INTRODUCTION

West Indian arrowroot (Maranta arundinacea L., Marantaceae) is a herbaceous, perennial tropical plant from tropical America (Delin & Kennedy, 2000; Handler, 1971; Tan & Zaharah, 2015). It is characterized by an edible starchy flesh tuber (Delin & Kennedy, 2000). Morphologically, the plant is straight herb with 30-130 cm in high; rhizomes sympodial and cylindric; stem erect, often apically branched, slender; leaf blade ovate-oblong; inflorescences several per leafy shoot, each subtending 2 or 3 flower pairs; corolla white, and sepals green (Wu & Kennedy, 2000). The West Indian arrowroot tubers contain more than 20 % starch (Rahman et al., 2015) which is higher than another member of family Marantaceae, Calathea allouia, which has 6.6 % starch (Bridgemohan, 2011). The starch from West Indian arrowroot flour had a nutrition composition of 25.9 % amylose, 0.14 % protein, 0.84 % fat, 11.9 % water, 0.58 % ash, 8.7 % insoluble dietary fiber, and 5.0 % soluble dietary fiber (Kumalasari et al., 2012). The starch also has a similar characteristic with cassava, potato, and banana starch (Rohandi, Budiadi, Hardiwinoto, Harmayani, and Sudrajat, 2017). The starch from West Indian arrowroot flour had higher protein content than cassava flour (Aprianita, Vasiljevic, Bannikova, & Kasapis, 2014). The West Indian arrowroot is well known as medicinal plant used against diarrhoea, dysentry, and urinary related diseases (Cooke, Carr, Abrams, & Mayberry, 2000; Shintu, Radhakrishnan, & Mohanan, 2015). Mashed rhizomes are applied topically for wounds from poisoned arrows, black spider, and scorpion bites (Lim, 2016). Arrowroot tubers are sources of fibrous food and have low glycemic index thus it is a healthy food (Lestari, Huriyati, & Marsono, 2017). The flour from tubers of the crop has been widely used in culinary products such as crackers, cookies, cakes, puddings, and porridge. It is also a potential source of prebiotics (Harmayani, Kumalasari, & Marsono, ...
The high starch and amylose contents in tuber are extremely important for the formation of strong polymeric matrices to be used in membrane production (Gordillo, Valencia, Zapata, & Henao, 2014).

Nowadays, West Indian arrowroot can be found in many tropical regions of the world, including South-East Asia, South Africa, Australia, India, Sri Lanka, and Florida (United States) and it can grow up to 1,000 m above sea level (asl) (Djaafar, Sarjiman, & Pustika, 2010; Shintu, Radhakrishnan, & Mohanan, 2015; Villamayor & Jukema, 1996). In Indonesia, it can be found in Java, Sulawesi, and Maluku, thus it has different local names for every region such as arut/ jelarut/ irut/ larut/ garut (East Java); larut/ pata sagu (West Java); labia walanta (Gorontalo); and huda sula (Ternate). The productivity of West Indian arrowroot in Indonesia ranges from 9 – 12 t/ha with a starch content of 1.92 – 2.56 t/ha (Djaafar, Sarjiman, & Pustika, 2010). Its productivity needs to be improved considering the high economic and health values of the crop. Cultivation of arrowroot has not been intensive, mostly left to grow wildly without maintenance in the yard which has low productivity. In addition, improving West Indian arrowroot productivity may contribute to achieving food security. Exploration of new accessions is needed for increasing crop productivity. Rohandi, Budiadi, Haridwinoto, Harmayani, & Sudrajat (2017) reported that in Garut District, there are three populations of arrowroot which have high tuber yield. Cilawu, Cikajang, and Cibatu populations have good potential to produce the high quality and quantity for arrowroot cultivation.

