Chemical Attributes of *Gigantochloa scortechinii* Bamboo Rhizome in Relation with Hydraulic Conductance

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Chemical changes during the maturation period of bamboo are believed to affect its conductance ability. However, prior studies on the bamboo's chemical changes were inconclusive in implying that the maturation period affects the rhizome's conductance ability. The rhizome's conductivity is crucial to rapidly grow a new bamboo sprout. The aim of this study was to determine the variation of chemical attributes among study sites during the maturation period of bamboo rhizome (*Gigantochloa scortechinii*), and investigate the possibility of a relationship between the chemical attributes and hydraulic conductance. Destructive sampling was conducted using the selective random sampling method on four consecutive rhizomes. The chemical attributes were determined according to the TAPPI standard methods, except for the holocellulose. The results indicated that the ash content, alcohol-acetone solubility, and holocellulose were significantly different ($p < 0.01$) among the three study sites. In addition, the results indicated that decreasing ash content with age could not be used as a determinant factor for the decrease in the hydraulic conductance. However, increasing the hot water solubility, alcohol-acetone solubility, lignin, and holocellulose with the rhizome age were suggested to be related to decreasing the rhizome's hydraulic conductance.

Keywords: Age-related; Bamboo; Rhizome; Chemical Attributes; Hydraulic Conductance

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INTRODUCTION

Bamboo has no secondary growth to increase its size in areas such as girth parameter; however, new bamboo culms produced from a vegetative reproduction system are interconnected with each other. Their conductivity may be particularly sectorial to consecutive rhizome branches. Previous studies explain that the translocation of nutrients, photosynthates, and water takes place from a mature bamboo to a new sprout (Ding *et al*. 1995; Kai *et al*. 2012; Umemura and Takenaka 2014). Zhao *et al*. (2017) used a modified version of the thermal dissipation probe (TDP) method to indicate a strong translocation function of the *Phyllostachys pubescens* rhizome. They found that the water used by new sprouts includes water self-absorbed through the soil, and more than 20% of the water used during the summer was transferred from older culms through its connected rhizome. The contribution of five consecutive culms that connected underground on water transfer and water use of *Bambusa vulgaris* and *Gigantochloa apus* bamboo species was also demonstrated by applying the deuterium tracing method; however, the water transfer between culms could be influenced by the culm's age (Mei *et al.* 2019).

In contrast with woody plants, a nocturnal-based hydraulic strategy was found in some bamboo species, such as *Guadua angustifolia*, *Chusquea ramosissima*, *Merostachys* *claussenii*, and *Sinarundinaria nitida*, and was induced by positive root pressure, thus agreeing with several instances of nocturnal hydraulic events (NHEs) on several grasses (Tyree *et al*. 1986; Cochard *et al*. 1994; Stiller *et al*. 2003; Marine 2009; Saha *et al*. 2009; Yang *et al*. 2012). Positive root pressure during the NHE was high enough to refill the embolism and was suggested to be responsible as the mechanism for cavitation repair. The NHE could also be an effective mechanism to recharge the culm water storage for replacing transpirational water losses on a daily basis (Yang *et al*. 2015). However, the hydraulic event, more specifically the determining factors for hydraulic conductance and resistance at different ages of individual bamboo rhizomes, has been studied much less.

However, the structural development and chemical changes, such as lignification due to aging, occur on individual bamboo culms. The structural development and chemical changes are known to affect the functional efficiency of conductance elements, which must function for several years without a secondary meristem, like woody plant species (Grosser and Liese 1971; Chen *et al.* 1985; Itoh 1990; Liese 1998; Hisham *et al*. 2012; Xu *et al*. 2014; Liese and Tang 2015; Wang *et al*. 2016). Several studies showed that plant hydraulics and the hydraulic conductance can limit the entire plant's growth efficiency and physiological activities, such as photosynthesis, respiration, transpiration, plant water potential, and carbon assimilation (Hubbard *et. al*. 2001; Phillips *et al*. 2003; Martínez-Vilalta and Garcia-Forner 2017).

The soil-plant-atmosphere continuum model and the cohesion-tension theory explain the consistent relationship between the plant's hydraulic conductance with leaf water potential, soil water potential, transpiration, and plant hydraulics resistance, thus explaining that a plant with a high plant hydraulic conductance has a low plant hydraulic resistance (Tyree and Zimmermann 2002; Tyree 2003). Plant size, xylem dysfunction, growth condition, and the genetics within and between species were among the factors that influence the plant hydraulic conductance (Tyree and Sperry 1989; Tyree *et al*. 1991, 1998; Sperry and Pockman 1993; Yang and Tyree 1993; Machado and Tyree 1994; Meinzer *et al*. 1995; Domec and Gartner 2002; Tyree and Zimmermann 2002; Tyree 2003; Brodribb and Cochard 2009).

This study assumed that the culm hydraulic resistance (*i.e.*, reciprocal of culm hydraulic conductance) that increases during aging also happens on the belowground part (rhizome) due to the aboveground parts (culms) being interconnected by the rhizomes, which enables transportation from a mature bamboo to a new sprout. In addition, this study attempted to determine the relation of plant hydraulic conductance to the chemical changes regarding several consecutive rhizomes that represented the different rhizome ages of the bamboo species *Gigantochloa scortechinii*.

