

## **Flooding tolerance of Japanese *Hosta* in relation to habitat preference**

by

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*ABSTRACT* 1) Thirteen species of Japanese *Hosta* are compared for flooding tolerance and respiratory and oxidative activities of roots in relation to habitat preference from the viewpoint of adaptation.

2) Growth retardation and root damping are ill effects of flooding on plants. Plants of all the examined species survived with a healthy appearance of roots under flooding in sand culture though all were checked for growth. On the other hand, under ordinary soil conditions containing organic matter, it was found that there are interspecific differences in flooding tolerance. The growth of some species is hastened; others exhibit growth inhibition; the remainder show, what is worse, root damping which is finally conducive to death. These differences may be ascribed chiefly to those of susceptibility to reductive conditions produced by flooding in the soil.

3) Root damping is correlated with a decrease in oxidizing power of roots which may be attributable to the lowering of respiratory activities.

4) The species show three grades of flooding tolerance. There is a good correlation between habitat preference and flooding tolerance. The habitat range of each species is roughly determined by its adaptability to the soil moisture conditions of its environment.

### **Introduction**

Adaptation is a general feature of relationships between organisms and their environments. The reason why each kind of organisms is restricted in nature to its own habitat is that it is specialized or adapted for making a living under one particular set of environmental conditions (Grant, 1963). Each species has its own morpho-physiological characteristics which form the foundation of performing its life functions in its habitat. In order to explain how each species adapts itself to conditions of its habitat, it is necessary to determine the concrete relationship between these characteristics and its environmental conditions.

In a previous paper (Fujita, 1976) I reported the habitat range and the water

economy of Japanese *Hosta* species and examined their relationships in *Hosta* species from the viewpoint of adaptation. Characteristics of this water economy are mainly limited to those which are related to the adaptation to dry and moist soil conditions. Habitats of Japanese *Hosta* species are diverse, especially in relation to soil moisture conditions, which range from extremely wet to relatively dry. In *Hosta*, therefore, it is also necessary to analyze how each species responds to wet soil conditions, or flooding, so as to give a full account of adaptation to the soil moisture conditions of its habitat.

Soil aeration decreases if the soil is flooded. When the soil contains decomposed organic matter (as a result of active decomposition of soil organic matter by microbes),  $O_2$  content decreases further and reduced products, such as  $S^{2-}$ ,  $Fe^{2+}$  and  $Mn^{2+}$ , which attack plant roots harmfully, are produced in the flooded soil (Robinson, 1930; Sato & Yamane, 1960). Hence, the flooded soil gives a complex of critical conditions with which plants can cope only if they have some specialized tolerance.

Flooding tolerance of plants has been studied. Marshy plants living at low levels of dissolved oxygen in ground water show lower respiration rates than those at high levels (Hogetsu et al., 1954). Many plants which grow best in muddy soil where the  $O_2$  concentration is extremely low have especially low  $O_2$  requirements for germination (Morinaga, 1926). Helophytes are metabolically adapted to flooded condition by avoiding excess ethanol accumulation (Crawford, 1966 & 1967; Crawford & McManmon, 1968; Crawford & Tyler, 1969; Tyler & Crawford, 1970; McManmon & Crawford, 1971). Judging from growth experiments, seedlings of rice are found to be more tolerant of ethanol than those of wheat (Taylor, 1942) and those of oat (Nagao & Ohwaki, 1953). Flooding-tolerant plants display higher oxidizing activities of roots than plants that are less tolerant of flooding (Yamasaki, 1952).

In this paper I have determined flooding tolerance, and respiratory metabolism and oxidizing activity of roots in order to account for the ability to withstand flooding in *Hosta* species, and examined the relationships between these characteristics and habitat preference of the *Hosta* species from the viewpoint of adaptation.

