

# STUDY ON THE SURVIVAL AND ADAPTATION OF *CANNA INDICA* L. TO DIFFERENT LIGHT ENVIRONMENTS AND HERBIVORE ATTACKS

<sup>1</sup>YORIANITA SASAERILA, <sup>2</sup>ANGELIA YULITA, <sup>3</sup>SASKIA ASRI, <sup>4</sup>TEUKU TAJUDDIN

<sup>1,2,3</sup>Department of Biology, Universitas Al Azhar Indonesia Jalan Sisingamangaraja, KebayoranBaru, , Jakarta, Indonesia, 12110

<sup>4</sup>Laboratory for Biotechnology, Agency for the Assessment and Application of Technology Indonesia. Building 630, Puspiptek Area, Setu, South Tangerang, Banten, Indonesia 15314

E-mail: <sup>1</sup>yshidayat@uai.ac.id, <sup>2</sup>angelia.yulita@gmail.com, <sup>3</sup>saskia.asri28@gmail.com, <sup>4</sup>teuku.tajuddin@bppt.go.id

**Abstract** –*Canna indica* (African arrowroot or Indian shot), a multi-use tropical herb with worldwide distribution, has great potential to be an intercropping plant, but little is known about its growth light environment. Here, we investigated the effect of light on the survival of *C. indica* and its susceptibility to insect attacks. This experiment was set on an open field with two light treatments: 100% natural full sunlight and 25% full sunlight (shade-grown). Insects that attacked the plant were from the natural populations. We found that all *C. indica* plants survived both treatments. Full-sunlight-grown *C. indica* produced thicker leaves, heavier fresh rhizomes and yielded an earlier flowering time, whereas shade-grown *C. indica* produced longer shoots, higher leaf area, and better branching frequency. A higher incidence of insect attacks was observed on the leaves of full-sunlight-grown plants, with about 17% of the total leaves being consumed, compared to ~1% of the leaves of shade-grown plants. No insect attack was found on the roots. The prime herbivore attack on *C. indica* was by *Valanga* sp. This study found that *C. indica* showed a remarkable ability to adapt to different light environments and is suitable as an intercropping plant under the shade of tree canopies.

**Keywords** - *Canna Indica*, Full Sun-Grown, Shadegrown, Herbivore Attack, Intercropping Species

## I. INTRODUCTION

Originally indigenous of South America, *Canna indica* is now distributed worldwide, especially in tropical and subtropical regions. Various local names that were given to this plant show how well spread and used this species is. It is called Achira in Spain, Balisier in French, Biri or Cana in Portugal, Queensland root in Australia, Sagu in Thailand, Chisqua in Columbia, Ganyong in Indonesia, to name a few. One of the reasons this species is well spread is that all parts of this plant are beneficial. The rhizome can be boiled or processed to make flour, pasta, and a variety of snacks. The young leaves are eaten as a vegetable. The seeds are used as an ingredient in tortilla mixtures, and the stems and older leaves are used as animal feed. As a food source, *C. indica* is the best-known edible canna among its congeneric, and provides a high amount of carbohydrates that could be used as an alternative to rice. The starch-rich rhizomes of *C. indica* contain about 94–96% starch, 0.05–0.20% protein, 0.01–0.15 % fat, 0.40–0.90% fiber, and 0.70–0.90% ash per dry weight basis [1]. The leaves and roots of this plant also have pharmaceutical benefits that have been used as home remedies for many generations. Another reason for its wide distribution is its soil conservative characteristics. *C. indica* is a fast growing species producing large leaves that are capable of protecting the soil from the impact of direct rainfall. This species also survives well on dry and marginal soils. With the continuous increase in the human population and rapid degradation of forested areas for agricultural

production, it is just a matter of time before a shortage of food occurs in the near future. *C. indica* has the potential to be used as a food crop, hence, to help to solve the world food crisis while conserving the soil.

An effective solution to reducing deforestation for the mass planting of food crops is by selecting shade-tolerant species, so they can be planted under tree canopies without the need to clear-cut forests, an activity also known as the agroforestry system. Such crops can be planted under the stands of commercial plantation, for example in areas under rubber or oil palm trees that are generally unused.