Crop productivity is determined by the pattern of dry matter allocation among plant organs (Tekalign & Hammes, 2005). Furthermore, environmental factors may influence the pattern of dry matter distribution through changes in photosynthesis rate and strength of various sinks (Bridgemohan, 2011; Lemoine et al., 2013). Zheng et al. (2016) reported that plant growth and accumulation of dry matter is different under different ecological conditions. Ecological conditions such as different altitudes cause differences of environmental conditions like intensity of sunlight, temperature, and wind speed (Kumar, Kumar, Vats, & Ahuja, 2006; Oktafani, Supriyono, Budiausti, & Purnomo, 2018; Shi, Haworth, Feng, Cheng, & Centritto, 2015). The environmental factor, light intensity, influenced the dry matter accumulation of another member of family Marantaceae, Guinea arrowroot (Calathea allouia (Aubl.) Lindl.) (Bridgemohan, 2011). Growth performance, tuber yield, and starch content of arrowroot have multi component characters greatly influenced by genetic system and some agro-climate conditions (Rohandi, Budiadi, Haridwinoto, Harmayani, & Sudrajat, 2017).

However, knowledge on how growth and development of the crop are affected by environmental factors is still limited. Therefore, studies comparing physiology, growth and tuber yield of West Indian arrowroot in different environmental conditions i.e. altitude are needed, due to the variations in sunlight, temperature and wind conditions. This study analysed the effect of environmental factors at different altitudes on physiological response of West Indian arrowroot. Growth rate and tuber yield were measured to examine the distribution of photosynthate in West Indian arrowroot at different altitudes. Area in lowland and highland might be a way to improve crop productivity of West Indian arrowroot.

**MATERIALS AND METHODS**

**Study Site and Plant Materials**

This research was conducted from September 2014 to December 2015 in West Java, Indonesia, at sites with altitudes of 250 m asl and 1,100 m asl. Climatic conditions at the planting areas at 250 m asl and 1,100 m asl during the study were different and are presented in Table 1.

The plant materials used were four accessions of West Indian arrowroot: Bantul, Krajan, Kemalang, and Begawat. The accession Bantul was from Yogyakarta (60 m asl). Accession Krajan was from Tegal, Central Java (270 m asl), Kemalang was from Klaten, Central Java (680 m asl) and Begawat was from Tegal, Central Java (854 m asl).

**Experimental Design**

This study used a split plot arrangement in a randomized block design with three replications. Altitude was the main plot and accessions were the subplots. The altitudes were 250 m asl (lowland) and 1,100 m asl (highland). The accessions of arrowroot plant consist of four levels i.e. accessions of Bantul, Krajan, Kemalang, and Begawat.

**Planting**

Prior to planting, the tubers were cut into smaller pieces of approximately 10-20 g in weight, with each piece having 6 buds. Pieces of tuber were soaked in a fungicide solution (Mankozeb 80 % 1 g/L water, Dithane™ M-45 80WP) for 5 minutes, then...
embedded in a nursery of size 5 m x 2 m which has been treated with cow dung (2 kg/m²) and shaded by paranet 60 %. The seven week old seedlings were planted in experimental plots sized 9 m x 3.2 m with spacing of 60 cm x 40 cm and depth of 7 cm (Sutoro & Hadiatmi, 2011). The experimental plots contained basic manure (700 g per hole), urea (290 kg/ha), Super Phosphate 36 (375 kg/ha), and KCl (300 kg/ha) (Djaafar, Sarjiman, & Pustika, 2010). Application of fertilizers during planting were manure and Super Phosphate 36, 1/3 dosage of urea, and 1/3 dosage of KCl. Urea and KCl (2/3 dosage) were given at 3.5 month after planting (MAP) (Suhartini & Hadiatmi, 2011).

Weeding was done to keep the plots clean at the experimental plot until harvest time. Combating pests with pesticide spraying (Deltamethrin 1 ml/L water, Decis® EC 25) was done when there were any attacks. Harvesting was done at 7 MAP in accordance with farmers practice.