EXPERIMENTAL

Materials

Sampling

This study was conducted at three different locations of Peninsular Malaysia, namely Amanjaya Forest Reserve (Hulu Perak, Perak, Malaysia), Kenaboi Forest Reserve (Kenaboi, Negeri Sembilan, Malaysia), and Ayer Hitam Forest Reserve (Puchong, Selangor, Malaysia). The destructive sampling of four consecutive rhizomes of the bamboo species *G. scortechinii* was conducted using a selective random sampling method from three healthy clumps for three replicates. The four consecutive rhizomes were represented as four different rhizome ages: a) new sprout, b) young, c) premature, and d) mature rhizome. The age estimation was based on the characters of culms (Banik 1993) and the number of rhizomes in a consecutive rhizome from the new sprout (Liese 1998). Only complete sets (four consecutive rhizomes) of a sectorial rhizome with complete plant parts (above and below ground) were chosen.

Methods

Determination of chemical attributes

The chemical attributes consisted of the determination of ash content, cold water solubility, hot water solubility, alcohol-acetone solubility, lignin, holocellulose, and alpha-cellulose. The ash content analysis was conducted according to the standard American Society for Testing and Materials (ASTM) E1755-95 (2001). Determining the cold and hot water solubility was conducted according to the Technical Association of the Pulp and Paper Industry (TAPPI) T207 cm-99 standard (1999). Determining the alcohol-acetone solubility was conducted according to the TAPPI T204 cm-97 standard (2007). Determining the lignin content was completed according to the TAPPI T222 om-02 standard (2006). Determining the holocellulose was conducted according to Wise *et al*. (1946). Determining the alpha-cellulose was conducted according to the TAPPI T203 cm-74 standard (1999).

Determination of hydraulic conductance

Determining the hydraulic conductance was conducted *in-situ* using a high-pressure flow meter (HPFM). Water was placed under pressure by compressed air that was controlled with a pressure regulator into the culm base with rapidly changing the delivery pressure, P (MPa), simultaneously measuring water flow, F (kg s^{-1}), and hence hydraulic conductance was estimated from the slope of the F *versus* P plot. The untested culms and belowground parts were avoided when making a cut or any major injuries as to reduce the degree of disturbance of the interconnected rhizome system.

Statistical analysis

The data were analyzed using a factorial analysis of variance (ANOVA). The relationship between the chemical attributes and the different study sites, rhizome ages, and the hydraulic conductance was analyzed using Bivariate (Pearson) Correlation and then analyzed further with regression analysis. The statistical analysis was conducted using IBM SPSS Statistics software version 21.0 (Armonk, NY, USA).

RESULTS AND DISCUSSION

The chemical attributes included the ash content, cold water solubility, hot water solubility, alcohol-acetone solubility, lignin, holocellulose, and alpha-cellulose. The attributes are discussed separately for ease and convenience. The results of the ANOVA and Duncan's multiple range tests are shown in Tables 1 and 2. The correlation coefficient analysis of the chemical attributes for the study sites, ages, and hydraulic conductance are shown in Table 3.

Table 1. Results of ANOVA for the Chemical Attributes

		F-Values and Statistical Significance							
S.O.V	DF	Ash Content	Cold Water Sol.	Hot Water Sol.	Alcohol-acetone Sol.	Lignin	Holo-cellulose	Alpha-cellulose	Hydraulic Cond.
Site	2	78.22 **	0.94 ns	2.17 ns	7.97 **	0.24 ns	23.62 **	0.04 ns	22431.88**
Age	3	314.54 **	1.63 ns	10.50 **	747.32 **	231.44 **	8.80 **	0.10 ns	158174.13**
Site × Age	6	3.24 *	0.82 ns	1.03 ns	2.26 ns	5.10 **	0.60 ns	0.02 ns	6162.85**

Note: S.O.V = Source of Variation, Sol. = Solubility, Cond. = Conductance, ns = not significant at p < 0.05, * = significant at p < 0.05, and ** = highly significant at p < 0.01; DF = degrees of freedom

Table 2. Results of Duncan's Multiple Range Test for the Effects of Study Site and Age on the Chemical Attributes

	Site *			Age *			
Attributes	Amanjaya FR	Kenaboi FR	Ayer Hitam FR	New Sprout	Young Rhizome	Premature Rhizome	Mature Rhizome
Ash content	2.54 ± 0.18a	2.03 ± 0.16c	2.33 ± 0.13b	3.14 ± 0.09a	2.27 ± 0.08b	1.90 ± 0.08c	1.89 ± 0.07c
Cold water solubility	11.39 ± 0.30a	11.72 ± 0.21a	11.33 ± 0.11a	11.33 ± 0.38a	11.12 ± 0.14a	11.64 ± 0.19a	11.84 ± 0.20a
Hot water solubility	14.01 ± 0.33a	13.82 ± 0.23a	13.49 ± 0.14a	13.05 ± 0.19b	13.44 ± 0.12b	14.05 ± 0.23a	14.55 ± 0.28a
Alcohol-acetone solubility	4.36 ± 0.31a	4.23 ± 0.33b	4.14 ± 0.31b	2.92 ± 0.04d	3.67 ± 0.04c	4.70 ± 0.08b	5.67 ± 0.06a
Lignin	24.32 ± 1.22a	24.06 ± 1.56a	24.15 ± 0.98a	17.97 ± 0.56d	23.40 ± 0.29c	26.45 ± 0.23b	28.88 ± 0.45a
Holocellulose	69.37 ± 0.28a	67.21 ± 0.32c	67.97 ± 0.27b	67.29 ± 0.40c	67.85 ± 0.46bc	68.52 ± 0.33ab	69.06 ± 0.39a
Alpha-cellulose	47.46 ± 0.19a	47.41 ± 0.11a	47.39 ± 0.11a	47.50 ± 0.20a	47.44 ± 0.15a	47.37 ± 0.15a	47.37 ± 0.16a
Hydraulic Conductance	3.07 ± 0.38c	3.39 ± 0.20b	3.80 ± 0.30a	4.80 ± 0.14a	3.68 ± 0.07b	3.07 ± 0.10c	2.14 ± 0.21d

* Mean values with the same letter in the same row for each factor are not significantly different at p < 0.05; ± = standard error; FR = Forest Reserve

Ash Content

Regardless of the study site and age, the ash content of the *G. scortechinii* rhizome ranged from 1.54% to 3.67%, which was within the range of the ash content of bamboo culms of the same species (1.10% to 4.70%) (Abd-Latif 1996; Hisham *et al*. 2006; Wahab *et al*. 2013).

