

Short communication

Do freshwater plants have adaptive responses to typhoon-impacted regimes?

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ABSTRACT

In tropical regimes, cyclones exert great influence on the local aquatic habitats. The objective of our study was to investigate if aquatic plants have an adaptive response to typhoon influence. Population traits of six aquatic species in different life-forms (emergent species: *Scirpus triangulatus*, *Eleocharis plantagineiformis*, *Rotala rotundifolia*, *Eriocaulon buergerianum*; submerged: *Blyxa echinosperma*; floating-leaved: *Nymphoides indica*) were investigated to compare intraspecific variations in high and low typhoon-impacted regions on Hainan Island in southern China. In the high typhoon-impacted region, there was greater belowground biomass allocation in both emergent and floating-leaved species. The ratio of belowground to total biomass of each emergent was 41% ($P = 0.028$), 38% ($P = 0.034$), 27% ($P = 0.040$), 19% ($P = 0.043$) greater respectively, and floating-leaved *N. indica* was 40% ($P = 0.014$) greater than in the low typhoon region. The stem height of relatively tall emergent species (*S. triangulatus* and *E. plantagineiformis*) was 35% ($P = 0.033$), 42% ($P = 0.046$) lower, and floating-leaved species *N. indica* had decreased leaf area (49%, $P < 0.001$) and number (30%, $P < 0.001$) on water surface in the high typhoon-impacted region than in the low. These adaptations of the plants will reduce their risk of mechanical damage from strong winds or wind-induced currents. Submerged species in the study showed no variation in traits between the high and low typhoon-impacted regions.

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1. Introduction

In tropical or subtropical areas, tropical cyclones (e.g. typhoons and hurricanes) are one of the strongest forces of nature, and they can exert great influence on landforms and ecology aspects (Li, 1983; Kubota et al., 2004). The heavy rainfall, flooding and high winds that accompany cyclones or typhoons can severely affect biota (Sanchez and Islebe, 1999). Vegetation is especially vulnerable. Many researchers have studied the biological effects of these catastrophic windstorms on terrestrial ecosystems. Moreover, many studies have focused on canopies and the density of tropical rain forests under the effect of heavy cyclones. Such studies have compared the traits of vegetation found across geographical cyclone-impacted areas, and found that shorter canopy heights and higher tree densities were found in frequent cyclone-impacted tropical rain forest ecosystems (Whitmore, 1984; Richards, 1996; Gouvenain and Silander, 2003). Few studies have, however, acknowledged the impact that cyclones may have on inland aquatic vegetation (Havens et al., 2001; Wang et al., 2008).

Phenotypic plasticity is a feature which allows aquatic plants to cope with environmental heterogeneity (Sculthorpe, 1967; Barrett et al., 1993). Population studies on patterns of variation in many aquatic species have revealed the existence of localized populations each adapted to the particular local environment (Cook, 1968; Oyama, 1996; González-Rodríguez and Oyama, 2005). Heavy rainfall, flooding and intense winds associated with typhoons can impact the hydrology of aquatic habitats. Hydrology is known to have a strong influence on aquatic plant community composition and processes (Keddy, 2000). Therefore, aquatic plant phenotypic responses in regions with a high frequency of typhoons can be expected.

Hainan Island in South China is a tropic island subjected to frequent typhoons that form over the tropical southwest Pacific Ocean (Li, 1983). While a century of deforestation has led to the disappearance of lowland rain forests along the island's edge. Fragmented wetlands and shallow waters are vastly developed in this region. Due to the impact of typhoon direction and the conical topographical structure of the land, the island sustains both natural barrier-protected and wind exposed treatments. In this paper, our objectives are to determine if aquatic plants in wetland or shallow water possess an adaptive response to typhoon by comparing the variation in population traits in high and low typhoon-impacted regions.

