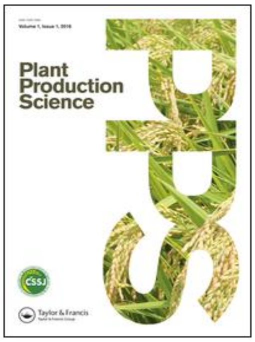

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Morphological and physiological traits of seeds and seedlings in two rice cultivars with contrasting early vigor

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ABSTRACT
Early vigor is important for crop establishment in rice. This study was conducted to determine the seed and seedling traits in relation to early vigor in rice. Laboratory tests and pot experiments were carried out in 2013 and 2014. Morphological and physiological traits of seeds and seedlings were compared between two contrasting rice cultivars, Yuxiangyouzhan with superior early vigor and Huanghuazhan with general early vigor. For seed traits, Yuxiangyouzhan had lower seed hull weight but higher seed amylose content, seed amylase activity, and plumule–radicle ratio than Huanghuazhan, and consequently, Yuxiangyouzhan had about 10% higher germination percentage and velocity and 37% longer plumule than Huanghuazhan. For seedling traits, leaf area, specific leaf weight, leaf chlorophyll and soluble protein contents, leaf net photosynthetic rate, and shoot–root ratio were higher in Yuxiangyouzhan than in Huanghuazhan, and as a result, seedling shoot biomass was 23–32% higher in Yuxiangyouzhan than in Huanghuazhan. These results indicate that Yuxiangyouzhan has both superior seed and seedling vigor. The former is attributed to the low mechanical strength of seed hull, high conversion efficiency of seed reserve, and high mobilization of seed reserve to plumule, while the latter is due to large leaf area, high leaf photosynthetic capacity, and high partitioning of dry matter to shoot. This study enriches the physiological understanding of superior early vigor in rice.

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CLASSIFICATION
Crop Physiology

Introduction

Rice is the staple food for more than 65% of the population in China. Over the past few years, the expansion of cities has led to a labor shortage for agricultural production (Peng et al., 2008), and the simple and labor-saving method of direct seeding has become very popular in rice production (Huang et al., 2011; Liu et al., 2015). Meanwhile, the frequency of natural disasters such as drought has increased partially because of global climate change (Du et al., 2015; Tao et al., 2003). Therefore, great efforts should be made to improve rice cultivars to adapt to the changes in socioeconomic and physical environments.

Poor crop establishment is one of the major constraints in the direct-seeded rice systems and particularly in adverse growing environments such as drought (Du & Tuong, 2002; Kumar et al., 2009). Improving crop early vigor is recognized as the most promising and effective strategy to relieve the constraint (Balasubramanian & Hill, 2002; Namuco et al., 2009; Okami et al., 2015; Zhang et al., 2005). Early vigor is a combination of the ability of the seed to uniformity germinate and emerge after planting (i.e. seed vigor) and the ability of the young plant to grow and develop after emergence (i.e. seedling vigor). It has been well documented that seed vigor is associated with seed structure in rice (Chen et al., 2015; Pandey et al., 1994). In general, rice seeds with large embryo and thin hull are desirable for seed vigor. Moreover, seed carbohydrate reserve is also important for seed vigor in rice since carbohydrates for germination and heterotrophic growth are provided by breakdown of the starch stored in the endosperm (Cui et al., 2002). This has been indirectly supported by a number of investigations showing a close relationship between early vigor and seed size or weight in rice (Lu et al., 2007; Namuco et al., 2009; Wang, Wang et al., 2010), but direct evidence is lacking. The starch stored in rice seed is a mixture of two polysaccharides: amylose and amylopectin. Amylose is composed mainly of linear chains of α-1, 4-linked glucose residues and can be

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converted completely by the amylase into maltose, while amylopectin is a highly branched glucan with α-1, 4 and α-1, 6-linkages and cannot be split completely into maltose leaving some fraction of dextrins. According to these facts, we hypothesized that the rice cultivars with higher seed amylose content and amylase activity may have superior seed vigor. After seedlings gain the ability of photoautotrophy, seedling vigor is considered to be positively associated with canopy photosynthetic capacity and dry matter partitioning to leaves (Asch et al., 1999; Caton et al., 2003; Dingkuhn et al., 1999). However, previous studies on early vigor-related canopy characteristics, mostly focusing on the morphological traits such as leaf area and specific leaf area, usually did not consider the leaf photosynthetic traits.