The range of ash content of both the rhizome (present study) and culms (previous study) is from 1.26% to 4.20% among other bamboo species (Abd-Latif 1996; Li 2004; Li *et al*. 2007; Scurlock *et al*. 2000; Wahab *et al*. 2013; Wang *et al*. 2016). Table 2 shows that the ash content in the *G. scortechinii* rhizome was highly significantly different ($p < 0.01$) with the study site. A higher ash content was found in Amanjaya FR (2.54%), followed by the rhizome in Ayer Hitam FR (2.33%) and Kenaboi FR (2.03%). However, the results in Table 3 indicate that no significant relationship was found between the ash content and the study site ($r = -0.146$).

Table 3. Correlation Coefficient of Chemical Attributes with Study Site, Rhizome Age, and Hydraulic Conductance

Attributes	Site	Age	Hydraulic Conductance
Ash content	-0.146 ns	-0.823 **	0.747 **
Cold water solubility	-0.033 ns	0.307 ns	-0.241 ns
Hot water solubility	-0.253 ns	0.688 **	-0.706 **
Alcohol-acetone solubility	-0.083 ns	0.986 **	-0.914 **
Lignin	-0.0160 ns	0.945 **	-0.857 **
Holocellulose	-0.436 **	0.510 **	-0.567 **
Alpha-cellulose	-0.058 ns	-0.106 ns	0.077 ns

Note: ns = not significant at p < 0.05, * = significant at p < 0.05, and ** = highly significant at p < 0.01

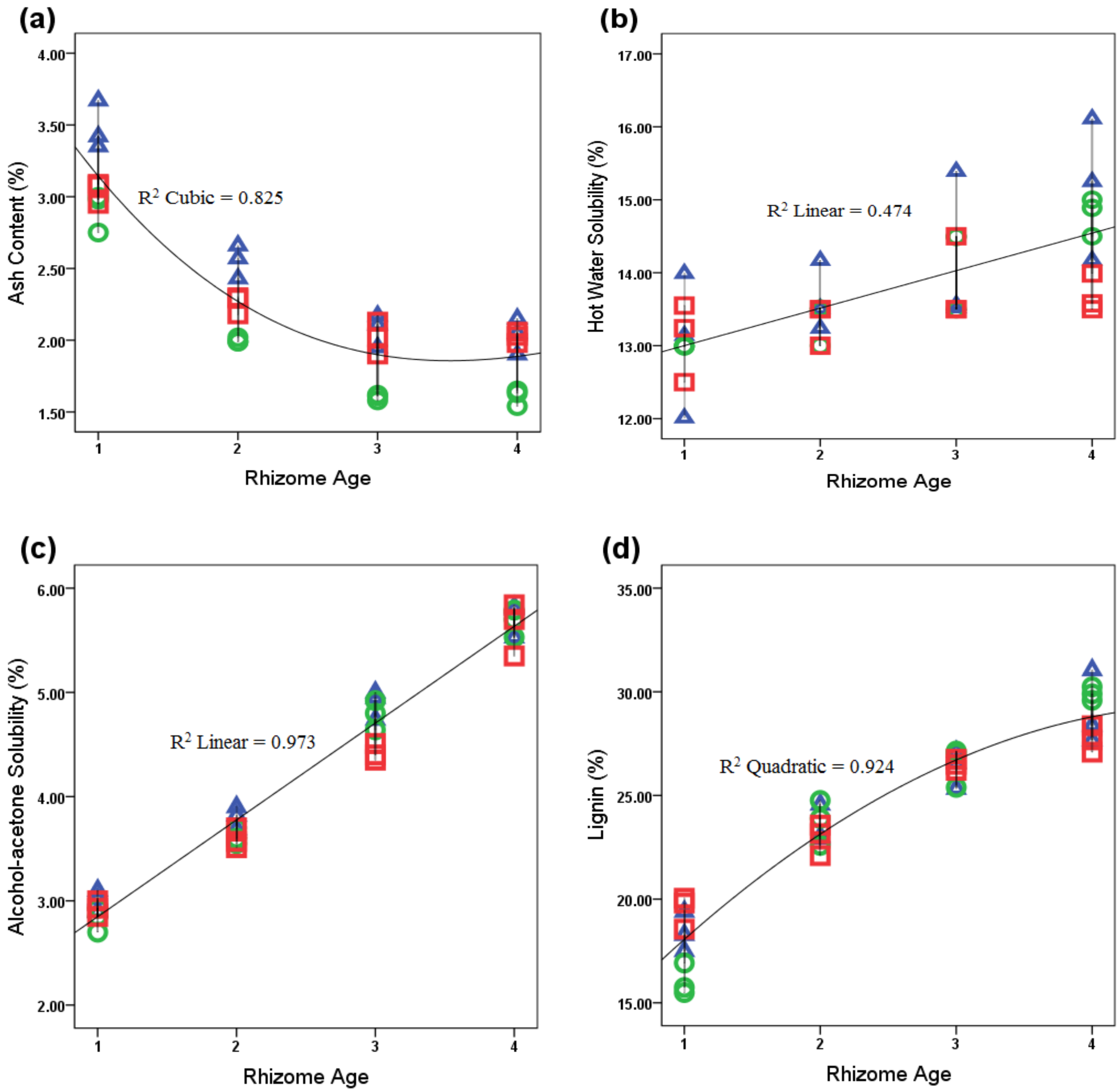
In addition, the ash content was highly significantly different ($p < 0.01$) with the rhizome age. A higher ash content was found in the youngest rhizome, while the lowest ash content was found in the oldest rhizome. Table 2 shows that the ash content was significantly different between the rhizomes at all four ages, but no difference was found between the premature (1.90%) and mature (1.89%) rhizomes. The ash content was also different ($p < 0.05$) with the interaction between the study site and the age.

