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The fluctuation of carbohydrates and nitrogen compounds in flooded wax-apple trees

Yu-Mei Hsu[1], Menq-Jiau Tseng[2] and Chin-Ho Lin[1,3]

[1]Department of Botany and [2]Department of Horticulture, National Chung Hsing University, Taichung, Taiwan 40227, Republic of China

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Abstract. The present study associates the response to flooding of potted wax-apple trees, *Syzygium samarangense* Merr. et Perry, with changes in carbon and nitrogen metabolism. In wax-apple leaves, the starch content conspicuously increased after 14 days of flooding, and the total nitrogen content decreased after 35 days of flooding. In roots, concentrations of total soluble sugars significantly increased after 14 days of flooding. The accumulation of starch in flooded wax-apple leaves and increased soluble sugar content in roots apparently were the result of the reduction of growth and metabolic activities in roots after flooding, which reduced the sink demand of carbohydrates. Soluble protein concentration significantly decreased after 7 days of flooding, but remained similar among 14-, 28- and 42-day flooding treatments. Free amino acid content of flooded plants was significantly higher than that of the control at all sampling dates. The activity of glutamine synthetase in leaves significantly decreased after 7 days of flooding, but was higher than the control's at 14, 28 and 42 days of flooding. In wax-apple roots, content of soluble protein, free amino acids, ammonia and the activity of nitrate reductase and glutamine synthetase all decreased significantly after flooding. Apparently, nitrogen metabolism was restricted in the roots during flooded conditions.

Keywords: Carbon/nitrogen ratio; Free amino acid; Glutamine synthetase; Nitrate reductase; Nitrogen; Soluble protein; Soluble sugar; Starch; *Syzygium samarangense*.

Introduction

In general, flooding has an adverse effect on fruit trees. In Taiwan, constant flooding of wax-apple tree (*Syzygium samarangense* Merr. et Perry) for 45 days during the summer not only advances the harvest period to the following December, but also increases harvest intervals and productivity (Wang, 1983). Long-term flooding results in soil anoxia, which restricts root growth and causes a metabolic imbalance between shoots and roots. Zvareva and Bartkov (1976) demonstrated that flooding decreased carbohydrate translocation from the leaves to the roots of soybean. Similar effects have also been found in *Saxifraga tormentosa* (Quereshi and Spanner, 1973), purple flower alfalfa (*Medicago sativa* L.) and *Lotus corniculatus* L. (Barta, 1987). The reduction of photosynthate translocation to roots under flooding stress might have been due to the reduction of carbohydrate utilization in roots (Wample and Davis, 1983) or to depression of the photosynthate transport system (Saglio, 1985; Topa and Cheeseman, 1992a). Therefore, under flooding conditions, although the photosynthetic rate in leaves declines, starch accumulates (Barta, 1987; Topa and Cheeseman, 1992b; Vu and Yelenosky, 1991; Wample and Davis, 1983).

[3]Corresponding author. Tel: 886-4-2862511; Fax: 886-4-2862511; E-mail: chlin@mail.nchu.edu.tw

Restriction of the absorption of mineral nutrients in roots under flooding usually results in lower nitrogen content in the tissues of flood-intolerant plants (Kozlowski and Pallardy, 1984). Oxygen deficiency restricts protein synthesis in roots (Lin and Key, 1967; Sachs et al., 1980) and accelerates anoxic metabolism (Crawford and Baines, 1977; Jackson et al., 1982). Therefore, under flooding stress, the composition and quantity of proteins and amino acids, and the activities of key enzymes involved in nitrate reduction and ammonia assimilation, will all be affected (Buwalda et al., 1988; Garcia-Novo and Crawford, 1973; Reggiani et al., 1988).

Wax-apple tree, a flood-tolerant species, is expected to have a different carbon and nitrogen metabolism response to flooding than flood-intolerant plants. Thus, the present study analyzed the variation of carbon and nitrogen contents in the leaves and roots with and without flooding. It also evaluated the impact of flooding on the activities of nitrate reductase and glutamine synthetase.