In this study, morphological and physiological traits of seeds and seedlings were compared between two rice cultivars with contrasting early vigor using laboratory tests and pot experiments. The objective of this study was to determine the seed and seedling traits in relation to early vigor in rice.

Materials and methods

Plant materials

Two contrasting rice cultivars, Yuxiangyouzhan with superior early vigor and Huanghuazhan with general early vigor, were chosen for this study. Both the cultivars are inbreds developed by Guangdong Academy of Agricultural Sciences, Guangdong Province, China and released in 2005. Huanghuazhan was developed from a cross of Huangxinzhan/Fenghuazhan, while Yuxiangyouzhan from a backcross of TY36/IR100//IR100. The seeds used in this study were hand collected from Yuxiangyouzhan and Huanghuazhan plants grown under the same management practices in an experimental field at Bingyang (23°09′N, 108°52′E, 110 m above sea level), Guangxi Province, China in early rice-growing season (from 12 March to 18 July) in 2013. The collected seeds were sun-dried for 3 days and then stored at 4 °C.

Laboratory experiments

Three samples (replications) of 50 g of the stored seeds were taken for each cultivar to determine seed traits in August in 2013. Twenty seeds were taken from each sample to measure seed length and width using a photoenlarger magnified at 10 x. All seeds in each sample were counted and then separated into hull, embryo, and endosperm by hand. Each of them was oven-dried at 70 °C to constant weight to determine dry weight. The dried endosperm was ground into flour with a grinder (FW100, Tianjin Taisite Instrument Co., Ltd, Tianjin, China) and passed through a 100-mesh sieve for measuring amylose, amylopectin, starch, and protein contents. The amylose and amylopectin contents were determined by a triple wavelength colorimetric method according to that described by Wang, Li et al., (2010). The starch content was calculated as the sum of amylose and amylopectin contents.

Eighteen samples (replications) of 25 seeds were taken for each cultivar. Each sample was soaked for 24 h in tap water at room temperature (mean temperature 27.1 °C) on 17 August in 2013. The soaked seeds of each sample were uniformly placed on a moist filter paper in a glass petri dish (10 cm diameter) and then put into an incubator (LRH-70, Shanghai Yiheng Technology Co., Ltd, Shanghai, China) at 30 °C. The filter paper was kept moist by daily addition of distilled water throughout the incubation period (from 18 to 22 August). Three samples were taken daily for each cultivar to determine seed amylase activity. The amylase activity was determined by measuring the amount of maltose liberated from soluble starch with the dinitrosalicylic acid procedure (Bernfeld, 1955). At 5 days after soaking (22 August), three samples were taken for each cultivar to determine germination percentage (number of germinated seeds/total number of seeds × 100) and length of plumule and radicle. Germination velocity (germination percentage/germination period) and plumule–radicle ratio (plumule length/radicle length) were calculated.

Pot experiments

Outdoor pot experiments were conducted at the experimental farm of Guangxi University (22°51′N, 108°17′E, 78 m a.s.l.), Guangxi Province, China in 2013 and 2014. Average daily mean temperatures during the experimental period (from 15 August to 9 September) were 27.4 °C in 2013 and 28.3 °C in 2014 (Vantage Pro2 weather station, Davis Instruments Corp., Hayward, CA, USA). The soil used in the experiment was collected from the upper 20 cm of an area of .5 m^2 of a rice paddy field at the experimental farm. The soil was an Ultisol (USDA taxonomy) with pH 6.33, organic matter = 24.2 g kg^{-1}, NaOH hydrolysable N = 142 mg kg^{-1}, Olsen p = 34.8 mg kg^{-1}, and NH_4OAc extractable K = 123 mg kg^{-1}. The collected soil was fertilized and then filled into 12 plastic trays (30-cell tray with 5-cm diameter and 7.5-cm depth cells) on 14 August. The fertilizers used were urea for N, single superphosphate for P, and potassium chloride for K at doses of 4.5 g N, 2.5 g P_2O_5, and 4.0 g K_2O. All fertilizers were incorporated into the soil. Pre-germinated seeds were sown on 15 August with one seed per cell. Each cultivar was planted in six trays (replications). The soil was kept moist by watering for the duration of the experiment.

