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Survival and Growth of the Seedlings of *Phragmites australis* (Cav.) Trin. ex Steud. Germinated on Well-drained Upland

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Abstract An outdoor experiment was conducted to investigate whether typical wetland species, *Phragmites australis*, could survive and grow on well-drained upland. Seeds of *P. australis* and typical upland species *Miscanthus sinensis* were sown separately in plots established on well-drained upland where all plants had been removed in advance. From half the plots, all emerged plants other than *P. australis* and *M. sinensis* were kept removed (" weeded plots "), while the other half were left unweeded (" unweeded plots "). Seeds were also sown in submerged pots filled with upland soil (" inundated plots "). Although seeds of *P. australis* sown in all plots germinated well, number of surviving seedlings considerably decreased in both unweeded and weeded plots. Increase in dry weight of surviving *P. australis* in both unweeded and weeded plots was also low. Only *P. australis* in inundated plots actively grew and propagated. Contrary to *P. australis*, seedlings of *M. sinensis* positively grew and propagated in both unweeded and weeded plots. These results indicated that although *P. australis* seeds could germinate on well-drained upland seedlings could not survive nor grow sufficiently thereafter. As the survival and growth rate in weeded plots were not much higher than those in unweeded plots, edaphic condition of the well-drained upland itself might be more responsible for the absence of *P. australis* than competition with other species.

Key words : competition, habitat segregation, *Miscanthus sinensis, Phragmites australis*, seedling, soil water content, survival, upland, wetland.

Phragmites australis (Cav.) Trin. ex Steud. is well known as one of the typical emergent aquatic perennials forming dense stands in littoral zones of lakes, along rivers and in shallow wetlands throughout the world. *P. australis* is so productive species that it can be frequently observed to form nearly monodominant closed stands under favorable conditions. In spite of its worldwide distribution and vigorous reproductive capacity, its habitat is strictly confined to wetlands. *P. australis* can seldom be found growing in grass lands formed on mesic but well-drained uplands such as those dominated by *Miscanthus sinensis* Andersson in temperate Japan. As diaspores of *P. australis* are light and hairy, they can be easily dispersed to terrestrial sites as well as aquatic sites by wind (Cook, 1987). The fact that *P. australis* can hardly found on well-drained uplands suggests that the environmental conditions characteristic of those area are too harsh for *P. australis* to germinate or grow. Low water content of the soil and／or competition with upland species are assumed to be the main factors responsible for the absence of *P. australis* from well-drained uplands.

Abiotic or biotic factors which might cause injurious effects on plants of xeric and mesic habitats under flooding or submergence have been extensively studied so far (e.g. Crawford, 1982 ; Jackson and Colmer, 2005). On the contrary, effects of the desiccation or drainage of soil on wetland species have not been closely investigated. Actually, there were some studies investigating the effects of low water level on the growth or performance of wetland species including *P. australis* (Lieffers and Shay, 1981 ; Yamasaki and Tange, 1981 ; Squires and van der Valk, 1992 ; Coops and van der Velde 1995 ; Coops *et al.*, 1996 ; van der Putten *et al.*, 1997). In those studies, however, the maximum depths of the water table which plants were subjected to at the experiments were no more than 1m, since the purpose of those studies was to compare the effects of water level among different species of wetland, not the comparison between wetland and upland species. Especially,