Data Measurements

Physiological responses such as stomatal conductance, rate of transpiration, and photosynthesis were measured using a LI-COR 6400XT portable photosynthesis system (LI-COR Biosciences, Lincoln, Nebraska, USA) at 2000 µmol/m²/s of photosynthetically active radiation (PAR). Measurements were done on fully expanded leaves for 5 in each accession and replication at 2, 5, and 7 MAP. For soluble sugar measurement, 9 fully expanded leaves were taken from 3 arrowroot plants in each accession in each replication, dried at 80 ºC and ground to powder using a blender. Soluble sugar content in leaves were measured at 2 MAP and 5 MAP using phenol-sulfuric acid method (Jain, Karibasappa, Dodamani, & Mali, 2017).

Growth variables measured were plant height growth, number of leaves, tiller number, leaf area per plant, tuber growth rate, shoot and tuber dry weight. The plant height growth as well as leaf number and tiller number were performed on five plants in each accession and replication at ages 2, 5, and 7 MAP. For leaf area per plant measurement, 5 fully expanded leaves were taken from 5 plants in each accession in each replication at 2, 5, and 7 MAP. Fresh leaf samples were made into replicas by drawing the outline on white, unlined paper. To determine leaf area, the leaf replicas were scanned and calculated using ImageJ software.

Measurement of tuber growth rate, shoot dry weight, and tuber dry weight were done by taking 5 plants in each accession and replication at 2, 5, and 7 MAP. Shoot dry weight was derived from sum of leaf dry weight and stem dry weight (Condori et al., 2008). The shoot and tubers were dried at 80 ºC until for constant dry weight. Tuber growth rate (mg/m²/day) was measured using the equation of Tekalign & Hammes (2005):

\[ \text{Tuber growth rate} = \frac{1}{\text{GA}} \times \frac{(T_2 - T_1)}{(t_2 - t_1)} \times 1000 \]

where \( T_1 \) and \( T_2 \) are, respectively, tuber dry weight (g) on initial (\( t_1 \)) and final (\( t_2 \)) measurement, and GA is ground area covered by crop.

Tuber yield was measured by taking fresh tubers on 12 plants of each accession in one plot in each replication. Production of fresh tuber was measured at 7 MAP.

Statistical Analysis

The data were analysed using analysis of variance (ANOVA) at 95 % confidence intervals and it continued with Duncan’s multiple range test (DMRT) at \( \alpha = 5 \% \) when significant ANOVA results were obtained. All statistical analyses were performed using SAS 9.1.3 (SAS Institute Inc., Cary, NC, USA).

RESULTS AND DISCUSSION

The results showed that altitudes significantly affected (\( P < 0.05 \)) the stomatal conductance of West Indian arrowroot. The stomatal conductance in the highland was higher than that in the lowland (Fig. 1). Transpiration rates were influenced by interaction between altitudes and plant ages (\( P < 0.05 \)). The highest and the lowest transpiration rates occurred at 2 MAP in the highland and lowland, respectively (Fig. 2). The differences in stomatal conductance and transpiration rate were affected by climatic condition such as wind speed at different altitude. The wind speed in the highland was higher than in the lowland (Table 1), so that affected the leaf boundary layer conductance. Strong wind led to reduce leaf boundary layer resistance thus increasing transfer of water vapor through stomata (Anten, Alcalá-Herrera, Schieving, & Onoda, 2010; Kuo, Lee, & Yang, 2011; Schymanski & Or, 2016). The higher stomatal conductance in the highland generally followed by the higher transpiration rate (Shi, Haworth, Feng, Cheng, & Centritto, 2015). This result in line with...
the statement of Gale (2004) that the highland with elevation 1000 m asl where stomata remain open and water is available may bring about a doubling transpiration rate. The transpiration rate and stomatal conductance had close relationship which can influenced the photosynthesis rate (Xie & Luo, 2003).

Photosynthesis rate were influenced by interaction between altitudes and plant ages (P < 0.05). The West Indian arrowroot exhibited the highest rate of photosynthesis at 7 MAP in highland, while the lowest one was in the lowland at 2 MAP (Fig. 2). The stomatal conductance and sink strength affected the photosynthesis rate. The highest photosynthesis rate in the highland at 7 MAP was possibly affected by increasing sink strength i.e. tuber enlargement. The increased demand of photosynthate in the tuber sink might have caused the raising of photosynthesis rate (Darvishi, 2016). Thus, the lower stomatal conductance and sink strength at 2 MAP became factors that limited photosynthesis rate in the lowland. There was no tuber formed, and the growth of vegetative organs was still going on at this time, so sink demand was low.