### Materials and Methods

All the plants of each species examined were derived from native sites, and the localities are the same as previously mentioned (Fujita, 1976). Plants were grown from rhizomes with winter buds in pots in a greenhouse where the air temperature ranged from 15 to 27°C. The soil used for cultivation was composed of sandy loam and humus in 3:1 volume ratio. The soil moisture was maintained at 60-50% based on the maximum water capacity which was 42% on a dry weight base after 5 days' drying at 105°.

Flooding experiments were begun about 50 days after the planting, when new roots and leaves had fully developed. Flooding was accomplished by adding water to the pots so that the soil moisture would be maintained at slightly higher than the maximum water capacity. Half of all the cultivated plants of each species were used in the flooding experiments; the other half were continuously raised under the original conditions of soil moisture to serve as controls. Flooding tolerance of each species was determined after 30 days' flooding not only from the appearance of flooded roots but also by determining the ratio of relative growth rate of flooded plants to that of unflooded ones.

Respiratory and oxidative activities were measured 7-10 days after initiation of flooding for both flooded and unflooded plants. Only new roots were used in order to eliminate differences in their activities due to age. Roots were cut from plants and cleansed with running water. After rinsing for 2 min. in 0.02%  $\text{HgCl}_2$  solution, they were washed thoroughly with deionized water. Then, roots were cut to 5 cm lengths from the tip and used for the measurements, followed by blotting and weighing. For respiratory measurements root tips were cut further into 3 mm sections with a multiple razor blade cutter.

Oxygen uptake during aerobic respiration and  $\text{CO}_2$  output during anaerobic respiration were determined by Warburg manometry, using M/15 phosphate buffer (pH 6.0) in the former and McIlvaine's buffer (0.1 M citric acid-0.2 M  $\text{Na}_2\text{HPO}_4$ ) (pH 4.8) in the latter. For each Warburg flask of 15-17 ml in volume, 0.2 g of root sections were suspended in 1.3 ml of each buffer. In the measurement of  $\text{O}_2$  consumption, 0.2 ml of 20% KOH solution and a fringed filter paper strip were placed in the center well of the flask;  $\text{CO}_2$  evolution was measured by subsequently gassing with  $\text{N}_2$  the flask which contained 0.2 ml of McIlvaine's buffer in the center well in place of the KOH solution. The flasks, covered with aluminium foil to establish a dark condition, were shaken at 30°C.

Oxidizing activities of roots were determined from  $\alpha$ -naphthylamine oxidation; for it has been reported that the oxidizing power of roots under paddy field conditions is correlated positively with the degree of coloring of roots in  $\alpha$ -naphthylamine solution (Doi, 1952) and that a method for the quantitative estimation of  $\alpha$ -naphthylamine was devised (Sakai & Yoshida, 1957). Approximately 1 g of root tips were put into a test tube filled with 8 ml of M/15 phosphate buffer (pH 6.0) and 1 ml of 180 mg/l  $\alpha$ -naphthylamine solution. This tube was then placed in an incubator, followed by 2 hr's shaking in the dark at 37°C. Oxidation reaction was stopped by the addition of 1 ml of 50% acetic acid. To check the automatic oxidation of  $\alpha$ -naphthylamine, a similar sample was placed in a duplicate tube and treated similarly except that the root tips were not added. Oxidizing activity of roots was determined from the concentration change in  $\alpha$ -naphthylamine in the bathing medium

before and after incubation. After the measurements of respiratory and oxidative activities the root tips were dried for 2 days at 95°C to obtain dry weight.

A quantitative estimation of  $\alpha$ -naphthylamine was conformable to Briess' method (Sakai & Yoshida, 1957). After placing 3 ml of 1% sulphanic acid solution in 30% acetic acid and 4 ml of 0.01%  $\text{KNO}_2$  solution in a measuring flask of 10 ml in volume, the flask was shaken and left for several min. at room temperature. 1 ml aliquot of the sample and 2 ml of deionized water were then added to the flask with shaking, followed by leaving for 5 min. at room temperature. Absorptimetry was carried out at 520 nm with a spectrophotometer.