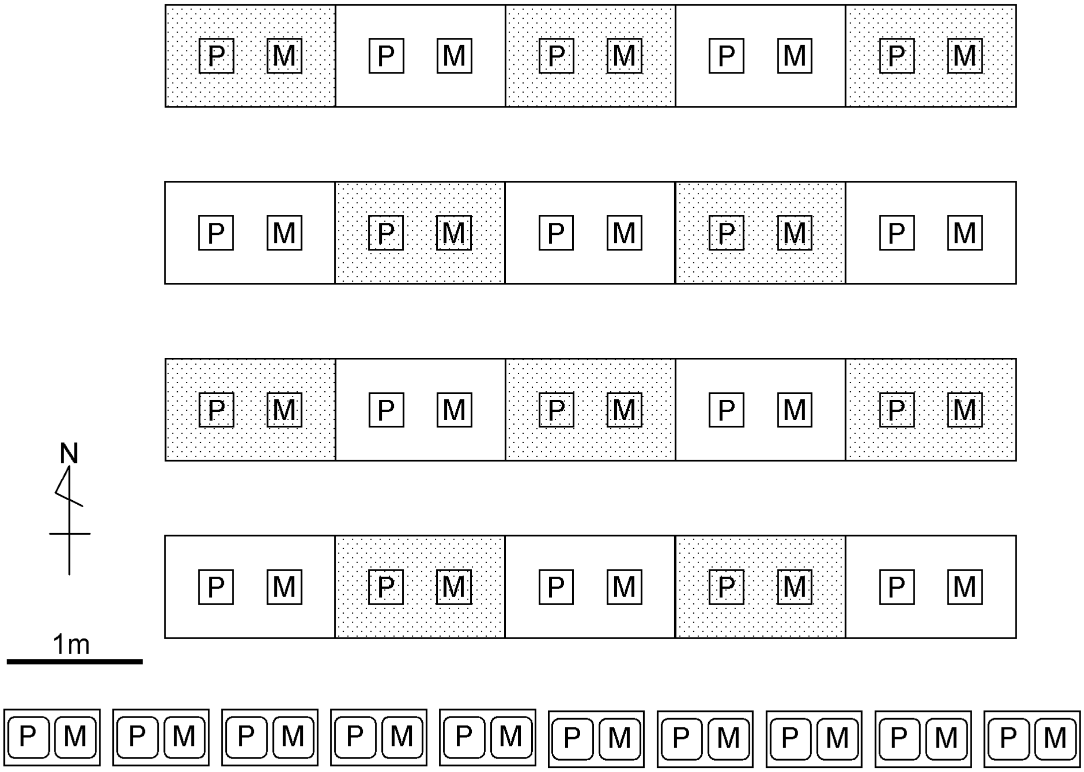

Fig. 1. Spatial arrangement of plots and treatments. Five rectangular plots were arranged in four rows. A pair of small squares in the plots represents quadrats where seeds of *Phragmites australis* (P) and *Miscanthus sinensis* (M) were sown. Hatched and open rectangles represent " weeded plots " which all plants except *P. australis* or *M. sinensis* were kept removed and " unweeded plots " where any plants were left unweeded, respectively. Ten small rectangles at the bottom are " inundated plots " which are water filled containers buried in the ground. In every container, a pair of pots sown with seeds of *P. australis* (P) and *M. sinensis* (M) was submerged.

no previous reports of the fate of wetland species whose seeds were dispersed on well-drained uplands, where water table was usually at the depth of a few meters to tens of meters, could be found.

In this study, an outdoor experiment was conducted to elucidate whether the absence of *P. australis* from well-drained upland is caused by the inferior competitive ability of P. australis against the other species inherent to upland or by the edaphic condition of upland itself. Seeds of *P. australis* were sown and number of emerged seedlings was counted in two contrasting plots–one where other plants were weeded intensively and the other where all the emerged plants were left unweeded–established on well-drained upland. With seeds of *P. australis*, seeds of *M. sinensis* were also sown in the same plots to compare the survival and growth of the seedlings of two contrasting perennials, where one is from wetland and the other inherent to well-drained uplands. Additionally seeds of *P. australis* and *M. sinensis* were also sown in inundated soil in order to record the number and growth of the seedlings under an inundated condition.

Materials and Methods

In early spring of 1997, an area of 7 m×10 m in the experimental field of Ecology Park of Natural History Museum and Institute, Chiba (35°35′N, 140°08′E) were weeded and tilled. This field, located on heights of 20 m a. s. l. was well-drained, and it had never been flooded even after a spell of heavy rain. Vegetation that originally covered this field was mostly composed by perennials typical of well-drained, mesic sites, such as *Solidago altissima* L., *M. sinensis*, *Imperata cylindrica* (L.) Raeusch and *Artemisia indica* Willd. var. *maximowiczii* (Nakai) H. Hara. They were removed as thoroughly as possible together with roots and rhizomes during the weeding and tilling of the field.