It has been reported that the quantity of light under tree canopies of established (6–15 years) rubber or oil palm is limited to less than 30% of full sunlight above the canopies [2]. A great deal of research has been done on *C. indica*, for example, [3] and more recent topics include: starch quality, physicochemical properties and genetic characteristics of *C. indica* starch [1]; [4]; [5], organogenesis and ultra-structural features [6], the effect of water deficiency and nutrients [7]; [8], pollination biology with respect to morphology of the style [9], and the use of *C. indica* for domestic waste treatments [10].

Unfortunately, little is known about the adaptability of this species to different lighting conditions for its growth. In fact, there are conflicting reports on the ability of *C. indica* to tolerate shade [11, 12]. If *C. indica* were to be used as an intercropping plant, it is imperative that its adaptability to light growing conditions for its growth be investigated. Similarly, there are no data available regarding the sensitivity of

*C. indica* to insect attack when grown under various lighting environments. Several insect species that have been reported to feed on *C. indica* leaves are grasshoppers, Japanese beetles (*Poppilia japonica*), and leaf rollers (*Calpodeseethlius*) [13]. In the present paper, we report the effects of different growth lighting conditions on the phenotypic adaptability and survivability of *C. indica* as well as its susceptibility to insect attacks. The main focus of this research is to provide information on the suitability and potential use of *C. indica* as an intercropping plant, with the aim of taking advantage of idle spaces under the canopies of commercial rubber plantations.

## II. MATERIALS AND METHOD

This research was conducted at the Center for Agricultural Production Technology, in the Agency for the Assessment and Application of Technology (BPPT), Puspiptek, Serpong, Banten, Indonesia (6°S, 106°E).

### General Preparation of Plant Materials and Growth Condition

Rhizomes of wild *C. indica* white cultivar were obtained from Trubus Co., in Jakarta, Indonesia. The rhizomes were cut into smaller pieces (~5cm, weight  $\pm 50$ g), each with a growing nodal point, planted on rice husks for seven days, watered daily with 50ml of tap water, twice daily until the sprout was visible. Then, watering was reduced to once daily. After seven days, *C. indica* seedlings were transferred into poly bags (15cm in diameter, 10cm in height) containing ~300g sandy clay soil (pH 6.9), mixed with organic compost, one plant per pot, and placed in the shade with about 50% reduction of full natural sunlight, at 0.5m x 0.5m spacing. After one month, *C. indica* seedlings were randomly selected and placed under the two light treatments: full sun, or 100% sunlight, and 25% of full sunlight, or 75% shade. Light treatments were created by constructing two shelters, each measuring 6m in length, 3m in height, and 3m in width on an open field. One shelter was used for 25% of full sunlight (75% shade) in which two layers of black polyethylene net meshes were placed (as a roof) on the top of the shelter to reduce acceptance light by about 75% of full sunlight. The other shelter was used for full sunlight, or 0% shade treatment in which the upper part of the shelter was not covered with any polyethylene mesh. Thus, it was left open. The percentage of the light reduction under the net meshes was measured at five points above and below the nets by using a light meter (Krisbow, KW 06-228). The distance between the two treatment shelters was  $\pm 50$ m.

### Experiment 1. The Adaptability of *C. indica* to Light Treatments

For this experiment, ten *C. indica* seedlings were divided into two groups, that is, five seedlings in each

group. The first group was grown in full sunlight (0% shade) treatment; the second group was grown in 25% of full sunlight. Once a month, the conditions of the environment in each group were measured, including light intensity, air and soil temperature, and humidity. Light intensity was measured in the morning from 8:00 to 9:00 a.m. and in the afternoon from 12:30 to 1:30 p.m., while air and soil temperature, and humidity were measured only in the afternoon. Plants heavily fed by herbivores were excluded from the experiment. Prior to the light treatments, *C. indica* seedlings were screened to ensure phenotypically more or less homogeneity in plant height and number of leaves.

### The Phenotypic Trait Measurements

Measurements of the phenotypic traits were completed six months after planting, and consisted of the following parameters: shoot length, leaf area, leaf length, leaf width, leaf thickness, branching frequency, leaf orientation, bud formation, flowering time, and fresh weight of harvested rhizomes, that is, measured after the rhizomes were harvested and cleaned from soils and root hair. Plants heavily attacked by herbivores were excluded.

### Experiment 2. Susceptibility of *C. indica* Grown under Different Lighting Conditions to Insect Attacks

This experiment was conducted about 50m away from Experiment 1. The setting and construction of light treatments were similar to those of Experiment 1. Five seedlings were grown in each light treatment, full sunlight and 25% of full sunlight environment. The distance between treatments was 5m.