At 25 days after sowing (9 September), three trays were randomly selected for each cultivar to determine leaf photosynthetic traits. Net photosynthetic rate and chlorophyll and soluble protein contents were measured on the uppermost fully expanded leaves of five representative seedlings in each tray. The net photosynthetic rate was determined at 9:00–10:30 using a portable photosynthesis system (Li-6400, Li-Cor, Lincoln, NE, USA) at a light intensity of 1200 μmol m^{-2} s^{-1}, a leaf temperature of 28.4 ± 1.2 °C, a constant CO_2 concentration of 380 ± 5 μmol mol^{-1}, and a relative humidity of 75 ± 5%. The chlorophyll content was determined by extracting with a mixture of ethanol: acetone: distilled water = 4.5: 4.5: 1 (v/v/v) for 24 h and then measuring the absorbance of the solution at 663 and 646 nm (Arnon, 1949). The soluble protein content was determined by the protein dye binding method introduced by Bradford (1976). On the same date, dry matter production and leaf morphological traits were measured in another three trays for each cultivar. Ten representative seedlings were sampled in each tray and then separated into leaves, stems, and roots. Leaf area was measured using a leaf area meter (CI-203, CID, Inc., Camas, WA, USA). Each organ was oven-dried at 70 °C to constant weight to determine dry weight. Shoot–root ratio (shoot dry weight/root dry weight), specific leaf area (leaf area/leaf dry weight), and specific leaf weight (leaf dry weight/leaf area) were calculated.

Statistical analysis

Data were analyzed following analysis of variance (Statistix 8.0, Analytical software, Tallahassee, FL, USA). Means of cultivars were compared based on the least significance test at the .05 probability level.

Results

Seed morphological and physiological traits

Seed length and dry weight of seed, hull, embryo, and endosperm were lower in Yuxiangyouzhan than in Huanghuazhan, but only the difference in hull dry weight was significant (Table 1). Seed width was higher, but not significantly, in Yuxiangyouzhan than in Huanghuazhan. Yuxiangyouzhan had 41% higher seed amylose content but 17% lower seed amylopectin content than Huanghuazhan.

Yuxiangyouzhan had significantly higher seed amylase activities than Huanghuazhan (Figure 1). Averaged across the 5 days of testing, seed amylase activity was 1.14 times higher in Yuxiangyouzhan than in Huanghuazhan. Germination percentage and velocity in Yuxiangyouzhan were about 10% higher than that in Huanghuazhan (Table 2). Yuxiangyouzhan had 37% longer plumule but 9% shorter radicle than Huanghuazhan. Plumule–radicle ratio was 50% higher in Yuxiangyouzhan than in Huanghuazhan.

Table 1. Seed traits in two rice cultivars: Yuxiangyouzhan and Huanghuazhan.

Trait	Yuxiangyouzhan	Huanghuazhan
Seed length (mm)	6.53 (.06)	6.70 (.10)
Seed width (mm)	2.10 (.06)	2.00 (.02)
Seed dry weight (mg seed^{-1})	21.2 (.3)	21.8 (.5)
Hull dry weight (mg seed^{-1})	4.00 (.08)*	4.43 (.16)
Embryo dry weight (mg seed^{-1})	.69 (.02)	.73 (.03)
Endosperm dry weight (mg seed^{-1})	16.5 (.2)	16.7 (.5)
Seed starch content (mg seed^{-1})	14.5 (.2)	14.9 (.4)
Seed amylose content (mg seed^{-1})	4.96 (.19)*	3.51 (.12)
Seed amylopectin content (mg seed^{-1})	9.5 (.1)*	11.4 (.3)

Note. Data are means (SD) ($n = 3$).
*indicates significant difference between the two cultivars according to LSD at $p = .05$.

