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Short article

An Experimental Approach to Clarify the Reason for the Absence of a Wetland Species, *Phragmites australis*, from Well-Drained Upland

Hiroshi Yura

Natural History Museum and Institute, Chiba
955-2 Aoba-cho, Chou-ku, Chiba-shi, 260-8682 Japan
E-mail: expplntecol@gmail.com

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Abstract This study aims to elucidate why a typical emergent aquatic plant, *Phragmites australis*, cannot grow on well-drained upland through pot culture experiments. In the first experiment, *P. australis* and typical upland species, *Miscanthus sinensis*, were grown in the pots under various water regimes in a glasshouse. Even though *P. australis* was grown in the pots from which excess water drained out freely through the drainage hole, the growth of *P. australis*, which was evaluated by the average dry weight of the seedlings, was higher than *M. sinensis*. The average dry weight of *P. australis* seedlings was higher than that of *M. sinensis* even in the pots whose water content was maintained low. In the second experiment, a newly developed method, named the “hydroearth method”, was introduced to simulate the water condition of the soil of the upland. *Phragmites australis* and *M. sinensis* were grown in the pots pushed down into the ground until the drainage hole made contact with the fine sand previously laid on the ground. Only when the two species were grown in the pots under the hydroearth method, the growth of *P. australis* seedlings was considerably lower than *M. sinensis* seedlings. Low growth of *P. australis* under the hydroearth method, however, could be ameliorated by adding nutrients. The fact that the growth of *P. australis* was inhibited in the pots under the hydroearth method indicated that *P. australis* could not grow sufficiently in the soil from which water swiftly infiltrates into the deep soil.

Keywords: Hydroearth method, leaching, perched water, plant distribution, pot-culture experiment, soil water.

It is well known that species composing the wetland vegetation are completely different from those growing on the surrounding uplands. The injurious effects of flooding or submergence on plants have been studied extensively and various physiological or morphological features of wetland plants to cope with such anaerobic conditions have been elucidated so far (e.g. Crawford, 1982; Jackson and Colmer, 2005). It can be reasonably speculated that such injurious effects might be the main factor inhibiting the upland species to invade and grow on wetlands.

On the contrary, the reason why wetland species cannot survive and grow on well-drained upland is not clear. Even *Phragmites australis* (hereafter referred to as *Phragmites*), one of the most widespread and invasive wetland species, can be rarely found on a mesic and fertile upland. As hairy and light diaspores of *Phragmites* are widely dispersed by wind, some of them can be assumed to land on the ground of nearby upland. The absence of *Phragmites* from the upland indicates that there should be characteristic biotic and/or abiotic factors inhibiting *Phragmites* from germinating or growing on the upland. As *Phragmites* was reported to have the ability to tolerate prolonged drought (Pagter *et al.*, 2005; Saltmarsh *et al.*, 2006), water stress itself caused by the relatively low water content of the soil of upland might not be the direct factor responsible for the absence of *Phragmites* from the upland.

In the previous study, I had sown the *Phragmites* seeds on a well-drained upland site and surveyed the survival and growth of the seedlings (Yura, 2010). To compare with upland species, seeds of *Miscanthus sinensis* (hereafter referred to as *Miscanthus*), a typical upland species in middle Japan, were also sown at the same time in nearby plots. Although a sufficient number of *Phragmites* seedlings emerged almost simultaneously with *Miscanthus* seedlings, the growth rate of *Phragmites* seedlings was much lower, and the difference in dry weight of the seedlings between surviving *Phragmites* and *Miscanthus* was remarkable at the end of the growing season. As seeds of both species were sown on the ground where other plants had been removed previously and kept weeded, a shortage of competitive ability against other species could not be the main reason for the poor growth of *Phragmites* seedlings. The environment of the upland itself seemed to be unsuitable for *Phragmites* seedlings to grow.