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2. Methods

2.1. Study site

Hainan Island is located in the South China Sea off, southern China (18°10′–20°09′N, 108°36′–111°03′E). The island covers an area of 33 900 km², with mountainous hills and peaks located in the center and plains along its periphery. Typhoons and tropical cyclones that affect the South China Sea region frequently hit the eastern and southern coasts of Hainan Island. The typhoon season on the island lasts from June to November, with the peak frequency in July to September (Zeng and Zeng, 1989). The northeastern Wenchang-Haikou region (19°28′–20°09′N, 110°04′–111°03′E) has the highest frequency of typhoon land-fall incidents on the island; locals call it the ‘Typhoon Corridor’ (Zeng and Zeng, 1989). From 1945 to 2005, three to four typhoons on average have landed in the region per year (Shanghai Typhoon Institute of China Meteorological Administration, 2005). Due to its wind-exposed location and high frequency of typhoon landings, Wenchang-Haikou is designated as a “high typhoon-impacted region”. In contrast, the Dongfang-Ledong region (18°42′–19°30′N, 108°36′–109°12′E) located on the west of the island rarely has typhoon landings. The obstruction provided by the central mountains makes Dongfang-Ledong a barrier-protected region. Hence, Dongfang-Ledong is a “low typhoon-impacted region” (Fig. 1).

We collected meteorological records during typhoon landing and substrate fertility data (total nitrogen and total phosphorus) from online database in both study regions. Meteorology data sourced from Shanghai Typhoon Institute of China Meteorological Administration (2005). Substrate fertility data was from Tropical Crop Science Data Center (2005). We also had field surveys on water acidity in the two regions. (Using HORIBA U10, HORIBA Instruments Inc., Japan.) The three factors were test differences respectively between the two regions using independent samples t-test.

2.2. Representative species selected

We selected representative species of aquatic plants in different niches, to study how their population traits differed between the high and low typhoon-impacted regions. Communities with three-dimensional structure in wetlands or shallow waters consist of submerged, floating-leaved, and emergent life-forms (Cook, 1990). Species in different life-forms are expected to experience different disturbances due to typhoons, depending on the littoral zone in which they occur. We selected representative species based on

being both abundant and occurring in both study regions to could compare intraspecific variation under different typhoon influences.

We selected *Blyxa echinosperma* (Hydrocharitaceae) as a representative for submerged species and *Nymphoides indica* (Menyanthaceae) for floating-leaved species. In addition, *Scirpus triangulatus* (Cyperaceae), *Eleocharis plantagineiformis* (Cyperaceae), *Rotala rotundifolia* (Lythraceae) and *Eriocaulon buergerianum* (Eriocaulaceae) were selected to represent emergent species. There is a considerable variation in body size of the emergent species. Relatively tall emergent species such as *S. triangulatus* (height 50–120 cm; Yan, 1983) and *E. plantagineiformis* (height 40–100 cm; Yan, 1983) were assumed to belong to a different niche than the relatively short species, *R. rotundifolia* (heights up to 30 cm; Qin and Chen, 2005) and *E. buergerianum* (heights 10–25 cm; Yan, 1983). Hereafter, the former species will be designated as tall emergents and the latter as short emergents.

2.3. Measurements of population traits

In 2006, we surveyed a total of 101 populations of six selected species found in relatively stable wetlands and shallow waters in both study regions on Hainan Island. Ten populations of every emergent species, five populations of floating-leaved species *N. indica*, and six populations of submerged species *B. echinosperma* surveyed at each site. Three surveys were conducted in July, August and October when are the months of high typhoon frequency and the growing season of the plants. All populations were measured at each of the three sample times, and mean values of the three separate measurement was taken. In each population, we randomly established 1 m × 1 m plots to obtain values for population traits.

Traits were measured differently by species type because of morphological variation among species. For submerged and emergent species, the stem height (cm) (leaf length for submerged species *B. echinosperma*), density (No m⁻²), total biomass and belowground biomass (dry weight) were measured. We used the ratio of belowground to total biomass as the parameter to determine biomass allocation. For the floating-leaved species *N. indica*, we measured area of mature leaves using a LI-3100 Area meter (LI-COR, Inc. USA), number of floating leaves on the water surface (number per plant), and ratio of belowground/total biomass. Height and petiole length of *N. indica* were not measured as its trait depends mainly on water depth which varies temporally.