A strong ($p < 0.01$) negative relationship ($r = -0.823$) was found between the ash content and the rhizome age. Table 3 shows that an increase in the rhizome age resulted in the ash content decreasing. However, the ash content significantly decreased from the new sprout to the premature rhizome. Later, it had fewer changes and was more constant (Fig. 1a).

These could be related to metabolically active vascular tissues that translocate the inorganic minerals (*e.g.*, boron, calcium, potassium, and magnesium) to the growing organ (Li 2004; Li *et al*. 2007; Umemura and Takenaka 2014). A similar trend of the ash content was found in a previous study on the same species of bamboo culms and in bamboo culms of other bamboo species such as *Dendrocalamus brandisii*, *Phyllostachys pubescens*, *Phyllostachys bambusoides*, *Phyllostachys bissetti*, and *Phyllostachys nigra* (Abd-Latif 1996; Scurlock *et al*. 2000; Li *et al*. 2007; Wang *et al*. 2016).

Cold and Hot Water Solubility

Cold water solubility of *G. scortechinii*'s rhizome ranged from 9.53% to 13.01%. It was not significantly different with the study site, rhizome age, and the interaction between the study site and the rhizome age (Table 1). However, the hot water solubility was relatively higher than that of the culms of the same species (4.00% to 7.00%) (Abd-Latif 1996).



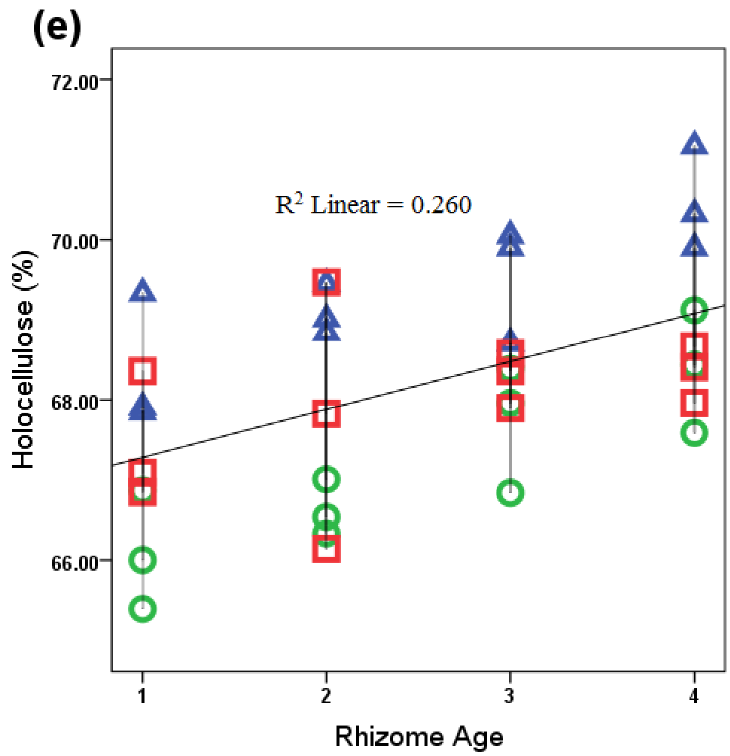


Fig. 1. Chemical attributes: (a) ash content, (b) hot water solubility, (c) alcohol-acetone solubility, (d) lignin, and (e) holocellulose; changes in rhizome from age-1 (new sprout) to Age-4 (mature rhizome). Different shapes indicate variation of the study site: triangle (Amanjaya FR), circle (Kenaboi FR), and square (Ayer Hitam FR)

These could be related to the difference in the microstructure and its arrangement between the bamboo rhizome and culms, such as increased ground tissue parenchyma (62%) and conducting element (18%) and a lower fiber (20%) composition in the rhizome compared with that of bamboo culms (Liese and Tang 2015). Both cold and hot water solubility are substances that dissolve in water and the extractives content, such as tannin, starch, coloring matter, and phenolic compounds (Browning 1963; Janes 1969; Li 2004).

The hot water solubility was not significantly different with the study site; however, it did significantly increase from the younger- to older-aged rhizome (Table 2). Abd-Latif (1996) shows how a relatively small variation of hot water solubility among the different study sites implies that the stability of the chemical component was not significantly influenced by environmental factors. A strong ($p < 0.01$) positive relationship ($R = 0.688$) with a moderate coefficient of determination ($R^2 = 0.474$) indicated that the hot water solubility increased because of the increased rhizome age. Li (2004) shows that the hot water solubility increased from the young (5.35%) to mature (6.41%) bamboo culms (*P. pubescens*) and later gradually decreased. However, this contradicts the finding by Abd-Latif (1996) on *G. scortechinii* culms that hot water solubility had a significantly ($p < 0.05$) moderate negative relationship ($R = -0.36$) with the culms' ages, while an insignificant ($R = 0.05$) increase with age was found with *B. vulgaris* culms.

