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Effects of water depth and substrate type on growth dynamics and biomass allocation of *Oryza rufipogon*

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ABSTRACT

Oryza rufipogon is known as the ancestor of Asian cultivated rice (*Oryza sativa*) and the most important germplasm for rice improvement. In this study, we investigated its growth and biomass allocation in response to water depth and substrate type. The results demonstrated that individual plant had an average weight of 18.98 g, 9.36 g, and 10.59 g and produced 77.7 seeds, 35.5 seeds, and 41.6 seeds in deep-, fluctuated-, and shallow water, respectively. Root-to-shoot ratios were 0.37 in deep water, 0.61 in fluctuated water level, and 0.56 in shallow water, reflecting larger investment in roots under water-level fluctuation and shallow water conditions. However, biomass allocation for sexual reproduction was no significant different among the three water levels. In substrates experiment, total biomass and seed production were significantly different between sediment types, and the averages were 10.59 g, 3.56 g, and 0.76 g in biomass and 41.6 seeds, 13.8 seeds, and 0.5 seeds per plant in lake sediment, river sand and clay, respectively. The number of tillers was significantly fewer in sandy and clay substrates than in lake sediments. Individual plant in clay substrates was significantly shorter than those in sandy and in lake sediment substrates. Our study suggests that the plasticity in morphology and biomass allocation of *O. rufipogon* appears to be an adaptation to the variability in water level and substrate conditions.

1. Introduction

Oryza rufipogon, known as the ancestor of Asian cultivated rice (*Oryza sativa*), has been proven to be a valuable gene pool for rice genetic improvement and thus plays a critical role in rice breeding in the future. It was formerly a common wetland plant in the south of China; however, populations have decreased severely in recent decades and the species is now endangered in China, mainly due to disappearance of habitat [4,5]. Many studies on this species have focused on the discovery and utilization of favorable genes [1–3]. Previous studies have also demonstrated that habitat condition is very important for maintenance and development of populations of *O. rufipogon* [6,7]. A suitable environmental condition is essential for *O. rufipogon* to win the competition with its companion species [8,9]. It is therefore important to understand the mechanism that *O. rufipogon* responses to changes of habitat condition.

Water level and substrate condition of habitat are major determinant of plant community development and patterns in wetlands [10,11]. The morphological adaptations and resource allocation patterns reflect the influence of environmental constraints on wetland plants. Optimal partitioning models and theories suggest that plants respond to variation in the environment by partitioning biomass among various plant organs to optimize the capture of nutrients, light, water, and carbon dioxide in a manner that maximizes plant growth rate [12–16]. Morphological plasticity is, therefore, one of the traits allowing plants to adapt to environment change and help maintenance and development of population.

Here, the morphological adaptations and resource allocation patterns of *O. rufipogon* in response to water depth and substrate type were investigated. We describe and compare (1) the variation of plant height, tiller number to determine the growth response of *O. rufipogon* to different planting condition; (2) the variation of number of tassel, seed number per ramet and 100 seed weight to determine the response of reproductive output; (3) the variation of allocation pattern of biomass to determine the response of morphological plasticity.

2. Materials and methods

2.1. Material

Seeds were collected from Anjiashan Reserve of *O. rufipogon*, located in Dongxiang County, Jiangxi Province (26°14′N, 116°36′E) in

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late October, 2007. The collected seeds were stored in darkness at 4 °C.

To obtain similar sized seedlings, the seed germination was conducted in incubator at 20 °C with a 12 L:12 D photoperiod on May, 2008. When the seedlings was approximately 15 cm tall, similar sized vigorous seedlings were transplanted singly into plastic pots (diameter 20 cm and height 15 cm) filled with one of the three sediment types (see Section 2.3). Four seedlings were planted per pot initially.

2.2. Water-level experiment

The experiment was set up with three water-level treatments in each of five replicate pools. Fifteen plastic pots, filled with lake sediment collected from Lake Donghu in Wuhan, were suspended in fifteen 2 m × 2 m × 1 m deep cement pools, respectively. Three water-level treatments were designed as follow: (1) 60 cm stable water level (deep); (2) 10 cm stable water level (shallow); (3) alternating water level of 60 cm or 10 cm each day (fluctuating). Twenty individuals (5 pots × 4 individuals) were used in each water-level treatment. The experiment was conducted on early-June.

2.3. Substrate type experiment

The experiment was set up with three substrate types in each of five replications. The three substrate types were: (1) lake sediment collected from Lake Donghu in Wuhan; (2) commercially-available washed river sand; (3) clay collected from nursery garden of Wuhan Botanical Garden, CAS. Five replicated pots were suspended at 10 cm water level, in five 2 m × 2 m × 1 m deep cement pools, respectively. Twenty individuals (5 pots × 4 individuals) were used in each substrate treatment. The experiment was conducted on early-June.

