Effect of Low pH on the Growth, Physiological Characteristics and Nutrient Absorption of Sago Palm in a Hydroponic System

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Abstract: The dry matter production, photosynthetic characteristics and nutrient concentrations in the plant tissues of sago palm seedlings cultured for 4.5 months in a hydroponic system at pH 5.7, 4.5, and 3.6 were examined. Plant growth in weekly increment of length, leaf emergence, leaf senescence, and total leaflet area was similar at all pHs. There was no significant effect of pH on the dry matter weight, although it tended to be lighter at pH 3.6 than at pH 5.7. Similarly, the photosynthetic rate and its related parameter were not significantly affected by the pH. However, the photosynthetic rate at pH 3.6 tended to be lower than that at pH 5.7, which was attributed to a decrease in the stomatal conductance. The effect of the low pH on the nutrient concentration in plant tissues was not distinct. We concluded that sago palm seedlings could maintain leaf morphogenesis and nutrient uptake in growth media at a pH ranging from 5.7 to 3.6 for 4.5 months, which led to a high growth rate and maintenance of dry matter production even at pH 3.6.

Key words: Growth, Low pH, Nutrient concentrations, Physiological characteristics, Sago palm.

Sago palm (Metroxylon sagu Rottb.) stores large quantities of starch in its trunk. The total starch storage in one trunk is approximately 300 kg dry weight (Ehara, 2005). Sago palm has long been cultivated for food, fulfilling a need similar to banana and taro (Barrau, 1959; Takamura, 1990). This palm species is a carbohydrate resource and is one of the oldest crops used by humans since ancient times (Takamura, 1990). The importance of sago palm as a staple food has not changed in areas such as Siberut Island in west Sumatra, the eastern archipelago of Indonesia, Maluku and Papua, and western Melanesia, Papua New Guinea. As a staple food, sago palm continues to be important in parts of Southeast Asia and in areas inhabited by the Melanesian people (Ehara et al., 2000). The carbohydrate or starch can be further processed into various basic raw materials for human and animal consumption as well as for use as an industrial energy source, such as ethanol.

Sago palm grows in swampy, alluvial, and peaty soils where almost no other major crops can grow without drainage or soil improvement (Sato et al., 1979; Jong and Flach, 1995). This palm is one of the most important bioresources for sustainable agriculture and rural development in swampy areas of the tropics. However, sago palm is recognized as an unexploited or underexploited plant because it has been harvested from natural forests and / or has been semi-cultivated under very simple maintenance. Further increase in its production is expected to be economically valuable in land development in swampy areas.

Since sago palm can grow in acid conditions, it is assumed to be resistant to acid (Purwanto et al., 2002; Osaki et al., 2003). However, few studies have compared the growth characteristics of sago palm in growth media at various pHs. The analysis of the effect of low pH on the growth characteristics with related physiological features may contribute to the development of a sustainable method of cultivation that is essential for the improvement of sago palm as an economic plant. We designed an experimental study to compare the physiological features and growth characteristics of young seedlings of sago palm at different pHs using a hydroponic system.

Materials and Methods

1. Plant materials and pH treatment

Fruits of sago palm were collected in the swampy areas of Rattapum, Songkhla, Thailand, on 1 August 2006. Fertilized and well-developed fruits were selected and treated physically to remove seed coat tissues. The cleaned seeds were placed in a plastic tray filled with tap water and then kept in darkness in a room kept at 30°C in Thammasat University, Pratumbanee, Thailand, as reported by Ehara et
The germinated seeds were brought to Mie, Japan, and transplanted to a 1/5000 a Wagner pot filled with vermiculite and Kimura B culture solution containing (µM) 36.5 (NH₄)₂SO₄, 9.1 K₂SO₄, 54.7 MgSO₄, 18.3 KNO₃, 36.5 Ca(NO₃)₂, 18.2 KH₂PO₄, and 3.9 FeO₃ (Baba and Takahashi, 1958). The culture solution was adjusted to an initial pH of 5.5 using 1.0N HCl before irrigation into pots, as reported by Ehara et al. (2006). The pots were placed in a greenhouse under natural sunlight and maintained at over 15ºC, even at night, at Mie University. Culture solution was added daily in an amount equal to that consumed, and the culture solution was renewed twice weekly.

