

The Effect of Light and Water Supply on Growth, Net CO₂ Assimilation Rate and Mineral Content of Salak (*Salacca zalacca* (Gaertn.) Voss) Seedlings

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Abstract

The study was carried out in a greenhouse of at the Institute for Horticultural Sciences of the Humboldt Universität zu Berlin. Seven-months-old seedlings of salak cultivars “pondoh” from Indonesia were used for the study. At this age, plants are usually transferred from the nursery to the field in the growing region. An experimental block design was arranged for the study. A total of 48 experimental plants was separated into two blocks, namely shading (S) and non-shading (N). Three water supply treatments were assigned to each block. At the beginning of the study, the seedlings for N treatment were moved from shading to non-shading tables in the greenhouse. Three water supply treatments were assigned to each block. At the beginning of the study, the seedlings for N treatment were moved from shading to non-shading tables in the greenhouse. Two additional 400 W lamps (HQI-TS/D, OSRAM, Germany) were placed 2 m above the seedlings in the N treatment. Three watering treatments, applied to each block, were W1 (100 ml distilled water per plant every 2 days), W2 (100 ml per plant every 4 days) and W3 (100 ml per plant every 6 days). Therefore, the combinations of the treatments were SW1, SW2, SW3, NW1, NW2 and NW3. Responses to be analysed were shoot and root dry weight, increment of shoot length and leaf area, net CO₂ assimilation rate (P_N) and plant mineral contents, i.e. N, P, K, Ca and Mg. In addition, water content of the growing media was recorded. The study results showed that shading, which reduced sunlight by 70 %, was not beneficial for 7-months-old salak seedlings, due to lower growth rate, P_N and N content as compared with plants in non-shading conditions. On the other hand, light intensities above 800 μmol m⁻² s⁻¹ (PAR) possibly cause leaf bleaching and should be avoided. Salak plants did not tolerate drought conditions. However, different water supply did not affect P_N and mineral uptake (N, P, K, Ca, Mg) of salak plants.

Keywords: *Salacca zalacca*, Light, Water supply, Growth, Photosynthesis, Mineral content

1. Introduction

Environmental conditions, such as water availability and solar irradiation may become stress factors for plants if the dosage is too high or too low (Lüttge, 1997). However, the major factor in terms of plant stress is the complex interaction between plant and environment (Lüttge, 1997; Biswal and Biswal, 1999). Many environmental factors individually may not provoke any stress but in combination they can cause harmful situations for plants.

Water is among the most limiting factors for plant productivity and growth rate worldwide (Pugnaire et al., 1999), because of its essential role in plant metabolism, both at cellular and whole-plant level. Any decrease in water availability has an immediate effect on plant growth and physiological processes such as photosynthesis or mineral transport and accumulation (Hsiao et al., 1976). Water loss by transpiration causes transient water deficit, therefore the most plants suffer at least regular and daily water shortages. When drying, soil causes water absorption to lag behind transpiration and permanent water deficit may result in wilting and plant death due to dehydration (Pugnaire et al., 1999).

Photosynthesis is the fundamental physiological process for plant growth and production. Besides plant-related factors, environmental conditions influence net CO₂ assimilation rate (P_N), including irradiance, water availability, CO₂ concentration and temperature (Baswal and Baswal, 1999). Excessively high solar irradiance can damage the photosynthetic system, particularly in shade-adapted leaves or in leaves where the photosynthetic CO₂ assimilation has been inhibited by other stressors such as extreme temperature or water deficit (Jones, 1992). The damage can be a result of photooxidation where bleaching of chlorophyll occurs. Leaf injury not accompanied by bleaching is usually termed as photoinhibition (Jones, 1992).

Salak (*Salacca zalacca* (Gaertn.) Voss) is an understory palm tree species growing at low light conditions in tropical rain forests of South-East Asia. Salak belongs to a group of palms, which are 1.5 - 5 m high, extremely spiny and sprout their leaves from the ground level. There are 30 cultivars of salak, which distribute across the Indonesian islands (Sudaryono et al., 1993; Kusumo, 1995). The availability of superior quality fruit of selected cultivars will promote the marketing of salak, such as cultivars “pondoh” from Yogyakarta and “gula pasir” from Bali provinces. “Pondoh” is cultivated in the sub district Sleman of the Yogyakarta province. In Indonesia, salak has been cultivated throughout the islands and the fruit is widely used as fresh fruit. Salak production in Indonesia has increased from 423.5 t in 2000 to 862.5 t in 2009 (Ministry of Agriculture, 2011). Fresh salak fruits have been exported to Singapore, Middle-East, Malaysia, Hongkong and China (Ministry of Agriculture, 2009).

In Indonesia, research on many aspects of salak fruit including pre- and postharvest have been carried out. Up to now, there is only limited knowledge about the physiological responses of salak to environmental factors. To promote production and fruit quality of salak, knowledge about ecophysiological aspects is very important. Thus, the purpose of this study was to investigate the effects of light and water supply on growth and physiological responses of salak seedlings.

2. Material and Methods

2.1 Location and experimental design

The study was carried out for a period of 6 weeks (April to May 2003) in a greenhouse at the Institute for Horticultural Sciences of the Humboldt Universität zu Berlin. The temperature of the greenhouse were adjusted to 20 °C/25 °C (day/night) and the relative humidity was between 40 and 80 %.

