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Growth, Leaf Chlorophyll Concentration, and Morphological Adaptation of Selected Wax Apple Cultivars in Response to Flooding

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ABSTRACT

Growth, leaf chlorophyll concentration and morphological adaptation of young wax apple (*Syzygium samarangense* (Blume) Merrill & Perry) cvs. Plastic (PT), Thunklao (TK), Phetnamphueng (PP) and Thapthimchan (TC) and Malay apple (*Syzygium malaccense*) (MA) plants under flooding conditions were investigated. Potted wax apple and Malay apple plants were flooded to 5 cm above the soil surface for 70 days continuously. MA, TK, PP and TC plants survived under this flooding duration while PT plants had gradually died after flooding for 30 days. Vertical splitting of the outer bark was observed immediately above and below the flood level in all cultivars after flooding for 12 – 21 days followed by a development of adventitious roots at stem base below the flood level in most cultivars except for MA plants. Flooded PT plants formed adventitious roots faster than other cultivars while flooded TC plants had greatest mass of adventitious roots. Flooding significantly decreased shoot length, leaf number, leaf area, leaf chlorophyll concentration and dry weight of leaves and roots but increased shoot to root ratio. Severe growth restriction was observed in flooded MA and PT plants. Based on the ability to maintain growth under flooding conditions, PP was the most flood tolerance cultivar with profuse adventitious roots followed by TK and TC, respectively, while PT was the least flood tolerance in this study. MA plants restricted their growth and maintained leaf chlorophyll level to survive flooding without adventitious root formation. The results suggested that these selected wax apple cultivars and Malay apple tolerated to flooding differently and flooding tolerance was not generally associated with the ability to form adventitious roots under flooding conditions.

Key words: adventitious roots, flood tolerance, lenticel, *Syzygium malaccense, Syzygium samarangense* (Blume) Merrill & Perry

INTRODUCTION

Wax apple is a tropical fruit tree commercially grown in Taiwan, Thailand, Malaysia, Indonesia, Australia, and Central and South America (Nakasone and Paull, 1998). In Taiwan, wax apple plants were flooded routinely for 30 to 40 days in summer to induce flowering without any report on tree damage or adverse physiological impact (Wang, 1983). A survey of fruit orchards in the central lowland areas of Thailand after a heavy flooding also reported that wax apples were flood tolerance (Sethpakdee, 1997). Flooding generally decreases growth of

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many woody perennials by suppressing new leaf formation and expansion of leaves and internode, causing leaf chlorosis, premature leaf senescence and abscission, inhibiting root formation and growth of existing roots and inducing root decay (Kozlowski and Pallardy, 1997). Shoot to root ratio is typically increased as low oxygen conditions of waterlogged soil had adverse affect on growth of roots more than the above ground portion (Kozlowski, 1997). Morphological changes in response to flooding include epinasty, formation of lenticels and adventitious roots, stem hypertrophy and aerenchyma formation in root tissue (Kawase, 1981). Flood-tolerant plants survive waterlogging by interaction of morphological, anatomical, and physiological adaptation. Examples are the formation of lenticels at the stem base to facilitate gas exchange between submerged stem and flooded water (Hook, 1984), formation of intercellular air spaces in roots or root aerenchyma for more efficient transport of oxygen gas within the roots (Lin and Lin, 1992) and formation of adventitious roots to increase water absorption (Tsukahara and Kozlowski, 1985) and to increase supply of root-synthesized gibberellins and cytokinins to the leaves (Reid and Bradford, 1984).