Alcohol-acetone Solubility

Regardless of the study site and rhizome age, the alcohol-acetone solubility ranged from 2.70% to 5.84%, which was comparable with the bamboo culms of the same species

(2.70% to 5.80%) in previous studies (Abd-Latif 1996; Hisham *et al*. 2006). The alcohol-acetone-soluble portion of bamboo contains substances that include general alcohol extractives, such as wax, fat, resin, gum, and some water-soluble extractives (Li 2004). The results indicate that alcohol-acetone solubility was significantly ($p < 0.01$) different with the study site and rhizome age, but not significantly different with the interaction between the study site and rhizome age (Table 1). Regardless of the rhizome age, a higher alcohol-acetone solubility (4.36%) was found in Amanjaya FR while the lowest (4.14%) was found in Ayer Hitam FR. Table 2 shows that the alcohol-acetone solubility in Amanjaya FR was significantly different from that in Kenaboi FR, and Ayer Hitam FR. The alcohol-acetone solubility in Kenaboi FR and Ayer Hitam FR were not significantly different and grouped in same rank according to Duncan's multiple range test.

The correlation coefficient analysis indicated an insignificant relationship ($R = -0.083$) between the alcohol-acetone solubility and the study site. However, a significantly ($p < 0.01$) strong positive relationship ($R = 0.986$) was found between the alcohol-acetone solubility and the rhizome age (Table 3). Figure 1c demonstrates that the alcohol-acetone solubility increased with rhizome age with a strong coefficient of determination ($R^2 = 0.973$). The results supported the finding by Abd-Latif (1996), where the alcohol-benzene soluble of the culms of both the *G. scortechinii* and *B. vulgaris* bamboo species had increased ($R = 0.52$) significantly ($p < 0.01$) with the culms' age. The results agreed with studies by Li (2004) and Wang *et al*. (2016). However, a fluctuating pattern was found by Hisham *et al*. (2006).

Lignin

Bamboo lignin is made up of three phenyl-propane units that synthesize from glucose through the shikimic acid pathway (Higuchi 1969; Liese 1987). Lignin was found as the second most abundant chemical attribute in bamboo and was not significantly different between vascular bundles and ground tissue parenchyma (Higuchi *et al*. 1966). In the present study, lignin ranged from 15.49% to 31.05%. The measured range of lignin was slightly lower than that in the *G. scortechinii* culms (21.90% to 34.00%) of previous studies (Abd-Latif 1996; Hisham *et al*. 2006). The results in Table 1 indicate that lignin may imply that the stability was not significantly influenced by the environmental factor, which agreed with a previous study by Abd-Latif (1996). Table 1 further indicates that lignin was highly significantly different ($p < 0.01$) with both the rhizome age and the interaction between the study site and the rhizome age.

The four rhizome ages were classified into four different ranks *via* Duncan's multiple range test. These indicate that the lignification process gradually took place, from new sprout (17.97%) to young (23.40%), premature (26.45%), and mature (28.88%) (Table 2). The increment of lignin through the aging of the rhizomes is shown in Table 3 and had a significantly ($p < 0.01$) strong positive relationship ($R = 0.945$). Figure 1d illustrates that the lignin dramatically increased from the new sprout to the young rhizome before gradually increasing to the mature rhizome. Abd-Latif (1996) found a significantly ($p < 0.01$) strong relationship ($R = 0.98$) between the bamboo culms' (*G. scortechinii*) lignin with ageing from one year to four years. The observed results agreed with a study by Hisham *et al*. (2006) for bamboo culms of the same species (*G. scortechinii*). However, the lignin in a monopodial bamboo species (*e.g.*, *P. pubescens*) is noted to increase during the elongation phase of the bamboo culms, and the lignification process is completed within one growing season with no significant changes occurring later (Itoh and Shimaji 1981; Li 2004). Li *et al*. (2007) suggest that the lignification in the bamboo species *P.*

pubescens continues to occur in two-year and three-year culms, during which more of the cell walls continue to depose of additional lamella, eventually reaching the maximum degree of deposition and lignification after three years.

Holocellulose and Alpha-cellulose

Holocellulose is the most abundant of the chemical attributes and reaches up to 80% content in bamboo (Abd-Latif 1996; Vena *et al*. 2013; Liese and Tang 2015). Holocellulose is a homo-polysaccharide composed of β-D-glucopyranose units that aggregate together in the form of microfibrils (Sjostrom 1981). Holocellulose consists of alpha-cellulose, which is the main source of mechanical support in bamboo, and hemicellulose, which is a supporting material in the cell wall (Janssen 1981; Sjostrom 1981; Li 2004).

Regardless of the study site and the rhizome age, the holocellulose and alpha-cellulose ranged from 65.39% to 71.17% and 46.52% to 48.24%, respectively. The ranges of the holocellulose and alpha-cellulose observed in the rhizomes of the present study were similar to the ranges of the holocellulose (66.00% to 82.30%) and alpha-cellulose (40.00% to 64.60%) in the culms of the same species of previous studies (Abd-Latif 1996; Hisham *et al*. 2006).

Table 1 shows that holocellulose was highly significantly different ($p < 0.01$) with the study site and rhizome age, but not significantly different with the interaction between the study site and the rhizome age. However, the alpha-cellulose was not significantly different with the study site, rhizome age, and the interaction between the study site and the rhizome age. Higher levels of holocellulose were found in Amanjaya FR (69.37%) followed by in Ayer Hitam FR (67.97%) and Kenaboi FR (67.21%) (Table 2). Although statistically significant differences could be found with the holocellulose between the study sites and was separated into three different ranks (Table 2), the results indicate that the difference was relatively small. The previous study by Abd-Latif (1996) found that the holocellulose of *G. scortechinii* culms is not significantly different among the four study sites.

