seedlings, and it enables A3-1 to strongly uptake soil water either in dry or wet season, resulting in good adaptation to drought prone environment.

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