In parallel with these experiments designed to test flooding effects in normal soil, another experiment on flooding in sand culture (which contained no soil organic matter) was carried out with some species. Flooding tolerance in sand culture was determined from growth and survival rates of seedlings. In each experiment, 100 seedlings selected after germination were cultivated in sand culture in pots. The maximum water capacity of the sand used was 16% on a dry weight base. Experimental conditions were as follows: flooded condition; high water table made by maintaining water surface 1 cm below the sand surface; unflooded condition; low water table 15 cm below. These experiments were begun in spring and ended in autumn, the pots being sheltered from rain with a vinyl cover in the open air through the growth season. After the experiments the surviving seedlings were counted and harvested to obtain dry weight.

Respiratory and oxidative activities of flooded plants in sand culture were obtained from the same collections of adult plants as those treated similarly under normal soil cultivation except that flooding conditions were produced by keeping the water surface 1 cm below the sand surface in pots.

## Results

Table 1 presents relative growth rates of plants grown under flooded and unflooded soil conditions and flooding effects produced on plant roots in each species. It is found in some species that flooding checks plant growth and induces root damping. Japanese *Hosta* species may be classified into the following three types as to differences in these flooding effects: (1) the species which maintain good growth and healthy appearance of roots even if grown under flooded conditions; (2) those which show arrested growth to some extent but whose roots are not harmed by flooding; (3) those which show deleterious effects of flooding on both growth and roots and ultimately die. It is thought that the degree of flooding tolerance of species decreases in this order of types. The first type consists of *H. albomarginata* and *H. longissima*. *H. sieboldiana* and *H. kiyosumiensis* belong to the second type.

Table 1. Some characteristics of the flooding tolerance of each *Hosta* species. Each figure for relative growth rate (given as the mean value of 5 plants) stands for fresh weight percentage of the plants before to after 30 days' treatments given by remaining unflooded and flooding in U and F respectively. Soil moisture conditions during the treatment are as follows: U, unflooded condition in which the soil moisture was maintained at 60-50% based on the maximum water capacity; F, flooded condition, slightly higher than the maximum water capacity. Root damping determined from the flooding experiment is indicated as in the following: +, occurrence of damping;  $\pm$ , occurrence of partial damping; —, non-occurrence of damping or maintenance of a healthy appearance of roots.

Species	Relative growth rate		F/U	Root damping
	U	F		
<i>H. albomarginata</i>	112	118	1.05	—
<i>H. longissima</i>	103	110	1.07	—
<i>H. sieboldiana</i>	114	104	0.91	—
<i>H. kiyosumiensis</i>	110	102	0.93	—
<i>H. tsushimensis</i>	109	100	0.92	$\pm$
<i>H. tibai</i>	106	95	0.90	+
<i>H. kikutii</i>	106	94	0.89	+
<i>H. hypoleuca</i>	104	96	0.92	$\pm$
<i>H. pulchella</i>	103	96	0.93	+
<i>H. capitata</i>	103	90	0.87	+
<i>H. pycnophylla</i>	103	91	0.88	+
<i>H. longipes</i>	104	92	0.88	+
<i>H. shikokiana</i>	104	94	0.90	+

The other species except *H. tsushimensis* are all included in the last type. *H. tsushimensis* is intermediate between the second and the last type.

Tables 2 and 3 give aerobic and anaerobic respiration rates respectively for roots of flooded and unflooded plants. These tables show that species differences are found in the ratio of respiration rate of flooded plants to that of unflooded ones: first, the species which show the respiration rate reduced by flooding and, second, those which show little change of the rate regardless of flooding. The former consists of the species susceptible to flooding (the third type in respect to flooding tolerance of *Hosta*) and the latter (consisting of the species tolerant of flooding) or the first and second types, especially in the rate of O<sub>2</sub> absorption in aerobic respiration. In CO<sub>2</sub> output in anaerobic respiration, not all but many flood-susceptible species show a decrease in the rate by flooding. The remainder and flood-tolerant species are not changed in the rate.

