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Morpho-physiological characterization of cultivated rice (*Oryza* spp.) during early vegetative growth under different soil water conditions

David Montcho[1,2*], Koichi Futakuchi[1], Gustave Djedatin[3], Mamadou Fofana[4], Baboucarr Manneh[5], Clement Agbangla[2], Corneille Ahanhanzo[2]

[1]*Physiology Unit, Africa Rice Center, Cotonou, Benin*

[2]*Department of Genetic and Biotechnology, University of Abomey-Calavi, Cotonou, Benin*

[3]*Department of Genetic, Polytechnic University of Abomey, Dassa, Benin*

[4]*Physiology Unit Africa Rice Center Ibadan, Nigeria*

[5]*Irrigated Rice Breeding Unit, Africa Rice Center, Sahel Station Saint Louis Senegal*

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Abstract

In rainfed rice cultivation, weeds, low or no fertiliser inputs and no water control can be production constraints. Vegetative early vigor may favour weed competitiveness. Since *Oryza glaberrima* is considered as genetic resources for this characteristic, growth analyses of three lines were made from seeds to juvenile plants of 35 days after seed soaking (DAS) in a pot experiment with two *O. sativa* under two soil water regimes: soil of water saturation without standing water (SAT) and soil of a wet surface without water saturation (WET). After germination, total dry weigh decreased (heterotrophic phase using carbohydrate reserve in kernels) then increased during autotrophic phase. Start of autotrophic phase was earlier in SAT than in WET (6.2 vs 7.6 DAS) and kernel weight lost was also higher in SAT (93 vs 82 %). Total dry weight was smaller in SAT than in WET at 5 DAS but larger at and after 11 DAS. The carbohydrate reserve in kernels was more rapidly and sufficiently used for seedling growth in SAT than in WET; the growth phase more quickly shifted from the heterotrophic to autotrophic in SAT than in WET then growth after the sift was better in SAT. Leaf area (determined at and after 13 DAS) was always larger in SAT than in WET. Varietal difference in total dry weight became significant ($P<0.05$) at 28 DAS; the *O. glaberrima* lines showed larger total dry weight than *O. sativa* varieties and difference between the two species was more obvious in SAT.

* **Corresponding Author:** Montcho David ✉ montchodav@yahoo.fr

Introduction

Weeds are one of the most important constraints to rice production in a range of major agro-ecosystems, i.e. upland, rainfed lowland and irrigated lowland in West Africa (WA). Direct seeding is commonly practiced in upland and in most cases of rainfed lowland so that weeds suppress rice plant growth particularly in these ecosystems. Since a number of rice farmers in irrigated systems in the tropics are shifting from transplanted to direct-seeded culture (Erguiza *et al.*, 1990), weeds are increasingly becoming important constraints in irrigated lowland too. Yield loss of rice due to weed problems ranges from 12% to 100% (Becker and Johnson, 2001,Becker *et al.*, 2003). Weeding is the most labor-intensive activity in Africa and large yield loss is mainly attributed to the limited availability of labor for hand weeding and to the unavailability and limited affordability of herbicides for farmers (Rodenburg and Johnson, 2009). It is therefore highly desirable to develop rice varieties with strong weed competitiveness which may reduce labor inputs for manual weeding.

Oryza glaberrima Steud., which is the other cultivated rice species from *Oryza sativa* L. and indigenous to West Africa, is known to be a rich genetic source for high weed competitiveness (Fofana and Rauber, 2000). Efforts to introduce weed competitiveness of *O. glaberrima* into *O. sativa* with high yield potential have been made (Jones *et al.*, 1997). Early growth vigor is considered as the most important trait in weed competitiveness (Saito *et al.*, 2010), particularly for short-duration genotypes (Dingkuhn and Asch, 1999). Dingkuhn *et al.* (1998; 1999) have shown the importance of specific leaf area (SLA), which has a close correlation with leaf area (LA), and tillering in early growth vigor and Saito *et al.* (2010) have done biomass accumulation. Such information can be directly used for the selection of weed competitive rice. However, these observations were made after the start of the tillering stage. This study was motivated by the possibility to have varietal differences in biomass and SLA in earlier stages. Furthermore, there will be a possibility that varietal differences in other traits in earlier seedling stage can be catalysts of the differences in biomass accumulation, SLA and number of tillers observed in the past studies (Dingkuhn *et al.*, 1998, Dingkuhn *et al.*, 1999, Saito *et al.*, 2010). If such traits of seedlings can be identified, mass screening for weed competitiveness at the seedling stage may become possible using them. Asch *et al.* (1999) have characterized rice in the seedling stage in relation to dry weight partitioning, SLA and other growth characteristics with genetically diverse materials (one *O. glaberrima* cultivar, three *O. sativa* cultivars, of which two were *japonica* types, one *indica*, and one interspecific cultivar between the two species). In that experiment, however, total dry weight did not vary widely among cultivars used, although SLA was significantly higher in the *O. glaberrima* cultivar than the others.