In this study, to elucidate the reason for the absence of *Phragmites* from the upland, I conducted three kinds of experiments. Firstly, seedlings of *Phragmites* and *Miscanthus* were grown in pots under three different soil moisture regimes. In any pot, the growth of *Phragmites* seedlings was higher than *Miscanthus* seedlings, indicating that an ordinary pot-culture experiment was inappropriate for reproducing the results of the field experiment. Secondly, I introduced a new method, which would be called the "hydroearth method", to control water moisture in the pot, and grew seedlings of the two species under the hydroearth method with three nutrient levels. By introducing the hydroearth method, the extremely low growth rate of *Phragmites* seedlings compared to *Miscanthus* seedlings could be reproduced. To estimate the nutrient level of the soil under those experimental conditions, the electrical conductivity of the soil extract was measured. Results of these experiments indicated that the movement of both water and nutrients characteristic to the soil of the upland might be the main reason for the low growth rate of *Phragmites* on the upland.

Materials and Methods

1. Growth of *Phragmites* and *Miscanthus* under different water regimes

The experiment was conducted at the experimental field of the Natural History Museum and Institute, Chiba (35º35′N, 140º08′E) in Chiba-shi, Japan. Thirty pots 20 cm high and 12 cm in diameter (1/10000 a Wagner pot) with a drainage hole of 2.2 cm in diameter on the bottom were filled with an equal weight of organic andosol which was common soil of upland in this area. A sheet of 3 mm mesh made of plastic was placed on the bottom of the pot in advance to retain the soil. On 8 May 2009, an appropriate number of seeds of *Phragmites* was sown in 15 pots, and an appropriate number of *Miscanthus* seeds was sown in the other 15 pots. Seeds of *Phragmites* and *Miscanthus* were collected last autumn from wild plants growing not far from the experimental field. Prior to the sowing, the soil was saturated with deionized water till drainage began. Deionized water was added to each pot every few days to keep the soil wet. On 3 June, when almost all seeds germinated, the number of the seedlings of the two species was thinned out to 10 per pot. After thinning, 10 pots with *Phragmites* seedlings and 10 pots with *Miscanthus* seedlings were moved into the glasshouse where windows were always opened for ventilation but rainfall was avoided. The remaining 5 *Phragmites* and 5 *Miscanthus* pots were left outdoors.

Pots in the glasshouse were divided into two groups. Water contents of the soil in 5 *Phragmites* and 5 *Miscanthus* pots in the glass house were kept nearly saturated by refilling the pots with deionized water after weighing the pots once or twice a week ("high water content"). The water content of the soil at saturation was 98 % (dry-weight basis). The other 10 pots were kept unwatered until the pot weight decreased to the weight equivalent to the soil water content of 70%. These pots were also weighed and watered thereafter once or twice a week until the pot weight attained a water content of 70% ("low water content"). Ten pots left outdoors were also weighed and saturated with deionized water

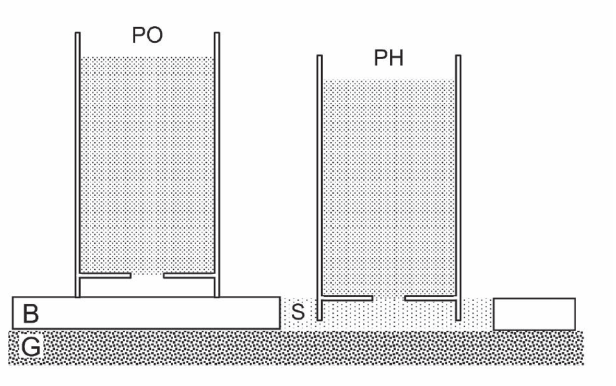
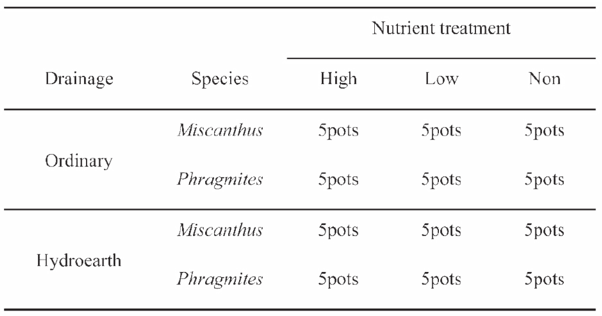


Fig. 1. Profile of the pots under the ordinary (PO) and hydroearth (PH) methods. Pots under the ordinary method were placed on concrete blocks (B), while those under the hydroearth method were pushed down into the fine sand (S) previously laid on the ground (G) until the soil in the pot made contact with the sand through the hole on the bottom.