2.4. Data analyses

Comparisons of intraspecific variations between the different typhoon-impacted regions were made using ANOVA and a post hoc Tukeys HSD test for samples of unequal size was used to determine significant differences ($P < 0.05$). Statistical analyses were performed using SPSS 13.0 for Windows (SPSS Inc., USA).

3. Results

Maximum wind speed and precipitation during typhoon landings were significantly ($\alpha = 0.05$) higher in high than in low typhoon-impacted region. Substrate fertility (total nitrogen and total phosphorus) was similar in high and low typhoon-impacted regions, and both regions had similar neutral water acidity (Table 1).

The comparison of population traits of the representative species between high and low typhoon-impacted regions is shown in Table 2. For emergent species, the population traits differed in the size of the plants. The stem heights of both *S. triangulatus* and *E. plantagineiformis*, the tall emergents, were significantly lower in

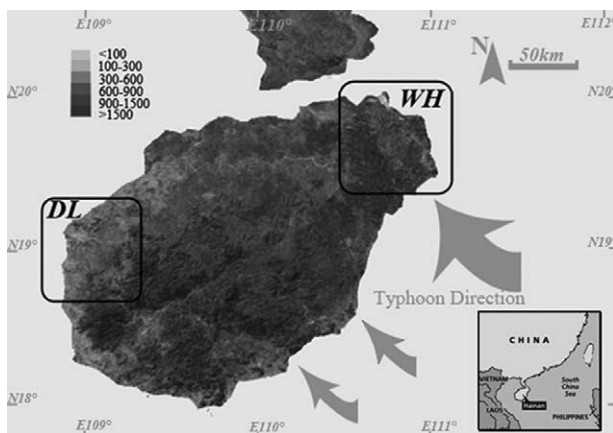


Fig. 1. Locations of high typhoon-impacted region WH (Wengchang-Haikou) and low typhoon-impacted region DL (Dongfang-Ledong) due to topography of Hainan Island and typhoons pathway.

Table 1
Meteorological record during typhoon landing and sediments conditions^a in high and low typhoon impact regions.

Typhoon impact	Maximal wind speed (m s ⁻¹)	Precipitation (mm)	Total nitrogen (mg g ⁻¹ sediment dry weight)	Total phosphorus	pH (water)
High	42 ± 13 ^b	136.2 ± 44.7 ^b	0.88 ± 0.31	0.094 ± 0.031	6.52 ± 0.33
Low	22 ± 11 ^b	97.5 ± 30.2 ^b	0.92 ± 0.25	0.113 ± 0.047	6.61 ± 0.25

^a Means ± SD: the differences in mean population traits analyzed using independent samples *t*-tests.

^b *P* < 0.05.

Table 2
Population traits^a of the representative aquatic species in high and low typhoon impact regions.

Population traits	Typhoon impact	<i>Scripus triangulatus</i>	<i>Eleocharis pantagineiformis</i>	<i>Rotala rotundifolia</i>	<i>Eriocaulon buergerianum</i>	<i>Nymphoides indica</i>	<i>Blyxa echinosperma</i>
Stem height (cm)	High	36.8 ± 13.1	42.8 ± 8.2	18.4 ± 3.1	17.8 ± 2.9	N/A	16.3 ± 3.3
	Low	56.7 ± 18.8 ^b	73.2 ± 17.6 ^b	20.1 ± 2.9	17.2 ± 3.3		16.6 ± 3.6
Population density (No m ⁻²)	High	93.5 ± 28.7	127.2 ± 27.4	87.6 ± 15.4	54.1 ± 8.9	N/A	39.5 ± 15.9
	Low	88.4 ± 16.3	132.8 ± 24.2	91.3 ± 34.8	48.2 ± 14.4		41.2 ± 18.4
Below/total biomass	High	0.62 ± 0.07	0.58 ± 0.06	0.52 ± 0.04	0.50 ± 0.08	0.56 ± 0.07	0.76 ± 0.02
	Low	0.44 ± 0.08 ^b	0.42 ± 0.09 ^b	0.41 ± 0.05 ^b	0.42 ± 0.04 ^b	0.40 ± 0.06 ^b	0.72 ± 0.02

^a Means ± SD: the differences in mean population traits analyzed using independent samples *t*-tests.