Seven-months-old seedlings of salak cultivars “pondoh” from Indonesia were used for the study. At this age, plants are usually transferred from the nursery to the field in the growing region. The plant growing media was compost/sand (1/1, weight/weight). The compost media (pH 6) comprised of 320 mg/l N, 320 mg/l P₂O₅ and 450 mg/l K₂O and was mixed with quartz sand (0.6 – 1.2 mm). Salt content was less than 3 g/l NaCl. Seedlings were planted in 14.5 cm x 11 cm pots. All plants tested were kept on greenhouse tables under shade nettings from germination until the beginning of the treatments. Shading was achieved using double shading net (Varia N2 9011, Wunderlich, Germany), 2 m above the seedlings. Full sun light was reduced by 70 %.

An experimental block design was arranged for the study. A total of 48 experimental plants was separated into two blocks, namely shading (S) and non-shading (N). Three water supply treatments were assigned to each block. At the beginning of the study, the seedlings for N treatment were moved from shading to non-shading tables in the greenhouse. Two additional 400 W lamps (HQI-TS/D, OSRAM, Germany) were placed 2 m above the seedlings in the N treatment. Three watering treatments, applied to each block, were W1 (100 ml distilled water per plant every 2 days), W2 (100 ml per plant every 4 days) and W3 (100 ml per plant every 6 days). Therefore, the combinations of the treatments were SW1, SW2, SW3, NW1, NW2 and NW3.

Responses to be analysed were shoot and root dry weight, increment of shoot length and leaf area, net CO₂ assimilation rate (P_N) and plant mineral contents, i.e. N, P, K, Ca and Mg. In addition to that, water content of the growing media was recorded.

2.2 Water content of the media

Water content of the media was measured with Time Domain Reflectometry (TDR), Soil Moisture Meter (70M/m/92, Easy Test Ltd., Poland) before the plants were watered according to the treatments. Digital readings ranged from 0 % (dry) to 100 % (saturated). During the study, 5 sets of TDR data were recorded (replicates of three media per treatment) from week 1 until week 5 of the experiment.

2.3 Growth

Shoot and root dry weight were measured at the end of the study after drying the fresh samples at 103 °C to constant weight (Maier, 1990). Leaf samples were weighed after drying at 65 °C for 8 h and were later used for the analysis of mineral contents. Shoot length and leaf area were first measured immediately after the seedling had been transplanted into the growing media. The second measurement was 14 weeks later. Shoot length was measured with a ruler, leaf area was measured with a leaf area meter (CI – 202, CID Inc., USA).

2.4 Net CO₂ assimilation rate

Net CO₂ assimilation rate (P_N) of the leaves were measured at week 1, 2, 4 and 6 after the onset of treatments with a portable photosynthesis measuring system (CI-301PS, CID Inc., USA). The measurements were conducted starting from 10 am until 12 am, except at week 6 when measurements were taken from 11 am until 1.30 pm.

2.5 Mineral content

Leaf mineral contents were analysed from dried and ground samples (Mikro-Feinmühle-Cullati DCFH 48, Janke & Kunkel, Germany). N content was determined following a modified Kjeldahl method as has been described by Okoye (1980). 500 mg leaf powder were digested (Büchi 430 Digestor, Büchi Labortechnik AG, Switzerland) in boiling 98 % H₂SO₄ (20 ml) and selenium catalyst (15348 Merck, Germany). The samples were thereafter distilled in a Büchi-Scrubber B-412 (Büchi Labortechnik AG, Switzerland) into 0.1 mol H₃BO₄ and subsequently were titrated with 0.1 N HCl. N content was calculated and expressed as % of DM.

P, Ca, Mg and K were analysed according to a modification method as described by Evenhuis and de Waard (1980). The samples were dry-ashed at 490 °C for 4 h. Ashes were dissolved in 25% HCl and were evaporated in a sand bath for 20 min until the complete disappearance of solid residues. P was determined photometrically (Eppendorf 1101 M, Germany). The other minerals were analysed using atomic absorption spectrophotometry (AAS) (905 A, GBC, Australia). The data of the minerals were expressed as mg/g DM.

2.6 Statistical analyses

All sample data were subjected to compare means and further analysed with least significant difference (LSD) test (Steel et al., 1997), with significant difference between means determined ($P \leq 0.05$) using the Statistic Program MINITAB 14 (Minitab Inc., State College, USA, 2001). The analyses comprised of solely the effect of light conditions or water supply treatments on growth, P_N and mineral content of salak seedlings. The effect of interactions between light conditions and water supply on growth, P_N and mineral content of salak seedlings was also analysed.

3. Results and Discussions

3.1 Water content of the media

Water content of the growing medium of salak seedlings grown under different light conditions is summarised in Table 1. No differences in water content of salak seedlings media were found between shading and non-shading treatments up to week 3. From this time on, medium moisture of non-shading treatment (20.51 %) was always slightly lower than that of shading treatment (24.39 %).

Water content of the growing medium of salak seedlings grown under different water supply variants is presented in Table 2. W1 represented a root zone moisture content of 30.83 % (29 - 33 %), W2 was 20.48 % (16 - 25 %) and W3 was 16.38 % (11 - 25 %).