Flood tolerance varies greatly with woody plant species and genotypes (Ranney and Bir, 1994; Kozlowski and Pallardy, 1997). Variation of flooding tolerance among wax apple cultivars commercially grown in Thailand has never been investigated. The objective of this study was to compare growth, leaf chlorophyll concentration and morphological adaptation of four wax apple cultivars of different growth and fruit characteristics in response to flooding. Four wax apple cultivars used in this study were Thapthimchan, Phetnamphueng, Thunklao and Plastic. Thapthimchan and Phetnamphueng are important seedless cultivars with an attractive glossy red long bell-shaped fruit. Thapthimchan, in particular, becomes more popular for most domestic and export markets due to their excellent fruit quality. Thunklao is an early bearing seedless cultivar with a glossy light green bell-shaped fruit, fast growing habit and ease of flowering manipulation. Cultivar Plastic is well known for its small flat bell-shaped fruit with bright red or pink skin that makes it look like a plastic fruit. Malay apple (*Syzygium malaccense*) with distinctively larger fruits and leaf sizes compared to other wax apple cultivars was also included in this study for comparison.

MATERIALS AND METHODS

Rooted cuttings of Malay apple (*Syzygium malaccense*) (MA) and wax apple (*Syzygium samarangense* (Blume) Merrill & Perry) cvs. Plastic (PT), Thunklao (TK), Phetnamphueng (PP) and Thapthimchan (TC) were planted in 3-L plastic pots (20 cm dia.) using a medium consisted of sand, rice hull, rice hull charcoal, coir dust and manure (1:1:1:1:1 by volume) and supplemented with 10 g/pot of 14-14-14 controlled release fertilizer (Osmocote®, Scotts Europe B.V., The Netherlands). Plants were grown in a lath-house receiving natural sunlight.

When plants were 7 months old, flooding treatments were randomly assigned. Half of the plants in each cultivar were put in a 40-L plastic bucket (4 plants/bucket) and flooded to 5 cm above the soil surface for 70 days with tab water and the flood level was maintained constantly by adding water daily to compensate for evaporative loss. The other half of the plants were irrigated daily and served as non-flooded controls. Representative shoots of each plant were marked at the tip and shoot elongation from the mark during the experiment was monitored. Adaptive morphological characteristics at stem base related to flood tolerance such as formation of lenticel and adventitious roots were observed daily and the first appearance time of such characteristics was recorded. After flooding for 14 and 70 days, 4 or more plants from each treatment combination were sampled to measure shoot length, leaf number, leaf area, plant dry weight and leaf chlorophyll concentration. Leaf area was measured using a leaf area meter (Li-3001; Li-Cor Inc., Nebraska, USA). Dry weight of leaves, stems and roots were recorded separately after drying in a forced air oven at 70 °C for 72 hours. Relative growth rate (RGR) of shoots and roots of flooded wax apple and Malay apple plants during day 0 - 14 and day 14 - 70 after flooding was calculated from changes of dry mass (Hunt, 1990). The most recently expanded leaves (3^{rd} – 5^{th} leaves from the top) were sampled and their chlorophyll was extracted by using *N,N* - dimethylformamide (DMF) and the total chlorophyll concentration was determined as described by Moran (1982).

The experiment was conducted in a 2 × 5 factorial in a completely randomized design (2 levels of flooding × 5 cultivars). Data were subjected to analysis of variance (SAS Institute, 1989) and degree of flood tolerance was ranked among cultivars based on growth responses and morphological adaptation after flooding for 70 days in comparison with their respective non-flooded control plants.

RESULTS

Morphological changes

After flooding for 12–21 days, splitting of the outer bark at stem base above and below the flood level was observed in flooded wax apples and Malay apples. The bark initially cracked randomly at 3-4 spots around the stem base and the cracks expanded vertically. Some cracks merged together to form a larger crack and opened wider. Hypertrophy of the stem bases was observed as a result of spongy tissues that developed from the inner bark underneath the cracks. PT plants showed bark splitting within 12 days after flooding followed by TK and PP plants on day 13^{th} and TC plants on day 14^{th} after flooding, respectively. Bark splitting was observed on flooded MA plants after flooding for 21 days. The differences in crack density among cultivars were not quantified in this study.