Materials and Methods

Plant Preparation and Flooding Treatments

Experiments were performed under open field conditions without fertilization on three-year-old wax-apple plants (*Syzygium samarangense* Merr. et Perry), grown in 16-L non-woven fabric bags with bark compost as a growth medium. Eighteen bagged plants were randomly divided into two groups: (A) 9 non-flooded plants, and (B) 9 flooded plants. Plants in Group A were watered once daily until runoff. Plants in Group B were flooded by immersing the bags in 30-L plastic buckets for up to 42 days and then draining. Four fully expanded leaves on the most recent emerged flushes of each tree were sampled before flooding, and at the 7th, 14th, 21st, 28th, 35th, and 42nd days of flooding and also, at the 7th and 14th days after the pots were drained. Leaves from three plants were pooled to make a single replicate. Each treatment had 3 replicates. The leaves were oven-dried and ground to powder for the determination of reducing sugars, total soluble sugars, starch, and total nitrogen.

An additional twenty two-year-old trees, about 150 cm in height, were grown in 7-L pots containing a field soil : bark compost : peat (2 : 1 : 1, v/v/v) mixture. Trees were randomly divided into five groups. Except for the non-flooded control group, plants of the other four groups were individually flooded in 17-L plastic buckets for 7, 14, 28 or 42 days, respectively, and then allowed to drain. Right after drainage, leaves and fibrous roots from each plant were immediately sampled to analyze the contents in free amino acids, soluble proteins, ammonia-nitrogen, and the activities of nitrate reductase and glutamine synthetase. About 10 g of fibrous roots from each plant were washed and dried for the determination of carbohydrates. Each tree was treated as a replicate, and each treatment had four replicates.

Carbohydrates and Total Nitrogen Analyses

Oven-dried leaf or root powder of 0.1 g was put into a 50 ml centrifuge tube, 10 ml of distilled water was added, and the mixture incubated at 30°C in a water bath shaker for 3 h. After incubation, the liquid sample was centrifuged at 12,000 *g* for 10 min. The supernatant was then used to determine the content of reducing sugars by the dinitrosalicylate method (Luchsinger and Cornesky, 1962), and the content of total soluble sugars by the method of Dubois et al. (1956). The residue, oven-dried at 80°C overnight, was used to determine the content of starch by the method of Yoshida et al. (1976). The total nitrogen was determined by the micro-Kjeldahl method (Horwitz, 1980).

Analyses of Nitrogen Compound and Nitrate Reductase and Glutamine Synthetase Activities

Leaves and fibrous roots of 2 g each were individually mixed with 1 g of sea sand and ground in 5 ml cold 0.1M phosphate buffer (pH=7.0) at 4°C. Crude extract was centrifuged at 20,000 *g* at 2°C for 20 min. The supernatant was filtered with Miracloth (Calbiochem, CA, USA) and was used with the Lowry method (Lowry et al., 1951) to determine the amount of soluble protein, with the Rosen method (Rosen, 1957) to determine the amount of free amino acids, and with by Nessler‘s reagent (Thompson and Morrison, 1951) to determine the amount of ammonia-nitrogen. The nitrate reductase activity was analyzed according to the method of Jaworski (1971), and the glutamine synthetase activity was determined by the method of Elliott (1953).

