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Ability of *Limnocharis flava* to escape from episodic submersion by rapid elongation of its leaf petiole

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Abstract

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Limnocharis flava commonly known as yellow velvetleaf plant is a promising vegetable for cultivation at riparian wetlands. However, this plant is also considered as noxious weed at paddy field during rice growing season. Socio-economically, this plant cannot compete with rice; therefore, cultivation of velvetleaf plant should be done during rice off-season, i.e. at early rainy season, with risk of total submersion if depth of floodwater is beyond expected level. Objective of this research was to investigate probable morphological adaptation of the velvetleaf plant to episodic submersion. Plants with relatively uniform height were submerged for 3, 6, 9, and 12 consecutive days in an outdoor experimental pool. Untreated plants were used as control. After submersion, all treated plants were allowed to recover for 7 days. Results of this study indicated that velvetleaf plant was able to escape from submersion condition by rapid elongation of their petioles; consequently, increased its height. It took less than two days for at least one leaf blade per plant had raised above water surface. The plant survived as long as at least one leaf had escaped out of water. However, number and size of leaves reduced during submersion. Chlorophyll concentration index (CCI) increased for compensating smaller leaf area. Long but weak petioles developed during submersion were immediately collapsed as soon as submersion treatments were terminated, failed to support weight of leaf blade. Velvetleaf plants gradually developed new normal leaves during recovery period.

Keywords: aquatic plants; yellow velvetleaf; wetland vegetable; morphological adaptation

Introduction

Low plant species diversity at tropical riparian wetlands is mainly associated with limited species which have ability to adapt to two extreme conditions, i.e. prolonged flooding during rainy season and severe drought during dry season (Lakitan et al., 2018a). Occurrences of these two extremes are also unpredictable (Widuri et al., 2017), in term of their intensity, timing, and duration. Furthermore, shallow soil water table condition also limits crop choices for local farmers to cultivate (Meihana et al., 2017; Lakitan et al., 2018c). Agriculture-wise, these conditions make it really hard for local smallholder farmers to schedule their farming activities. Therefore, most of local farmers only grow one rice crop annually (Kartika et al., 2018a; 2018b; Lakitan et al., 2018b). Floating culture of annual vegetable crops is possible to do (Siaga et al., 2018) since it does not require large acreage as rice does.

Velvetleaf is a perennial aquatic plant, classified as helophytes, rooting in mud at the bottom of flooded land. However, its leaves and inflorescences are above water surface. Leaves are initiated at base of the plant. Leaf blade is supported by long and spongy petiole with numerous internal air chambers. Inflorescence is axillary with long and erect peduncle up to 90 cm, consists of 5 to 15 flowers. Flowers have 3 sepals and 3 yellow petals. Compound fruit is 1.5-2.0

cm in diameter, enclosed by the sepals. Seeds are numerous, minute, and dark brown colour (CABI, 2018).

The velvetleaf plants are commonly found at frequently flooded riparian wetlands. Suitable depth of floodwater should not be more than 50 cm, such that it is less than the length of its leaf petiole. Abhilash et al. (2008) observed that velvetleaf plant was an aggressive colonizer, which had ability to outcompete native species. Nutrients, water depth and land use patterns were major factors responsible for growth and proliferation of this aggressive plants.

The velvetleaf plant is suspected to have ability to mitigate fluctuating depth of floodwater, as this condition naturally occurs at riparian wetland ecosystem. However, it is unclear on which mechanism(s) employed by the plant in mitigating submersion condition. Objective of this study was to investigate probable morphological adaptation of velvetleaf plants to episodic submersion.