Three seedlings at the 7th leaf stage, with the 8th leaf emerging and the mean plant length of all plant materials at 39 cm, were cultured in Kimura B culture solution adjusted to pH 5.7, 4.5 and 3.6 with 1.0 N HCl as required. The pots were placed in the same greenhouse under natural sunlight. An air pump was connected to the pots to provide air to the roots. Culture solution equal to that consumed was supplemented daily and each solution was renewed every other day from 23 May to 9 October, 2007.

2. Photosynthetic rate, transpiration rate, and stomatal conductance

On 5 October 2007, 18 weeks after the start of culture, the leaflets of the most active leaves or the 4th leaf position from the top were selected for measuring the net photosynthetic rate, transpiration rate, and stomatal conductance using a portable photosynthetic meter (Analytical development Co., Ltd., LCA-4, England) at saturation irradiance with incident photosynthetically active radiation (PAR) of 800–1,000 µmol m⁻² s⁻¹. As a light source, a halogen lamp was used. The appropriate PAR was obtained by changing the distance between the projector and leaves.

3. Chlorophyll content of the leaflets

The chlorophyll content of the leaflets at each leaf position was measured by the method of Mackinney (1941). An area of 0.25 cm² from each leaflet was punched out from each leaf and soaked in 10 mL of 80% (v/v) acetone to extract chlorophyll. The chlorophyll content was expressed as the content per unit leaflet area.

4. Sampling and nutrient concentrations in plants

The treated plants were sampled and washed thoroughly in distilled water. The plants were separated into three parts: leaflets, petioles including rachis, and roots. The fresh weight of each part was recorded. The leaflet areas were measured using an automatic area meter (Hayashi-Denko AAM-9, Japan). The roots were divided into lateral roots and adventitious roots, and the adventitious root was divided into stele and cortex (epidermis, exodermis, suberized sclerenchyma cell). Adventitious and lateral roots were classified according to the method of Nitta et al. (2002) as follows: adventitious roots were about 6 to 11 mm in diameter, and lateral roots, less than 6 mm in diameter. The separated samples were dried in an oven at 80ºC for 72 hours to measure the dry weight and then ground into powder in order to analyze the ion concentrations. The ground samples were reduced to ash in a furnace and extracted with 1.0N HNO₃, and the K⁺, Ca²⁺, and Mg²⁺ concentrations were determined using a high-performance liquid chromatograph (HPLC) with a conductivity detector (Shimadzu CDD-6A, IC-C3, Japan). The concentration of P was evaluated by atomic absorption spectrophotometry. The total N concentration was determined by the semi-micro Kjeldahl method, while the Al³⁺ concentration was determined calorimetrically by the aluminon method.

5. Statistical analysis

The statistical difference of the data was determined using NCSS 2001 (Number Cruncher Statistical Systems). The effects of treatments were determined by one-way ANOVA (analysis of variance), and the differences among the mean values of treatment were determined using the Tukey-Kramer test.

Results and Discussion

1. Plant growth

The numbers of emerged leaves, live leaves, and dead leaves were counted throughout the treatments (Table 1). During the experiment, approximately 7 leaves emerged at each pH. The number of dead leaves counted during the experiment was 4, 4, and 3 at pH 5.7, 4.5, and 3.6, respectively. There were no significant differences in the numbers of emerged, dead, and live green leaves among the three pHs. These results indicate that the low pH
conditions had no effect on leaf emergence and senescence.

The weekly increment of plant length from the 19th to the 20th week, and total leaflet area and dry matter weight of the leaflets, petioles, roots, and whole plant at the end of the pH treatments are shown in Table 2. The weekly mean increment of plant length did not change at any pH throughout the experiment. The leaflet area at the end of the treatment was the same at all three pHs. The total dry matter weight tended to be heavier at pH 4.5 than at pH 5.7. On the other hand, the total dry matter weight at pH 3.6 tended to be lighter than that at pH 5.7. There was no significant difference in the total dry matter weight between pH 5.7 and pH 3.6, the mean difference being 9%; the comparatively large variation in the value among the individuals in each treatment might be related to this variation. It is difficult to obtain uniform sago palm seedlings because of the low germination percentage and very large variation in the days of germination; therefore, there is a comparatively large variation in the growth parameters, which is a general characteristic of wild plants.