In our study, we focused on *O. glaberrima* using three cultivars and attempted to confirm their early vigor and explain the vigor through detailed growth characterization of seedlings in comparison with *O. sativa*. In the humid and savannah zones of WA, peneplains are prevailing and rice can be cultivated on the whole toposequence from the inland valley bottom to upland. Although our experiment was conducted in pots, materials were raised under two different environments simulating the situations of upland and bottom fringe, where no flooding water exists and only direct-seeding is an applicable practice.

Materials and methods

Experimental site

The experiment was conducted in February–March 2010 in a screen house at Africa Rice Center (AfricaRice) research station. The station is located at Togoudo (6°25 N in latitude and 2°20 E in longitude), southern Benin, in the coastal savannah zone, with a subequatorial climate. The south of Benin is characterized by bimodal rainfall pattern, i.e. a big rainy season from April/May to July and a small rainy season from September to October/November (Adam and Boko, 1993).

Plant material

Three *O. glaberrima* cultivars, i.e. CG 17, TOG 9280 and TOG 12303, were used. CG 17, TOG 9280 and TOG 12303 showed the large number of spikelets (to estimate potential productivity eliminating the effect of grain shattering, which is always arising in *O. glaberrima*, number of spikelets before shattering was used unpublished data) compared to high yielding *O. sativa* cultivars in upland, fringe of lowland and lowland, respectively, in the previous field study. As *O. sativa* checks, Moroberekan, traditional tropical *japonica* type cultivar, and WITA 4, improved *indica* type cultivar, were included in the materials. For each cultivar, hundred seeds were randomly taken from winnowed seeds produced in the field during the preceding wet season of 2009. From the hundred seeds, seeds weighing less than 16 mg were excluded (Asch *et al*., 1999)

Methods

In the experiment, two ecosystems, upland (WET) and fringe of lowland or hydromorphic (SAT) were supposed. Regarding upland, soil collected from the upland ecosystem was filled in pots with their bottoms perforated and the surface of the soil was maintained to be wet without water saturation (WET). For the lowland fringe (hydromorphic) situation, soil of the fringe of lowland area was used to fill non-perforated pots and the soil was maintained water saturated conditions without flooded water (SAT).

The seeds of the five (5) rice cultivars were soaked in distilled water for 24 hours on 15 February in petri dish and then incubated in oven at 25°C for 48 hours. Before soaking, the seed sample for each cultivar was weighted to determine kernel weight. Seed weighing less than 16 mg were excluded (Asch *et al*., 1999). The seedlings were dibbled into the pots according to the different water managements. No fertilizer was applied. To avoid root entanglement, the seedlings were separated by plastic sheets. Randomized complete block design with five replications were performed. Climatic conditions (air temperature and moisture) in the screen house during the experiment were monitored three times a day using a thermo-hygrometer. For each replication, one entire seedling was sampled (retrieved from the pot) at 3, 5, 8, 9, 11, 13, 17, 21, 28 and 35 days after soaking (DAS). Sampled seedlings were separated into roots, stems (including leaf sheath) and leaves (leaf blades). The roots were rinsed to remove soil particles. All fractions (roots, stems and leaves) were separately oven-dried at 70°C for 72 hours and weighed by precision balance. Leaf area (LA) was determined at 13, 21, 28, and 35 DAS using a leaf area meter (LI-3000, LI-COR). Specific leaf area (SLA) was calculated dividing LA by leaf dry weight. A dry matter partitioning coefficient for each organ (leaf, stem and root) was calculated on the basis of a relative change in dry weight of each organ to that of the whole plant for each sampling interval.

In addition fifty grains were selected for each cultivar. Each grain was dehusked manually and separated to embryo and endosperm using a dissection needle. Embryo and endosperm was oven dried and the dry weight of each organ was separately determined for single grain.