The results shown in Tables 2 and 3 indicate that the holocellulose slightly increased with a significantly ($p < 0.01$) strong positive relationship ($R = 0.510$) from a new sprout (67.29%) to young (67.85%), premature (68.52%), and mature (69.06%) rhizome. However, Fig. 1e indicates a weak coefficient of determination, where the rhizome ages explain only approximately 26.00% variation of the holocellulose. A relatively low amount of holocellulose was found from younger (one-year) to older (four-year) culms of the *G. scortechinii* species (Abd-Latif 1996; Hisham *et al*. 2006). In previous studies, the holocellulose of the young culms of *P. pubescens* were not significantly different between the three- and five-year culms, but were significantly different between one- and three-year culms (Li 2004; Li *et al*. 2007).

Hydraulic Conductance

Regardless of different study sites and rhizome ages, the hydraulic conductance of *G. scortechinii* rhizomes varied from 1.289 $m^2 s^{-1} MPa^{-1}$ to 5.333 $m^2 s^{-1} MPa^{-1}$. ANOVA (Table 1) indicates that the hydraulic conductance was different ($p<0.01$) with different study sites, rhizome ages, and also their interaction (study sites with rhizome ages). Regardless of different rhizome ages, higher hydraulic conductance (in averages) was found in Ayer Hitam FR followed by Kenaboi FR and Amanjaya FR; 3.797, 3.390, and 3.073 $m^2 s^{-1} MPa^{-1}$, respectively. All three study sites exhibited a difference in ($p<0.01$)

hydraulic conductance (Table 2), where it could be related with the rhizome morphological characteristics that are significantly different among study sites (data not shown). Factors that might be important include the distance from young to older rhizome, rhizome length, number of internode, rhizome diameter (upper, middle and lower portion), rhizome lumen diameter (middle and lower portion), rhizome wall thickness (upper, middle and lower portion), number of buds (active and damaged), and number of branches.

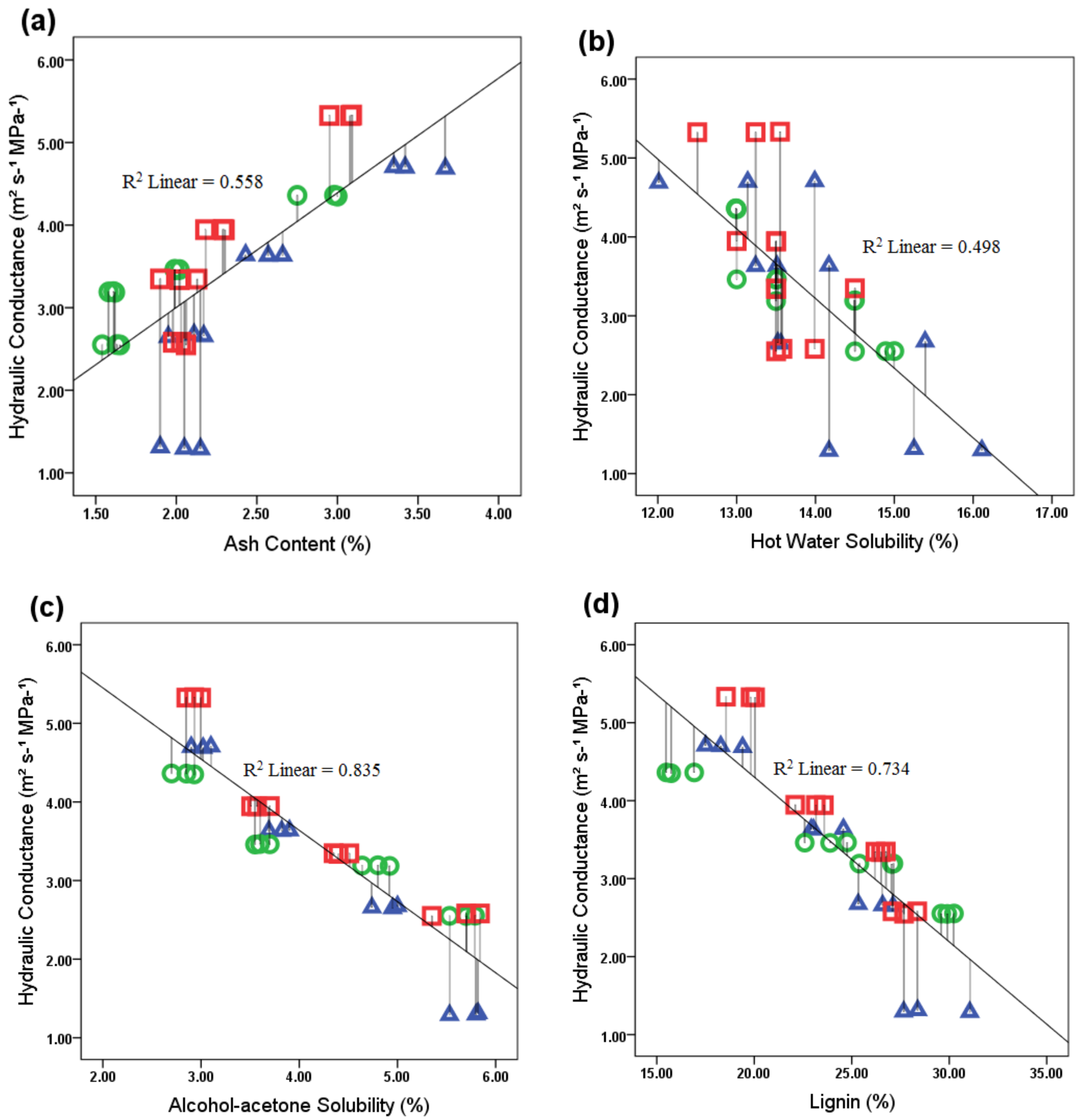
The differences of rhizome morphological characteristics among study sites may be further related to the intrinsic condition at each study site. Different site conditions may depict differentiations in temperature (air and soil temperature) (Kim *et al*. 2009), moisture/humidity, radiant or light (quality, intensity, and duration) (Franklin and Whitelam 2005), water stress (El-Soda *et al*. 2014), wind and soil/media physico-chemical properties (Tomlinson and O'Connor 2004), biotic factors *i.e* animals, insects, soil organism, fungi, and disease (Johnson and Agrawal, 2005; Crutsinger *et al*. 2008), vegetation composition and disturbance gradient (Volker and David 2001; Kang *et al*. 2015), and plant-animal interaction (Daniel *et al*. 2011). As a consequence, soil surface depth or topmost soil layer profusely influences the elongation of the subterranean part and effective rooting zone itself; *i.e.* fine roots and root hairs. Thus, those factors or their interactions play an important role in plant physiological activities such as hydraulic conductance and its ability to accumulate and sequester nutrient elements (Kumar and Divakara, 2001). Furthermore, an individual rhizome or belowground culm may be matured, but the form in an immature clump may be the reason for significantly smaller sizes (length and girth), such as the rhizome in Ayer Hitam FR (planted).