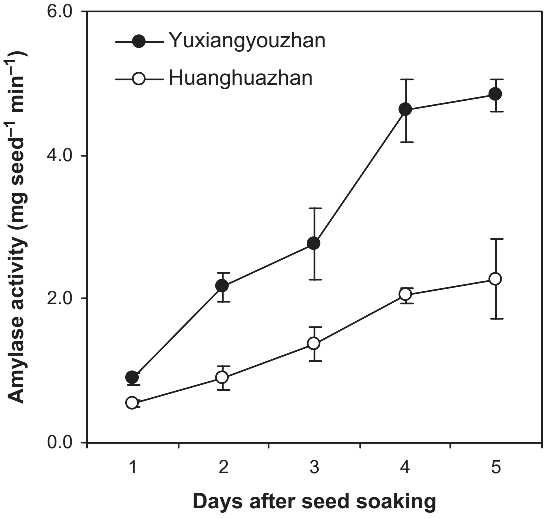

Figure 1. Seed amylase activity in two rice cultivars: Yuxiangyouzhan and Huanghuazhan. Each data point and vertical bar show mean and SD ($n = 3$).

Table 2. Germination percentage and velocity, plumule and radicle length, and plumule–radicle ratio in two rice cultivars: Yuxiangyouzhan and Huanghuazhan.

Trait	Yuxiangyouzhan	Huanghuazhan
Germination percentage (%)	96 (4)*	87 (2)
Germination velocity (% d^{-1})	19.2 (.8)*	17.3 (.5)
Plumule length (mm)	34.3 (.6)*	25.0 (1.4)
Radicle length (mm)	18.9 (.6)*	20.7 (.4)
Plumule–radicle ratio	1.82 (.06)*	1.21 (.05)

Note. Data are means (SD) ($n = 3$).
*indicates significant difference between the two cultivars according to LSD at $p = .05$.

Seedling morphological and physiological traits

Dry weights of shoot, stem, and leaf were higher in Yuxiangyouzhan than in Huanghuazhan by 23–24% in 2013 and by 30–34% in 2014 (Table 3). Root dry

Table 3. Dry matter production and canopy traits in seedlings of two rice cultivars: Yuxiangyouzhan and Huanghuazhan in 2013 and 2014.

Trait	2013		2014	
	Yuxiangyouzhan	Huanghuazhan	Yuxiangyouzhan	Huanghuazhan
Shoot dry weight (mg seedling^{-1})	214 (3)*	173 (4)	276 (28)*	208 (17)
Stem dry weight (mg seedling^{-1})	118 (2)*	96 (6)	145 (18)*	108 (12)
Leaf dry weight (mg seedling^{-1})	96 (2)*	78 (2)	131 (10)*	101 (5)
Root dry weight (mg seedling^{-1})	82 (5)*	97 (6)	103 (4)*	114 (4)
Shoot–root ratio	2.62 (.20)*	1.79 (.11)	2.67 (.17)*	1.84 (.09)
Leaf area (cm^2 seedling^{-1})	33.0 (1.6)*	29.0 (1.4)	45.9 (2.5)*	40.5 (1.5)
Specific leaf area (cm^2 mg^{-1})	.34 (.01)*	.37 (.01)	.35 (.01)*	.40 (.01)
Specific leaf weight (mg cm^{-2})	2.91 (.09)*	2.68 (.06)	2.84 (.11)*	2.49 (.08)
Leaf chlorophyll content (g m^{-2})	.44 (.01)*	.41 (.01)	.42 (.02)*	.38 (.01)
Leaf soluble protein content (g m^{-2})	3.94 (.12)*	3.64 (.09)	3.93 (.15)*	3.56 (.12)
Leaf photosynthetic rate (μmol CO_2 m^{-2} s^{-1})	21.4 (.7)*	18.7 (.4)	20.7 (.8)*	18.4 (.6)

Note. Data are means (SD) ($n = 3$).
*indicates significant difference between the two cultivars according to LSD at $p = .05$.