Data analysis

The linear regression was performed for kernel dry weight reduction (Regression I) and the total dry matter decrease (Regression II) in the heterotrophic phase. The following parameters were calculated according to Asch *et al*. (1999):

Efficiency of reserve mobilization.

$$1-\frac{slope\ of\ regression\ II}{slope\ of\ regression\ I}$$

Kernel dry weight loss

$$1-\frac{Final\ kernelweight}{Initial\ kernel\ weight}$$

Principal Component Analysis (PCA) was performed using the kernel mean, the efficiency of reserve mobilization, Kernel dry weight loss and the onset of autotrophy to access their relationship.

Results

From the soaking to end of the experiment, a daily average humidity ranged between 35.3 and 61.8% and a daily temperature between 29.5 and 40.3°C. Fig. 1 shows time courses of humidity and temperature during the experiment.

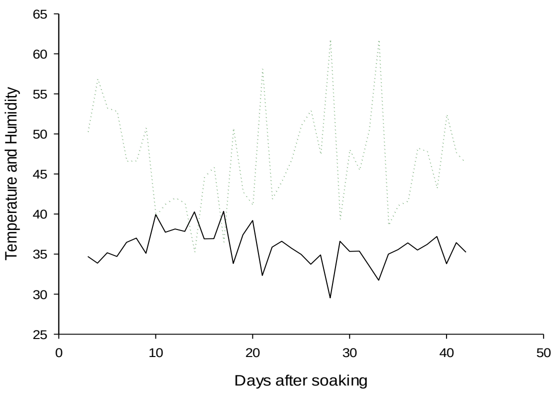

Fig. 1. Time courses daily temperature and humidity in the screen house.

Table 1 indicates the summary of two-way analysis of variance for total dry weight, leaf dry weight, stem dry weight and root dry weight under WET and SAT conditions. From soaking to 9 DAS, total dry weight decreased. The decreasing period was considered as the heterotrophic phase; a day when total dry weight was lowest and started to increase was considered the onset of the autotrophic phase. After 11 DAS (autotrophy phase), total dry weight was higher under water saturated conditions in all cultivars other than Moroberekan. At 28 DAS, there was a significant varietal difference. *Oryza glaberrima* showed higher values than *O. sativa*. This difference was more obvious in water saturated conditions than in upland conditions. At 35 DAS, a similar tendency with 28 DAS was observed though the difference was not significant.

Table 1. Analysis of variance for total dry weight, leaf dry weight, stem dry weight and root dry weight in different water regimes.

Parameters	0 DAS	3 DAS	5 DAS	8 DAS	9 DAS	11 DAS	13 DAS	17 DAS	21 DAS	28 DAS	35 DAS
Total Dry weight											
Variety	**	**	*	ns	ns	ns	ns	ns	ns	*	ns
Water regimes	**	**	***	ns	ns	*	**	***	***	***	***
Variety x water regime	ns	ns	**	ns	ns	ns	ns	ns	ns	*	ns
Leaf dry weight											
Variety	-	-	ns	ns	ns	ns	*	ns	*	**	**
Water regimes	-	-	***	***	**	***	***	***	***	***	***
Variety x water regime	-	-	ns	ns	ns	ns	ns	ns	ns	**	*
Stem dry weight											
Variety	-	-	***	*	ns	ns	ns	ns	ns	ns	ns
Water regimes	-	-	ns	ns	**	***	**	***	***	***	***
Variety x water regime	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns
Root dry weight											
Variety	-	-	**	***	ns	ns	ns	ns	ns	ns	ns
Water regimes	-	-	ns	ns	***	ns	*	***	**	***	***
Variety x water regime	-	-	ns	ns	ns	ns	ns	ns	ns	ns	ns

* : P<0.05 ; ** : P<0.01 ; *** : P<0.001 ; ns : no significant ; - : no fraction.

Leaf dry weight was always larger in water saturated conditions. For stem and roots, dry weight became larger from 9 and 13 DAS, respectively. There was no varietal difference in stem and root dry weight. At 21 DAS, TOG 12303 and TOG 9280 showed larger leaf dry weight than the others especially in water saturated conditions. The *O. glaberrima* cultivars had larger leaf dry weight than the *O. sativa* especially in water saturated conditions.