Table 1. Experimental design of "Growth of *Phragmites* and *Miscanthus* at different nutrient levels under the hydroearth method."



		Nutrient treatment		
Drainage	Species	High	Low	Non
Ordinary	*Miscanthus*	5pots	5pots	5pots
	Phragmites	5pots	5pots	5pots
Hydroearth	*Miscanthus*	5pots	5pots	5pots
	Phragmites	5pots	5pots	5pots

("outdoors") once or twice a week. As pots left outdoors were subjected to occasional rainfall, the amount of water necessary to saturate the pots was often smaller than that to saturate the pots of high water content in the glasshouse. Total precipitation from June to September of the year the experiment was conducted was 589.5 mm, which was obtained from the nearby meteorological station of Japan Meteorological Agency, "Chiba weather station"* ca. 3 km west of the experimental field.

*(Japan Meteorological Agency, https://www.data.jma.go.jp/stats/etrn/view/monthly_s1.php?prec_no=45&block_no=47682&year=2009&month=&day=&view=.; accessed 30 March 2023.)

On 25 September, *Phragmites* and *Miscanthus* seedlings were harvested from the 3 treatments. From randomly chosen 2 pots under each treatment, all 20 seedlings were dug out. Almost all *Phragmites* seedlings had rhizomes and new sprouts developed from terminal buds of the rhizomes. Almost all *Miscanthus* seedlings had new sprouts developed from the lateral buds on the base of the shoots. As the whole roots could not be sampled completely from the soil, all roots were cut off from the base of the shoots and rhizomes. Harvested seedlings (shoots + rhizomes) were washed under running tap water, dried at 70 ºC, and weighed.

2. Growth of *Phragmites* and *Miscanthus* at different nutrient levels under the hydroearth method

A new method to control the water condition of the soil in the pot outdoors was introduced. By pushing down the pot into the fine sand laid thick on the ground until the hole on the bottom made contact with the sand, the water content of the soil in the pot could be kept lower than the soil of the ordinarily set pot, whose hole on the bottom made no contact (Fig. 1). When the same soil as in the previous experiment was saturated with water in the same pot and pushed down on the fine sand, the weight of the pots decreased by nearly 200 g, which is equivalent to the soil water content of nearly 20%, in 24 hours, while the pots stand ordinarily at the same time lost almost no weight. A considerable amount of water in the pot under the hydroearth method was swiftly drained out by active infiltration into the fine sand laid under the pot.

Pots, soil, seeds, and the location where the experiment was conducted were all the same as those in the previous experiment. An appropriate number of seeds of *Phragmites* and *Miscanthus* was sown separately on 28 April in two groups of 18 pots each placed on flat concrete blocks outdoors, respectively. Prior to the sowing, the soil was saturated with water by adding deionized water to the extent that drainage began. Deionized water was added to all pots every few days to keep the soil wet.

On 26 May, when almost all seeds germinated, the number of the seedlings of the two species was thinned out to 10 per pot. After thinning, 15 pots with *Phragmites* seedlings and 15 pots with *Miscanthus* seedlings were pushed down into the fine sand 6 cm thick to start the hydroearth method (Table 1). Fine sand with no nutrients had been previously laid on the andosol ground surrounded by flat concrete blocks 6 cm thick. The remaining 9 *Phragmites* and 9 *Miscanthus* pots were left on the surrounding blocks as control, which will be referred to as the "ordinary method" hereafter. All 60 pots were weighed once a week and an equal volume of deionized water was added to all pots. The amount of water added was necessary to saturate the most dried pot under the ordinary method. Pots under the hydroearth method were pushed down into the sand again immediately after weighing and watering.