As described above, the dry matter weight of plants grown for 4.5 months at pH 4.5 was slightly heavier, and that at pH 3.6 was slightly lighter than that at pH 5.7. However, differences in plant size, not only shoot elongation, leaf emergence, and leaf area expansion but also dry matter increase, were statistically negligible. Therefore, we considered that the decrease of the pH in the growth media in the range from pH 5.7 to pH 3.6 might not have a marked effect on the growth rate of sago palm seedlings in the early stage of growth.

2. Physiological characteristics

The mean values of the chlorophyll content per unit leaflet area at upper, middle, and lower leaf positions were 74.7, 73.5, and 76.0 µg cm\(^{-2}\) at pH 5.7, 4.5, and 3.6, respectively (Table 3). The highest value of the chlorophyll content was observed in the 5th leaf from the top at each pH. The differences, then, in the chlorophyll content among the three pHs were not significant at any leaf position (data not shown).

The photosynthetic rate, transpiration rate, and stomatal conductance were measured at the 4th leaf position from the top, which was considered to be the most active physiologically according to the leaf development and chlorophyll content. All the measured values decreased slightly under lower pHs, but the extent of the decrease was not distinct (Table 3). In sugar maple (Hogan, 1998), red oak (Reich et al., 1986), and hybrid poplar (Hogan and Taylor, 1995), the photosynthetic rate, transpiration rate, and stomatal conductance did not decrease markedly in the pH range from 5.5 to 3.0. Generally, reduction in the photosynthetic rate of several plants has been recorded when the pH is extremely low, i.e., lower than the soil pH in field conditions (Taylor et al., 1986; Hogan and Taylor, 1995). The soil pH of peat soil planted with sago palm in Salawak, Malaysia has been reported to be acidic, in the range of 3.9 to 4.5, and did not result in the appearance of symptoms or growth inhibition (Kawahigashi et al., 2003).

As described above, although there was no significant difference in the total dry weight per plant among the three pHs, the total dry weight at pH 3.6 tended to be smaller than that at pH 5.7. Similarly, the photosynthetic rate at pH 3.6 tended to be lower than that at pH 5.7. The difference in photosynthetic rates among the three pHs

### Table 2. Effect of low pH on weekly increment of plant length, leaflet area and dry matter weight.

| Treatment | Weekly increment of plant length (cm) | Leaflet area per plant (cm\(^2\)) | Dry matter weight per plant (g) |
|-----------|--------------------------------------|-----------------------------------|---------------------------------|
| pH 5.7    | 2.0 ± 0.1 a                          | 2,400.6 ± 420.5 a                 | 18.2 ± 5.7 a                    |
| pH 4.5    | 2.0 ± 0.1 a                          | 2,457.2 ± 346.9 a                 | 19.5 ± 1.3 a                    |
| pH 3.6    | 2.0 ± 0.1 a                          | 2,418.8 ± 728.0 a                 | 17.3 ± 5.9 a                    |

Mean ± standard deviation (n=3). Values with the same letters in a given column are not significantly different at the 0.05 level by the Tukey-Kramer test.

### Table 3. Chlorophyll content per unit leaflet area, photosynthetic rate, transpiration rate and stomatal conductance at different pHs.