The soil of this field was composed of fine sand and andosol - soil that contained materials rich in volcanic ash and humus. Weeded and tilled area was smoothed by trampling on the soil.

Five rectangular plots of 0.75 m × 1.25 m were arranged in four rows in the weeded and tilled area (Fig. 1). Within those 20 plots, one pair of quadrats of 0.25 m × 0.25 m was placed at the interval of 0.25 m.

On the south side of the field, 10 open top containers made of plastic of 33 ㎝ wide, 57 ㎝ long and 22 ㎝ deep were buried at the depth of 20 ㎝ in one row. Soil that was dug out for each container was filled into two square pots of 27 ㎝ × 27 ㎝ and 25 ㎝ deep to the depth of 24 ㎝. After filling the buried containers with well water, a pair of pots filled with soil was submerged into them. All containers were filled up with water once to twice a week, if necessary, during the study to maintain the soil under inundated conditions such as wetland. A quadrat of 0.25 m × 0.25 m was placed on the soil surface of every pot. Hereafter these pots in water filled containers will be called " in undated plots " .

On 17 March 1997, 87 mg of the seeds of *P. australis* was sown evenly in one of the pair quadrats in every plot. On the same day, 121 mg of the seeds of *M. sinensis* was sown into the other quadrats. After sowing, half of the twenty plots on well-drained area were assigned alternatively as " weeded plots ", from which all the emerged seedlings except for those of *P. australis* or *M. sinensis* were kept removed whether they emerged inside or outside the quadrats. The other half were assigned as " unweeded plots ", where any emerged seedlings were left unweeded. Any seedlings emerged in the inundated plots were left unweeded.

Five weeded and five unweeded plots were randomly chosen as plots for counting the number of surviving aboveground shoots during the studying period. Total numbers of the aboveground shoots of *P. australis*, *M. sinensis* and other plants emerged in the quadrats were counted every other week. When a new sprout of *P. australis* or *M. sinensis* emerged from the base of shoots or rhizomes, it was counted as separate shoots whether they emerged inside or outside the quadrats. In the same way, the number of the shoots of *P. australis* and *M. sinensis* emerged in the quadrats of randomly chosen five inundated plots were also counted. The counting was continued for one and a half years except in winter when almost all shoots died back.