Throughout the experiment, incidents of insects that fed on any parts of the *C. indica* (flower, leaves, stem, roots, etc.) were recorded, beginning one month after the shade treatment was applied. Samples of immature insects and imago were captured and sent to the Indonesian Institute of Sciences (LIPI) for identification. The observation was terminated after six months, because many new leaves that had emerged—as the older leaves at the bottom senesced—made it difficult to measure insect damage to the leaves.

At the end of the experiment, seedlings were measured for the following parameters: shoot length, leaf area, and root conditions. Any condition resulting from insect infestation was carefully recorded. Damage to leaves, shoots and roots of the *C. indica* caused by insect infestation was analyzed. Reduction of leaf area as a result of insect feeding was measured by using the method described by [14].

### Statistical Analysis

A randomized complete block design was implemented in this study. Data of plant height, shoot lengths, number of leaves, leaf area were analyzed using Microsoft Excel 2016. The effects of light

treatments on these measured parameters were tested by using a One-Way ANOVA, and test of Least Significant Difference (LSD) was conducted to determine the statistical significance between the two light treatments. The level of statistical significance was set at  $p \leq 0.05$ .

### III. RESULTS AND DISCUSSION

#### Environmental Conditions

The average maximum and minimum air temperatures during these experiments were  $38.5^{\circ}\text{C}$  and  $25.1^{\circ}\text{C}$ , with an average air temperature of  $31 \pm 5^{\circ}\text{C}$ . There was a temperature different between the Full sun and the 25% of Full sun environment from  $5^{\circ}\text{C}$  during the cloudy day to about  $15^{\circ}\text{C}$  during hot sunny days. The average relative humidity was  $74 \pm 2.3\%$ , and the total precipitation was 984mm. The averages of morning sunlight intensity were  $173.3 \mu\text{mol.s}^{-1}.\text{m}^{-2}$  and  $53.2 \mu\text{mol.s}^{-1}.\text{m}^{-2}$  for sunny clear days and cloudy days, respectively. The average of afternoon light intensities for clear sunny days was  $1810 \mu\text{mol.s}^{-1}.\text{m}^{-2}$  and on cloudy days  $240 \mu\text{mol.s}^{-1}.\text{m}^{-2}$ . Soil water contents measured from five hot sunny days during drought were  $19\% \pm 0.02$  and  $26\% \pm 0.02$  for 25% shade and Full sun soils, respectively.

#### Morphological Adaptation of *C. indicain* Shade and Direct-Sunlight Treatments

In these experiments, *C. indica* showed remarkable ability to adapt and survive in a wide range of growth lighting conditions. Although there were some morphological differences between *C. indica* grown in each treatment, not a single *C. indica* died, including those that were attacked by insects. The effects of light treatments on the morphology of *C. indica* are depicted in Table 1. *Canna indica* grown in the shade display significantly higher plant height, leaf area, leaf length-to-width ratio and branching frequency, whereas the plants grown in full sunlight have thicker leaves, and heavier fresh rhizome weight and earlier bud formation (Table 1).

Morphological adaptation	Full sunlight	25% of full sunlight
Mortality (%)	0	0
Plant height (cm)	$100.66 \pm 1.0^a$	$168.10 \pm 3.5^b$
Leaf area ( $\text{cm}^2$ )	$2.80 \pm 0.15^a$	$6.20 \pm 0.12^b$
Leaf length-to-width ratio	$1.92 \pm 0.03^a$	$2.17 \pm 0.04^b$
Leaf thickness (mm)	$0.23 \pm 0.04^a$	$0.18 \pm 0.03^b$
Branching frequency	$8.8 \pm 0.40^a$	$10.14 \pm 0.31^b$
Leaf orientation	More vertical	More horizontal and disperse around the stem
Bud formation	$4.69 \pm 0.47^a$	$2.36 \pm 0.29^b$
Flowering time	Earlier	12 Days delayed
Rhizome fresh weight (kg)	$2.35 \pm 0.10^a$	$0.58 \pm 0.03^b$

Table 1. Morphological adaptation of *Canna indica* to different light environments (mean  $\pm$ SE, n=5).