On the same day watering was conducted, nutrient solution was also added. Ingredients of the reagent in the nutrient solution were 4 mM $Ca(NO_3)_2$, 6 mM KNO_3, 1 mM $MgSO_4$ and 2 mM $NH_4H_2PO_4$ (Epstein, 1972). To 10 *Phragmites* and 10 *Miscanthus* pots under hydroearth and ordinary treatment, 5 ml of nutrient solution was added to each pot ("high nutrient treatment"). To the other 10 *Phragmites* and 10 *Miscanthus* pots under hydroearth and ordinary treatment, 5 ml of nutrient solution diluted 1/10 was added to each pot ("low nutrient treatment"). To the remaining pots, 5 ml of deionized water was added as the control ("no nutrient treatment"). Total precipitation from June to September of the year the experiment was conducted was 681.5 mm, which was obtained from "Chiba weather station".*

*(Japan Meteorological Agency, https://www.data.jma.go.jp/stats/etrn/view/monthly_s1.php?prec_no=45&block_no=47682&year=2008&month=&day=&view=.; accessed 30 March 2023.)

On 25 September, all 20 seedlings for one species were harvested from randomly chosen 2 pots under each treatment. Almost all *Phragmites* seedlings had rhizomes and new sprouts. Almost all *Miscanthus* seedlings had new sprouts. As the whole roots could not be sampled completely from the soil, all roots were cut off from the base of the shoots and rhizomes. Harvested seedlings (shoots + rhizomes) were washed under running tap water, dried at 70 ºC, and weighed.

3. Electrical conductivity of the soil extract

Pots, soil, and the location where the experiment was conducted were all the same as those in the previous experiment. In early April, 12 pots filled with the same amount of soil were placed on flat concrete blocks outdoors. On 21 May, after all pots were watered with equal amounts of deionized water till the soil saturated, 6 pots were moved into the glass house, 3 pots were pushed down into the fine sand to start the hydroearth method and 3 pots were left on the concrete blocks to start ordinary method. Any seedlings germinated were weeded to keep the soil bare till the end of the experiment.

As for the 6 pots in the glass house, the water content of the soil in 3 pots was kept high by refilling the pots with deionized water after weighing the pots once a week to the weight equivalent to the soil water content at near saturation of 83% ("high water content"). The other 3 pots were kept unwatered until the pot weight decreased to the weight equivalent to the soil water content of 67%. These pots were also weighed and watered thereafter until the pot weight attained a water content of 67% ("low water content") once or twice a week. Also, 6 pots left outdoors - 3 pots under the hydroearth method and 3 pots under the ordinary method - were weighed once a week, and an equal volume of deionized water was added to all pots. The amount of water added was necessary to saturate the most dried pot under the ordinary method. Total precipitation from May to October was 589.5 mm, which was obtained from "Chiba weather station".*

*(Japan Meteorological Agency, https://www.data.jma.go.jp/stats/etrn/view/monthly_s1.php?prec_no=45&block_no=47682&year=2009&month=&day=&view=.; accessed 30 March 2023.)

On 18 October, soil in each pot was emptied into a bucket, stirred, and part of the soil was sampled and dried at 105ºC to determine water content. Almost 20 ml of each wet soil was weighed and put into a plastic tube. Deionized water was measured and added to the soil as the ratio of dry soil and water to be strictly 1:2 by weight. Tubes were stirred well and allowed to stand for more than 3 hours. The electric conductivity of the supernatant was measured with a conductivity meter (B-173 Horiba, Ltd.).