In order to evaluate the growth of the seedlings in

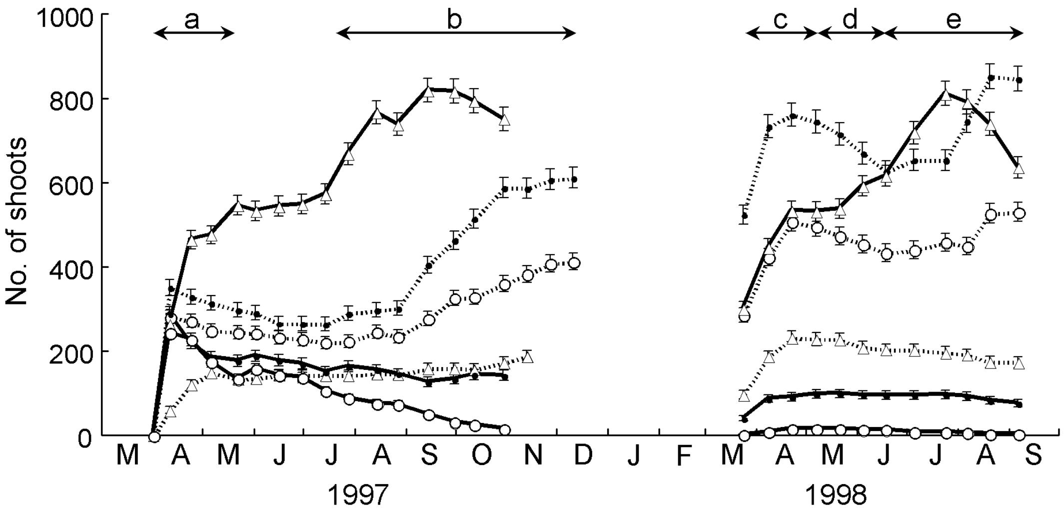

Fig. 2. Seasonal changes in the total number ± s.d. of surviving shoots of *Phragmites australis* (solid line) and *Miscanthus sinensis* (dotted lines) in five plots where all other species except *P. australis* or *M. sinensis* were kept removed (weeded plots, closed dots), five plots where any plants were left unweeded (unweeded plots, open circles) and five plots under inundated conditions (inundated plots, open triangles). Seeds were sown on 17 March 1997. Counting was withheld during the season of winter dormancy. Increments in number of shoots, if any, during the periods a, b, c and e were due to germination of sown seeds, sprouting from the bases or rhizomes of the seedlings, sprouting from overwintered rhizomes and sprouting from the bases or rhizomes of grown shoots, respectively. Decrements, if any, during the periods d and e were due to the death of overwintered or grown shoots.

weeded, unweeded and inundated plots, ten randomly chosen seedlings of *P. australis* and *M. sinensis* were harvested from one pair of quadrats in the remaining plots on 15 May, 20 July and 14 October. As whole roots of the seedlings could not be excavated completely, the aboveground parts and rhizomes, if present, were collected. After soil was rinsed off, they were dried at 70°C and then weighed.

Results

Changes in shoot number

Seeds of *P. australis* and *M. sinensis* sown in all plots began to germinate in early April. Totally 250 to 350 seedlings of *P. australis* and *M. sinensis* emerged in both five weeded and five unweeded plots on well-drained area (period a in Fig. 2). In inundated plots only *P. australis* seeds germinated plentifully. Initial seedling number of *M. sinensis* in early April was far smaller than those in other plots. Seeds of both species sown in inundated plots kept on germinating till June, while germination of the seeds of the two species sown in weeded and unweeded plots terminated by the middle of April.

In inundated plots germination of the seeds of *P. australis* almost terminated in early summer. The number of shoots, however, began to increase again in August due to new sprouts from rhizomes or the base of the growing seedlings (period b in Fig. 2). As almost all *P. australis* seedlings sprouted new shoots, the number of total above ground shoots eventually doubled by the end of autumn. On the contrary, *M. sinensis* shoots in inundated plots did not increase after the termination of germination. After May, no new sprout or germination was observed in the first year.

In weeded and unweeded plots, total number of the seedlings of the two species began to decrease soon after germination. However, as new shoots sprouted from the base of the surviving *M. sinensis* seedlings in both weeded and unweeded plots, total number of aboveground shoots of *M. sinensis* began to increase in early autumn again (period b in Fig. 2). The increase in the number of shoots was more rapid in weeded plot. Finally, number of surviving *M. sinensis* shoots in December was higher than that of the germinated seedlings in spring. On the contrary, the number of *P. australis* shoots in weeded and unweeded plots gradually decreased without any marked increase till early November, when shoots began to die back due to winter dormancy. Decreasing rate was higher in unweeded plots than in weeded ones. No sprouting of new shoots of *P. australis* was observed in unweeded plots, indicating that the number of shoots was representing the number of seedlings. No more than 16 seedlings of *P. australis* were surviving at the end of the first year in 5 unweeded plots.