| Treatment | Chlorophyll content per unit leaflet area (µg cm\(^{-2}\)) | Photosynthetic rate (µmol m\(^{-2}\) s\(^{-1}\)) | Transpiration rate (mmol m\(^{-2}\) s\(^{-1}\)) | Stomatal conductance (mol m\(^{-2}\) s\(^{-1}\)) |
|-----------|----------------------------------------------------------|-----------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| pH 5.7    | 74.7 ± 5.7 a                                             | 2.418.8 ± 728.0 a                             | 74.7, 73.5, and 76.0 µg cm\(^{-2}\) at pH 5.7, 4.5, and 3.6, respectively (Table 3). The highest value of the chlorophyll content was observed in the 5th leaf from the top at each pH. The differences, then, in the chlorophyll content among the three pHs were not significant at any leaf position (data not shown). The photosynthetic rate, transpiration rate, and stomatal conductance were measured at the 4th leaf position from the top, which was considered to be the most active physiologically according to the leaf development and chlorophyll content. All the measured values decreased slightly under lower pHs, but the extent of the decrease was not distinct (Table 3). In sugar maple (Hogan, 1998), red oak (Reich et al., 1986), and hybrid poplar (Hogan and Taylor, 1995), the photosynthetic rate, transpiration rate, and stomatal conductance did not decrease markedly in the pH range from 5.5 to 3.0. Generally, reduction in the photosynthetic rate of several plants has been recorded when the pH is extremely low, i.e., lower than the soil pH in field conditions (Taylor et al., 1986; Hogan and Taylor, 1995). The soil pH of peat soil planted with sago palm in Salawak, Malaysia has been reported to be acidic, in the range of 3.9 to 4.5, and did not result in the appearance of symptoms or growth inhibition (Kawahigashi et al., 2003). As described above, although there was no significant difference in the total dry weight per plant among the three pHs, the total dry weight at pH 3.6 tended to be smaller than that at pH 5.7. Similarly, the photosynthetic rate at pH 3.6 tended to be lower than that at pH 5.7. The difference in photosynthetic rates among the three pHs
could be attributed to differences in the stomatal conductance, which tended to be lower than that at pH 5.7 (Table 3). Yamamoto et al. (2003) reported that sago palm growth was slower and starch yield was smaller in acid peat soil than in mineral soil. Generally, the time from planting to harvesting (maturity), is longer in acid peat soil than in mineral soil, but even so sago palm grown in acid peat soil can be harvested even when the growth rate is depressed by environmental stress, such as low pH or poor fertility per soil volume. Our findings on the dry matter weight and photosynthetic rate with related parameters suggest that the lower growth rate and lower yield of sago palm under acid conditions in the field is due to lower photosynthetic rate caused by the small stomatal conductance of the leaflet.

3. **Nutrient concentrations in different plant parts**

The concentrations of Al$^{3+}$, N, P, K$^+$, Ca$^{2+}$, and Mg$^{2+}$ in the leaflets, petioles, roots, and whole plant at each pH are shown in Table 4. We did not add Al to the culture solution, although Al$^{3+}$ was detected in the plant tissues probably due to its elution from vermiculite. The Al$^{3+}$ concentration in plant tissues tended to be higher in the root than in the leaflet and petiole, and the difference between the root and top parts, petiole and leaflets, was significant at both pH 4.5 and 3.6. A similar tendency was found in tea plants, in which the concentration of Al$^{3+}$ in the root was higher than that in the shoot or leaves, especially in the large-leaf variety that grows in low pH soil (Fung and Wong, 2001). However, there was no significant difference in the Al$^{3+}$ concentration in any of the plant parts among the three pHs. Considering the results from our experiment, such as the difference in the Al$^{3+}$ concentration in the root and top parts under a lower pH condition and the lack of a significant difference in the Al$^{3+}$ concentration in the top parts among the three pHs, the translocation of Al$^{3+}$ from the root to the top parts might be restricted.