3.2 Growth

The effect of light on growth parameters of salak seedlings is summarised in Figure 1 and Table 3. Root and shoot dry weight as well as the increment of leaf area of seedlings growing in non-shading conditions were higher as compared with those in the shading variant (46 %, 31 % and 14 % respectively). Similar results were reported by Stoneman and Dell (1993) and Stoneman et al. (1995) on *Eucalyptus marginata* seedlings, i.e. growth of all plant

parts increased in response to higher light level. In grape (*Vitis vinifera*), leaf, shoot, trunk, root and total plant dry weights were reduced when growing under lower light level (Van den Heuvel et al., 2004); root growth decreased by 84 % in vines that had been shaded for a period of 16 weeks (Van den Heuvel, 2002). Root dry weight of vines growing under 80 % shading were reduced by 51 % in the following year (McArtney and Ferree, 1999). The increment of shoot length of seedlings in the non-shading variant was smaller as compared with those under shading conditions (29 %). This can be explained as etiolation effect indicating that under the shading net, light intensity was too low for proper growth of salak seedling.

The effect of water supply on growth of salak seedlings is presented in Table 4. No differences of growth parameters were found among water supply treatments. However, there was a strong effect of water supply on leaf area. The reduction by 26 % in the increment of leaf area of both W2 (watered every 4 days) and W3 (watered every 6 days) treatments as compared with W1 (watered every 2 days) was found. The reduction of leaf area appears to be largely affected by soil water status and by root hydration (Termaat et al., 1985). This could be correlated with the result of water content of the media that more frequent watering resulted in higher water content of the media. On the other hand, Levitt (1980) stated that decreased cell turgor (cell enlargement) is the most sensitive plant response to water stress, since cell growth is quantitatively related to cell turgor, and cell turgor decreases with any dehydration-induced decrease in cell water potential. Factors which postpone dehydration by reducing water loss, such as a decrease in leaf area, are known to decrease productivity (Turner, 1979). Moreover, it was found, that salak plants are drought susceptible, since the plants began to wilt during a 2 to 3 weeks drought period (Lestari and Ebert, 2002)

The growth parameters affected by light and water supply treatments are summarised in Table 5. Seedlings growing in full light with highest water supply had the highest root and shoot weight as well as leaf area increment. This result indicated non-shading and high water supply were the most suitable conditions for growth of salak seedlings. On the other hand, seedlings of the shading variant and high water supply developed the lowest root and shoot dry weight. Shading in the study obviously reduced too much light, which was required by seedlings for growing more vigorously. On the other hand, more frequent water supply and shading caused excessive high water content of the growing media which possibly lead to oxygen depletion. These conditions are regarded to cause the inhibition of leaf extension and cessation of root growth (Marschner, 1995).

3.3 Net CO₂ assimilation rate

Net CO₂ assimilation rate (P_N) of salak seedlings under different light conditions is presented in Figure 2. Under non-shading (N) condition during the measurements photosynthesis active radiation (PAR) was about 400 to 700 $\mu\text{mol m}^{-2} \text{s}^{-1}$, whereas shading (S) reduced PAR by 70 %. Until week 4, P_N of seedlings in non-shading (varying in between 3.4 and 3.6 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) was higher as compared with in shading condition (varying from 2.2 to 3.0 $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$). This result gave evidence that shading limited P_N in salak seedlings. Higher light intensity led to higher P_N in salak seedlings of non-shading condition as compared with that of seedlings under a shading net, except the midday P_N measurement at week 6. A great number of publications give evidence, that photosynthetic CO₂ – assimilation is limited by light intensity (Wong et al., 1978; von Caemmerer and Farquhar, 1981; Stoneman et al., 1995). Higher P_N resulted in more chemical energy in the form of carbohydrates and other organic compounds, which are ultimately used for plant growth. Similar results have been reported for banana plants, where P_N was lower under shading conditions as compared to plants in full sun light (Thomas and Turner, 2001). This was due to the limitation of P_N by low photosynthetic photon flux density. The mesophyll resistance, which is usually regarded as the sum of biophysical and biochemical resistances to CO₂ movement between the mesophyll cell wall and the site of carboxylation in the chloroplast, was reported to be higher in plants grown at low light intensities (Holmgren, 1968, Crookston et al., 1975).

There was no net CO₂ gain in non-shaded plants at week 6, measured over midday hours (Figure 2). The phenomenon of low P_N at intensive solar irradiation and high water vapour saturation deficit is well known for many plants species (“midday depression”). In our experiment, this effect was induced by high light radiation (up to PAR of 1636 $\mu\text{mol m}^{-2} \text{s}^{-1}$) during the P_N measurement. The “midday depression” in plants subjected to water stress is associated with photoinhibition. Both light and water stress evidently initiate an activation of the primary photochemical pathway associated with photosystem II (Björkman and Powles, 1984). This could be proved by the occurrence of bleaching in some salak leaves subjected to full sun light. It is well established that photobleaching is a secondary phenomenon following photoinhibition (Powles, 1984). Similar photoinhibitory effects or midday reduction of P_N at high photon flux density (more than 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) have been reported for water-stressed carambola (Ismail et al., 1994) and citrus plants (Brakke and Allen Jr., 1995). This was typically attributed to large leaf-to-air vapour pressure difference or high atmospheric vapour pressure deficit. Therefore, in the case of light-susceptible salak, shade is an important factor for the survival of plants especially with respect to water stress.

As known from a previous study, salak palms are very susceptible to high light intensities (Lestari and Ebert, 2003).