Regarding different rhizome ages, the hydraulic conductance was found to be different among ($p<0.01$) different rhizome ages. Youngest-age (new sprout) rhizome showed the highest hydraulic conductance (4.795 $m^2\ s^{-1}\ MPa^{-1}$), followed by young (3.680 $m^2\ s^{-1}\ MPa^{-1}$), pre-mature (3.065 $m^2\ s^{-1}\ MPa^{-1}$), and mature rhizome (2.140 $m^2\ s^{-1}\ MPa^{-1}$). Results also indicate that there was a significant correlation ($r = -0.918$) between rhizome hydraulic conductance with different rhizome ages (Table 3). A negative correlation shows that the hydraulic conductance decreased with the increment of rhizome age. Linear regression ($y = 5.56 - 0.86*x$) analysis indicated a strong coefficient of determination (R^2 value) where rhizome ages (x-axis) influenced about 84.3 % of the variability of rhizomes hydraulic conductance (y-axis), with F-ratio, $F(1,34) = 182.985$, $p<0.0005$. The difference in the hydraulic conductance in this study illustrates that the hydraulic resistance increased up to an average of 23% at each increment of age.

Intercorrelation of Chemical Attributes with Hydraulic Conductance

According to Table 3, all chemical attributes had significant relationships ($p < 0.01$) with the hydraulic conductance except cold water solubility ($R = -0.241$) and alpha-cellulose ($R = 0.077$). The significantly strong positive relationship ($R = 0.746$) between ash content and the hydraulic conductance indicates that the hydraulic conductance increased due to the ash content increasing. Figure 2a illustrates the linear relationship between ash content and the hydraulic conductance with a strong coefficient of determination ($R^2 = 0.558$). In the real world, however, the relationship between ash content and the hydraulic conductance should be manifested inversely, with the hydraulic conductance decreasing when the ash content decreases because of the increasing of age from younger- to older-aged rhizomes. The ash content is an indicator when determining the existence of inorganic nutrient elements in bamboo (Wahab *et al*. 2013).

Therefore, the decrease in ash content from the new sprout to the mature rhizome is suggested to be related with the concentration of inorganic nutrients (especially the macronutrients) and is crucial for the fast growth of organs (Li 2004; Li *et al*. 2007; Wu *et al*. 2009; Umemura and Takenaka 2014). In the case of the rhizome, the decreasing of nutrients through ageing could also be related to its function for storage and translocation (Wu *et al*. 2009). It is therefore suggested that the changes in the ash content might not exactly associate with the changes that occur in the microstructural elements during the maturation period, which are believed to reflect the rate of hydraulic conductance (Abd-Latif 1996; Hisham *et al*. 2006; Li *et al*. 2007; Liese and Tang 2015; Wang *et al*. 2016).



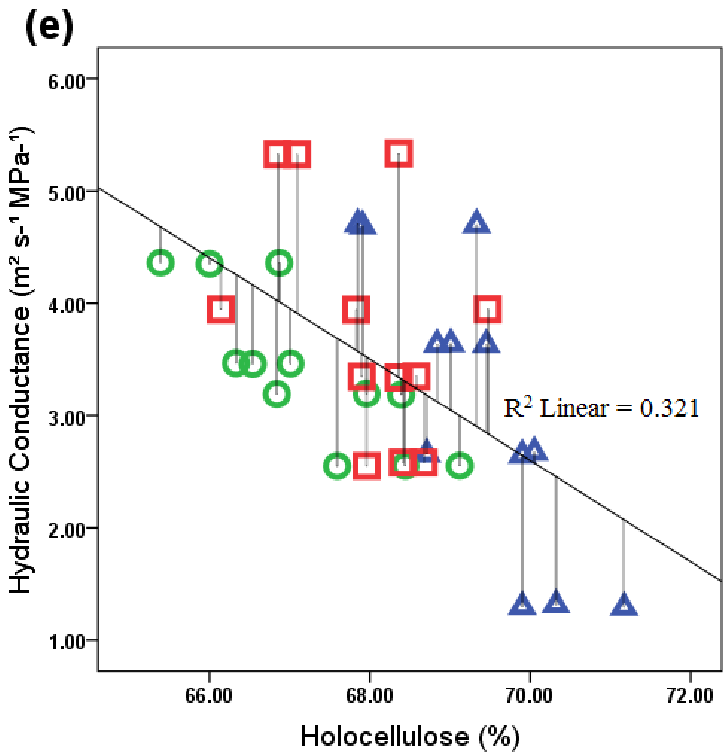


Fig. 2. Linear regression of hydraulic conductance with (a) ash content, (b) hot water solubility, (c) alcohol-acetone solubility, (d) lignin, and (e) holocellulose. Different shapes indicate variation of the study site: triangle (Amanjaya FR), circle (Kenaboi FR), and square (Ayer Hitam FR)