The rate of photosynthesis declined at 5 MAP in the highland, possibly due to the environmental stress. Strong wind and low temperature for long time periods caused plant stress. The higher wind speed in the highland caused leaves to roll up, thus it reduced leaf area for photosynthesis (Schymanski & Or, 2016). At low temperature, plants reserve more nitrogen in RuBP regeneration processes than in Rubisco, hence limiting carboxylation reaction by Rubisco, causing photosynthetic decline (Yamori, Hikosaka, & Way, 2014). At 7 MAP, the photosynthesis rate of West Indian arrowroot in highland increased, possibly because it had been able to adapt.

![Stomatal conductance of West Indian arrowroot (Maranta arundinacea L.) at different altitudes](image)

**Fig. 1.** Stomatal conductance of West Indian arrowroot (Maranta arundinacea L.) at different altitudes

<p>| Table 1. Climatic condition of planting areas at 250 m asl and 1,100 m asl from October 2014 - June 2015 (Station of climatology at Dramaga, Bogor and Pasir Sarongge, Cianjur) |</p>
<table>
<thead>
<tr>
<th>Location</th>
<th>Duration of solar radiation (%)</th>
<th>Temperature (°C)</th>
<th>Relative humidity (%)</th>
<th>Wind speed (km/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>250 m asl</td>
<td>39.0 - 84.0</td>
<td>25.0 - 26.8</td>
<td>75.0 - 88.0</td>
<td>3.7 - 4.7</td>
</tr>
<tr>
<td>1,100 m asl</td>
<td>54.0 - 79.0</td>
<td>21.0 - 23.0</td>
<td>65.0 - 81.0</td>
<td>47.0 - 58.0</td>
</tr>
</tbody>
</table>

Remarks: Value indicates minimum and maximum
Plants growing in the highland generally had a higher photosynthetic capacity despite the fact that conditions of temperature and partial pressure of CO₂ in the highland were lower than that in the lowland (Shi, Liu, Liu, & Centritto, 2006). Plants acclimate at low temperature by increasing amounts of photosynthetic enzymes such as Rubisco, sedohexulose-1, 7-bisphosphatase (SBPase), and stromal fructose-1, 6-bisphosphatase (Yamori, Hikosaka, & Way, 2014). On the other hand, photosynthesis rate of West Indian arrowroot in the lowland still increased at 5 and 7 MAP. The suitable condition and increasing sink strength become factors that cause the photosynthesis rate of West Indian arrowroot at 5 and 7 MAP in lowland to still increase.

Soluble sugar content in leaves was influenced by the interaction between altitudes and accessions (P < 0.05) at 2 MAP and 5 MAP (Fig. 3).
Most of the accessions showed higher levels of leaf soluble sugar at 5 MAP in the highland. These results support the suggestion that the West Indian arrowroot suffered stress at this time. High levels of leaf soluble sugar have been suggested as the mechanism for stress tolerance in the highland. Soluble sugar acts as osmoprotectants and protect cell membrane from damage (de Oliveira Mello, Barbedo, Salatino, & de Cássia Leone Figueiredo-Ribeiro, 2010; Garvey, Lenné, Koster, Kent, & Bryant, 2013). Plants growing in the highland require high energy to respond to the environmental stresses and generally accumulate high soluble sugar content in leaves as one of the mechanisms of stress tolerance (Ma et al., 2015). Soluble sugar content in leaves at 5 MAP was higher than that at 2 MAP in the two locations. This may be related to the change in photosynthetic demand which increased along with plant age. Furthermore, soluble sugar was translocated to the sink for growth activity (Braun, Wang, & Ruan, 2014; Hossain et al., 2012).