Table 4 shows oxidative activities of roots obtained from  $\alpha$ -naphthylamine oxida-

Table 2. Aerobic respiration rates ( $Q_{O_2}$ ) in  $\mu\text{l O}_2$  uptake/h/mg dry weight of roots. Each figure shows the mean value with its standard deviation. The number of samples is given in parentheses. U, unflooded roots; F, roots flooded in the soil.

Species	U	F	F/U
<i>H. albomarginata</i>	1.21 $\pm 0.02$ (3)	1.37 $\pm 0.10$ (3)	1.13
<i>H. longissima</i>	1.23 $\pm 0.02$ (3)	1.21 $\pm 0.04$ (3)	0.98
<i>H. sieboldiana</i>	1.23 $\pm 0.05$ (3)	1.28 $\pm 0.06$ (3)	1.04
<i>H. kiyosumiensis</i>	1.06 $\pm 0.08$ (3)	1.09 $\pm 0.12$ (3)	1.03
<i>H. stushimensis</i>	1.21 $\pm 0.04$ (3)	1.13 $\pm 0.10$ (3)	0.93
<i>H. tibai</i>	1.36 $\pm 0.05$ (3)	1.13 $\pm 0.02$ (3)	0.83
<i>H. kikutii</i>	1.24 $\pm 0.04$ (3)	0.93 $\pm 0.05$ (3)	0.75
<i>H. hypoleuca</i>	1.33 $\pm 0.06$ (2)	1.08 $\pm 0.12$ (2)	0.81
<i>H. pulchella</i>	1.09 $\pm 0.05$ (2)	0.88 $\pm 0.10$ (2)	0.81
<i>H. capitata</i>	1.12 $\pm 0.13$ (3)	0.67 $\pm 0.08$ (3)	0.60
<i>H. pycnophylla</i>	1.12 $\pm 0.03$ (3)	0.76 $\pm 0.01$ (3)	0.68
<i>H. longipes</i>	1.05 $\pm 0.01$ (3)	0.84 $\pm 0.02$ (3)	0.80
<i>H. shikokiana</i>	1.00 $\pm 0.03$ (2)	0.80 $\pm 0.02$ (3)	0.80

tion. The activities are reduced also in flood-sensitive species when grown under flooded condition while flood-tolerant species do not decrease in activity despite flooding.

Variation of flooding tolerance in relation to habitat differences within a species was determined in *H. sieboldiana* (Table 5). This species occupies the most varied habitats of any of the Japanese species of the genus. Significant variation is not found in this species. The intraspecific variation is small enough to consider characteristics of *H. sieboldiana* given in Tables 2, 3 and 4 as peculiar to it, not to mention the other species growing in narrower habitats.

Table 3. Anaerobic respiration rates ( $Q_{CO_2^{N_2}}$ ) in  $\mu l$   $CO_2$  output/h/mg dry weight of roots. Notes are as in Table 2.

Species	U	F	F/U
<i>H. albomarginata</i>	0.91 $\pm 0.02$ (3)	1.04 $\pm 0.08$ (3)	1.14
<i>H. longissima</i>	1.03 $\pm 0.07$ (3)	0.98 $\pm 0.03$ (3)	0.95
<i>H. sieboldiana</i>	1.00 $\pm 0.06$ (3)	0.96 $\pm 0.10$ (3)	0.96
<i>H. kiyosumiensis</i>	0.83 $\pm 0.01$ (3)	0.88 $\pm 0.02$ (3)	1.06
<i>H. tsushimensis</i>	0.83 $\pm 0.10$ (3)	0.84 $\pm 0.02$ (3)	1.01
<i>H. tibai</i>	0.87 $\pm 0.02$ (3)	0.90 $\pm 0.03$ (3)	1.04
<i>H. kikutii</i>	0.92 $\pm 0.03$ (3)	0.67 $\pm 0.05$ (3)	0.73
<i>H. hypoleuca</i>	0.89 $\pm 0.07$ (2)	0.83 $\pm 0.07$ (2)	0.93
<i>H. puichella</i>	0.68 $\pm 0.02$ (2)	0.73 $\pm 0.10$ (2)	1.07
<i>H. capitata</i>	0.83 $\pm 0.04$ (3)	0.42 $\pm 0.06$ (3)	0.51
<i>H. pycnophylla</i>	0.82 $\pm 0.11$ (3)	0.62 $\pm 0.04$ (3)	0.85
<i>H. longipes</i>	0.94 $\pm 0.02$ (3)	0.80 $\pm 0.08$ (3)	0.72
<i>H. shikokiana</i>	0.65 $\pm 0.04$ (3)	0.47 $\pm 0.03$ (3)	0.72