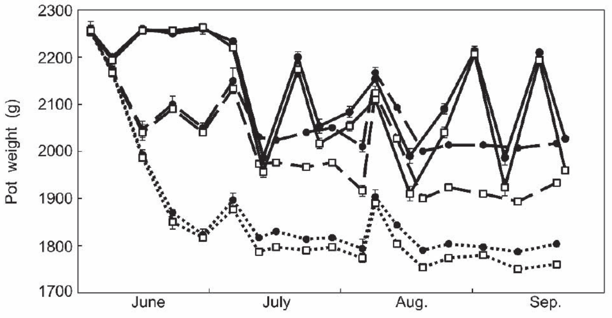


Fig. 2. Seasonal changes in the average weight of the pots (±SD, N=5) of high (dash lines) and low (short-dash lines) water contents in the glasshouse, and the pots left outdoors (solid lines), in which *Phragmites australis* (open square) and *Miscanthus sinensis* (closed circle) were grown. Pots were irrigated with deionized water immediately after measuring the weight until the soil in the pots of high water content and outdoors was nearly saturated, and the soil in the pots of low water content attained the water content equivalent to 70%, if necessary.

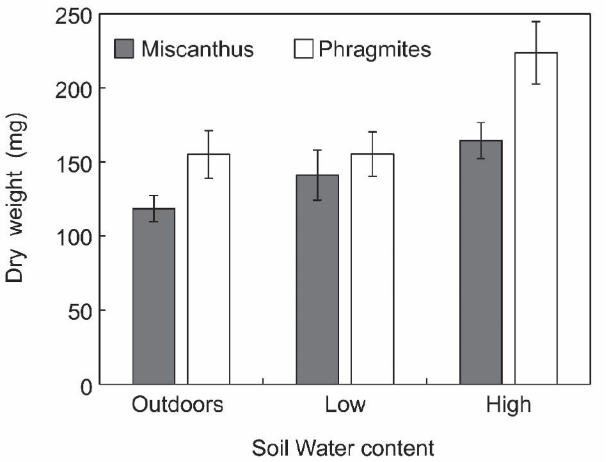


Fig. 3. Average dry weight (±SE, N=20) of the seedlings (shoot + rhizome) of *Phragmites australis* (open bars) and *Miscanthus sinensis* (closed bars) grown in the pots of high and low water contents in glasshouse, and pots left outdoors.

Results

1. Growth of *Phragmites* and *Miscanthus* under different water regimes

Changes in the weight of the pots are shown in Fig. 2. Average weight of the pots of high water content was always higher than those of low water content, as intended. Calculated minimum soil water content was 71%, 60%, 49%, and 46% for the pots of *Miscanthus* under high water content, *Phragmites* under high water content, *Miscanthus* under low water content, and *Phragmites* under low water content, respectively. As the pots outdoors were frequently exposed to rainfall, the average weight of the pots rarely fell below the weight of the pots of high water content. The average weight of the pots of *Miscanthus* was always equal to or higher than pots of *Phragmites* due to the difference in the rate of evapotranspiration. Especially, the difference was large for the pots with high water content.

Differences in dry weight of the seedlings (shoot + rhizome) between the two species ($F_{1,\ 114}$=8.40, P less than 0.005, two-way ANOVA) and among the three treatments ($F_{2,\ 114}$=7.68, P less than 0.001) were both significant without significant interaction ($F_{2,\ 114}$=1.06, P more than 0.3; Fig. 3). In every treatment average dry weight of *Phragmites* seedlings was higher than that of *Miscanthus* seedlings. Even in the pots of low water content, *Phragmites* seedlings had grown faster than *Miscanthus* seedlings, and the final dry weight was slightly higher than that of *Miscanthus* seedlings. The average dry weight of the *Phragmites* seedlings grown under high water content was higher than those under the two other treatments. The average dry weight of *Phragmites* seedlings left outdoors was not different from those of low water content even though the water content of the soil in the pots left outdoors was much higher. Although there was no eminent difference among the three treatments, the average dry weight of the *Miscanthus* seedlings was the highest under high water content and lowest in the pots outdoors.

2. Growth of *Phragmites* and *Miscanthus* at different nutrient levels under the hydroearth method

Although equal amount of water was added to all pots periodically, the average weight of the pots under the hydroearth method was always equal or lower than those of the pots under ordinary treatment (Fig. 4). Calculated maximum-minimum soil water content was 99–68%, 99–60%, 81–59% and 81–62% for the pots of *Miscanthus* under ordinary method, *Phragmites* under ordinary method, *Miscanthus* under the hydroearth method and *Phragmites* under the hydroearth method, respectively.