The growth in plant height was influenced by altitude and West Indian arrowroot accessions independently. The height growth in the lowland was significantly higher ($P < 0.05$) compared to those in the highland. The Krajan accession had the height growth significantly different ($P < 0.05$) from that of Bantul accession, but it was not different ($P > 0.05$) from those of Kemalang and Begawat accessions. The height growth in the lowland and highland were 20.00 and 9.11 cm/month, respectively. The West Indian arrowroot in the lowland exhibited faster plant height growth than that in the highland (Fig. 4a). Temperature and wind speed were the factors which affected plant growth. The lower plant height in the highland was possibly due to the low temperature which caused inhibition of carbon storage for growth (Atkin, Loveys, Atkinson, & Pons, 2006). Low height growth in the highland may be associated with a self-defence mechanism against abiotic stress i.e. high wind speed (Sharaf, Khafagi, Hatab, & Moursy, 2013; Shi, Haworth, Feng, Cheng, & Centritto, 2015; Smith & Ennos, 2003). The reduction of plant height, which has been reported by several studies (Dierig, Adam, Mackey, Dahlquist, & Coffelt, 2006; Onoda & Anten, 2011) is a strategy of plants to survive the harsh conditions such as strong wind and low temperature at high altitudes.

There was no significant effect of altitude and accessions on the leaves and tiller number ($P > 0.05$) (Fig. 4b and Fig. 4c). The West Indian arrowroot increased leaf number at both altitudes from the beginning until 5 MAP and decreased after 5 MAP. Furthermore, altitudes significantly affected leaf area per plant ($P < 0.05$). Leaf area per plant in the lowland was higher than that in the highland (Fig. 5).
Fig. 4. Growth of a) plant height, b) leaves, and c) tillers of West Indian arrowroot (*Maranta arundinacea* L.) at different altitudes.

Remarks: A = 250 m asl, B = 1,100 m asl, BT = Bantul accession, KR = Krajan accession, KM = Kemalang accession, BG = Begawat accession. Values show mean ± SD.

Fig. 5. Leaf area of West Indian arrowroot (*Maranta arundinacea* L.) at different altitudes.

Remarks: Bars represent mean ± SD.
Along with the increased altitude gradient, the smaller leaf area was detected as a response to strong wind (Pan et al., 2009). Lower leaf area can be an advantage for the plant if suffered high wind speed, they can avoid serious damage. This result is in line with Yuliani, Soemarno, Yanuwidi, & Leksono (2015), that Asteraceae such as Ageratum conyzoides, Pluchea indica, and Elephantopus scaber in low altitude tends to have wider leaves than that in high altitude.

The tuber growth rate was affected by altitude and West Indian arrowroot accessions independently (P < 0.05). The tuber growth rate in the lowland was significantly higher (P < 0.05) compared to that at highland, while tuber growth rate of Krajan accession was different (P < 0.05) from the rate of Bantul accession, but it did not differ significantly (P > 0.05) from the rate of Kemalang and Begawat accessions (Table 2).

Table 2. Tuber growth rate of West Indian arrowroot (Maranta arundinacea L.) at different altitudes

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Tuber growth rate (mg/m²/day)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitudes</td>
<td></td>
</tr>
<tr>
<td>250 m asl</td>
<td>39a</td>
</tr>
<tr>
<td>1100 m asl</td>
<td>30b</td>
</tr>
<tr>
<td>Accessions</td>
<td></td>
</tr>
<tr>
<td>Bantul</td>
<td>27a</td>
</tr>
<tr>
<td>Krajan</td>
<td>41a</td>
</tr>
<tr>
<td>Kemalang</td>
<td>37a</td>
</tr>
<tr>
<td>Begawat</td>
<td>35a</td>
</tr>
</tbody>
</table>

Remarks: Values in the same column in different treatments followed by different letters indicate a significant difference (P < 0.05) on DMRT test (α = 5 %)

Tuber growth of West Indian arrowroot in the lowland showed higher rate (30 %) than that in the highland. It was caused by a high photosynthesis rate entering 5 MAP. The tuber of West Indian arrowroot was formed at this time, so the higher photosynthesis rate was needed to supply the demand of photosynthe in sink organs i.e. tuber. The temperature in the lowland appeared to be more suitable for West Indian arrowroot; it possibly supported the phloem-loading process (Bilska-Kos, Grzybowski, Jończyk, & Sowiński, 2016). The tuber growth rate of Bantul accession was the lowest among the accessions and this was caused by differences in the ability of accessions in translocating photosynthate to the tuber (Lambers, Chapin III, & Pons, 2008).