Table 6 gives growth and survival of seedlings obtained in sand culture. Flooding tolerance is lowered in sand culture in all the species examined regardless of flooding tolerance displayed under normal soil conditions and the decreasing rate is nearly equal among the species. However, a healthy appearance is maintained in flooded roots in all the species, and root damping was not caused even after the experiment.

Table 7 represents respiratory and oxidative activities of flooded roots in sand culture for adult plants of some species. In contrast to normal soil cultivation, flooding in sand culture does not cause a drop in respiratory or oxidative activities in any species.

Table 4. Oxidation rates of  $\alpha$ -naphthylamine in mg/6h/g dry weight of roots. Each figure represents the mean value of two experiments. Symbols are the same as in Table 2.

Species	U	F	F/U
<i>H. albomarginata</i>	0.58	0.61	1.05
<i>H. longissima</i>	0.55	0.55	1.00
<i>H. sieboldiana</i>	0.61	0.59	0.97
<i>H. kiyosumiensis</i>	0.59	0.54	0.92
<i>H. tsushimensis</i>	0.47	0.41	0.87
<i>H. tibai</i>	0.52	0.40	0.77
<i>H. kikutii</i>	0.47	0.29	0.62
<i>H. hypoleuca</i>	0.64	0.41	0.64
<i>H. pulchella</i>	0.38	0.25	0.66
<i>H. capitata</i>	0.50	0.20	0.40
<i>H. pycnophylla</i>	0.51	0.32	0.63
<i>H. longipes</i>	0.56	0.42	0.75
<i>H. shikokiana</i>	0.48	0.39	0.81

Table 5. Intraspecific variation of *H. sieboldiana* in respiratory and oxidative activities owing to habitat differences. Symbols and units of the activities are the same as in Tables 2, 3 and 4. Standard deviation of each figure is omitted. Localities and habitats are as follows: Mikata (Fukui Pref.), fairly wet places in a stream bed; Noma (Kyoto Pref.), moist grassland on forest margin; Chomonkyo (Yamaguchi Pref.), dry rock cliff in a valley; Hirasan (Shiga Pref.), rather dry rocky soil on mountain ridge; Uraresan (Iwate Pref.), fairly dry grassland on mountain slope; Tsukude (Aichi Pref.), low moor.

Locality	Q <sub>O<sub>2</sub></sub>		Q <sub>CO<sub>2</sub>N<sub>2</sub></sub>		Oxidation	
	U	F	U	F	U	F
Mikata	1.23(3)	1.28(3)	1.00(3)	0.96(3)	0.61	0.59
Noma	1.24(3)	1.20(3)	0.86(3)	0.88(3)	0.62	0.71
Chomonkyo	1.23(3)	1.34(3)	0.78(3)	0.80(3)	0.47	0.38
Hirasan	1.35(2)	1.44(2)	1.00(2)	1.11(2)	0.60	0.54
Uraresan	1.04(2)	1.03(2)	0.85(2)	0.77(2)	0.59	0.53
Tsukude	1.05(3)	1.09(3)	0.68(2)	0.75(3)	0.49	0.48



Table 6. Seedling growth under low and high water table conditions in sand culture. Seeds were planted in spring and seedling weight was measured in autumn. Each figure of biomass shows the average value of 100 seeds or all surviving seedlings. Biomass is expressed in mg dry weight. Growth and survival ratios are given as rates of seedling weight and surviving seedling number of high water table to low water table respectively.