For all cultivars, partitioning coefficients (PC) for stems and roots increased and decreased with the time course, respectively. For leaves, PC slightly increased up to 21 DAS then decreased. PC for leaves was always high in water saturated conditions than upland conditions irrespective of cultivars. PC for roots was high in upland conditions up to 11 DAS but high in water saturated from 21 DAS afterward. PC for stems was higher in upland conditions from 11 DAS afterward. Table 2 shows the summary of two-way analysis of variance.

Table 2. Partitioning coefficient of leaf, stem and root.

Fraction	5-8 DAS	8-9 DAS	9-11 DAS	11-13 DAS	13-17 DAS	17-21 DAS	21-28 DAS	28-35 DAS
Leaf								
Variety	ns	ns	ns	ns	ns	ns	ns	ns
Water regimes	***	***	***	***	***	***	***	***
Variety x Water regime	ns	ns	ns	ns	ns	ns	ns	ns
Stem								
Variety	ns	ns	ns	ns	ns	ns	ns	*
Water regimes	ns	ns	ns	***	***	***	***	***
Variety x Water regime	ns	ns	ns	ns	ns	ns	*	ns
Root								
Variety	ns	ns	ns	ns	**	ns	ns	ns
Water regimes	**	***	***	ns	*	ns	***	***
Variety x Water regime	ns	ns	ns	ns	ns	ns	ns	ns

* : P<0.05 ; ** : P<0.01 ; *** : P<0.001 ; ns : no significant.

Table 3 shows time courses of leaf area (LA) in both hydrological conditions. LA was large in water saturated condition compared to that in upland condition. LA was always large in *O. glaberrima* compared to *O. sativa*. This tendency was similarly observed in both upland and water saturated conditions at 13 and 21 DAS but more clearly in water saturated condition than in upland conditions at 28 and 35 DAS.

Table 3. Time courses of leaf area in different water regimes (cm²).

Variety/water regime	13 DAS	21 DAS	28 DAS	35 DAS
Upland				
TOG 12303	6.41	21.10	52.90	86.05
TOG 9280	9.75	21.10	47.40	68.33
CG 17	7,79	18.30	42.90	61.13
Moroberekan	6.58	13.30	31.70	45.58
WITA 4	5.57	15.40	34.30	47.98
Water saturated				
TOG 12303	11.09	41.30	229.50	493.40
TOG 9280	13.55	53.70	266.20	364.38
CG 17	15.09	38.80	256.90	602.53
Moroberekan	9.05	29.60	96.10	233.12
WITA 4	10.20	30.30	120.80	283.64
Variety	***	*	***	**
Water regimes	***	***	***	***
Variety x water regime	ns	ns	**	**

* : P<0.05 ; ** : P<0.01 ; *** : P<0.001 ; ns : no significant.

Table 4 shows time course of specific leaf area (SLA) in both water regimes. It was generally high in *O. glaberrima* than in *O. sativa*. At 28 and 35 DAS, SLA was higher in upland conditions than in water saturated conditions, while no difference was observed at 13 and 21 DAS (larger LA in water saturated was not due to higher SLA larger but to leaf dry weight).

Table 4. Time courses of specific leaf area in different water regimes (m²/kg).

Variety/water regime	13 DAS	21 DAS	28 DAS	35 DAS
Upland				
TOG 12303	41.1	36.3	34.3	25.1
TOG 9280	40.6	38.1	33.0	26.6
CG 17	38.5	37.5	34.6	26.5
Moroberekan	30.7	27.5	23.8	21.6
WITA 4	33.1	29.8	24.8	20.6
Water saturated				
TOG 12303	37.3	34.9	29.2	24.2
TOG 9280	43.3	27.6	23.9	23.6
CG 17	40.0	32.8	26.1	22.6
Moroberekan	32.6	27.8	23.7	20.4
WITA 4	33.7	32.3	20.5	17.0
Variety	**	*	***	**
Water regimes	ns	ns	***	*
Variety x water regime	ns	ns	ns	ns

* : P<0.05 ; ** : P<0.01 ; *** : P<0.001 ; ns : no significant.

Table 5 shows characterization of rice used in the vegetative growth on WET and SAT conditions. No difference in mobilization efficiency among cultivars or between the two water regimes. Moroberekan had larger kernel dry weight than the others (no difference between the other cultivars). Kernel dry weight loss was larger in water saturated conditions than in upland conditions. *O. glaberrima* showed earlier start of the autotrophy only in water saturated conditions.

Table 5. Characterization of rice used in the growth on WET and SAT condition.