New adventitious roots emerged at stem base below the flood level mainly through the cracks and a few from the non-crack area 2-3 days after the first appearance of bark splitting. Some adventitious roots elongated, branched and extended down to the soil surface while some roots still floated near the water surface. Distinctive white adventitious roots were relatively larger in size and less branching as compared to regular roots formed in the non-flooded soil. Flooded PT plants formed adventitious roots faster than other cultivars but flooded TC had larger and greater number of adventitious roots followed by flooded TK and PP plants, respectively, while flooded MA plants did not form adventitious roots at all. Despite earlier formation of stem splitting and adventitious roots, flooded PT plants began to die after flooding for 30 days.

Growth and leaf chlorophyll concentrations

Flooding for 14 days did not significantly affected shoot length, leaf number and leaf area of each cultivar. Shoot length of PT, TK, PP and TC plants was even increased by flooding while leaf area was slightly increased in flooded MA, TK and PP plants and was slightly decreased in flooded PT and TC plants. Plant dry mass was initially different among cultivars but dry mass allocation to leaves, stems and roots was not significantly affected during day 0 – 14 of flooding (Table 1). Flooding up to 70 days significantly restricted shoot elongation and expansion of leaf area of all cultivars, particularly for MA and PT plants (Table 2). Leaf and stem dry mass of flooded MA, PT, TK and TC plants was lower than that of non-flooded controls while flooded PP plants slightly gained leaf and stem dry mass over their non-flooded controls (Table 2). Flooding for 70 days severely decreased root dry mass of all

Table 1 An increase in shoot length, leaf number, leaf area, dry weight partitioning to leaves, stems and roots and shoot to root ratio of Malay apple and four wax apple cultivars after 14 days of flooding.

Flooding-cultivars	Shoot length (cm)	Leaf number (no./plant)	Leaf area (cm^2)	Dry weight (g)			Shoot:root
				Leaves	Stems	Roots	
Control - MA	6.5±3.5	41.0±2.3	2137.2±110.8	16.9±2.1	12.1±1.9	10.1±2.6	3.2±0.5
Flooded - MA	0.1±0.1	46.7±0.9	2662.3±54.8	23.2±1.7	18.9±2.7	12.5±2.6	4.0±0.7
Control - PT	3.0±1.2	67.0±2.7	2523.3±237.1	13.9±1.8	7.2±1.2	8.5±1.8	2.7±0.5
Flooded - PT	6.8±0.7	48.8±1.7	1329.1±69.0	9.5±0.6	6.0±0.7	7.0±1.5	2.4±0.4
Control - TK	2.5±0.8	46.5±2.2	1758.7±224.7	14.5±1.9	14.3±3.1	10.1±2.2	3.0±0.3
Flooded - TK	6.9±3.7	44.0±0.4	1876.1±124.7	18.0±2.4	15.9±2.8	9.5±1.7	3.8±0.5
Control - PP	2.6±0.5	40.5±2.0	1736.3±96.7	14.9±0.8	11.5±1.1	8.3±0.6	3.2±0.2
Flooded - PP	3.0±1.8	44.3±2.2	2104.7±259.1	18.2±2.9	13.2±2.1	7.0±0.7	4.4±0.4
Control - TC	2.6±1.3	48.5±3.0	4088.8±384.1	28.5±2.1	25.1±2.7	17.0±1.5	3.2±0.2
Flooded - TC	5.0±3.6	50.5±2.2	3324.7±190.1	29.3±1.3	32.9±2.5	18.6±3.3	3.6±0.4
Significance							
Flooding	0.5190	0.1798	0.1586	0.1264	0.0239	0.9397	0.0367
Cultivars	0.8606	<0.0001	<0.0001	<0.0001	<0.0001	0.0001	0.0533
Interaction	0.1601	<0.0001	0.0007	0.0907	0.2291	0.8304	0.4746

MA = Malay apple, PT = Plastic, TK = Thunklao, PP = Phetnamphueng, TC = Thapthimchan. Values are mean±SE.

Table 2 An increase in shoot length, leaf number, leaf area, dry weight partitioning to leaves, stems, roots and adventitious roots and shoot to root ratio of Malay apple and four wax apple cultivars after 70 days of flooding.