In unweeded plots, many shoots of other species, which were seedlings germinated from buried seeds or shoots sprouted from the fragments of rhizomes, began to emerge simultaneously with the germination of *P. australis* and *M. sinensis* in early April. There was not much difference in the number of other species emerged inside the quadrats of *M. sinensis* and *P. australis*. Total number of the shoots of other species inside the quadrats of five plots was totally almost 120 in early April. Major species in spring were *Calystegia pubescens* Lindl., *Oenothera parviflora* L. and some annuals such as *Setaria faberi* R.A.W. Herrm. and *Ambrosia artemisiifolia* L. In summer dominant species were *S. faberi*, *A. indica* var. *maximowiczii* and *Digitaria ciliaris* (Retz.) Koeler. Total number of the shoots of other species fluctuated, since some of the plants grew fast and sprouted new shoots from the base of the stem, while some of shoots died out. However, total number of other species was always in the range of 100 to 150 without any extreme increase or decrease till the end of October, when more than hundred of seedlings newly emerged in every quadrat. Most of the emerged seedlings in autumn were those of winter annuals. Eventually, total numbers of the shoots of other species including new seedlings inside the five quadrats of *P. australis* and *M. sinensis* became to be in the ranges of 650 to 780 and 500 to 750, respectively. Dominant species in late November were *O. parviflora, A. indica* var. *maximowiczii, S. altissima, I. cylindrica*. Contrary to unweeded plots, only few other species emerged in inundated plots. Most of them were species of *Typha*. As it seemed to have not much influence, the number of other species in inundated plots was not counted.

In late March of the second year, new shoots of *P. australis* and *M. sinensis* were found sprouting from overwintered rhizomes (period c in Fig. 2). As shoots of *M. sinensis* sprouted in autumn of the first year kept green till the early spring of the second year, those shoots were included as surviving shoots at the counting. On the contrary, as almost all shoots of *P. australis* sprouted in the first year withered during winter, only newly emerged ones were counted.

Patterns of the seasonal changes in shoot number of *M. sinensis* in weeded and unweeded plots were almost similar. Although the number increased rapidly in spring due to new sprouts, the number of

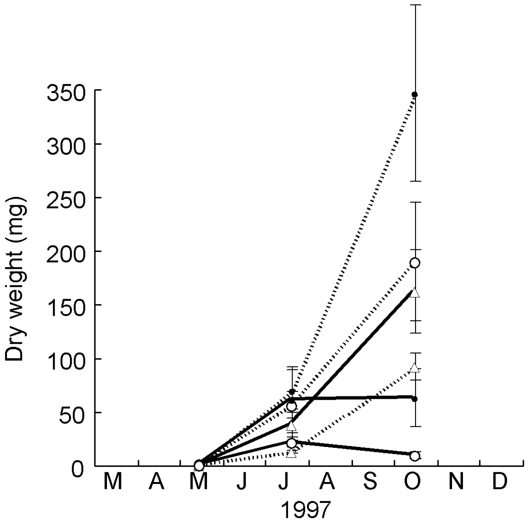

Fig. 3. Seasonal changes in dry weight of shoots+rhizomes of the seedlings of *Phragmites australis* (solid line) and *Miscanthus sinensis* (dotted lines) harvested from plots where all other species except *P. australis* or *M. sinensis* were kept removed (weeded plots, closed dots), plots where any plants were left unweeded (unweeded plots, open circles) and plots under inundated conditions (inundated plots, open triangles). Values are mean ± s.e. of ten plants.

total shoots decreased in early summer, as those shoots sprouted in the first year began to die out one after another (period d in Fig. 2). In summer, new shoots began to sprout from the base of grown shoots and, as a result, total number of shoots began to increase in late summer again (period e in Fig. 2). In both weeded and unweeded plots, final numbers of *M. sinensis* shoots in early September were the highest during the two years. In spite of the similar temporal pattern in the number of the shoots in both plots, total number of *M. sinensis* in weeded plots was always as twice as those in unweeded plots.

Contrary to the great fluctuation of the number of shoots on well-drained area, *M. sinensis* shoots in inundated plots did not increase in autumn of the second year. Rather the number gradually decreased from spring to autumn. Final number was almost equal to that of the first year.

In the second year, the mere plots in which shoot number of *P. australis* drastically changed were those in inundated plots. Although total number rapidly increased from April to July, some grown shoots withered in late summer (period e in Fig. 2). The final total number was 636 in early September. Contrary to the inundated plots, shoot numbers in weeded and unweeded plots were considerably low and stable throughout the growing season. Total numbers of emerged shoots in the second year were always lower than the minimum numbers in the first year. Numbers of the shoots slightly decreased and final numbers were both smaller than those in the first year, indicating that the population was declining. In unweeded plots *P. australis* seedlings were almost extinct.