Shoot dry weight was affected by altitude, while tuber dry weight and tuber yield were affected by altitude and accessions independently. Shoot dry weight, tuber dry weight, and tuber yield in the lowland were significantly higher (P < 0.05) compared to those in the highland (Table 3). Tuber dry weight of accession of Krajan did not differ (P > 0.05) from the accession of Kemalang, but it was different (P < 0.05) from the accessions of Begawat and Bantul. On the other hand, tuber yield of Krajan accession was different (P < 0.05) from that of Bantul accession, but it did not differ (P > 0.05) from those of Kemalang and Begawat accessions. Shoot and tuber dry weight of West Indian arrowroot were higher in the lowland compared to those in the highland. It may be caused by the higher plant height of West Indian arrowroot in the lowland due to the high height growth. The high plant height tends to have a larger storage capacity which supports the replenishment of food reserves to tuber (Dordas & Sioulas, 2009).

Table 3. Effect of altitudes and accessions on shoot dry weight, tuber dry weight, and tuber yield of West Indian arrowroot (Maranta arundinacea L.)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Shoot dry weight (g)</th>
<th>Tuber dry weight (g)</th>
<th>Tuber yield (t/ha)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitudes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>250 m asl</td>
<td>152.79a</td>
<td>165.04a</td>
<td>27.04a</td>
</tr>
<tr>
<td>1,100 m asl</td>
<td>64.31b</td>
<td>125.59b</td>
<td>18.90b</td>
</tr>
<tr>
<td>Accessions</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bantul</td>
<td>101.89a</td>
<td>109.74b</td>
<td>17.53c</td>
</tr>
<tr>
<td>Krajan</td>
<td>110.51a</td>
<td>169.71a</td>
<td>23.14c</td>
</tr>
<tr>
<td>Kemalang</td>
<td>112.81a</td>
<td>153.90a</td>
<td>24.73c</td>
</tr>
<tr>
<td>Begawat</td>
<td>108.98a</td>
<td>147.91ae</td>
<td>26.48c</td>
</tr>
</tbody>
</table>

Remarks: Values in the same column in different treatments followed by different letters indicate a significant difference (P < 0.05) on DMRT test (α = 5 %)
Tuber yield of West Indian arrowroot in the lowland was higher (43.07 %) than those in the highland. The accession of Bantul had the lowest tuber yield compared to accessions of Krajan, Kemalang, and Begawat. This may be attributed to the tuber growth rate and accumulation dry matter in tuber. Accessions of Krajan, Kemalang, and Begawat were considered to have a higher capability in translocating photosynthate toward tuber that was shown by the tuber growth rate and tuber dry weight was higher than that accession of Bantul. Differences of photosynthate translocation to tuber were affected by the differences of each accession in starting the process of photosynthate translocation towards tuber and the ability of accession in distributing the photosynthate (Condori et al., 2008).

CONCLUSION AND SUGGESTION

The climatic conditions at different altitudes such as temperature and wind speed affected the physiological response such as stomatal conductance, photosynthesis and transpiration rate, and photosynthate distribution of West Indian arrowroot. Those factors also influenced the plant height and leaf area. The tuber growth rate in the lowland was higher (30 %) than that in the highland. Furthermore, the tuber yield in the lowland was higher (43.07 %) than those in the highland, due to the higher distribution of photosynthate to the tuber. It is suggested that West Indian arrowroot tends to be more suitable to grow in lowland. Accessions of Begawat, Kemalang, and Krajan have the potential to be cultivated both in the lowland and highland with high tuber yield.

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