Mean  $\pm$ SE, with different letters within rows, are significantly different based on LSD ( $p \leq 0.05$ ). Light treatments had significant effects on shoot length and leaf area of *C. indica*. Those grown under 25% of full sunlight had longer shoot length (168cm) than those grown under full sunlight (100.8cm) (Figure 1). Similarly, higher leaf area was observed in 25% of full-sunlight-grown *C. indica* ( $6.2\text{cm}^2$ ) compared to those grown under full-sunlight treatment ( $2.8\text{cm}^2$ ) (Figure 1). These results were consistent with the previous findings on *C. edulis*, where it was capable of growing under a wide range of lighting environmental conditions [15,16]. *Canna edulis* was previously considered as the synonym for *C. indica* [17]. However, based on the Integrated Taxonomic Information System (ITIS), *edulis* is not the accepted name for this species [18]. Higher leaf area and shoot length were also observed in *C. indica* grown under 6-year-old rubber trees in a commercial plantation as compared to those grown on an open area (Sasaerila, unpublished).

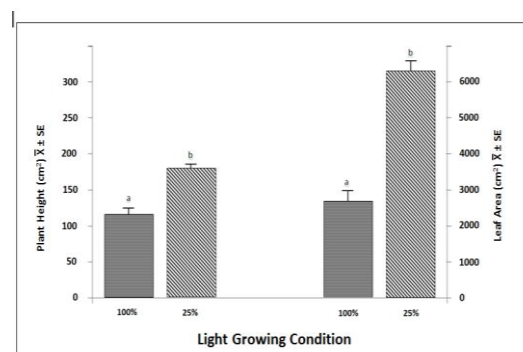


Figure 1. Shoot length (cm) and leaf area ( $\text{cm}^2$ ) of *C. indica* grown under Full sun (100% light) and 25% of full sunlight. Mean  $\pm$ SE with different letters are significantly different based on LSD ( $p \leq 0.05$ ).

The leaf length-to-width ratio is an indicator of the direction of leaf growth, whether medial-lateral axis (wider) or proximal-distal axis (longer). The average leaf length-to-width ratio of full sunlight- and shade-grown *C. indica* was significantly different ( $p \leq 0.05$ ) (Table 1). Shaded plants have longer leaves or have ratios more than 2, whereas the full-sunlight-grown plants have wider leaves or have ratios less than 2. Higher leaf length-to-width ratio in low-light-grown plants indicates that these plants have longer leaves, whereas high-light-grown plants have wider leaves. Similar results were reported by [19] in *Nothofagus cunninghamii* and [20] in *Zoysia japonica*. It is interesting that in this experiment, shade-grown *C. indica* tended to have a smaller leaf angle and appeared to be flatter (nearly horizontal) compared to the leaves of high light-grown *C. indica*, which had a larger leaf angle and more vertically oriented leaves. This is probably an adaptation to reduce light through self-shading by growing their leaves in a linear orientation and a more

overlapping leaf position when viewed from above. On the other hand, the plants grown in low light adapt by growing leaves around the stem to maximize light capture, that is, arranging leaves around the stem[21]. Thicker leaves in full-sunlight-grown plants may be caused by the presence of a waxy coating that protects the leaves against water loss and photodamage of the photosynthetic apparatus by increasing diffuse reflectance, reducing the amount of energy and heat absorption by the leaves [21]. A similar finding was reported in *Coffea arabica*, where full-sunlight-grown plants have increasing outer periclinal cell walls, and adaxial epidermis produced a thick epicuticular wax[22];[23]. In contrast, shade-grown *C. indica* had thinner but longer leaves that have a mass lower than that of thicker leaves because of fewer cells per unit area. These thinner leaves are more efficient in capturing light at low-level availability, hence optimizing the use of carbon gain[24]; [25].

Both groups displayed a contrasting pattern in branching. The majority of shaded *C. indica* had more than nine leaves, whereas the full-sunlight-grown *C. indica* had fewer than nine. Nine was used as the standard to classify the branching pattern since the number appeared often among plants in full sunlight and shade-grown *C. indica*. The higher number of branching in shade-grown *C. indica* compared to that of the full-sunlight-grown ones may indicate an adaptation to maximize the capture of light in low-light growth condition. On the other hand, full-sunlight-grown plants minimize the captures of light energy. This result was similar to that of a study on soybean, a shade-intolerant plant that showed decreasing in branching frequency in a shade-grown experiment[26];[27].