Under the ordinary method, differences in dry

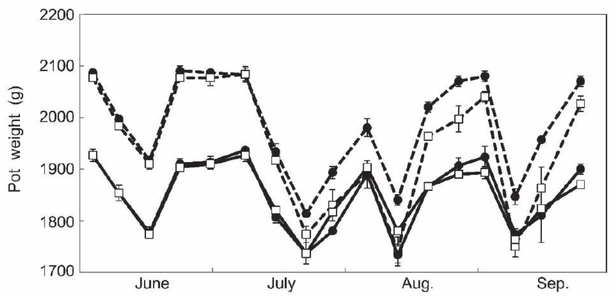


Fig. 4. Seasonal changes in the average weight of the pots (±SD, N=5) of no nutrient treatment under the ordinary (dash line) and hydroearth (solid line) methods, in which *Phragmites australis* (open square) and *Miscanthus sinensis* (closed circle) were grown. All pots were irrigated with the same amount of deionized water necessary to saturate the lightest pot immediately after measuring the weight, if necessary.

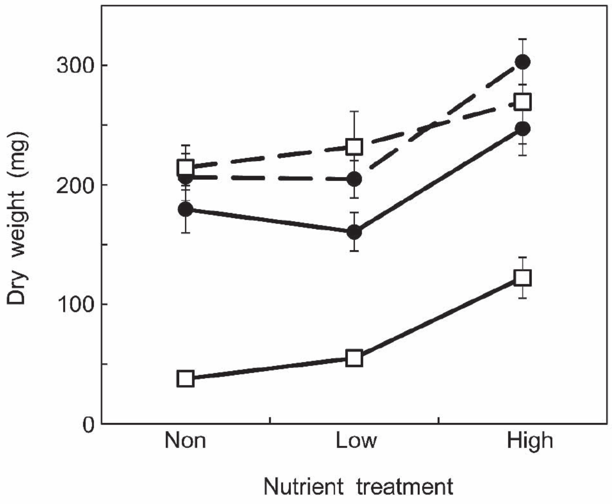


Fig. 5. Average dry weight (±SE, N=20) of the seedlings (shoot + rhizome) of *Phragmites australis* (open square) and *Miscanthus sinensis* (closed circle) grown in the pots of high, low, and no nutrient treatments under the ordinary (dash line) and hydroearth (solid line) methods.

weight of the seedlings (shoot + rhizome) between the two species were not significant ($F_{1, 114}$=0.0007, P more than 0.97, two-way ANOVA; Fig. 5). Difference in dry weight of the seedlings among three nutrient levels was significant ($F_{2, 114}$=6.00, P less than 0.003). The dry weight of the seedlings of both species was the highest at high nutrient treatment. The interaction was not significant ($F_{2, 114}$=0.83, P more than 0.4).

Under the hydroearth method, differences in the dry weight of the seedlings (shoot + rhizome) between the two species were conspicuous ($F_{1, 114}$=92.30, P less than 0.0001, two-way ANOVA). The difference in dry weight of the seedlings among the three nutrient levels was also significant ($F_{2, 114}$=6.00, P less than 0.0001). The interaction was not significant ($F_{2, 114}$=0.65, P more than 0.5). The growth rate of *Phragmites* under the hydroearth method was very low. The average dry weight of *Phragmites* seedlings grown under no nutrients was 21% of that of *Miscanthus* (t=6.90, df=22, P less than 0.0001, t-test). The growth rate of *Miscanthus* seedlings under the hydroearth method was, however, nearly equal to those under the ordinary method. Although the difference in dry weight between the two species decreased with the increase in nutrient level due to the higher growth of *Phragmites* seedlings under high nutrient treatment, the dry weight of *Phragmites* seedlings of high nutrient was still 49% of that of *Miscanthus* seedlings.