Materials and Methods

Plant materials and agro-climatic conditions

Seedlings of the wild velvetleaf plant were gathered from paddy field at the Agricultural Training Centre (ATC), Universitas Sriwijaya, Inderalaya, Indonesia. The seedlings were selected for homogenous size and number of leaves. Seedlings were selected and transplanted into 60 PVC pots, containing muddy soil previously used for rice cultivation. Two seedlings were planted in each pot. Upper and base diameters of pots are 17 cm and 13 cm, respectively. Height of the pot is 32 cm. Soil pH was around 5.5 to 6.0 (slightly acidic), similar to soil commonly found at riparian wetlands in South Sumatera, Indonesia. NPK was applied at rate of 5 g/plant as base fertilizer.

The research was conducted at outdoor research facilities during rainy season in 2017, using an experimental pool dedicated for water-related research. The velvetleaf plants were directly exposed to unfavourable soil (acidic) and climatic (heavy rainfall) conditions which are mimicking frequent submerging condition experienced by the plants at riparian wetlands in Indonesia. The research facility is located at Jakabaring (104°46’44”E; 3°01’35”S), Palembang, Indonesia.

Research setup and experimental design

At two weeks after transplanting, one of the two seedlings was cut for increasing uniformity of plant population prior to application of treatments. Since the velvetleaf plant is a perennial plant, further effort to minimize heterogeneity of the population with regard to plant age is by rejuvenating all plants used in this experiment. Technically, all above ground organs of the whole population were cut at base of their petioles. The plants are ready to be treated after each rejuvenated plant had developed its third new leaf.

Prior to transplanting, all pots had been filled with soil to 24 cm height (3/4 of pot height), leaving 8 cm (1/4 of pot height) space at upper part of the pots to be filled with water. This setup was used as control plant (S_0). Our previous study indicated that velvetleaf plant grew and produced higher yield at shallow flooding condition.

All plants subjected to submersion treatments were placed in experimental pool, filled with water such that all treated plants were fully submerged. Durations of submersion treatments were 3 days (S_3), 6 days (S_6), 9 days (S_9), and 12 days (S_{12}). At the end of each submersion treatment, the plants were allowed to recover by taking the pots out of experimental pool and placing them at the pre-assigned plot next to control plants (S_0). Water regime applied during recovery period of the S_3, S_6, S_9, and S_{12} plants were similar to that of the S_0 plant.

This submersion experiment consisted of five treatments (4 different durations of submersion plus control) randomly placed into each of 4 blocks. There were 3 plants represented each treatment within each block. Position of each block and position of treatments within each block were arranged following randomized block design (RBD) layout.

Data collection and analysis

Growth parameters measured were plant height, leaf midrib length, leaf area, length of upper and lower parts of petiole, chlorophyll concentration index (CCI), relative number of leaves developed during submersion, and percentage of broken petioles during recovery period. Based on architecture of above-ground organs of the velvetleaf plant, plant height is basically similar to length of petiole plus midrib of blade of the longest leaf. Leaf area (LA) was calculated based on regression model (Lakitan et al., 2017) using midrib length as predictor. CCI values were measured using a chlorophyll meter (Konica Minolta SPAD-502 Plus).

The analysis of variance and pairwise comparisons were carried out using statistical application developed by the SAS Institute Inc., Cary, NC, USA. Further test was performed using the Least Significant Differences test at $p \leq 0.05$ ($LSD_{0.05}$) for specifying differences amongst treatments for each parameter.

Results

Accelerated increase in plant height under submersion condition

Plant height was measured on the day prior to submersion treatment, at the end of each submersion treatment, and after a week of post-treatment recovery. Since durations of treatment were varied at 3, 6, 9, and 12 days, then paired measurements of treated and controlled plants were made on each specified day of treatments were terminated.

Pairwise comparison between treated and controlled plants prior to submersion treatments indicated that there were no differences in height between each pair of controlled and treated plants (Table 1). It implies that the plant population used in this study was statistically uniform before the treatments were commenced. Population uniformity is a good foundation for justifying differences in height after treatments and during recovery period is truly caused by the treatments.