P_N of salak seedlings at different water supply is presented in Figure 3. Until week 4 of the treatment, there was no clear influence of water supply on P_N (ranging from 2.5 to 3.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). However, P_N decreased at week 6, in all water supply treatments. Moreover, in some P_N measurements at week 6, there was no net CO_2 gain in W3 plants, but only leaf respiration. Some studies have suggested that the change in stomatal conductance was the main cause for the decrease in P_N in water-deficient plants (Boyer, 1976; Cornic, 2000). In *Nerium oleander* plants, subjected to water stress, full sun light resulted in an inhibition of non-stomatal components of photosynthesis. This was manifested as a reduced photon yield and light-saturated capacity of photosynthetic CO_2 uptake, measured after restoration of high leaf water potential and partial reopening of the stomata (Björkman and Powles, 1984). Either stomatal closure or non-stomatal limitation might have induced midday depression of P_N as observed in non-shaded salak plants. In case of stomatal closure, CO_2 supply from ambient air becomes the limiting step in the CO_2 assimilation process (Pugnaire et al., 1999).

P_N of salak seedlings affected by interaction of light and water supply are presented in Table 6. P_N of plants in all water supply treatments with non-shading condition tended to be higher than that of the interactions with shaded plants. P_N of NW2 plants at week 1 and 4 was found to be the highest. The midday measurement of week 6 indicated that plants under full sun light failed to assimilate CO_2 . The results indicate that light had a stronger effect on P_N in salak seedlings than water supply. Some studies also reported that “midday–depression” of P_N under high irradiance can be observed either in stressed or non-stressed young carambola plants (Ismail et al., 1994), in well-irrigated *Protea acaulos* (Herppich et al., 1994) and in young, well-watered *Welwitschia mirabilis* (Herppich et al., 1996).

P_N of salak is generally low, even at high PAR. This phenomenon is a characteristic of shade plants, which have very low light compensation points i.e. 0.5 – 2 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ in the extreme shade species *Alocasia macrorrhiza* (Jones, 1992). At high PAR, P_N of some other tropical tree species, such as peach palm (*Bactris gasipaes* Kunth) is about 10 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Oliveira et al., 2002), oil palm 25 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Dufrene and Saugier, 1993), mango 8 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Fukamachi et al., 1998), banana is 19 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Thomas and Turner, 2001) and citrus is 11 $\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (Brakke and Allen Jr., 1995).

3.4 Mineral content

N content of leaves was strongly influenced by light conditions. There was no influence on the uptake of other ions (Table 7). Estimates of the quantity of nutrients supplied to plants by mass flow are not only based on the nutrient concentration in the soil solution but also on the transpiration (Marschner, 1995). Movement of nutrients to the root surface via mass flow and subsequently from the root into leaves are predominantly influenced by transpiration (Shaner and Boyer, 1976). Higher transpiration rates under full-light condition will result in higher nutrient uptake. These could possibly explain the increased N concentration in the leaves of non-shaded plants as compared to that of shaded plants. This result might also relate with reduced growth and lower P_N of salak seedlings in shading as compared with in non-shading conditions. A strong relationship exists between total plant N concentration and the fraction of plant dry matter that is produced in leaf tissue (Agren and Ingestand, 1987). Furthermore, Agren (1985) and Hirose (1988) modelled the plant relative growth rate as a linear function over a wide range of whole-plant internal N concentrations. There is also a tight relation between leaf N and maximum photosynthetic activity (Le Bot et al., 1998). Mathematical functions have been applied for modelling the effect of N on P_N (DeJong and Doyle, 1985; Hirose and Werger, 1987; Sage and Pearcy, 1987; Hirose et al., 1988; Lim et al., 1990). Since the growth of plants is a function of their photosynthetic capacity and allocation to leaf tissue, interrelationships between N productivity, leaf growth, net assimilation rate and relative growth rate can be modelled (Agren and Ingestand, 1987; Hirose, 1988).

On the other hand, there were no differences in mineral contents of salak seedlings in all water supply treatments (Table 8). This indicated that water supply did not limit the nutrient uptake of the seedlings.

The contents of N, P, K, Ca and Mg in salak seedlings affected by interaction of light and water supply are summarised in Table 9. N content of SW1 plants was lower than that of NW2 and NW3 plants, but not different to that of the other interactions tested. On the other hand, no differences of N content in salak leaf were found between similar water supply treatment in non-shading and shading condition. These results indicated that light had a stronger effect on N content of salak seedlings as compared to water supply. Interactions of light and water supply did not affect mineral contents of salak seedlings in this experiment.

According to Marschner (1995), the optimal ranges of mineral content in plant shoot for growth (in mg/g) are as follows: N = 20 – 50; P = 3 – 5; K = <20 – 50, Mg = 1.5 – 3.5, and Ca = 1 – 50, whereas optimal leaf element

concentration for oil palm (*Elaeis guineensis*) according to Fairhorst and Hårdter (2003) as follows (in mg/g): N = 14, P = 1.5 – 1.9, K = 10 – 13, Mg = 1.6 – 2.2, Ca = 1.4 – 2.5. In our experiments, salak seedlings showed nutrient contents being in the optimal range (Marschner, 1995), with the exception of Mg. This might be due to a limited availability of this element in the media, since there was no supply of nutrients to the seedlings during the experiment. Only N was found to be significantly lower in shaded plants. The results clearly indicate that under the experimental condition as explained above, nutrient uptake of salak seedlings was neither affected by shading nor by water supply.