Significantly lower bud formation in shade-grown *C. indica* may be associated with energy conservation as the shaded plants were experiencing lower available light energy. Thus, it is possible that the plants did not invest much energy for newly germinated plants. This is in accordance with the flowering time of full-sunlight-grown *C. indica*, which was 12 days earlier than for those that were shade grown. A similar finding was reported in *Mischantus sinensis* that experienced a delayed in flowering by an average of 14 days[28]. This observation differs with shade-intolerant or avoidance species that accelerate flowering time when grown in a low-light environment [29].

Full-sunlight-grown *C. indica* had significantly ( $p \leq 0.05$ ) heavier rhizomes despite having fewer leaves than shade-grown *C. indica*. It may also be an adaptation to drier soil environment under full-sunlight conditions that causes more allocation of dry matter to the lower ground biomass in order to maximize the search for water[30]. A similar result was reported in *C. edulis* [31] and also in *Triticum aestivum*[32]. A study on *C. edulis* showed that four uppermost leaves served as the main contributor to the dry matter of the plant[31]. It may serve to explain higher rhizomes in full-sunlight-

grown *C. indica* and indicate the remarkable plasticity of *C. indica* to survive and grow in a wide range of lighting conditions.

### Effects of Light Treatments on Insect Infestation

Growth lighting condition appeared to have a significant effect on the insect attack incidents on *C. indica*. In these experiments, the leaves of the high-light-grown *C. indica* were attacked by grasshoppers (*Valanga* sp.) 28 days earlier than for those grown under the shade treatment. Furthermore, the leaves of *C. indica* grown in full sunlight were significantly ( $p \leq 0.05$ ) damaged, with a total loss of leaves of about 478.69 cm<sup>2</sup> or about 17% of total leaves compared to only 63.87 cm<sup>2</sup> (1% of total leaves) for the shade-grown plants (Figure 2). It is noteworthy that these damaged leaves were quickly replaced with new leaves in the full-sunlight treatment as *C. indica* grown under this treatment had an earlier bud break compared to its counterpart under the shade treatment.

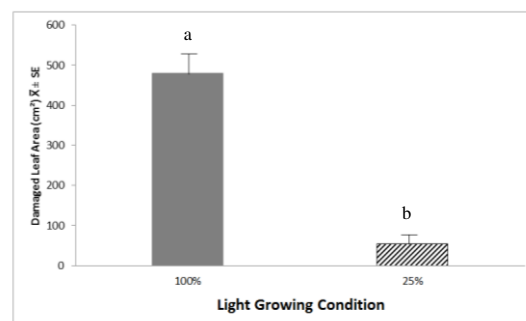


Figure 2. Damaged leaf area by insects on *C. indica* grown in Full sun and in 25% of Full sunlight. Mean ± SE with different letters are significantly different based on LSD ( $p \leq 0.05$ ).

Insects that were observed to attack the leaves of *C. indica* during these experiments were: *Valanga nigricornis* (Acrididae: Orthoptera), *Systoloderus* sp., larvae of Lepidoptera (Pyrilidae) and Psychidae. The most leaf-damage was caused by the *Valanga* sp. Larvae of Pyralids and Nymphalids were observed feeding on the young leaves of shade-grown *C. indica*. However, the damage was minimal. Similarly, feeding marks of Psychidae were also not serious. It is interesting that they were observed to be more attracted to the full-sunlight-grown plants. These three insects from the family of Pyralidae, Nymphalidae and Psychidae were, for the first time, reported to feed on *C. indica*. No infestation to any *C. indica* roots was observed in these experiments. This result is consistent with the previous report on the pest of *C. indica*[13, 3].

The shaded environment seems to be the best growth condition for *C. indica*, which increase its ability to defend itself against insect attacks, especially by its main pest, the grasshopper. Several factors may explain the significantly higher insect attack on *C. indica* grown under high-lighting environment. In these experiments, *C. indica* grown under full sunlight has a higher temperature, especially during

the day, at least about 5°C than the temperature of shade-grown plants.

This condition may have induced slight water stress in full-sunlight-grown plants. In fact, inspection of most of the leaves of full-sunlight-grown *C. indica* showed symptoms of chlorosis (data not shown), possibly an indication of drought stress that caused inhibition of chlorophyll [33].