At the end of all submersion durations, i.e. 3, 6, 9, and 12 days, height of treated plants were significantly taller than that of untreated plants (Table 1). Clearly, submersion enhanced vertical growth of the velvetleaf plants. The longer duration of submersion, the taller velvetleaf plant became, despite floodwater was set at constant level. This study revealed that the velvetleaf plant lengthen its petiole to raise leaf blade (lamina) above water surface; such that the leaf blade can function normally in capturing light and facilitating gas exchanges, i.e. photosynthesis, respiration, and transpiration.

Seven days after recovery from submersion, the newly developed leaves during post-submersion period were shorter but had not yet been as short as the height of control plants (Table 1). Rapid vertical elongation during submersion condition is an adaptive mechanism of the velvetleaf plant to escape from such unfavourable condition. The term of 'escape' during submersion is associated with ability of a plant to rapidly increase its height such that some of its leaves were uplifted above water surface. In velvetleaf plant, lengthening of leaf petiole is directly increasing plant height as shown in Table 1. Eventually, the newly developed leaves gradually return to normal height as the floodwater recedes to a level below leaf blade position.

Part of petiole that elongates during submersion

Height in velvetleaf plant is predominantly governed by length of its petiole plus midrib of leaf blade. However, prior to this study, it was unclear which part among midrib, upper petiole, and lower petiole contributed to rapid increase in plant height during submersion period. Lower petiole is characterized by presence of wings along both sides the petiole. Results of this study revealed that both upper and lower parts of petiole elongated during submersion but lower petiole elongated significantly more than upper petiole. For instance, after 12 days under submersion, lower petiole extended as much as 77.9 percent more compared to that of control plants; while upper petiole extended only 20.7 percent (Table 2).

Table 1. Pairwise comparisons of plant height between control and submerged *Limnocharis flava* plants at 3, 6, 9, and 12 days, measured prior to, after each treatment was terminated, and at the 7th day of post-treatment recovery

Pairwise[1] comparison	Average		Standard deviation			*t-calculated*	Significant level[3]	*t-table*	
	S_0	S_x	S_0	S_x	S_0/S_x [2]			0.05	0.01
Prior to submersion treatment									
S_0-S_3	33.68	33.43	3.54	4.39	0.808	0.224	ns	1.717	2.508
S_0-S_6		32.28		5.40	0.656	1.068	ns		
S_0-S_9		32.42		2.73	1.298	1.387	ns		
S_0-S_{12}		34.02		3.34	1.061	0.335	ns		
At the end of each submersion treatment									
S_0-S_3	38.75	47.75	3.14	4.51	0.696	8.018	**	1.717	2.508
S_0-S_6	40.81	51.85	2.96	3.65	0.811	11.512	**		
S_0-S_9	42.13	55.04	2.65	2.24	1.183	18.256	**		
S_0-S_{12}	43.48	57.79	3.37	2.36	1.424	17.050	**		
After 7 days of recovery for each treatment									
S_0-S_3	49.94	53.04	5.63	3.70	1.522	2.255	*	1.717	2.508
S_0-S_6	50.14	53.03	4.64	3.60	1.289	2.403	*		
S_0-S_9	50.37	52.27	4.69	7.24	0.647	1.079	ns		
S_0-S_{12}	51.08	54.31	4.57	5.96	0.766	2.103	*		

[1] Controlled (S_0) and treated plants (S_x) were compared as two independent samples.
[2] If standard deviation of S_0/S_x > 0.5 and < 2.0, then both samples are considered as having equal variance.
[3] Significant level: ns = not significant, * = significant at $p \leq 0.05$; ** = significant at $p \leq 0.01$.