Variety/water regime	Kernel mean (mg)	Kernel dry weight lost	Mobilization efficiency	Onset of autotrophy
Upland condition				
TOG 12303	32.6	0.85	0.88	8
TOG 9280	32.8	0.75	0.86	8
CG 17	32.6	0.83	0.93	9
Moroberekan	36.6	0.85	0.85	8
WITA 4	30.2	0.84	0.77	5
Means	32.96	0.82	0.85	7.6
Water saturated condition				
TOG 12303	29.4	0.96	0.87	5
TOG 9280	31.2	0.95	0.71	5
CG 17	29.6	0.93	0.82	5
Moroberekan	32.4	0.91	0.85	8
WITA 4	30	0.93	0.89	8
Mean	30.32	0.93	0.82	6.2
Significance	ns	***	ns	ns

*** : P<0.001 ; ns : no significant.

Principal Component Analysis (PCA) indicated that Kernel mean was negatively correlated with Kernel dry weight lost but positively correlated with mobilization efficiency and the onset of autotrophy. The coefficient of correlation between kernel mean and the onset of autotrophy was significant at P < 0.05. Kernel dry weight lost was negatively correlated with mobilization efficiency but not significantly at 5%. The efficiency of grain reserve mobilization was significantly (P<0.05) correlated with the onset of autotrophy (Fig. 2).

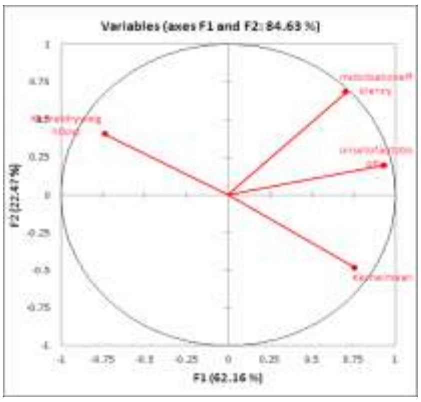

Fig. 2. Plot of factors pattern for factor 1 and factor 2.

Table 6 shows means of endosperm and embryo for each cultivar. Result indicated for embryo and endosperm of *O. glaberrima* had the largest dry weight and *O. sativa* showed the smallest (P < 0.001).

Table 6. Means of embryo and Endosperm.

Variety	Endosperm (mg)	Embryo (mg)
TOG 12303	20.44	1.85
TOG 9280	23.99	1.75
CG17	25.31	1.68
Moroberekan	17.69	1.21
WITA 4	16.61	1.35
Significance	***	***

*** : P<0.001

Discussion

Effect of water regime was clearly observed in leaf area and total dry weight; differences became significantly (P<0.001) more obvious in water saturated (SAT). This difference can be explained by the duration of plants in water. According to Sie (1991), the long stay in water increased vegetative development of plant as number of tillers and leaves.

The difference between water regimes was water accumulation in water saturated condition. Availability of water in SAT condition increased plant growth. Leaf area in upland and water saturated conditions increased throughout the vegetative growth for all cultivars because plants usually produced leaves and tiller during this stage. This result confirmed Asch *et al.* (1999) observations under upland condition. In both irrigation conditions, specific leaf area decreased during the vegetative development for all cultivars used from germination to 35 DAS. Various studies indicated a common and highly reproducible exponential decrease of specific leaf area in the course of vegetative growth (Dingkuhn *et al.*, 1998, Johnson *et al.*, 1998, Asch *et al.*, 1999, Dingkuhn *et al.*, 1999). The interaction SLA and cultivars is highly significant ($P < 0.001$). *Oryza glaberrima* had the largest SLA and *O. sativa* varieties had the smallest. Specific leaf area permits to discriminate rice cultivars. The discrimination was probably caused by early vigor of *O. glaberrima* (Asch *et al.*, 1999). It is a major determinant of growth vigor (Dingkuhn *et al.*, 1999). The largest SLA of *O. glaberrima* is explained by the superior vigor. African rice varieties were able to cover the soil to varying degrees and might, therefore be effective in limiting space, light and nutrients for weeds (Moukoumbi *et al.*, 2011). Our result indicated that *O. glaberrima* showed high dry weight of embryo as compared to *O. sativa*. Early vigor of *O. glaberrima* may be linked to larger embryo. Compared to Saito *et al.* studies (2010), early vigor was obtained at 42 and 63 DAS. Ni *et al.* (2000) indicated that early vigor was noticed at 5 Weeks after sowing in lowland condition and 6 weeks after sowing in upland condition. Zhao *et al.* (2006) got early growth at 6 weeks after sowing in upland condition. Our result confirmed Zhao *et al.* observation who showed early vigor between 2 - 4 weeks after sowing (Zhao *et al.*, 2006,Zhao *et al.*, 2006). Dingkuhn *et al.* (1999) indicated positive correlation ($P < 0.05$) between SLA and weed competitiveness and confirmed that SLA is one of the parameters most predictive of weed competitiveness. SLA relationship was uniform within the *O. glaberrima*. Same pattern was observed within *O. sativa* used but Dingkuhn *et al.* (1999) reported that SLA relationship was fairly uniform for *O. glaberrima* rices, *O. sativa japonica* rice and their interspecific progenies but differed from *O. sativa indica*. Jones *et al.* (1997) proposed to select cultivars with high SLA to improve competitiveness with weeds during vegetative growth because at this stage weed competition is severer and the plant are more affected.