Flooding-cultivars	Shoot length (cm)	Leaf number (no./plant)	Leaf area (cm^2)	Dry weight (g) Leaves	Stems	Roots	Adv.roots	Shoot:root
Control - MA	17.5±2.7	104.8±3.8	8053.7±1301.8	58.1±2.7	44.43±1.8	34.8±3.4	-	3.0±0.3
Flooded - MA	1.3±0.8	46.5±4.2	2261.3±204.1	26.4±2.5	31.5±4.5	14.0±2.6	-	4.4±0.7
Control - PT	16.7±3.0	139.3±6.3	5220.4±405.8	35.0±2.5	19.0±1.6	26.6±3.4	-	2.1±0.2
Flooded - PT	0.2±0.0*	51.0±0.0*	1945.6±0.0*	17.5±0.0*	8.3±1.0**	6.1±1.4**	1.02*	6.4±0.0*
Control - TK	21.0±2.6	89.5±8.1	4516.5±259.7	39.2±4.6	32.1±3.3	31.1±2.8	-	2.3±0.2
Flooded - TK	13.8±2.3	65.5±4.1	2896.9±164.7	35.4±1.8	31.9±2.0	12.4±0.1	0.96	5.4±0.3
Control - PP	17.0±3.3	82.0±4.9	4064.6±277.1	37.6±2.2	26.3±1.8	24.4±1.6	-	2.6±0.1
Flooded - PP	10.4±3.1	72.3±7.9	3520.4±300.4	43.4±4.0	28.2±6.8	12.8±3.4	0.64	6.0±0.6
Control - TC	17.7±6.6	79.5±1.2	5747.7±207.3	51.7±1.7	49.9±2.7	53.6±12.2	-	2.1±0.3
Flooded - TC	11.4±2.1	67.3±4.8	4210.4±449.6	46.7±4.8	49.3±6.1	15.1±2.1	1.10	6.5±0.7
Significance								
Flooding	0.0001	<0.0001	<0.0001	<0.0001	0.0641	<0.0001	-	0.0001
Cultivars	0.1200	0.0686	0.0149	0.0002	<0.0001	0.0045	-	0.5390
Interaction	0.4063	<0.0001	0.0003	<0.0001	0.1776	0.0735	-	0.0187

MA = Malay apple, PT = Plastic, TK = Thunklao, PP = Phetnamphueng, TC = Thapthimchan. Values are mean±SE.

* indicated the value from a single plant that survived until the end of the flooding duration.

** indicated the mean from both live and dead plants at the end of the flooding duration.

cultivars, particularly for PT and TC. Lower root dry mass under long-term flooding was associated with poor root growth, death and decomposition of roots, particularly those roots at the bottom portion of the container. Increased shoot to root ratio of flooded wax apples in all cultivars (Table 1-2) indicated that roots were more sensitive to flooding than the above ground portion. Dry mass of adventitious roots of flooded PT, TK and TC was comparable and followed by that of PP while flooded MA did not form adventitious roots (Table 2).

As four wax apple cultivars and Malay apples were different in the initial sizes, relative growth rate (RGR) of shoot and root was used to compare the effect of flooding on their growth rate. Shoot RGR of all cultivars was positive from days 0 - 14 and days 14 - 70 of the flooding regime indicating the gain of shoot dry mass from the initial one in each cultivar during the early flooding period (Figure 1). MA plants had highest shoot RGR followed by PP while PT, TK and TC had lower shoot RGR after flooding for 14 days (Figure 1). After flooding up to 70 days, shoot RGR decreased in all cultivars and PP plants had highest shoot RGR followed by TK, PT, TC and MA, respectively (Figure 1). Flooded MA also had highest root RGR followed by flooded PP and TC while flooded PT and TK had negative root RGR values indicating the loss of root dry mass during the 14-day flooding period. Root RGR during 14 – 70 days of flooding was highest in flooded PP followed by that of flooded TK, MA and TC, respectively while only flooded PT plants had negative value of root RGR (Figure 2).