3. Electrical conductivity of the soil extract

Differences in electrical conductivity (EC) among 4 treatments - the hydroearth method, the ordinary method, low water content, and high water content - were significant ($F_{3, 8}$=4.07, P less than 0.001, one-way ANOVA; Fig. 6). Average EC of two treatments conducted outdoors - the hydroearth method and the ordinary method - was far lower than the two treatments - low water content and high water content - done in the glasshouse. Higher EC indicated that soil in those pots holds considerably more ionic solvent than the other two.

Discussion

The results of the field experiment in the previous study (Yura, 2010), namely the extremely low growth rate of *Phragmites* seedlings compared to *Miscanthus* seedlings, could only be reproduced under the hydroearth method in the second experiment especially when no nutrients were added (Fig. 5). Although the soil in the pots under ordinary method was not constantly inundated with water as the wetland, growth of *Phragmites* seedlings was not significantly different from *Miscanthus* seedlings. As the water content of the pots under the hydroearth method was always lower than those under the ordinary method, shortage of water in the soil might have

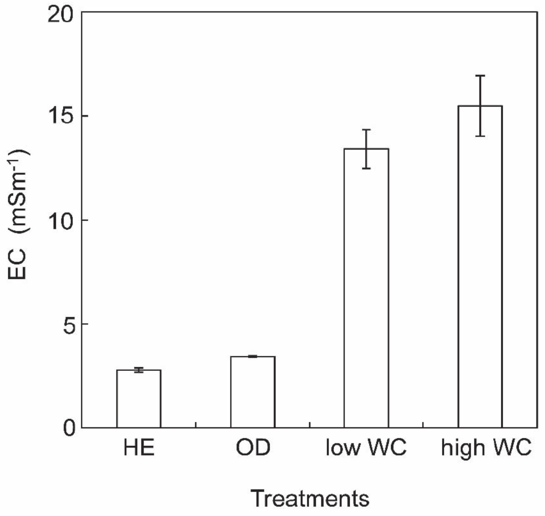


Fig. 6. Average electric conductivities (EC, ±SE, N=3) of the water extracted from the soil in the pots situated under the hydroearth (HE) and ordinary (OD) methods, and those in which soil water content kept low (lowWC) and high (highWC).

suppressed the growth of *Phragmites* seedlings, while such difference in water content had little effect on the *Miscanthus* seedlings (Fig. 4).

The relatively high water content of the soil in the ordinary pots might be caused by the formation of a "perched water table", a zone of soil soaked in water, at the bottom of the pot. It is known that the formation of a perched water table is unavoidable in ordinary pots after irrigation (e.g. Arthur Spomer, 1976; Arthur Spomer *et al.*, 1997). Contrary to ordinary pots, continuity of the soil from the ground to the soil in the pot would have inhibited the formation of a perched water table in the pots under the hydroearth method (Fig. 1). Theoretically, the water potential of the soil in the pots under the hydroearth method should be nearly equal to that of the mesic soil of the ground just under the pots.

Although low soil water content might be necessary for suppressing the growth of *Phragmites* seedlings, it was not, however, sufficient. In the first experiment, not only the difference in growth rate between *Phragmites* and *Miscanthus* seedlings was insignificant, growth of *Phragmites* seedlings was higher than *Miscanthus* seedlings even in the pots under low water contents (Fig. 3). Although water content of the soil in the pots of low water content was frequently lower than that in the pots outdoors, growth of *Phragmites* seedlings between the two pots was not much different (Figs. 2 & 3). Suppression of the growth of *Phragmites* seedlings could not be reproduced only by culturing them in soil of low water content.

Soluble nutrients are known to leach out from the upper soil with the infiltration of precipitated water (e.g. Greenland, 1958; Fried and Broeshart, 1967; Bourgeois and Lavkulich, 1972). Indeed, the electrical conductivity of the extraction of the soil in pots left outdoors (pots under the ordinary and hydroearth methods) was far lower than those in the glasshouse (pots kept high and low water contents; Fig. 6). As the amount of water added to the pots in the glasshouse was equal to that lost by evaporation, ionic solvents seemed to have accumulated in the soil without leaching out of the pots. Kachi and Hirose (1983) who conducted a pot-culture and field experiment on *Oenothera erythrosepala*, concluded that one of the factors responsible for the difference in growth between the two experiments was the leaching of specific nutrients from the soil in the field. The low growth of *Phragmites* seedlings under the hydroearth method might be caused by the synergistic effect of the leaching of available nutrients and the low water content of the soil.