4. Conclusions

From the study it is concluded that shading, which reduced sunlight by 70 %, was not beneficial for 7-months-old salak seedlings, due to lower growth rate, P_N and N content as compared with plants in non-shading conditions. Six weeks after the treatments, a photoinhibitory response of non-shaded plants was detected, which caused bleaching of salak leaves. Shading is to a certain extent required for raising salak seedlings. However, light intensities less than $250 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) may lead to retarded growth, decreased P_N and inhibited N uptake. Light intensities above $800 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR) possibly cause leaf bleaching and should be avoided. Salak plants did not tolerate drought conditions. However, different water supply did not affect P_N and mineral uptake of salak plants. Light had a stronger effect on P_N and nutrient uptake of salak seedlings as compared to water supply.

References

- Agren, G.I. (1985). Theory for growth of plants derived from the nitrogen productivity concept. *Physiol. Plant*, 64, 17-28.
- Agren, G.I. and Ingestand, T. (1987). Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant Cell Environ*, 10, 579-586.
- Biswal, B. and Biswal, U.C. (1999). Photosynthesis under stress: Stress signals and adaptive response of chloroplast. In: Pessaraki, M. (ed.). Handbook of plant and crop stress (2nd ed., revised and expanded). Marcel Dekker, Inc. New York and Basel, 315 – 336.
- Björkman, O. and Powles, S.B. (1984). Inhibition of photosynthetic reactions under water stress: Interaction with light level. *Planta*, 161, 490-504.
- Boyer, J.S. (1976). *Water deficit and photosynthesis*. In: Kozlowski, T.T. (ed.). Water deficits and plant growth, Vol. IV: Soil water measurements, plant responses and breeding for drought resistance, Academic Press, London and New York, 153-190.
- Brakke, M. and Allan Jr, L.H. (1995). Gas exchange of Citrus seedlings at different temperatures, vapour-pressure deficits and soil water contents. *J. Am. Soc. Hort. Sci.*, 120, 497-504.
- Cornic, G. (2000). Drought stress inhibits photosynthesis by decreasing stomatal aperture not by affecting ATP synthesis. *Trends Plant Sci.*, 5, 187-188.
- Crookston, R.K., Treharne, K.J., Ludford, P. and Ozbun, J.L. (1975). Response of beans to shading. *Crop. Sci.*, 15, 412-416.
- DeJong, T.M. and Doyle, J.F. (1985). Seasonal relationships between leaf nitrogen content (photosynthetic capacity) and leaf canopy light exposure in peach (*Prunus persica*). *Plant Cell Environ*, 8, 701-706.
- Dufrene, E. and Saugier, B. (1993). Gas exchange of oil palm in relation to light, vapour pressure deficit, temperature and leaf age. *Functional Ecol.*, 7, 97-104.
- Fairhorst, T. and Hårdter, R. (2003). Oil palm – Management for large and sustainable yields. Potash and Phosphate Institute (PPI), Potash and Phosphate Institute of Canada (PPIC) and International Potash Institute (IPI). Singapore.
- Fukamachi, H., Yamada, M., Komori, S. And Hidaka, T. (1998). Photosynthesis in longan and mango as influenced by high temperatures under high irradiance. JIRCAS Newsletter No. 17.
- Hirose, T. (1988). Modelling the relative growth rate as a function of plant nitrogen concentration. *Physiol. Plant*, 72, 185-189.
- Hirose, T. and Werger, J.A. (1987). Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiol. Plant*, 70, 215-222.
- Hirose, T., Werger, J.A., Pons, T.L. and van Rheenen, J.W.A. (1988). Canopy structure and leaf nitrogen distribution in a stand of *Lysimachia vulgaris* L. as influenced by stand density. *Oecologia*, 77, 145-150.