Leaf chlorophyll concentration was initially different among cultivars where TK and PP had greater chlorophyll concentration than the others. Chlorophyll tended to increase during a 70-day period of experiment in control plants. Flooding generally decreased leaf chlorophyll concentration and its effect was more pronounced

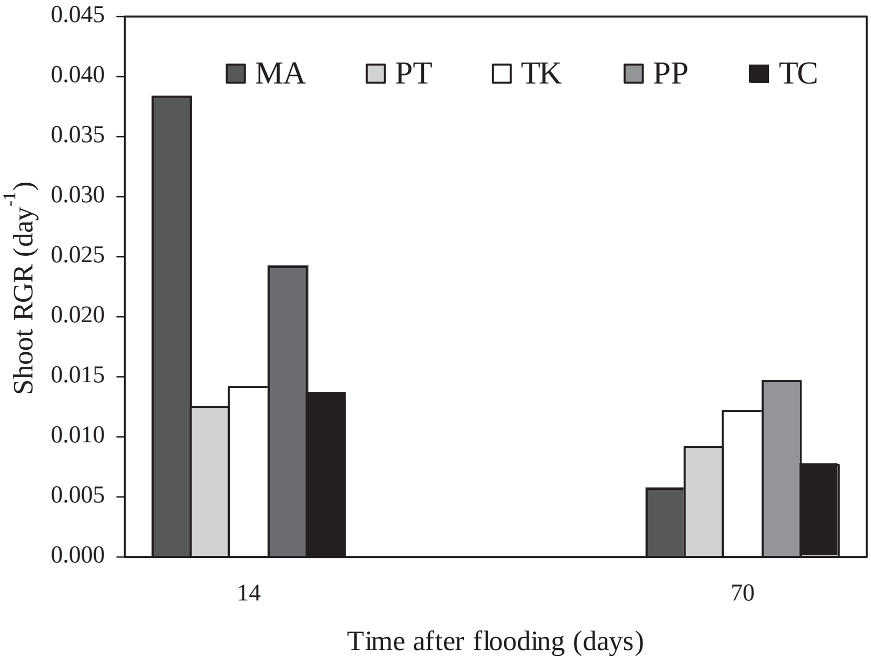

Figure 1 Shoot relative growth rate (RGR) of Malay apple and four wax apple cultivars under flooding for 14 days and 70 days. MA = Malay apple, PT = Plastic, TK = Thunklao, PP = Phetnamphueng and TC = Thapthimchan.

with time after flooding (Table 3); however, distinctive chlorosis was not observed in this study. Flooded MA, PT and TK better maintained leaf chlorophyll concentration at the end of the flooding period than flooded PP and TC (Table 3).

DISCUSSION

Vertical split of the outer barks and forming of larger cracks at stem base near the flood level in response to flooding were observed in all wax apple cultivars and Malay apples. Splitting of stem in response to flooding has been reported in other woody plants such as eucalyptus (Akilan *et al*., 1997). These cracks resembled lenticels that facilitated gas exchange between stem and flooding water as reported in other species under flooding conditions (Sena Gomes and Kozlowski, 1980). Lenticels appear to be more important site for oxygen entry and probably the site for releasing potentially toxic substances such as ethanol and acetaldehyde produced by anaerobic respiration of submerged plant parts (Coutts and Armstrong, 1976; Kozlowski, 1997). Covering of lenticels with Vaseline to restrict gas exchange significantly decreased growth of flooded wax apples (Ya-intr *et al*., 2006). Adventitious root formation observed in all flooded wax apple cultivars agreed with other reports on flooded woody perennials that produced adventitious roots on the original roots or on the submerged portion of the stem or both (Tsukahara and Kozlowski, 1985; Yamamoto *et al*., 1995). These adventitious roots could physiologically compensate for loss by decay of portions of the original root system following flooding. Potential roles of these adventitious roots included enhancing of water absorption, oxidizing the rhizosphere and transforming some soil-borne toxins to less harmful compounds and supplying of root synthesized gibberellins and cytokinins to