| Nutrient concentration | Plant part | pH treatment | pH 5.7 | pH 4.5 | pH 3.6 |
|------------------------|------------|--------------|--------|--------|--------|
| Al$^{3+}$ (µmol g$^{-1}$) | Leaflet    | 7.4 ± 1.8 aA | 7.7 ± 1.7 aB | 8.7 ± 0.1 aB |
|                        | Petiole    | 7.5 ± 1.1 aA | 8.7 ± 1.3 aB | 8.9 ± 0.3 aB |
|                        | Root       | 9.6 ± 2.4 aA | 10.2 ± 1.2 aA | 12.1 ± 0.6 aA |
|                        | Whole      | 7.8 ± 0.5 a  | 8.6 ± 1.2 a  | 9.4 ± 1.8 a  |
| N (mg g$^{-1}$)        | Leaflet    | 22.3 ± 1.8 aA | 22.3 ± 2.0 aA | 20.9 ± 2.5 aA |
|                        | Petiole    | 9.6 ± 1.6 aB | 9.6 ± 1.9 aB | 8.8 ± 0.6 aB |
|                        | Root       | 9.7 ± 1.7 aB | 9.7 ± 0.6 aB | 10.8 ± 2.5 aB |
|                        | Whole      | 13.9 ± 2.4 a  | 13.9 ± 1.7 a  | 13.6 ± 1.2 a  |
| P (mg g$^{-1}$)        | Leaflet    | 2.1 ± 0.2 aB | 1.8 ± 0.2 aAB | 1.8 ± 0.3 aA |
|                        | Petiole    | 2.6 ± 0.1 aA | 2.1 ± 0.3 aA | 2.2 ± 0.3 aA |
|                        | Root       | 1.1 ± 0.1 aC | 1.6 ± 0.1 aB | 1.6 ± 0.2 aA |
|                        | Whole      | 2.1 ± 0.1 a  | 1.9 ± 0.2 a  | 1.9 ± 0.2 a  |
| K$^+$ (µmol g$^{-1}$)  | Leaflet    | 97.7 ± 4.2 aC | 95.9 ± 5.6 aB | 93.5 ± 4.4 aB |
|                        | Petiole    | 182.9 ± 9.7 bB | 225.3 ± 3.6 aA | 219.6 ± 8.4 aB |
|                        | Root       | 245.5 ± 2.4 aA | 230.1 ± 2.0 aA | 253.4 ± 2.4 aA |
|                        | Whole      | 156.5 ± 9.7 a | 177.4 ± 7.6 a | 178.2 ± 4.2 a |
| Ca$^{2+}$ (µmol g$^{-1}$) | Leaflet    | 50.4 ± 2.6 aB | 47.0 ± 5.7 aB | 42.4 ± 4.8 aAB |
|                        | Petiole    | 68.8 ± 4.6 aA | 68.1 ± 6.7 aA | 55.7 ± 1.6 aA |
|                        | Root       | 30.1 ± 1.7 aC | 31.1 ± 3.2 aC | 28.8 ± 1.6 aB |
|                        | Whole      | 55.2 ± 2.8 a | 52.5 ± 5.4 a | 45.7 ± 3.2 a |
| Mg$^{2+}$ (µmol g$^{-1}$) | Leaflet    | 45.8 ± 3.6 aB | 43.2 ± 2.2 aB | 41.1 ± 4.3 aB |
|                        | Petiole    | 60.7 ± 3.7 aA | 63.3 ± 0.4 aA | 56.7 ± 2.6 aAB |
|                        | Root       | 64.4 ± 5.8 aA | 63.0 ± 5.8 aA | 63.9 ± 6.4 aA |
|                        | Whole      | 55.2 ± 4.3 a | 55.6 ± 6.2 a | 52.1 ± 5.2 a |

Mean ±standard deviation (n = 3). Values with the same letters in a given column are not significantly different at the 0.05 level by the Tukey-Kramer test. Lowercase letter indicates comparison among the pHs in each part of plant. Capital letter indicates comparison among plant tissues under the pH treatments.
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In contrast, the P concentration in the root was comparatively higher at pH 4.5 and 3.6 than at pH 5.7. Furthermore, the P concentration in different plant parts in the pH 5.7 treatment was significantly higher in the petiole, followed by the leaflet and root. In contrast, there was no significant difference between the P concentration in the petiole and leaflet or the leaflet and root, and there was no significant difference among the P concentration in the petiole, leaflet, and root in the pH 3.6 treatment (Table 4). This different trend, such as the vertical difference in the P concentration in the root and top parts, especially between the pH 5.7 and pH 3.6 treatments, suggests that the translocation of P from the root to the top parts will be affected and depressed at lower pH, which is a similar tendency to that observed in wheat (Malkanthi et al., 1995). The P concentration in the root tended to be higher at a lower pH, although the difference among the three pHs was not significant (Fig. 1). Generally, the available P in the culture solution is affected by the Al concentration at a lower pH, which may account for the low P absorption by the plant body (Fageria, 1985). The Al$^{3+}$ concentration in the root was significantly higher in the lateral root than in the stele or cortex of the adventitious root at pH 4.5 and 3.6 in our experiment. Even so, the absolute value of the Al$^{3+}$ concentration in the root was 10 to 12 µmol g$^{-1}$ in our experiment, which was a low level and might not significantly affect the P concentration.