A shortage of nutrients for the growth of *Phragmites* seedlings in the pots under the hydroearth method was also indicated in the second experiment. Although the growth of every seedling improved when the nutrient solution was periodically added, the addition of nutrients was most effective for *Phragmites* seedlings in the pots under the hydroearth method (Fig. 5). A marked increase in growth indicated that *Phragmites* seedlings grown under the hydroearth method were in the state of nutrient deficiency. On the contrary, the growth of *Phragmites* seedlings under the ordinary method was already high and did not much improve by adding nutrients. As the difference between the hydroearth and ordinary method was the water content of the soil, excess water in the soil might have functioned to alleviate the adverse effect of nutrient shortage.

Usually, the process in which the root surface makes contact with nutrients is divided into three components; root interception, mass flow, and diffusion (Marshner, 1995). From the results of this study, it could be assumed that *Phragmites* seedlings depended mostly on mass flow driven by the transpiration to acquire nutrients. When the soil was holding much available water, such as pots of high water content in the first experiment or pots under ordinary methods in the second experiment, *Phragmites* seedlings could acquire sufficient nutrients with a high rate of mass flow even though the concentration of the nutrients in the soil water was low. Also, when soil water contained many nutrients, *Phragmites* could acquire sufficient nutrients even though available water was limited. *Phragmites* seedlings in the pots of low water content in the first experiment may be under this condition, where sufficient nutrients accumulated in the soil without leaching out. Only in the case of pots under the hydro-earth method, where soil water was limited and nutrients frequently leached out, *Phragmites* seedlings could not acquire sufficient nutrients to grow as much as seedlings in other pots. Contrary to *Phragmites*, *Miscanthus* seedlings could be assumed to acquire nutrients mostly by another process than mass flow since *Miscanthus* seedlings are not much affected by the water condition of the soil. *Miscanthus* might be able to acquire much of the nutrients by absorbing insoluble nutrients adsorbed to the soil particles.

In conclusion, the extremely low growth rate of *Phragmites* seedlings sown on the well-drained upland was considered to be caused by the unsuitable mechanism of *Phragmites* seedlings in acquiring nutrients from the soil not inundated with water. Although depending on mass flow for acquiring nutrients may be suitable for growing in wetlands, it would be difficult to grow fast on the upland area where precipitated water swiftly infiltrates deep into the soil dissolving nutrients without being stagnant near the surface of the ground.

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抽水植物ヨシ（*Phragmites australis*）が，水はけの良い台地上で生存・成長できない理由の解明

由良　浩

千葉県立中央博物館 共同研究員
〒 260-8682　千葉市中央区青葉町 955-2
E-mail: expplntecol@gmail.com

典型的な抽水植物であるヨシ（*Phragmites australis*）が，水はけの良い台地上で生存・成長できない理由を解明するために栽培実験を行った．最初の実験では，ヨシと水はけの良い台地での優占種であるススキ（*Miscanthus sinensis*）とをいくつかの土壌含水量のもとで，種子から育てた．その結果，含水量を低く維持したポットでも，ヨシの成長は低下しないことが明らかとなった．次に，ポットの底の穴を屋外の地面に敷いた砂に接触するまでポットを押し付けた状態にした「ハイドロアース法」を考案し，その方法で実験を行った．その結果，「ハイドロアース法」でヨシを育てると，同様に育てたススキより明らかに成長が低下すること，また，栄養塩を加えると，ヨシの成長が回復することが明らかになった．以上の実験からヨシが水はけの良い台地上で成長できないのは，台地上では，水とともに栄養塩が土壌から溶脱するために，十分に栄養を得ることができないためであることが示唆された．