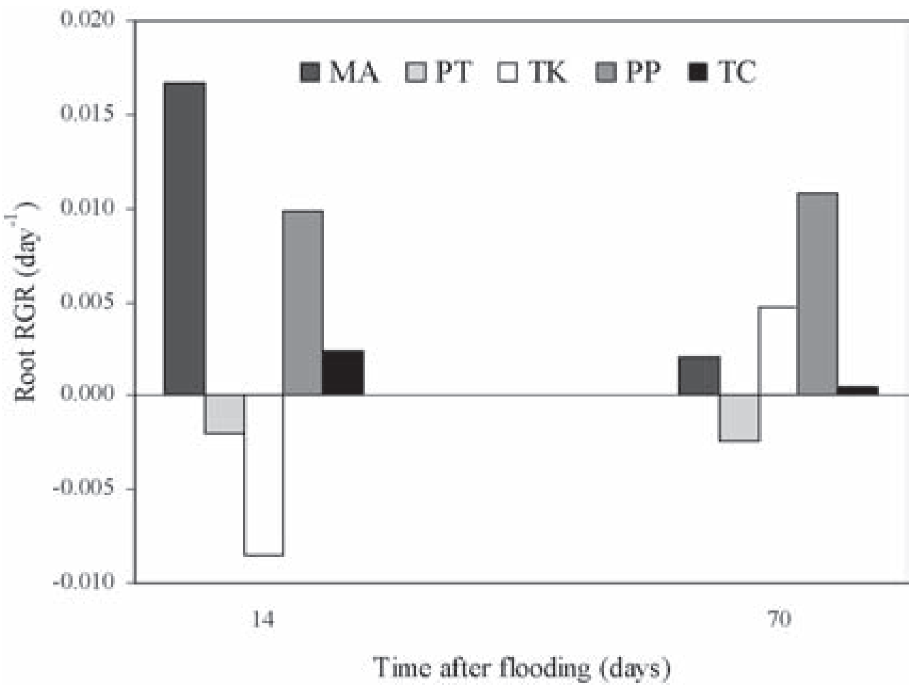

Figure 2 Root relative growth rate (RGR) of Malay apple and four wax apple cultivars under flooding for 14 days and 70 days. MA = Malay apple, PT = Plastic, TK = Thunklao, PP = Phetnamphueng and TC = Thapthimchan.

the leaves (Hook and Brown, 1973; Jackson and Drew, 1984; Reid and Bradford, 1984; Tsukahara and Kozlowski, 1985). However, flood-induced adventitious roots have not been mentioned for field grown wax apples (Wang, 1983; Sethpakdee, 1997). In this study, flooded Malay apples did not form adventitious roots at all suggesting that their survival may associate with other mechanisms besides adventitious root formation.

Flooding decreased growth of these four wax apple cultivars and Malay apples as previously reported in other woody perennials (Crane and Davies, 1988; Ismail and Noor, 1996). Leaf abscission was slightly observed in this study and lower shoot dry mass of flooded plants was mainly due to slow shoot growth. The detrimental effect of flooding was more pronounced to root system than to the above ground portion leading to an increase in shoot to root ratio. Plants with high shoot to root ratio would be susceptible to water stress after drainage. Although adventitious roots were formed in response to flooding to compensate for the loss of submerged roots, our observation from other experiments indicated that most of these flood-induced adventitious roots dried out after drainage due to lacking of moisture and only few were able to grow into the soil surface. Thus the role of flood-induced adventitious roots on growth recovery after flooding is still questionable.