Table 3 shows a significantly ($p < 0.01$) strong negative relationship ($R = -0.706$) between hot water solubility and hydraulic conductance, indicating that the hydraulic conductance decreased with the increase in hot water solubility. The increase of hot water solubility with rhizome age is illustrated in Fig. 1b, and the decrease of hydraulic conductance with the increase of hot water solubility ($R^2 = 0.498$) is illustrated in Fig. 2b. Compounds, such as tannin, starch, sugar, and other hot water extractives, increased and were deposited into the cell and cell wall during the maturation period, which reflects the conductance rate in the rhizomes (Browning 1963; Janes 1969).

According to Table 3, a significantly ($p < 0.01$) strong negative relationship ($R = -0.914$) between the alcohol-acetone solubility and the hydraulic conductance was observed. This indicates that the hydraulic conductance decreased when the alcohol-acetone solubility increased. Figure 1c illustrates the decrease of hydraulic conductance with a strong coefficient of determination ($R^2 = 0.835$). Similar to hot water solubility, the deposition of alcohol-acetone extractives was found to increase during the rhizome's maturation period.

In contrast, Table 2 indicates a lower alcohol-acetone solubility compared with hot water solubility from a new sprout to a mature rhizome, but a higher relationship and coefficient of determination for hydraulic conductance with alcohol-acetone solubility compared to hydraulic conductance with hot water solubility was observed. This could be due to the type of compounds with such a high accuracy (Fig. 1c) of concentration in the alcohol-acetone solubility rather than the type of compounds with a high variation (Fig.

1b) of concentration in hot water solubility (Browning 1963; Janes 1969; Li 2004). The type of compounds, such as wax, fat, resin, and gum, in general alcohol extractives is suggested to be a heavy substance in extractives and could result in a lower alcohol-acetone solubility compared with hot water solubility (Li 2004). Those compounds may be related to the presence of gum-like substances, slime, and callose substances in vessels, sieve tubes, and other tissues during the aging of bamboo and is suggested to be related to the decrease in the hydraulic conductance (Liese and Weiner 1996; Liese and Tang 2015). Furthermore, the deposition of various compounds is positively related with the density of the culms (Abd-Latif 1996). This implies a decrease in the porosity or space during the maturation period, which was presented as permeability and a pathway for solute conductance.

The results shown in Table 3 indicate a significantly ($p < 0.01$) strong negative relationship ($R = -0.857$) between lignin and hydraulic conductance. Figure 2d further illustrates this relationship with a strong coefficient of determination ($R^2 = 0.734$). The continuous deposition of lignin or the lignification process during the maturation period indicates that lignin is continuously sheathed, binds the microfibrils in bamboo, and continuously increases the strength and structural rigidity of the bamboo culms (Abd-Latif 1996; Scurlock *et al*. 2000; Li *et al*., 2007). A previous study on the relationship of lignin with the density of *G. scortechinii* and *B. vulgaris* culms found a moderately positive correlation coefficient ($R = 0.44$ and $R = 0.37$, respectively), which indicates that the density of bamboo increased because of an increase in lignin (Abd-Latif 1996). Therefore, the deposition of lignin from a new sprout to a mature rhizome significantly affected the hydraulic conductance.

A significantly ($p < 0.01$) strong negative relationship ($R = -0.567$) between holocellulose and hydraulic conductance is shown in Table 3. Figure 1e illustrates the decreasing of hydraulic conductance due to the increasing of holocellulose ($R^2 = 0.321$). An increasing trend of holocellulose from a new sprout to a mature rhizome was observed in Fig. 1e. Abd-Latif (1996) determines that the increasing ($R = 0.350$) of holocellulose during the maturation period of *G. scortechinii* culms is related to the increasing of the fiber cell wall thickness. Abd-Latif (1996) further indicates a positive relationship ($R = 0.34$) between the fiber cell wall thickness and the bamboo culms' density, which depicted that the density increases due to the increasing fiber cell wall thickness.

The thickening of the fiber cell wall during the maturation period of *G. scortechinii* culms has also been observed by Wahab *et al.* (2006). The anatomical changes during the development of the fiber structure on other bamboo species were reported in several studies (Fujii 1985; Alvin and Murphy 1988; Liese and Weiner 1996; Londoño *et al*. 2002; Gan and Ding 2005). The thickening of the fiber cell wall during the maturation period occurs due to the deposition of additional lamella layers but not due to the thickening of the existing cell walls, which was depicted to increase in the density (Liese 1998). The increase of holocellulose from a new sprout to a mature rhizome was related to the increasing of the fiber cell wall thickness and the density of the rhizome, therefore decreasing the hydraulic conductance.

CONCLUSIONS

1. The results showed that the ash content, alcohol-acetone solubility, and holocellulose of bamboo rhizomes significantly differed with the study site.

2. All the chemical attributes had significant differences, and therefore all, except cold water solubility and alpha-cellulose, showed a relationship with the rhizome age.
3. A significant relationship was found between the hydraulic conductance and all chemical attributes except for cold water solubility and alpha-cellulose.

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