Higher leaf temperature of high-light-grown plants may be a preferred spot, or ambience for insect activities, especially with the elevated morning temperature that could save some energy when insects are about to start their activities as compared to the ambience of a shaded area. This higher temperature may deter mutualistic microorganism, thus reducing natural enemy pathogen against the insects. Studies have shown that water-stressed plants attract insect defoliators because of their higher sugar and nitrogen content in the leaves [34]. Water stress, which is clearly shown on the growth of *C. indica* under high light, may cause a slight reduction of its ability to defend itself against defoliators [35].

Finally, in this research, *C. indica* showed remarkable ability to recover from insect attack despite being grown under the least favorable condition. These experiments have shown that *C. indica* has the potential to be used as intercropping food plants for the following reasons: 1) This species is shade-tolerant; 2) It does not have major pests or diseases and is capable of surviving insect attacks despite being grown under the least favorable condition; and 3) It is capable of protecting the soil through its fast-growing behavior, large leaf size and its contribution of soil nutrient from its above-ground biomass.

## ACKNOWLEDGEMENT

We would like to thank the Indonesian Directorate General of Higher Education, the Ministry of Research and Technology – Higher Education, and the Lembaga Penelitian dan Pengembangan (LPPM), Universitas Al Azhar Indonesia, for the supports for this project.

## REFERENCE

- [1] Piyachomkwan K., Chotineerant S., Kijkhunasatian. C., Tonwitawat R., Prammanee S., Oates, C.G., & Sriroth K., 2002. Edible canna (*Canna edulis*) as a complementary starch source to cassava for the starch industry. *Ind. Crop. Prod.* 16:11-21
- [2] Stür W.W., and Shelton H.M., 1990. Review of forage resources in plantation crops of Southeast Asia and the Pacific. In: Australian Centre for International Agricultural Research (ACIAR) Proceedings of a workshop: Forages for Plantation Crops. Sanur Beach, Bali, Indonesia. 27-29 June 1990. 168 p.
- [3] Imai K., 2002. Edible canna: a prospective plant resources from south America. *Jpn. J. Plant Sci.*, 2: 46-53.
- [4] Soni P.L., Sharma H. Srivastava H.C., & Gharia M.M., 1990. Physicochemical properties of *Canna edulis* starch – comparison with maize starch. *Starch*, 42: No. 12.S, 460-464.