Interactions between SLA and water regime (WET and SAT conditions) are not significant ($P=0.2216$). Specific leaf areas are not water regime dependent. Our study confirmed Asch *et al.* (1999) result reporting that SLA is a genetic characteristic.

The mean of material mobilized from the grain was 0.85 in upland condition and 0.82 in hydromorphic condition. No significant difference was observed between hydrological conditions. The mobilization efficiency values reported were overestimated because we supposed that seedling photosynthesis had little effect on growth before the plant became autotrophic. Asch *et al.* (1999) reported the mobilization efficiency value between 0.59 and 0.66 using upland rice (upland condition). Labusch *et al.* (1989) observed a mobilization efficiency value of 0.65 for winter wheat based on measurements with carbon isotope tracers. (Yoshida, 1981) estimated 0.60 as reserve mobilization efficiency for lowland rice from growth experiment in the dark.

The present study indicated that dry weight fraction in leaf blades was high at each ecology as compared to root and stem fraction. By comparison, leaf dry weight in water saturated condition was higher compared to upland condition ($P<0.05$). *Oryza glaberrima* had the high values because they have a much greater vigor in vegetative growth and early ground cover than the *O. sativa*.

Partitioning coefficient ($\Delta DW/\Delta DW$) among organ was important to explain variation of dry matter. Marked changes in PC occurred during the transition from heterotrophic to autotrophic growth as said by

Asch *et al.* (1999). The decrease of PC for root (PC_R) between 5 and 9 DAS in both water managements coincided with the onset of autotrophic phase and the cessation of reserve mobilization. At 5 DAS PC_R in upland and water saturated condition was respectively 0.84 and 0.80 and different statistically. Asch *et al.* (1999) reported that PC_R was 0.5 at 4 DAS and decrease to about 0.1 at 10 DAS and recovery to about 0.25 at 18 DAS. Asch *et al.* (1999) insist that the decrease of PC_R might be explained by assimilate investments in the establishment of the photosynthetic apparatus.

PC_S (PC for stem) increased gradually during vegetative growth and statistically different in upland condition as compared to water saturated at tillering stage (after 13 DAS). Asch *et al.* (1999) noticed that PC for stem was nearly constant at 0.3 but this experiment was not performed during tiller ability stage. The present study showed a variability of PC_S in both conditions at vegetative growth. PC_S was between 0.10 and 0.73 at upland and 0.10 and 0.39 at hydromorphic condition.

PC for leaves (PC_L) was 0.055 in upland condition and 0.093 in hydromorphic condition at 5 DAS. Then PC_L increased to 21 DAS and decreased to 35 DAS. The same trend was observed at both hydrological conditions. PC for leaves at upland was significantly different from PC_L at hydromorphic condition. PC_L in hydromorphic condition was high as compared to PC_L at upland condition. Asch *et al.* (1999) reported PC_L was 0.4 at 4 DAS and 0.65 between 10 and 18 DAS. Other reports insist that PC for leaves decreases during vegetative development (Dingkuhn *et al.*, 1998).

It can be concluded that early vigor of *O. glaberrima* at the juvenile stage compared to *O. sativa* is due to the high weight of embryo. *Oryza glaberrima* showed higher weight of embryo as compared to *O. sativa*. Water saturated condition showed larger LA than upland condition and higher total dry weight. We propose to screen for weed competitiveness on the basis of SLA and early vigor.

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Conflict of Interest

The authors declare that they have no conflict of interest

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