- Herppich, M., Herppich, W.B. and von Willert, D.J. (1994). Influence of drought, rain and artificial irrigation on photosynthesis, gas exchange and water relations of the fynbos plant *Protea acaulos* (L.) Reich at the end of the dry season. *Bot. Acta*, 107, 369-472.
- Herppich, W.B. (2000). Interactive effects of light and drought stress on photosynthetic activity and photoinhibition under (sub-) tropical conditions. *Acta Hort.*, 531, 135-142.
- Holmgren, P. (1968). Leaf factors affecting light-saturated photosynthesis in ecotypes of *Salidago virgaurea* from exposed and shaded habitats. *Physiol. Plant.*, 21, 676 – 698.
- Hsiao T.C., Acevedo, E., Fereres, E. and Henderson, D.W. (1976). Water stress, growth and osmotic adjustment. *Philos. Trans. R. Soc. Lond. Ser. B*, 273, 479-500.
- Ismail, M.R., Burrage, S.W., Tarmizi, H. and Aziz, M.A. (1994). Growth, plant water relation, photosynthesis rate and accumulation of proline in young carambola plants in relation to water stress. *Sci. Hort*, 60, 101-114.
- Jones, H.G. (1992). *Plants and microclimate, a quantitative approach to environmental plant physiology* (2nd ed.). Cambridge University Press. UK.
- Kusumo, S. (1995). Salak, a prideful fruit of Indonesia. *IARD Journal*, 17 (2), 19–23.
- Le Bot, J., Adamowicz, S. and Robin, P. (1998). Modelling plant nutrition of horticultural crops: A review. *Sci. Hort.*, 74, 47-82.
- Lestari, R. and Ebert, G. (2002). Salak (*Salacca zalacca* (Gaertn.) Voss) – The snakefruit from Indonesia, preliminary results of an ecophysiological study. Proceeding of the Deutscher Tropentag 2002, Kassel, Germany.
- Lestari, R. and Ebert, G. (2003). The snake fruit salak pondoh (*Salacca zalacca* (Gaertner) Voss.) – A new fruit species from Indonesia. *BDGL-Schriftenreihe* 21: 208.
- Levitt, J. (1980). *Responses of plants to environmental stress*. 2nd ed. Academic Press, New York, USA.
- Lim, J.T., Wilkerson, G.G., Raper, C.D. Jr. and Gold, H.J. (1990). A dynamic growth model of vegetative soya bean plants: Structure and behaviour under varying root temperature and nitrogen concentration. *J. Exp. Bot.*, 41, 229-241.
- Lüttge, U. (1997). *Physiological ecology of tropical plants*. Springer. Berlin-Heidelberg, Germany.
- Marschner, H. (1995). *Mineral nutrition of higher plants*. 2nd ed. Academic Press. CA, USA
- Mc Artney, S.J. and Ferree, D.C. (1999). Shading effects on dry matter partitioning, remobilization of stored reserves and early season vegetative development of grapevines in the year after treatment. *J. of Am. Soc. of Hort. Sci.*, 124, 591-597.
- Ministry of Agriculture of Indonesia. (2011). [Online] Available: http://database.deptan.go.id/bdsp/hasil_kom.asp (March 6, 2011).
- Ministry of Agriculture of Indonesia. (2009). [Online] Available: http://www.hortikultura.go.id/index.php?option=com_content&task=view&id=240&itemid=1 (March 6, 2011).
- Oliviera, M.A.J., Bovi, M.L.A., Machado, E.C., Gomes, M.M.A., Habermann, G. and Rodrigues, J.D. (2002). Photosynthesis, stomatal conductance and transpiration in peach palm under water stress. *Sci. Agric. (Piracicaba Braz.)*, 59, 59 – 63.
- Powles, S.B. (1984). Photoinhibition of photosynthesis induced by visible light. *Ann. Rev. Plant Physiol*, 35, 15-44.
- Pugnaire, F.I., Serrano, L. and Pardos, J. (1999). *Constraints by water stress on plant growth*. In: Pessaraki, M. (ed.). *Handbook of plant and crop stress* (2nd ed., revised and expanded). Marcel Dekker, Inc. New York, and Basel, 271 – 283
- Sage, R.F. and Pearcy, R.W. (1987). The nitrogen use efficiency of C₃ and C₄ plants: II. Leaf nitrogen effects on the gas exchange characteristics of *Chenopodium album* (L.) and *Amaranthus retroflexus* (L.). *Plant Physiol.*, 84, 954-958
- Shaner, D.L. and Boyer, J.S. (1976). Nitrate reductase activity in maize (*Zea mays* L.) leaves: 1. Regulation by nitrate flux. *Plant. Physiol.*, 58, 623-636
- Steel, R.G.D., Torrie, J.H. and Dickey, D. (1997). *Principles and procedures of statistics*. McGraw-Hill, New York, USA.

Stoneman, G.L. and Dell, B. (1993). Growth of *Eucalyptus marginata* (jarrah) seedlings in a greenhouse in response to shade and soil temperature. *Tree Physiol.*, 13, 239-252.

Stoneman, G.L., Dell, B. and Turner, N.C. (1995). Growth of *Eucalyptus marginata* (jarrah) seedlings in Mediterranean-climate forest in south-west Australia in response to overstorey, site and fertiliser application. *For. Ecol. Manage.*, (79), 173-184.

Sudaryono, T., Purnomo, S. and Soleh, M. (1993). Cultivar distribution and estimation of area development of *Salacca* (in Indonesian). *Penel. Hort.*, 5, 1-4.

Termaat, A., Passioura J.B. and Munns, R. (1985). Shoot turgor does not limit shoot growth of NaCl-affected wheat and barley. *Plant Physiol.*, 77, 869-872.

Thomas, D.S. and Turner, D.W. (2001). Banana (*Musa* sp.) leaf gas exchange and chlorophyll fluorescence in response to soil drought, shading and lamina folding. *Sci. Hort.*, 90, 93-108.

Turner, N.C. (1979). Drought resistance and adaptation to water deficits in crop plants. In: Mussel, H. and Staples, R. (Eds). *Stress physiology in crop plants*. Wiley-Interscience, New York, USA, 181-194.

von Caemmerer, S. and Farquhar, G.D. (1981). Some relationship between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, 153, 376-387.

Vanden Heuvel, J.E., K.H. Fisher, J.T.A. Proctor and J. A. Sullivan. (2004). Shading affects morphology, dry-matter partitioning, and photosynthetic response of greenhouse-grown 'Chardonnay' grapevines (*Vitis vinifera* L.). *HortScience*, 39(1):65-70.

Vanden Heuvel, J.E., E.D. Leonardos, K.H. Fisher, J.T.A. Proctor, and J.A. Sullivan. (2002). Translocation and partitioning patterns of ¹⁴C photoassimilate from light- and shade-adapted shoots in greenhouse-grown 'Chardonnay' grapevines (*Vitis vinifera* L.). *J. Amer. Soc. Hort. Sci.*, 127(6):912- 918.

Wong, S.C., Cowan, I.R. and Farquhar, G.D. (1978). Leaf conductance in relation to assimilation in *Eucalyptus pauciflora* Sieb. Ex Spreng. Influence of irradiance and partial pressure of carbon dioxide. *Plant Physiol*, 62, 670-674.