Results and Discussion

Carbohydrate content in wax-apple leaves showed inconsistent changes during flooding treatments. Reducing sugar content was significantly higher than the control’s at the 42nd day of flooding and the 7th day after draining (Figure 1A). The total soluble sugar content basically remained similar in the two treatments, except that the flooded treatment was significantly higher than that of control during the 4th week of flooding and the 1st week after pots were drained (Figure 1B); the starch content was significantly higher than control’s after 14 days of flooding (Figure 1C). Overall, flooding treatments increased the total carbohydrate content in leaves (Figure 1D), mostly due to the accumulation of starch. Similar leaf carbohydrate accumulation under flood conditions has been reported for sunflower (Wample and Davis, 1983), purple flower alfalfa (Barta, 1987), sweet orange (Vu and Yelenosky, 1991), pine (Topa and Cheeseman, 1992a,b), and bitter melon (Liao and Lin, 1994). Starch accumulation in leaves after flooding has been attributed to reduced translocation of carbohydrates from leaves to roots (Barta, 1987) and to the retardation of growth and metabolism in roots which decreased carbohydrates apparently demand (Wample and Davis, 1983).

Reducing sugars and starch content in roots did not vary significantly between the two treatments, but soluble sugar content did significantly increase after 14 days of flooding (Table 1). This is similar to the response of purple flower alfalfa (Barta, 1987; Castonguay et al., 1993). Barta (1987) noted that the anoxic condition in roots will restrict the translocation in phloem. Topa and Cheeseman (1992a) suggested that root systems possessing aerenchyma cells may facilitate translocation of photosynthates. Schumacher and Smucker (1985) have also indicated that the ^{14}C translocated to the roots of *Phaseolus vulgaris* under flooding was not metabolized by glycolytic enzymes in roots. Therefore, starch accumulation in wax-apple leaves and the increase of soluble sugars in the roots could be related to the reduction of growth and metabolic activity of roots under flooding, which further reduces carbohydrate demand in roots.

It has been reported that total nitrogen content in plant tissue usually decreases under flooding stress in various fruit trees, such as citrus (Labanauskas et al., 1972), apple (Olien, 1989), avocado (Slowick et al., 1979), and blueberry (Herath and Eaton, 1968). For the wax-apple tree in the present study, total nitrogen content in leaves after 35 days of flooding was significantly lower than the control‘s (Figure 2A) while total carbohydrate increased (Figure 1D), which resulted in a significant increase in C/N ratio (total carbohydrate / total nitrogen) (Figure 2B). The carbohydrate-nitrogen ratio in fruit trees has often been associated with bud formation, flowering, and fruiting, but this hypothesis has also been found to vary with species (Goldschmidt, 1982; Scholefield et al., 1985; Smith et al., 1986). There are no apparent references that elucidate the special response of flowering advancing to flooding.