Table 2. Length of midrib, upper petiole, lower petiole, leaf area (LA), and relative leaf number of *Limnocharis flava* as affected by submersion treatment and percentage of collapsed elongated petioles during recovery period

Treatment	Length (cm) at the end of submersion						LA (cm^2)	Relative leaf number during sub-mersion	Collapsed petiole (%)
	Midrib		Upper petiole		Lower petiole				
S_0	15.192	a[1]	18.108	b	12.258	bc	147.96	1.000	0
S_3	13.850	b	18.458	b	11.900	c	123.49	0.580	100
S_6	13.775	b	18.600	b	11.358	c	122.19	0.500	100
S_9	13.925	b	19.058	b	13.758	b	124.80	0.556	100
S_{12}	14.892	ab	21.858	a	21.808	a	142.30	0.605	100
LSD .05	1.265		2.426		1.833		–	–	–

[1] Means followed by the same letter are not significantly different at $p \leq 0.05$.

It is interesting to note that midrib length of newly developed leaves during submersion condition was shorter than that of leaves in control plants (Table 2). Shorter midrib meant smaller leaf size since shape of the leaf did not altered. This contrasting effect implied that petiole elongation was occurred at expense of leaf blade enlargement.

Forcing petiole to extend beyond its normal length has helped the velvetleaf plant to survive under submersion condition. However, abnormally longer petiole increases susceptibility to lodging problem. In this study, during post-submersion period, all (100%) elongated petioles of leaves developed during submersion were collapsed soon after the submersion treatment was terminated (Table 2).

At normal condition, the velvetleaf plant develops new leaf in every 3-day period. However, relative number of leaf developed during submersion was reduced to about half of that of control plant, i.e. 0.580, 0.500, 0.556, and 0.605 during 3, 6, 9, 12 days exposed to submersion, respectively (Table 2).

Table 3. CCI value of *Limnocharis flava* leaf measured at pre-treatment, during submersion treatment, and during recovery period

Treatment	Pre-treatment		During treatment[2]		During recovery[3]	
S_0	41.04	a[1]	41.86	a	34.85	a
S_3	40.22	a	37.03	a	38.34	b
S_6	36.76	a	38.76	a	38.82	b
S_9	39.17	a	36.16	a	39.29	b
S_{12}	37.24	a	36.04	a	39.24	b
LSD .05	4.915		6.702		3.046	

[1] Means followed by small letter is not significantly different at $p \leq 0.05$.
[2] Measurements during submersion treatments were done on leaf blades above water surface.
[3] Measurements during recovery period were done at 7 days after end of submersion.

CCI value prior to, during, and after submersion

CCI value was not affected by submersion treatments up to 12 days. However, it was surprising that CCI values of the velvetleaf plants which had been exposed to submersion condition for 3 to 12 days were significantly higher than that of control plant during recovery period (Table 3).

Discussion

Paradox of the velvetleaf plant

It has been observed that local farmers collected young unfolded leaf and inflorescence at flower bud stage of wild velvetleaf plants for their consumption as vegetable (Saupi et al., 2009; Ooh et al., 2015; Sukenti et al., 2016). During rice off-season, farmers let the velvetleaf plants to grow on the rice field and collected them for consumption. However, the velvetleaf plant was treated as a noxious weed during rice growing season (Juraimi et al., 2013; Chandran and Ramasamy, 2015; Panetta, 2015; Gilal et al., 2016) since it could establish strong competition on rice crops; therefore, farmers eradicated this plant at the rice field. Moreover, this plant had also been reported as a resistant weed to some herbicides, i.e., synthetic auxin herbicides, AHAS-inhibiting herbicides (Ruzmi et al., 2017). More recently, this aquatic plant has been intensively studied for its potential use in bioremediation of soils contaminated by heavy metals (Marrugo-Negrete et al., 2017; Retnaningdyah et al., 2017).

Velvetleaf plant can be perceived as paradoxical plant. It can be an unwanted noxious weed in rice cultivation but it can also be a promising vegetable crop at riparian wetlands, or as beneficial plant for cleaning up metal-contaminated soil. These conflicting issues are actually manageable issues. Solution includes growing the velvetleaf plant on lands that is not suitable for rice crop or growing the plant only during rice off-season. The velvetleaf plant may also be planted at buffer zone for protecting agricultural land from anthropogenic source of heavy metal pollution.