As some of the other plants had overwintered in unweeded plots, 425 and 279 shoots of them were already alive in five quadrats of *M. sinensis* and *P. australis*, respectively, at the first count in late March of the second year. Major species then were *Sonchus asper* (L.) Hill, *O. parviflora, S. altissima* and *A. indica* var. *maximowiczii*. As many new shoots began to sprout thereafter, the total number in *M. sinensis* and *P. australis* quadrats rose to 1358 and 1190 within a month, respectively. The number of other species gradually decreased partly due to the death of winter annuals during spring. Major species in summer were *S. altissima, A. indica* var. *maximowiczii, O. parviflora* and *I. cylindrica*. Final numbers in September were 501 and 806 for *M. sinensis* and *P. australis* quadrats, respectively.

Changes in dry weight

Average dry weights of the shoots + rhizome of 10 *M. sinensis* seedlings increased at every plot (Fig. 3). Rate of increment, however, differed among the three plots. Difference in average dry weights on the final day of the harvest was significant (one-way ANOVA, $p=0.015$). Dry weight that mostly increased was that of *M. sinensis* seedlings in weeded plots. Although there was an increase in dry weight at inundated plots, the increment was the least.

Although average dry weight of surviving *P. australis* seedlings in three plots increased from May to July, no increment in dry weight was noted thereafter in weeded and unweeded plots. Average dry weight of *P. australis* that significantly increased from July to October was only those in inundated plots (t-test $p=0.012$). There was no significant difference between the two harvests in weeded plots (t-test $p=0.96$). Even significant decrement was detected in unweeded plots (t-test $p=0.015$). Eventually, dry weights at the final harvest were significantly different among the three plots (one-way ANOVA, $p=0.018$). Final dry weights of surviving *P. australis* seedlings in weeded and unweeded plots in the first year were far lower than those of *M. sinensis*seedlings.

Table 1. Relative growth and survival rate of the seedlings of *Phragmites australis* and *Miscanthus sinensis* in weeded and unweeded plots on well-drained upland and in inundated plots.

species	plots		
	weeded	unweeded	inundated
P. australis	−	−	++
M. sinensis	++	+	−

++, very high ; +, high : −, low.

Discussion

Although the unweeded plots were bared artificially before the start of the study, many plants other than *P. australis* or *M. sinensis* germinated and sprouted naturally. Those species were all inherent to well-drained land in temperate Japan. Therefore, considering the vegetation composition and geographic location, the unweeded plots could be regarded as an area of typical well-drained upland under natural succession. Although *P. australis* seeds germinated and grew for a while in unweeded plots, those emerged seedlings could not keep growing nor propagate (Figs. 2, 3). *P. australis* seedlings started to die one after another soon after germination and finally they were almost totally extinct in autumn of the second year. These results are indicating that even though seeds of P. australis have a good chance to germinate on natural upland those seedlings can not survive and grow for a long period.

The low survival and growth rate of the seedlings of *P. australis* in unweeded plots could not be completely attributed to the effects of competition with other plant species, since decrement in shoot number or increment in dry weight did not markedly improved in weeded plots (Figs. 2, 3). In weeded plots there were completely no other plants to shade the sun nor intercept the absorption of water and nutrients in the soil. Although initial increment in dry weight of *P. australis* seedlings was higher than those in unweeded plots, increment in dry weight stopped by late July as in unweeded plots. Although a few new sprouts of *P. australis* were observed in weeded plots, emergence of new shoots could not exceed the decrement rate of the seedlings. As a result, total number of seedlings in weeded plots also decreased persistently after germination as in unweeded plots. Even though some rhizomes overwintered and start sprouting in spring of the second year, total number of shoots had not increased at all. These facts indicate that the environment characteristic to upland per se is unsuitable for *P. australis* seedlings to grow and propagate.