The N concentration in the leaflet was apparently higher than that in the petiole and the root at all pHs (Table 4). A tendency toward a higher N concentration in the leaf than in the other parts, such as the petiole or root, is generally found in various plant species, such as winged and velvet beans (Anugroho et al., 2010). Moreover, the N concentration in the leaflet tended to be higher at higher leaf positions than at lower leaf positions at all pHs (data not shown). This tendency toward a higher concentration of N in the young than older leaves was in agreement with the report of Purwanto et al. (2002), which suggested that N was retranslocated from the mature leaves to the young leaves of sago palm growing on the peat soils.

In the leaflet and petiole, the N concentration tended to decrease at a lower pH, while this tendency was not observed in the root. However, we were unable to find a significant difference among the three pHs in the N concentration in any plant part. Kueh (1995) also reported that the foliar N level of sago palm was unaffected even by the application of N fertilizer. Purwanto et al. (2002) suggested that the perennial nature of the crop may be responsible for the delay in the response of sago palm to fertilizer on the acid peat soil. In our experiment, the unclear effect of the pH of the culture solution on the N concentration in the plant tissues might be related to the absence of a difference with the pH in leaf appearance and shoot elongation in young sago palm seedlings.

![Fig. 1. Al$^{3+}$ and P concentrations in different parts of root (stele and cortex of adventitious root and lateral root) under different pHs. □, pH 5.7; ■, pH 4.5; ■, pH 3.6. Vertical bars indicate the standard deviation (n = 3). Values with the same letters are not significantly different at the 0.05 level by the Tukey-Kramer test. Lowercase letter indicates comparison among the pHs in each part of root. Capital letter indicates comparison among the parts of root under the pH treatments.](image-url)
The K⁺ concentration in the root and petiole was higher than that in the leaflet at all pHs. The effect of the pH on the K⁺ concentration in plant tissues was significant only in the petiole. The Ca²⁺ concentration in the top parts, the petiole and leaflet, was higher than that in the root under the three pHs. On the other hand, the Mg²⁺ concentration was higher in the root and petiole than in the leaflet (Table 4). There are several reports concerned with the effect of low pH on nutrient uptake in rice (Thawornwong and Diest, 1974), wheat, barley, chili, cowpea (Malkanthi et al., 1995), and tea plants (Fung and Wong, 2001). In these plant species, the Ca²⁺ and Mg²⁺ concentrations in the top parts decreased under strong acid conditions (pH lower than 4.0). These reports suggest that the suppressed uptake of Ca²⁺ and Mg²⁺ under a low pH condition is likely to be the result of a high H⁺ concentration. In our study, however, there was no significant difference in the Ca²⁺ and Mg²⁺ concentrations in the whole plant with the pH.

As described above, there was no significant difference in the chlorophyll content with the pH, presumably due to the small effect of the low pH on the Mg²⁺ and the total N concentrations in the leaflets. The structure of chlorophyll consists of a central magnesium atom surrounded by a nitrogen-containing structure called a porphyrin ring, which has a long carbon-hydrogen side chain attached, known as a phytol chain (Wu and Rebeiz, 1985). In this experiment, there was no significant difference in either the Mg²⁺ or total N concentration in the leaflets with the pH, which might be due to the small effect of the low pH and lack of a significant difference in the chlorophyll production in the leaflet. The chlorophyll production could be maintained for a comparatively long time, which may account for the ability to maintain growth under these adverse conditions.

In conclusion, sago palm seedlings can maintain leaf morphogenesis and nutrient uptake under a wide range of low pH conditions (pH 5.7 to pH 3.6) in culture solution for 4.5 months, which may account for the maintenance of dry matter production. However, a significant difference may occur in the growth rate of sago palm grown under unfavorable conditions, such as acid peat soil versus that under favorable conditions of mineral soil after culture for a longer time.

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