Adaptation strategy to submersion conditions

Shallowly flooded land is a preferable habitat for velvetleaf plant, therefore, it is obvious that this plant will not experience stress under such flooding condition. It has not been previously disclosed whether this plant can survive under fully-submerging condition, i.e. all parts of the plant are drowned under water. Jackson and Colmer (2005) stated that when flooding extended to submersion of the shoot, photosynthesis became severely restricted by a deficiency of external carbon dioxide and lower light intensity depending on clarity of floodwater. These might be also the case in the velvetleaf plant. Growth and development of the vast majority of vascular plant species were impeded by complete submersion which could result in death. However, numerous wetland species were well adapted to flood-prone areas. This was achieved by certain key physiological adaptations and acclimations such as physical escape from submerged environment, avoidance of oxygen-deficiency through effective internal aeration, and a capacity to prevent or repair oxidative damage during re-aeration (Jackson and Colmer, 2005).

Fast elongation at basal meristem of petiole

Based on results of this study, it was clear that the velvetleaf plant had ability to escape from submersion condition by rapid elongation of its petioles, especially at lower part of the petioles (Table 2). Each leaf petiole of velvetleaf plant has meristemic tissue at its base, called basal meristem. The fast elongation at lower part of petiole is associated with enhanced division and longitudinal elongation of meristematic cells at basal meristem. Stem of velvetleaf plant is fleshy, erect, and unbranched (Haynes et al., 1998). However, the stem is very short and not directly visible since it is fully covered by sheathing base of petioles from all direction. Stem has very limited physical contribution to rapid increase of plant height during submerging condition.

Ookawara et al. (2005) argued that faster elongation was probably predicated on ethylene-induced cell wall loosening which increased cell wall extensibility. Therefore, cell elongation can occur at faster rate. Cell wall extension and cell elongation are irreversible process. Since this faster elongation is at expense of cell wall structural loosening; therefore, the advantage of longer petiole in escaping from water submersion obscured by drawback of weak petiole for supporting weight of leaf blade as soon as floodwater subsides. However, it is still an effective way in escaping submersion for at least 12 days.

The long, slender, and weak petiole did not collapse while supporting weight of leaf blade during submersion due to lateral support by surrounding body of water from all direction. In addition, existence of air chambers within the petiole created buoyant force to uplift the weak petiole. However, soon after submersion was terminated, all of elongated petioles developed during submersion were collapsed, too weak to support weight of leaf blade (Table 3). Water was replaced by air as floodwater subsided. Bornette and Puijalon (2011) reminded that density of water was much higher than that of air. Therefore, the weak petiole lost lateral support and buoyant force as soon as submersion was terminated. As the plant continues to grow, during post-submersion or recovery period, petiole of newly developed leaves would gradually return to normal.

Conclusion

Velvetleaf plant has ability to escape from submersion at least for 12 days by rapid elongation at basal meristem of leaf petiole. The plant will survive as long as at least one of its leaf blades has been positioned above water surface. Number of newly developed leaves was cut by half and LA significantly decreased during submersion, however, CCI values increased, perhaps to compensate for LA reduction. Spongy petiole, rich in air chamber, may have similar function as aerenchyma in transferring oxygen internally from leaf to submerged organs. Long, slender, but weak petiole developed during submersion collapsed at its base and failed to support weight of leaf blade after submersion treatments were terminated. During recovery period, the velvetleaf plant gradually developed new leaves with normal petiole, comparable to that of control plants.

Cultivation of velvetleaf is recommended at wetland area during rice off-season, i.e. at early rainy season, such that it will not in direct competition with rice. Other possibility is growing the velvetleaf plant at area with deeper and longer period of annual flooding,

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