Loss of chlorophyll and leaf chlorosis are common symptoms observed in flooded plants (Kawase, 1981). Flooding conditions generally decreased uptake of mineral nutrients, especially nitrogen which is an important component in chlorophyll molecule (Kozlowski and Pallardy, 1997). Hsu *et al*. (1999) also reported a significant decrease in leaf nitrogen of wax apple plants after flooding for 35 days. This partly explained a decrease in leaf total chlorophyll concentration of flooded wax apples at the end of a 70-day flooding period. As chlorophyll measurement was performed destructively on recently matured leaves, different values observed among cultivars were also possibly due to variation of leaf ages. Flooded Malay apples grew very slowly with very

Table 3 Leaf total chlorophyll concentration of Malay apple and four wax apple cultivars after flooding for 14 days and 70 days.

Flooding - cultivars	Total chlorophyll concentration ($g.m^{-2}$)	
	14 days	70 days
Control - MA	0.34±0.02	0.40±0.03
Flooded - MA	0.30±0.03	0.37±0.03
Control - PT	0.45±0.02	0.50±0.02
Flooded - PT	0.38±0.02	0.46±0.00
Control - TK	0.60±0.01	0.71±0.03
Flooded - TK	0.47±0.02	0.64±0.06
Control - PP	0.51±0.01	0.77±0.03
Flooded - PP	0.43±0.02	0.56±0.05
Control - TC	0.43±0.03	0.71±0.03
Flooded - TC	0.41±0.02	0.48±0.01
Significance		
Flooding	<0.0001	<0.0001
Cultivars	<0.0001	<0.0001
Interaction	0.1235	0.0197

MA = Malay apple, PT = Plastic, TK = Thunklao, PP = Phetnamphueng and TC = Thapthimchan. Values are mean±SE.

few new leaves and maintained relatively stable leaf chlorophyll concentrations. Growth restriction and chlorophyll maintenance mechanism were reported in some submerged tolerance rice cultivars (Sarkar *et al*., 2006). These rice cultivars stopped growing and remained green to conserve energy and survived under water for a certain period of time. Their growth continued again after being released from flooding.

Ranking of flood tolerance among four wax apple cultivars and Malay apple in this study was based on growth, leaf chlorophyll concentration, morphological adaptation and survival after flooding for 70 days. The results indicated that PP was the most flood tolerance that could maintain growth and form lenticels and profuse adventitious roots, followed by TK and TC, respectively. MA was ranked as moderate flood tolerance that employed a strategy of growth restriction, leaf chlorophyll maintenance and lenticel formation to survive flooding without adventitious root formation. PT that formed lenticels and adventitious roots earlier than other cultivars was the least flood tolerance in this study. Some PT plants began to die after flooding for 30 days and only one plant survived until the end of the flooding duration (Table 2). Flood-induced adventitious roots have been reported in a wide range of both flood-intolerance and tolerant angiosperms and gymnosperms but more are usually produced by flood-tolerant species (Sena Gomes and Kozlowski, 1980; Kozlowski and Pallardy, 1997). Our results suggested that flood tolerance of wax apples and Malay apples is not generally associated with the ability to form lenticels and adventitious roots.

CONCLUSION

Flooding for 70 days decreased growth and leaf chlorophyll concentrations of young potted Malay apples and the other four cultivars of wax apples; Plastic, Thunklao, Phetnamphueng and Thapthimchan. Splitting of stems immediately above and below the flood level was observed in all cultivars followed by formation of adventitious roots at the stem base under the flood level in the four wax apple cultivars but not in Malay apples. Plastic was the only cultivar that some plants died as flooding progressed despite its ability to form adventitious roots faster than other cultivars. Flood tolerance of Thunklao, Phetnamphueng and Thapthimchan cultivars was associated with their ability to form profuse adventitious roots. Malay apples restricted their growth and maintained leaf chlorophyll level to survive flooding. Based on the ability to maintain growth and leaf chlorophyll concentration during flooding, morphological adaptation (splitting of stems and adventitious root formation) and survival, flood tolerance of selected wax apple cultivars and Malay apple commercially grown in Thailand was ranked in order as Phetnamphueng > Thunklao > Thapthimchan > Malay apple > Plastic.

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