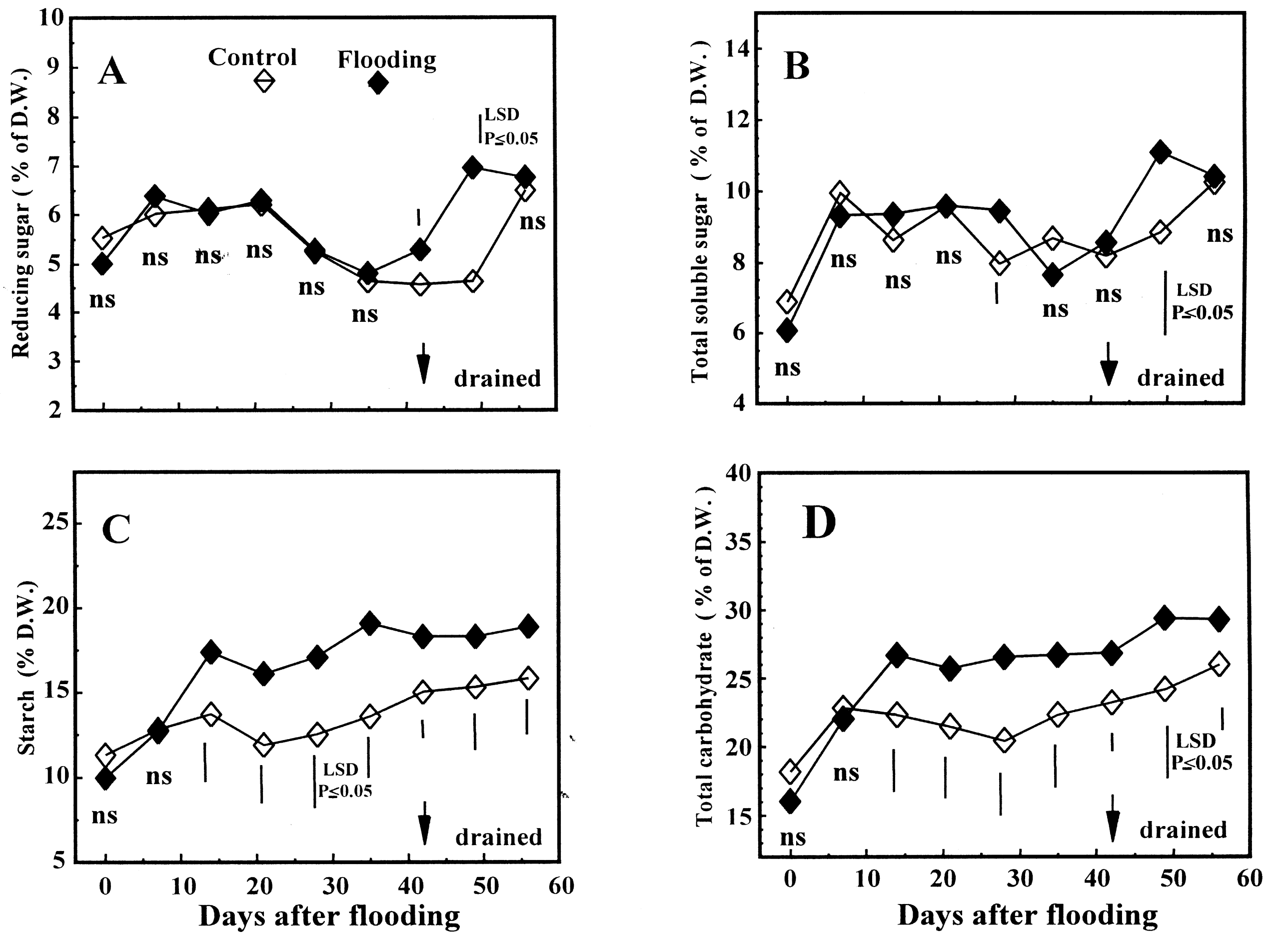

Figure 1. Reducing sugar (A), total soluble sugar (B), starch (C) and total carbohydrate (D) content of wax-apple leaves during 42 days of flooding and after 14 days of drainage.

Table 1. Effects of flooding duration on carbohydrates concentration of wax-apple roots. Root samples were collected at the end of flooding.

Flooding duration (days)	Reducing sugar	Total soluble sugar	Starch
		(% of dry weight)	
0	4.13 a*	3.86 a	7.21 a
14	5.58 a	6.00 b	6.96 a
28	4.62 a	5.25 b	6.92 a
42	4.91 a	4.93 ab	7.01 a

*Values within a column followed by different letters are significantly different according to Duncan's multiple range test, $P \leq 0.05$.

Table 2. Effects of flooding duration on nitrogen compound concentration and glutamine synthetase activity of wax-apple leaves. Leaf samples were collected at the end of flooding.

Flooding duration (days)	Soluble protein (mg B.S.A. equivalent/g F.W)	Free amino acid (μmol alanine equivalent/g F.W)	Ammonia nitrogen (μmol NH_4 equivalent/g F.W)	Glutamine synthetase activity (μmol glutamic acid-γ-mono-hydroxamate/g F.W/h)
0	54.6 a*	20.4 a	202 a	18.7 a
7	33.6 b	21.3 ab	222 a	12.4 b
14	50.0 a	27.4 cd	236 a	24.8 c
28	51.2 a	26.6 bd	242 a	27.6 c
42	59.0 a	32.9 c	268 a	27.9 c

*Values within a column followed by different letters are significantly different according to Duncan's multiple range test, $P \leq 0.05$.