2.4. Morphological measurements

The experiment lasted from 5 June to 29 September. The plant height (the longest branch) and tillers number of each individual were monitored on 14th June, 5th July, 26th July, 18th August, 10th September, 29th September, respectively.

Due to the spikelets (later called seed) of *O. rufipogon* shed easily after maturation, all tassels were wrapped by meshed bags in mid-September. All mature seeds were collected, and seed number and 100 seed weight were measured.

Plants were harvested at the end of experiment. To determine biomass allocation among plant parts, we divided each plant into tassels, leafs, shoots, and roots; dried them for 70 h at 80 °C; and then weighed the parts separately.

2.5. Statistic analysis

Phenological and morphological variables were analyzed using one-way ANOVA. Plant height and tiller variation were analyzed using a repeated measures ANOVA design. Comparison of the three reproductive attributes and biomass partitioning were assessed by Tukey's test. Plant morphogenetic responses to water level and sediment treatments were evaluated using a one-way ANOVA, with the total biomass as a covariate. All dependent variables were transformed to natural logarithms prior to analysis. All statistic analyses were performed by SPSS 16.0.

3. Results

3.1. Plant growth

Both water level and substrate type had significant effects on growth of *O. rufipogon* (Fig. 1). The plant height is always largest in deep water level and smallest in the shallow water level at all monitoring dates. Repeated measures analysis of variances indicated that plant height was significantly different among three water-level treatments ($F_{2,57} = 78.184$, $P < 0.001$). Tukey's test also showed significant difference each other among three water-level treatments ($P < 0.001$). In substrate type experiment, the plant height in clay treatment was significantly lower than that in other two treatments. Repeated measures analysis of variances indicated that significant difference was found among the three substrate type treatments ($F_{2,57} = 75.239$, $P < 0.001$).

Both water level and substrate type had significant effects on tiller of *O. rufipogon* (Fig. 2). The tillers number in fluctuated water level had an obvious decrease in the first three measurements. Repeated measures analysis of variances indicated that individual average number of tillers had significant difference among the three water-level treatments ($F_{2,57} = 8.098$, $P < 0.001$). Tukey's test also suggested that tillers number had significant difference between shallow water level and fluctuated/deep water level ($P < 0.001$). In substrate type experiment, repeated measures analysis of variances indicated that individual average number of tillers also had significant difference among the three substrate type treatments ($F_{2,57} = 128.383$, $P < 0.001$). Tukey's test showed significant differences each other in three substrate type treatments ($P < 0.001$). The individual tillers number of *O. rufipogon* was most in lake sediment treatments and fewest in clay treatments.

3.2. Reproduction output

Obvious changes in sexual reproduction output were detected (Fig. 3). In water-level treatments, the number of tassel per individual had no significant difference ($F_{2,57} = 1.968$, $P > 0.05$); the seed number per ramet had significant difference ($F_{2,57} = 7.854$, $P < 0.001$); the seed number in deep water level was significantly more than that in fluctuated- and shallow water level ($P < 0.05$, Tukey's test), 100 seeds weight had no significant difference in three water levels ($F_{2,57} = 1.691$, $P > 0.05$). In substrate type treatments, the number of tassels and seed number per ramet decreased significantly in the river sand than those in the lake sediment ($P < 0.05$, Tukey's test). Only one tassel occurred in clay substrate. No significant difference was found among the three substrates in 100 seed weight ($F_{1,38} = 0.736$, $P > 0.05$).

3.3. Biomass allocation

Total biomass and biomass allocation pattern had significant changes among the three water-level treatments (Fig. 4a). Individual average total biomass in deep water treatment was 17.98 g, which was significantly heavier than that in fluctuated water level (9.36 g) and shallow water treatments (10.59 g) ($P < 0.05$, Tukey's test). Root biomass allocation increased significantly in fluctuated and shallow water level, while leaf biomass allocation decreased significantly in fluctuated water level ($P < 0.05$, Tukey's test). Root-to-shoot ratios were 0.37 in deep water, 0.61 in fluctuated water level, and 0.56 in shallow water. No significant difference was found in biomass allocation of sexual reproduction ($P > 0.05$, Tukey's test). Analysis of covariance (total biomass as covariate) suggested that the biomass of root, stem and leaf had significant differences ($P < 0.05$, Table 1), but biomass of sexual reproduction