Species	Seed weight	Seedling weight		Growth ratio	Survival ratio
		Water table Low	Water table High		
<i>H. albomarginata</i>	2.8	109.0	25.7	0.24	0.62
<i>H. longissima</i>	2.7	130.9	23.8	0.18	0.75
<i>H. sieboldiana</i>	2.6	112.0	53.3	0.48	0.77
<i>H. kiyosumiensis</i>	2.8	118.1	35.4	0.30	0.70
<i>H. kikutii</i>	1.2	66.7	21.7	0.33	0.85
<i>H. hypoleuca</i>	1.4	37.7	15.4	0.41	0.71
<i>H. capitata</i>	4.3	171.0	44.3	0.26	0.83
<i>H. pycnophylla</i>	1.5	64.2	27.3	0.43	0.76
<i>H. longipes</i>	1.8	97.4	27.7	0.28	0.82

Table 7. Respiratory and oxidative activities in sand culture. Symbols and units of the activities are the same in Tables 2, 3 and 4, except that F shows flooded roots in sand culture. Standard deviation of each figure is omitted.

Species	Q <sub>o</sub>		Q <sub>o n</sub>		Oxidation	
	U	F	U	F	U	F
<i>H. albomarginata</i>	1.21(3)	1.09(3)	0.91(3)	0.93(3)	0.58	0.58
<i>H. longissima</i>	1.23(3)	1.34(2)	1.03(3)	1.14(2)	0.55	0.61
<i>H. sieboldiana</i>	1.23(3)	1.16(2)	1.00(3)	1.04(2)	0.61	0.55
<i>H. capitata</i>	1.12(3)	0.99(3)	0.83(3)	0.87(3)	0.50	0.50
<i>H. pycnophylla</i>	1.12(3)	1.06(2)	0.82(3)	0.92(2)	0.51	0.46
<i>H. longipes</i>	1.05(3)	1.16(2)	0.94(3)	0.70(2)	0.56	0.58

## Discussion

The ability to resist flooding is thought to minimize baneful effects which arise in flooded soil. According to Crawford and his school (Crawford, 1966, 1967; Crawford & McManmon, 1968; Crawford & Tyler, 1969; Tyler & Crawford, 1970; McManmon & Crawford, 1971), no distinct differences were found in rates of O<sub>2</sub> consumption in aerobic respiration between plants from wet and dry areas. This is

also true with *Hosta* in the present experiment. On the other hand, in CO<sub>2</sub> evolution in anaerobic respiration, increased rates were induced by flooding in plants from dry areas, while plants from wet areas showed little change of rate when flooded. They concluded that plants from wet areas can stand up better in anaerobic environments by having alternative metabolic pathways which enable them to avoid accumulation of toxic concentrations of ethanol. It is noteworthy that they indicated the existence of this metabolic adaptation to anaerobic environments in plants inhabiting wet places, but this metabolic adaptation is not found in *Hosta*.

Plants of all the examined *Hosta* species sustain their lives when deprived of O<sub>2</sub> by flooding in sand culture, maintaining a healthy appearance of their roots in spite of retardation of growth and promotion of CO<sub>2</sub> output in anaerobic respiration is not seen. In contrast, in flooding experiments performed in normal soil that holds organic matter, some *Hosta* species exhibit not only growth stunting but also root damping which eventually leads to death. Oxidizing power of roots declines in those species. On the other hand, the species that present a healthy appearance in flooded roots retain the capacity for oxidizing activities of roots. Prevention of root damping induced by flooding in normal soil may be attributable to oxidizing power which counteracts reductive conditions in flooded soil. The fall of oxidizing power of roots may come from the lowering of respiratory activities since this fall is usually accompanied by a reduction in the rate of O<sub>2</sub> demand in aerobic respiration. Moreover, not all but many of the species which show lower oxidizing power in roots show lowering of the rate of CO<sub>2</sub> output in anaerobic respiration also, though a few species exhibit a reverse tendency.