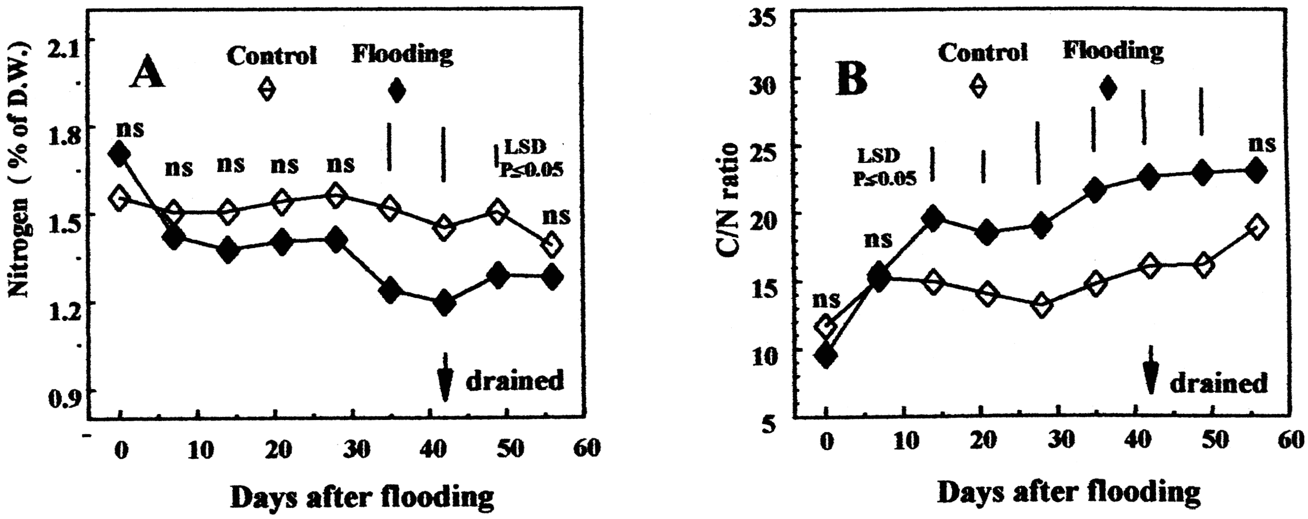

Figure 2. Nitrogen content (A) and C/N ratio (B) of wax-apple leaves during 42 days of flooding followed by 14 days of drainage.

Soluble protein content in the leaves significantly decreased in 7 days of flooding, but recovered afterward. Free amino acid content was significantly higher than the control's after 14 days of flooding, and ammonia-nitrogen did not differ significantly among flooding treatments (Table 2). The activity of glutamine synthetase in leaves significantly decreased after 7 days of flooding, but recovered to higher activity than the control's after 14 days of flooding (Table 2). We therefore suggest that the increase of leaf free amino acid after flooding is related to the increase of glutamine synthetase activity.

The soluble protein, free amino acid, ammonia-nitrogen contents and activities of nitrate reductase and glutamine synthetase in roots of flooded wax-apple tree significantly decreased (Table 3). The response of nitrogen metabolism in roots of flooded wax-apple tree was different from the anoxic effects, such as reduced protein synthesis (Brambilla et al., 1986; Lin and Key, 1967; Menegus et al., 1984) and increased amino acid levels (Reggiani et al., 1988), observed in the roots of most herbaceous plants. This difference might be related to the significant decrease in nitrate reductase and glutamine synthetase activities (Table 3).