^b *P* < 0.05

the high typhoon-impacted region (*P* = 0.033 and 0.046). The short emergents *R. rotundifolia* and *E. buergerianum* did not differ in stem height regardless of the region where they were found. In the high typhoon impacted region, the ratio of belowground to total biomass of each emergent was 41% (*P* = 0.028), 38% (*P* = 0.034), 27% (*P* = 0.040), 19% (*P* = 0.043) greater respectively than in the low. No significant difference in population density was observed for any of the four species.

For the floating-leaved species *N. indica*, the number of surface leaves on each plant was lower in the high impact region (17 ± 6) than in low impact region (33 ± 4) (*P* < 0.001). The average leaf area was significantly smaller in the high impact region (58.7 ± 3.9 cm²) than in low impact region (84.3 ± 4.7 cm²) (*P* < 0.001). The ratio of belowground to total biomass was higher in the high impact region (*P* = 0.014).

For the submerged species, no significant difference was observed between regions for all of the population traits.

4. Discussion

Plants in the high typhoon-impacted region experience strong winds, high precipitation and subsequent flooding during typhoon events. Due to the different niches where these species are found, the plants have adopted distinct strategies to survive the frequent typhoon landings.

4.1. Typhoon effects on emergent plants

Since emergent plants were more exposed to strong wind compared to the other types of plants, their response to high wind intensity seemed to be more similar to that exhibited by terrestrial plants. Previous studies in rain forests have reported a significant correlation between short vegetation canopies and occurrence of tropical cyclones (Gouvenain and Silander, 2003). In the present study, we found the heights of tall emergents (>25 cm in height), such as *S. triangulatus* and *E. plantagineiformis*, to be lower in the high typhoon-impacted region. The body sizes of these plants tended to be small in the typhoon exposed region, presumably to avoid wind-throw or breakage. The heights of short emergents (<25 cm) were not significantly correlated with typhoon effects. It is possible that increased water level due to the high precipitation

associated with typhoons submerges smaller plants. Hence, the short emergents would encounter less wind disturbance than the tall ones.

The response to typhoon in allocation of biomass of emergent species was also similar to that in terrestrial plants. Small individuals in a tropical forest were previously found to be the most affected by storms because their roots were not deep enough to resist the strength of the cyclones (Sanchez and Islebe, 1999). Emergent species had a higher belowground/total biomass in the high typhoon-impacted region, presumably they could develop more roots or clonal structures, such as tubers and rhizomes, to better anchor them and keep themselves from being washed away during strong storms. These stored belowground resources are withdrawn from the production process which implies a cost in terms of reduced current growth and performance. This trade-off between current growth and stored resources for future survival and recovery represents a key trait for understanding the evolution of plant life history (Suzuki and Stuefer, 1999). After the strong winds in a storm, the plants will experience subsequent flooding episodes. Many emergent plants respond to flooding above the canopy with stem or leaf elongation (Kirkman and Sharitz, 1993; Blanch et al., 1999) as failure to elevate the canopy above the surface may cause light limitation of photosynthesis or carbon starvation (Grace, 1989). This response is usually fuelled from subterranean storage that results in decreased proportional allocation to belowground weight (e.g. Vretare et al., 2001). Hence, plants in the high typhoon-impacted region showed higher belowground/total biomass ratio than in the low.

High belowground biomass allocation may also explain the similar population densities in both the high and low typhoon-impact regions. After a period of influence by typhoons, high levels of storage can quickly rebuild parts of plant body (leaves, stems, and roots). Furthermore, belowground clonal structures, such as tubers and rhizomes would produce new offspring and keep the population stable.