Table 1. Water content of the growing medium of salak seedlings grown under different light conditions (shading (S) and non-shading (N))

Treatment	Week 1	Week 2	Week 3	Week 4	Week 5	Average
N (%)	17.47± 2.11a	20.37± 2.20a	21.23± 2.33a	23.06± 1.23a	20.42± 2.18a	20.51
S (%)	21.01± 2.22a	23.91± 1.21a	23.66± 1.65a	27.29± 1.14b	26.09± 1.62b	24.39

Values represent means ± SE. Different letters in the same column indicate significant differences by LSD test ($P \leq 0.05$)

Table 2. Water content of the growing medium of salak seedlings grown under different water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3))

Treatment	Week 1	Week 2	Week 3	Week 4	Week 5	Average
W1 (%)	31.15± 1.16 c	29.08± 0.67b	29.58± 0.94c	31.58± 1.03 c	32.78± 1.46 c	30.83
W2 (%)	15.75± 0.77 b	19.54± 1.55a	25.19± 1.15b	20.80± 0.97 a	21.12± 0.92 b	20.48
W3 (%)	10.81± 0.49 a	16.71± 1.55a	13.93± 1.08a	24.56± 0.65 b	15.87± 1.66 a	16.38

Values represent means ± SE. Different letters in the same column indicate significant differences by LSD test ($P \leq 0.05$)

Table 3. Leaf area and shoot length increments of salak seedlings under different light conditions shading (S) and non-shading (N))

Growth parameter	Light condition	
	S	N
Leaf area (cm ²)	150.69 ± 19.40 a	171.99 ± 17.6 a
Shoot length (cm)	10.14 ± 1.56 a	7.15 ± 1.25 a

Values represent means + SE. No significant differences by least significant difference (LSD) test ($P < 0.05$) were found.

Table 4. Growth of salak seedlings under different water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3))

Growth parameter	Water supply		
	W1	W2	W3
Root (g DW)	0.89 ± 0.11 a	0.91 ± 0.08 a	0.89 ± 0.10 a
Shoot (g DW)	3.85 ± 0.34 a	3.76 ± 0.35 a	3.73 ± 0.24 a
Leaf area (cm ²)	195.26 ± 24.60 a	143.79 ± 23.90 a	144.96 ± 17.00 a
Shoot length (cm)	6.31 ± 2.09 a	11.00 ± 1.69 a	8.63 ± 1.30 a

Values represent means ± SE. No significant differences by least significant difference (LSD) test ($P \leq 0.05$) were found.

Table 5. Interactive effects of different light conditions (shading (S) and non-shading (N)) and water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3)) on growth of salak seedlings

Treatments	Growth parameter			
	Root (g DW)	Shoot (g DW)	Leaf area (cm ²)	Shoot length (cm)
SW1	0.65 ± 0.10 a	3.00 ± 0.29 a	165.05 ± 36.40 a	9.77 ± 3.68 a
SW2	0.81 ± 0.11 ab	3.34 ± 0.53 ab	141.90 ± 48.20 a	10.73 ± 2.51 a
SW3	0.72 ± 0.07 ab	3.48 ± 0.22 ab	145.11 ± 11.70 a	9.92 ± 2.23 a
NW1	1.12 ± 0.15 b	4.70 ± 0.35 b	225.48 ± 31.30 a	2.85 ± 0.93 a
NW2	1.01 ± 0.11 ab	4.17 ± 0.43 ab	145.69 ± 13.80 a	11.27 ± 2.49 a
NW3	1.05 ± 0.16 ab	3.98 ± 0.42 ab	144.80 ± 33.70 a	7.33 ± 1.34 a

Values represent means ± SE. Different letters in the same column indicate significant differences by LSD test ($P \leq 0.05$)

Table 6. Interactive effects of different light conditions (shading (S) and non-shading (N)) and water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3)) on net CO₂ assimilation rate of salak seedlings

Treatments	P _N (μmol CO ₂ m ⁻² s ⁻¹)			
	Week 1	Week 2	Week 4	Week 6
SW1	2.76 ± 0.33 a	2.43 ± 0.70 ab	3.05 ± 0.45 ab	3.05 ± 0.45
SW2	2.18 ± 0.25 a	1.53 ± 0.39 a	2.43 ± 0.40 a	2.57 ± 0.84
SW3	1.88 ± 0.25 a	2.56 ± 0.46 ab	2.62 ± 0.29 ab	3.32 ± 0.91
NW1	2.74 ± 0.38 a	2.88 ± 0.47 ab	3.72 ± 0.21 ab	nd
NW2	4.82 ± 0.53 b	3.37 ± 0.37 b	3.87 ± 0.40 b	nd
NW3	3.31 ± 0.29 a	3.95 ± 0.34 b	3.30 ± 0.36 ab	nd

Values represent means ± SE. Different letters in the same column indicate significant differences by LSD test ($P \leq 0.05$), nd = not detected

Table 7. Mineral content of salak seedlings under different light conditions (shading (S) and non-shading (N))

Light condition	N	P	K	Ca	Mg
	(mg/g DM)				
S	25.39 ± 0.3 a	2.78 ± 0.1 a	13.95 ± 0.5 a	4.28 ± 0.2 a	1.01 ± 0.03 a
N	27.27 ± 0.4 b	2.60 ± 0.1 a	12.51 ± 0.7 a	5.49 ± 0.6 a	1.10 ± 0.05 a

Values represent means ± SE. No significant differences by LSD test ($P \leq 0.05$) were found

Table 8. Mineral content of salak seedlings under different water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3))