Nitrate reductase is the most important enzyme in the nitrate reduction process. Garcia-Novo and Crawford (1973) and Lambers (1976) have reported that the activity of nitrate reductase in the roots of flood-tolerant plants increased rapidly during flooding, along with the amino acid synthetic ability. However, wax-apple trees tend to have different responses to flooding. The activity of nitrate reductase in the roots of flooded wax-apple tree did not increase with flooding period as in other plants, but significantly decreased (Table 3). This might be due to a reduced nitrate uptake by the roots as the synthesis of nitrate reductase is substrate regulated (Beevers and Hageman, 1969; Hewitt, 1975). The half-life of the newly synthesized enzyme is only a few hours (Taiz and Zeiger, 1991). Therefore, reduced nitrate uptake by roots would reduce the synthesis of nitrate reductase. The decrease of glutamine synthetase activity is correlated with the decrease in root respiration (unpublished data). The process for ammonia to be reduced to glutamine demands a supply of ATP (Zubay, 1993), which would decline in the anoxia root environment during flooding.

In summary, we found that starch content in leaves of potted wax-apple increased after flooding and contributed to an increase in total carbohydrates. A concomitant decrease in total nitrogen content led to a higher C/N ratio in flooded plants. Contents of soluble protein, free amino acid, ammonia-nitrogen, and activities of glutamine syn-

Table 3. Effects of flooding duration on nitrogen compound concentration, glutamine synthetase, and nitrate reductase activities in wax-apple roots. Root samples were collected at the end of flooding.

Flooding duration (days)	Soluble protein (mg B.S.A. equivalent/g F.W)	Free amino acid (∝mol alanine equivalent/g F.W)	Ammonia nitrogen (∝mol NH_4 equivalent/g F.W)	Glutamine synthetase activity (∝mol glutamicacid-γ-mono-hydroxamate/g F.W/h)	Nitrate reductase activity (μmoll NO_2/g F.W/h)
0	5.92 a*	4.29 a	9.04 a	7.23 a	1.79 a
7	3.56 b	3.68 b	5.21 bc	2.29 b	1.57 ab
14	1.26 c	1.98 c	3.74 c	2.03 b	1.07 b
28	3.94 b	1.96 c	5.12 bc	1.91 b	0.97 b
42	2.80 bc	3.23 b	5.08 b	3.69 b	0.85 b

*Values within a column followed by different letters are significantly different according to Duncan's multiple range test, $P \leq 0.05$.

thetase in leaves decreased at early flooding stage then recovered afterward. This recovery was not apparent in the roots and suggests that flooding results in decreased metabolism in flooded wax-apple roots.

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蓮霧在淹水逆境下葉片及根部碳水化合物及含氮化合物含量之變化

許玉妹[1] 曾夢蛟[2] 林金和[1]

[1] 國立中興大學植物學系

[2] 國立中興大學園藝學系

本試驗以盆栽蓮霧 (*Syzygium samarangense* Merr. et Perry) 為材料，探討淹水對葉片及根部的碳素與氮素代謝之影響。試驗結果顯示，葉片澱粉含量在淹水 14 天後顯著升高，全氮含量則在淹水處理後 35 天明顯降低；故在淹水 14 天後，淹水處理組之葉片碳／氮比顯著高於對照組。而根部還原糖含量與澱粉含量，在處理間則無顯著差異，但可溶性糖在淹水 14 天後顯著上升。由以上結果推測，蓮霧葉片澱粉的累積，及根部可溶性糖含量的上升，是由於淹水逆境下根部生長及代謝能力降低，對碳水化合物需求減少所致。葉片含氮化合物的變化方面，可溶性蛋白質含量經淹水 7 天顯著下降，但淹水 14、28 及 42 天處理者與對照組間則無顯著差異。淹水 14 天後，葉片游離胺基酸含量則均顯著高於對照組。而葉片麩醯胺合成酵素活性經淹水 7 天顯著下降，但淹水 14、28 及 42 天處理者顯著高於對照組。根部方面，可溶性蛋白質、游離胺基酸及氨態氮含量，經淹水處理後均顯著下降，顯示淹水會抑制蓮霧根部氮素之代謝。

關鍵詞：碳／氮比；游離胺基酸；麩醯胺合成酵素；硝酸鹽還原酵素；氮；可溶性蛋白；可溶性糖；澱粉；蓮霧。