4.2. Typhoon effects on hydrophilous plants

Submerged and floating-leaved plants are hydrophilous species living in a water column. Typhoon that would influence them are

strong wind-induced currents. Leaf area, leaf number, and belowground biomass allocation of the floating-species *N. indica* differed between the high and low typhoon-impacted regions. Wind-induced currents agitate the water column which can result in the petioles of the plant being broken. Long petioles increase this risk, but the petiole length was decided by the temporal water level of water body (Strand and Weisner, 2001). We thus excluded this characteristic of floating-leaved species from our analysis. The decreased leaf area and number on the water surface of *N. indica* in the high typhoon-impacted region can be considered an adaptive response to reduce the possibility of petiole breakage by strong winds or wind-induced currents.

The sequent flooding episodes may have a greater influence on hydrophilous species than emergent species. Floating-leaved species can respond to fluctuating water level by rapid petiole extension and continuous and rapid leaf recruitment (Cooling et al., 2001), as well as maintaining a disproportionately low belowground biomass relative to their total biomass (Brock et al., 1983). The increased allocation of belowground biomass in a high typhoon-impacted region may also play a role in anchorage and resource availability for rapid petiole growth to accommodate rapidly rising water levels during and immediately following the passage of a typhoon.

As shown in previous studies, wind disturbance affects submerged species through wave action that can fragment, undermine or uproot plants (e.g. Riis and Hawes, 2003). During flooding, many submerged species increase biomass allocation to shoot in response to the increasing water levels. This response probably allows the plant to grow longer shoots to stretch towards the water surface, and thus to maximize photosynthesis and survival (Strand and Weisner, 2001).

In our observation, there was no significant variation in the morphological traits of *B. echinosperma*. The reason may be that *B. echinosperma* populations always embed in emergent aquatic plant communities that provide protection from wind-generated waves. This protection is especially important in shallow waters as we found at our study site. And another reason may be the fact that the water is relatively clear resulting in relative little effect on photosynthetic radiation reaching these submerged plants. Since these plants grow among emergent vegetation, their light requirements may be relatively low. Or the water level increases associated with typhoons are relatively short lived thus not warranting stem elongation. Although we did not document a long-term functional response in *B. echinosperma*, the plants may have had transient or short-term variations in biomass allocation or leaf morphology in response to typhoon disturbance that were not recorded using our methods.

In conclusion, we observed that emergent and floating-leaved plants show adaptive responses to typhoon effects on Hainan Island. In comparison, submerged species in wetland and shallow water habitats on the island seemed to be subject to fewer typhoon-related disturbances. As our study was based on *in situ* analyses, other factors such as sediment characteristics, grazing and stress of competition may have potentially influenced results. Because typhoon season occurs during the peak growing season, further studies on plant phenology are needed to determine typhoon impacts on plant growth and reproduction.