Contrary to weeded plots, *P. australis* seedlings in inundated plots actively grew and sprouted. Since the soil used in inundated plots was collected from upland, active growth and sprouting of the seedlings in inundated plots could not be attributed to the type of the soil. The only difference between weeded and inundated plots was the content and movement of water in the soil. In inundated plots soil was constantly immersed in almost still water, but in weeded plots water which was provided by intermittent rainfall gradually infiltrated down into the deep soil, leaving the surface in moist condition at most. It is known that anaerobic conditions in inundated soils in some cases increase availability of nutrients such as ammonium ions, soil phosphorus and potassium ions for wetland species (Fitter and Hay, 1987). Unfavorable edaphic condition caused by the movement and low content of water in the upland soil might be one of the main reason for the low survival and growth rate of *P. australis* seedlings on well-drained but mesic upland.

Seedlings of *M. sinensis*, on the other hand, grew and propagated sufficiently in both weeded and unweeded plots. As could be attributed to the existence of other species, the increment rates of dry weight and shoot number in unweeded plots were half to two third of those in weeded plots. Although competition with other species had minus effects on the propagation of *M. sinensis* seedlings, it was not serious enough as to inhibit the growth or survival of them. Number of shoots in unweeded plots had a tendency to increase even in the second year. *M. sinensis* seems to have a potential ability to grow and dominate on the upland area, even under competition. Only under inundated condition, *M. sinensis* seedlings could not propagate. Although dry weight increased in inundated plots, shoot number did not increase even in the second year. As both growth and propagation rate of *P. australis* in inundated plots were far higher than those of *M. sinensis, P. australis* should have the ability to overwhelm *M. sinensis* and become dominant species under natural inundated condition.

The results of the study demonstrated the contrasting difference in the performance of *P. australis* and *M. sinensis* seedlings germinated in well-drained and inundated area (Table 1). The difference coincides to the well known difference in distribution of upland species, ***M. sinensis***, and wetland species, ***P. australis***. Although competition is certainly one factor adversely affecting the growth or propagation of the two species, water content or movement in the soil is considered to be more critical. Mechanism that leads to the promotion or inhibition of growth and propagation under contrasting environment could not be cleared in this study. It is to be elucidated under controlled experiments in the future.

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水はけの良い台地上で発芽したヨシ Phragmites australis の実生の生存と成長

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代表的な湿地の植物であるヨシは、湿地以外の立地、例えば，水はけの良い台地上で生育していることはまれであるが、その理由はほとんど解明されていない。本研究では、ヨシの種子を、水はけの良い台地上に播き、その後の発芽、実生の生存、増殖によるシュート数の増加等を１年半にわたり追跡した。また１年目には実生を定期的に３回掘り出し、根を除く実生の平均乾量を測定した。台地上にある実験圃場を裸地化し、プロットを 20 設置し、その中にヨシの種子と、台地上の代表的な優占種であるススキの種子を離して播いた。20 プロットのうち、半数を除草区とし、発生したヨシもしくはススキ以外のすべての植物を除去した状態に保った。残りの半数は放置区とし、すべての植物をそのまま放置した。これらのプロットの他、台地上の土を入れたポットを水没させた浸水区を設けて、そこにも両種の種子を播いた。ヨシは台地上で多数発芽したが、除草区でも放置区でも発芽直後から実生の数は減少し続けた。少数の実生は冬越ししたものの放置区では２年目の秋には実生はほぼ全滅し、除草区でも地上のシュート数に全く増加は見られなかった。実生の乾量は１年目の初夏の頃まで除草区でも放置区でも増加したが、その後は全く増加しなくなった。浸水区のヨシの実生の乾量のみ増加し続け地上のシュート数も増加した。一方のススキは、放置区除草区ともに、実生の乾量も、地上のシュート数も増加した。冬越しした２年目もシュート数は増加した。これらの結果から、ヨシは水はけの良い台地上では発芽はできるものの、長くは生きられないことが明らかになった。ヨシは除草区でも生育が良くないことから、他の種との競争だけが生育不良の原因ではなく、台地上の環境そのものもヨシの生育にとって好ましくないことが示唆された。