Fiedler (1935, 1951) found a lowering of the aerobic respiration rate in apples damaged by O<sub>2</sub> deficiency. Sakai & Yoshida (1957) presumed that  $\alpha$ -naphthylamine oxidation was brought about by a coupling enzyme system producing H<sub>2</sub>O<sub>2</sub> in the peroxidase system. Yamada & Ohta (1958) showed  $\alpha$ -naphthylamine oxidation was closely correlated with respiratory activity. Thus, although some indications are given, the cause of the decline of these activities in *Hosta* is not explained.

Two different components, O<sub>2</sub> shortage and a reductive state, characterize flooded soil conditions and flooding manifests two distinct deleterious effects on plants: growth inhibition and root damping. It is necessary to have an eye to resistability to reductive conditions of flooded soil when considering survivable tolerance at least in the case of *Hosta*.

*Hosta* species which commonly grow in wet habitats and continue to exhibit normal growth if flooded under ordinary soil condition, such as *H. longissima* and *H. albomarginata*, show retardation in growth and a chlorotic appearance in leaves only when flooded under sand culture. The same phenomenon is noted in rice plant. Chlorosis occurred in rice seedlings grown in water-logged, organic-matter-free

artificial soil and was ascribed to too little soluble iron in the soil as the result of undevelopment of reductive conditions (Takagi, 1966). In contrast, the same flooding in ordinary organic-matter-containing soil is contributive to the normal growth of rice plants because reductive conditions induced in the flooded soil facilitate the solubility of nutrients, such as Fe, Mn, Si and P (Clark et al., 1957; Shapiro, 1958; Mandal, 1962). This accounts for wholesome effects of reductive conditions in the flooded soil on plant growth. It is not clear that such is also the case in *Hosta* but the ability to endure and utilize reductive conditions may play an important role in the flooding tolerance of *Hosta*.

The species of Japanese *Hosta* were classified into three large groups according to habitat preference (Fujita, 1967), and the *Hosta* species, according to present results, represent three grades of tolerance when flooded under ordinary soil condition. There is a good correlation between habitat preference and flooding tolerance. *H. longissima* growing low moors and *H. albomarginata* often occurring on wet soils have high flooding tolerance, which is a logical conclusion. *H. sieboldiana* and *H. kiyosumiensis* which live on soil and rocks in various habitats show some flooding tolerance, at least as much as necessary for subsistence. *H. tsushimensis* which can be regarded as similar to these two species relative to habitat range, except for occasionally occurring on wet soils, proved less tolerant of flooding than these two species in these experiments. The other species which inhabit rocky places are easily affected by flooding. They are not necessarily restricted to dry places, and rather prefer moist conditions. However, they are limited to outcrops and rocky soils where natural ventilation is better and this limitation of habitat range may be set by their susceptibility to flooding, particularly to reductive conditions produced in the flooded soil.

If taking drought resistance of *Hosta* species (Fujita, 1976) into consideration with flooding tolerance, a clear account is given of the adaptability of each *Hosta* species to the soil moisture conditions of its habitat. The species which commonly grow under various soil moisture conditions of habitat display broad adaptability of water relations in respect to flooding tolerance survival as well as with a fairly high drought resistance. On the other hand, those species confined to rocky places are readily attacked by flooding but are resistant to drought. Those limited to wet places are highly resistant to flooding but susceptible to drought. Therefore, the species occurring in restricted habitats lack the adaptive plasticity of water relations but they adapt themselves to a particular environment successfully but rigidly. The habitat range of each species is roughly determined by its adaptability to soil moisture conditions of environment. Thus the *Hosta* species owes its prosperity of life partly to its capacity of water relations. Characteristics of water relations of the species may be a reflection of the mode of its life.

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