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References

- Barrett, S.C.H., Eckert, C.G., Husband, B.C., 1993. Evolutionary processes in aquatic plant populations. *Aquat. Bot.* 44, 105–145.
- Blanch, S.J., Ganf, G.G., Walker, K.F., 1999. Growth and resource allocation in response to flooding in the emergent sedge *Bolboschoenus medianus*. *Aquat. Bot.* 63, 145–160.
- Brock, T.C.M., Arts, G.H.P., Goossen, I.L.M., Rutenfeans, A.H.M., 1983. Structure and annual biomass production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). *Aquat. Bot.* 17, 167–188.
- Cook, C.D.K., 1968. Phenotypic plasticity with particular reference to three amphibious plant species. In: Heywood, V. (Ed.), *Modern Methods in Plant Taxonomy*. Academic Press, London, pp. 97–111.
- Cook, C.D.K., 1990. *Aquatic Plant Book*. SPB Academic Publishing, Amsterdam.
- Cooling, M.P., Ganf, G.G., Walker, K.F., 2001. Leaf recruitment and elongation: an adaptive response to flooding in *Villarsia reniformis*. *Aquat. Bot.* 70, 281–294.
- González-Rodríguez, A., Oyama, K., 2005. Leaf morphometric variation in *Quercus affinis* and *Q. laurina* (Fagaceae), two hybridizing Mexican red oaks. *Bot. J. Linn. Soc.* 147, 427–435.
- Gouvenain, R.C., Silander, J.R.J.A., 2003. Do tropical storm regimes influence the structure of tropical lowland rain forests? *Biotropica* 35, 166–180.
- Grace, J.B., 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *Am. J. Bot.* 76, 762–768.
- Havens, K.E., Jin, K.R., Rodusky, A.J., Brady, M.A., East, T.L., Iricanin, N., James, R.T., Harwell, M.C., Steinman, A.D., 2001. Hurricane effects on a shallow lake ecosystem and its response to a controlled manipulation of water level. *The Scientific World J.* 1, 44–70.
- Keddy, P.A., 2000. *Wetland Ecology: Principles and Conservation*. Cambridge University Press, Cambridge, UK.
- Kirkman, L.K., Sharitz, R.R., 1993. Growth in controlled water regimes of three grasses common in freshwater wetlands of the southeastern USA. *Aquat. Bot.* 44, 345–359.
- Kubota, Y., Murata, H., Kikuzawa, K., 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, southern Japan. *J. Ecol.* 92, 230–240.
- Li, X.Z., 1983. *Typhoon*. Meteorological Press, Beijing.
- Oyama, K., 1996. Quantitative variation within and among population of *Arabis serrata* Fr. & Sav. (Brassicaceae). *Bot. J. Linn. Soc.* 120, 243–256.
- Qin, H.N., Chen, J.R., 2005. *Lythraceae*. In: *Flora of China*. Science Press, Beijing.
- Richards, P.W., 1996. The tropical rain forest. *J. Ecol.* 27, 1–61.
- Riis, T., Hawes, I., 2003. Effect of wave exposure on vegetation abundance, richness and depth distribution of shallow water plants in a New Zealand lake. *Freshwater Biol.* 48, 75–87.
- Sanchez, O.S., Islebe, G.A., 1999. Hurricane Gilbert and structure changes in a tropical forest in south-eastern Mexico. *Global Ecol. Biogeogr.* 8, 29–38.
- Sculthorpe, C.D., 1967. *The Biology of Aquatic Vascular Plants*. Arnold, London.
- Shanghai Typhoon Institute of China Meteorological Administration, 2005. *Typhoon Almanac*. see at <http://www.typhoon.gov.cn/cn/ziliao.php>.
- Tropical Crop Science Data Center, 2005. *Soil Nutrient Data Pool of Hainan Province*. see at <http://trop.agridata.cn/A05/ShowClass.asp?ClassID=775&page=1>.
- Strand, J.A., Weisner, S.E.B., 2001. Dynamics of submerged macrophyte populations in response to biomanipulation. *Freshwater Biol.* 46, 1397–1408.
- Suzuki, J.I., Stuefer, J.F., 1999. On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biol.* 14, 11–17.
- Vretare, V., Weisner, S.E.B., Strand, J.A., Granéli, W., 2001. Phenotypic plasticity in *Phragmites australis* as a functional response to water depth. *Aquat. Bot.* 69, 127–145.
- Wang, Q., Yu, D., Li, Z.Q., Wang, L.G., 2008. The effect of typhoons on the diversity and distribution pattern of aquatic plants on Hainan Island, South China. *Biotropica* 40 (6), 692–699.
- Whitmore, T.C., 1984. *Tropical Rain Forest of Far East*. Clarendon Press, Oxford, England.
- Yan, S.Z., 1983. *Pictorial Handbook of Higher Water Plant of China*. Science Press, Beijing.
- Zeng, Z.X., Zeng, X.Z., 1989. *Nature Geography of Hainan Island*. Science Press, Beijing.