- [5] Zhang J., Wang Z-W, & Shi X-M, 2008. Effects of microwave heat/moisture treatment on physicochemical properties of *Canna edulis* Ker starch. *J. Sci. Food Agric.* 89:653-664.
- [6] Wafa S.N., Taha R.M., Mohajer S., Mahmud N., & Abdul A.A., 2016. *BioMed. Res. Intl.* 2016, 1-9.
- [7] Bruck H., Jureit C., Hermann M., Schulz A., & Sattelmacher B., 2001. *Plant Biology* 3:326-334.
- [8] Zhang Z., Rengel Z., & Meney K., 2007. Growth and resource allocation of *Canna indica* and *Schoenoplectus validus* as affected by interspecific competition and nutrient availability. *Hydrobiologia* 589:235-248.
- [9] Glinos E., & Cocucci A.A., 2011. Pollination biology of *Canna indica* (Cannaceae) with particular reference to the functional morphology of the style. *Plant Syst. Evol.*, 291: 49-58.
- [10] Konnerup D., Koottatep T., & Brix H. 2009. Treatment of domestic wastewater in tropical, subsurface flow constructed wetlands planted with *Canna* and *Heliconia*. *Ecological Engineering* 35:248-257.
- [11] Centre for Agriculture and Bioscience International (CABI), 2017. *Canna indica* (Canna lily). Available from CABI, <https://www.cabi.org/isc/datasheet/14575>.
- [12] Plant for a Future. 2017. Available from: <http://www.pfaf.org/user/Plant.aspx>
- [13] Reddy, P.P., 2015. Plant protection in tropical root and tuber crops.
- [14] Bakr E.M., “A new software for measuring leaf area, and area damaged by *Tetranychus urticae* Koch,” *J. Appl. Entomol.*, vol. 129, no. 3, pp. 173–175, 2005.
- [15] Ishida Y and Imai, K. 2003. Gas exchange characteristics in leaves of edible canna with special reference to carbon dioxide concentration. Proceedings of the Kanto Branch, the Crop Science Society of Japan. 18:94-95.
- [16] Sasaerila Y., Noriko, N., Sakinah, Saputra, A. 2012. Effect of shades on the growth and physiology of ganyong (*Canna edulis*). Proc. of International Seminar on Science and Technology Innovations. Jakarta: Universitas Al Azhar Indonesia.
- [17] Segeren, W. and Maas, P.J.M., 1971. The genus *Canna* in Northern South America. *Acta Bot. Neerl.* 20(6):663-680.
- [18] Integrated Taxonomic Information System. *Canna indica* L. (Taxonomic Serial No.: 42413). Available from: <http://www.itis.gov>. [Accessed 30 July, 2019].
- [19] Hovenden, M.J. and Vander Schoor, J.K. 2006. The response of leaf morphology to irradiance depends on altitude of origin in *Nothofagus cunninghamii*. *New Phytol.*, vol. 169, no. 2, pp. 291–297.
- [20] Ganesan, M., Han, Y.J., Bae, T. W., Hwang, O.J., Chandrasekhar, T., Shin, A.Y., and Song, P. S. 2012. Overexpression in phytochrome A and its hyperactive mutant improves shade tolerance and turf quality in creeping bentgrass and Zoysiagrass. *Planta*, 236:1135-1150.
- [21] James, S.A. and D. T. Bell, Leaf orientation, light interception and stomatal conductance of *Eucalyptus globulus* ssp. *globulus* leaves, *Tree Physiol.*, vol. 20, no. 12, pp. 815–823, 2000.
- [22] Bondada, B.R., D. M. Oosterhuis, J. B. Murphy, and K. S. Kim, “Effect of water stress on the epicuticular wax composition and ultrastructure of cotton (*Gossypium hirsutum* L.) leaf, bract, and boll,” *Environ. Exp. Bot.*, vol. 36, no. 1, pp. 61–65, 1996.
- [23] M. F. Pompelli, G. M. Pompelli, E. C. Cabrini, E. C. Arruda, M. C. Ventrella, and F. M. DaMatta, “Leaf anatomy, ultrastructure and plasticity of *Coffea arabica* L. in response to light and nitrogen availability,” *Biotemas*, vol. 25, no. 4, 2012.
- [24] Terashima I., and Hikosaka K. 1995. Comparative ecophysiology of leaf and canopy photosynthesis. *Plant Cell Environ.*, 18, 1111-1128.
- [25] Evans J. R., & Poorter H., 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant Cell Environ.*, 24:755-767.
- [26] E. Green-Tracewicz, E. R. Page, and C. J. Swanton, “Shade

- Avoidance in Soybean Reduces Branching and Increases Plant-to-Plant Variability in Biomass and Yield Per Plant,” *Weed Sci.*, vol. 59, no. 1, pp. 43–49, 2011.
- [27] C. M. M. Gommers, When growing tall is not an option contrasting shade avoidance responses in two wild Geranium species. 2013.
- [28] O. J. Hwang, S. H. Lim, Y. J. Han, A. Y. Shin, D. S. Kim, and J. Il Kim, “Phenotypic characterization of transgenic miscanthus sinensis plants overexpressing arabidopsis phytochrome B,” *Int. J. Photoenergy*, vol. 2014, 2014.
- [29] Franklin, K.A. 2008. Shade avoidance. *New Phytologist*. 179:930-944.
- [30] K. W. Tomlinson et al., “Biomass partitioning and root morphology of savanna trees across a water gradient,” *J. Ecol.*, vol. 100, no. 5, pp. 1113–1121, 2012.
- [31] Kato M., and Imai, K. 1996. Studies on matter production of edible canna (*Canna edulis* Ker.). IV. Leaf unrolling and changes in leaf photosynthetic rates with growth under field conditions. *Japanese Journal of Crop Science* 65: 253-259.
- [32] Laghrari, K.B., Munir, M., Farrar, J.F., and Mahar, A.N. 2004. *J. food, Agric. Env.* 2004. 2:149-156.
- [33] Kramer, P.J. 1983. *Water relations of plants*. Academic Press. New York.
- [34] Dale, A.G. and Frank, S.D. 2017. Warming and drought combine to increase pest insect fitness on urban trees. *PLoS ONE* 12(3):e0173844.
- [35] Mattson, J.M. and Haack, R.A. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience* 37:110-118.

★ ★ ★