Water supply	N	P	K	Ca	Mg
	(mg/g DM)				
W1	25.58 ± 0.6 a	2.74 ± 0.06 a	12.88 ± 1.07 a	3.85 ± 0.20 a	1.07 ± 0.05 a
W2	26.64 ± 0.7 a	2.83 ± 0.15 a	12.80 ± 0.85 a	5.30 ± 0.56 a	1.04 ± 0.06 a
W3	26.76 ± 0.6 a	2.49 ± 0.09 a	14.01 ± 0.22 a	5.50 ± 0.68 a	1.06 ± 0.04 a

Values represent means ± SE. No significant differences by LSD test ($P \leq 0.05$) were found

Table 9. Interactive effects of different light conditions (shading (S) and non-shading (N)) and water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3)) on mineral content of leaves of salak seedlings

Interaction	N	P	K	Ca	Mg
	(mg/g DM)				
SW1	24.98 ± 1.0 a	2.78 ± 0.05 a	14.74 ± 1.0 a	3.70 ± 0.35 a	1.04 ± 0.07 a
SW2	25.48 ± 0.1 ab	3.05 ± 0.09 a	13.21 ± 1.0 a	4.60 ± 0.22 a	1.00 ± 0.02 a
SW3	25.72 ± 0.2 ab	2.50 ± 0.03 a	13.90 ± 0.4 a	4.54 ± 0.47 a	1.00 ± 0.06 a
NW1	26.19 ± 0.6 ab	2.70 ± 0.13 a	11.03 ± 1.4 a	4.00 ± 0.23 a	1.10 ± 0.08 a
NW2	27.81 ± 0.4 b	2.61 ± 0.16 a	12.39 ± 1.5 a	6.00 ± 1.04 a	1.09 ± 0.11 a
NW3	27.81 ± 0.2 b	2.48 ± 0.21 a	14.12 ± 0.2 a	6.47 ± 1.14 a	1.12 ± 0.05 a

Values represent means ± SE. No significant differences by LSD test ($P \leq 0.05$) were found

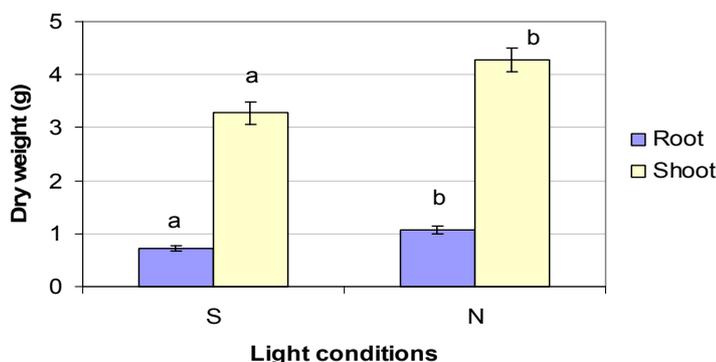


Figure 1. Root and shoot dry weight of salak seedlings under different light conditions (shading (S) and non-shading (N)). Different letters in the same column indicate significant differences by LSD test ($P \leq 0.05$)

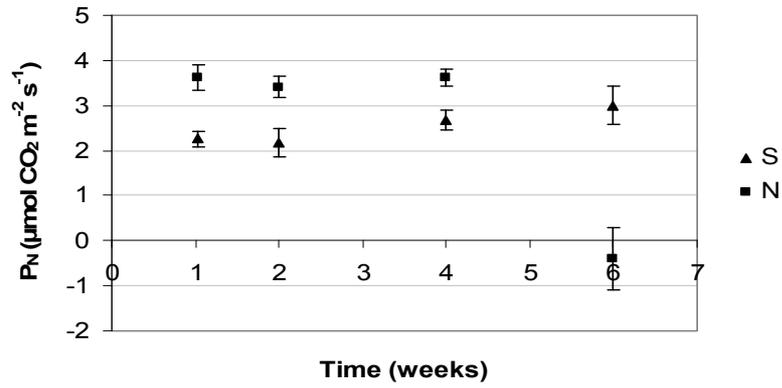


Figure 2. P_N of salak seedlings under different light conditions (shading (S) and non-shading (N))
 (Note: Recording P_N in week 6 was done during midday hours)

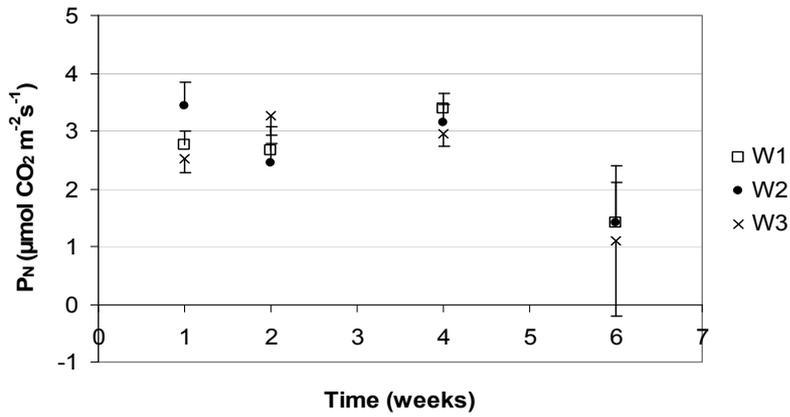


Figure 3. P_N of salak seedlings under different water supply (every 2 days (W1), every 4 days (W2) and every 6 days (W3)) (Note: Recording P_N in week 6 was done during midday hours)