weight in Yuxiangyouzhan was 16 and 9% lower than that in Huanghuahzan in 2013 and 2014, respectively. Yuxiangyouzhan had higher shoot–root ratio than Huanghuazhan by 46% in 2013 and by 45% in 2014. Leaf area was about 14% higher in Yuxiangyouzhan than in Huanghuazhan in both 2013 and 2014. Specific leaf area in Yuxiangyouzhan was lower than that in Huanghuazhan by 8 and 12% in 2013 and 2014, respectively. Specific leaf weight was 9 and 14% higher in Yuxiangyouzhan than in Huanghuazhan in 2013 and 2014, respectively. Leaf chlorophyll content in Yuxiangyouzhan was higher than that in Huanghuazhan by 6% in 2013 and 13% in 2014. Leaf protein content was 8 and 10% higher in Yuxiangyouzhan than in Huanghuazhan in 2013 and 2014, respectively. Leaf net photosynthetic rate in Yuxiangyouzhan was higher than that in Huanghuazhan by 14% in 2013 and by 13% in 2014.

Discussion

Rice cultivars with strong early vigor are desirable for crop establishment in the direct-seeded systems, especially in adverse growing environments (Balasubramanian & Hill, 2002; Namuco et al., 2009; Zhang et al., 2005). Consequently, many studies have been conducted to determine the factors that contribute to superior early vigor in rice (Asch et al., 1999; Caton et al., 2003; Namuco et al., 2009). However, these studies mostly focused on morphological factors. The physiological understanding of superior early vigor in rice is still limited. In this study, morphological and physiological traits of seeds and seedlings were compared between two contrasting rice cultivars, Yuxiangyouzhan with superior early vigor and Huanghuazhan with general early vigor.

On the one hand, Yuxiangyouzhan had faster germination velocity, higher germination percentage, and longer plumule than Huanghuazhan, indicating that seed vigor was stronger in Yuxiangyouzhan than in Huanghuazhan. It has been reported that several seed morphological traits, including seed size and weight, embryo size, and hull thickness, are associated with seed vigor in rice (Chen et al., 2015; Lu et al., 2007; Namuco et al., 2009; Pandey et al., 1994; Wang, Wang et al., 2010). In the present study, there were no significant differences between Yuxiangyouzhan and Huanghuazhan in seed size and weight and embryo weight, while seed hull weight was significantly lower in Yuxiangyouzhan than in Huanghuazhan. This indicated that seed hull was thinner in Yuxiangyouzhan than in Huanghuazhan, suggesting that low mechanical strength of seed hull might be partly responsible for the strong seed vigor in Yuxiangyouzhan. More interestingly, our results showed that although the difference in seed starch content between Yuxiangyouzhan and Huanghuazhan was not significant, Yuxiangyouzhan had higher seed amylose content and amylase activity than Huanghuazhan. These indicated that Yuxiangyouzhan had higher conversion efficiency of seed reserve than Huanghuazhan because amylose is composed mainly of linear chains of α-1, 4-linked glucose residues and can be converted completely by amylase into maltose. This might be an important reason for the strong seed vigor in Yuxiangyouzhan, and supports our hypothesis that the rice cultivars with higher seed amylose content and amylase activity may have superior seed vigor. In addition, our result showed that Yuxiangyouzhan had higher plumule–radicle ratio than Huanghuazhan, indicating that Yuxiangyouzhan allowed mobilization of more seed reserve to plumule during germination and heterotrophic growth than Huanghuazhan. This might also be an important reason why Yuxiangyouzhan had stronger seed vigor than Huanghuazhan.

On the other hand, seedling shoot biomass was higher in Yuxiangyouzhan than in Huanghuazhan, suggesting that Yuxiangyouzhan had stronger seedling vigor than Huanghuazhan. The stronger seedling vigor in Yuxiangyouzhan was partially attributed to improved leaf morphology and photosynthesis. Yuxiangyouzhan had higher leaf area than Huanghuazhan. Leaf area is a function of leaf dry weight and specific leaf area. In the present study, because specific leaf area was lower in Yuxiangyouzhan than in Huanghuazhan, the higher leaf area in Yuxiangyouzhan was attributed to higher leaf dry weight than in Huanghuazhan. This finding disagrees with previous studies (Asch et al., 1999; Dingkuhn et al., 1999), showing that superior early vigor in African rice is partly due to high specific leaf area. Specific leaf weight is the reciprocal of specific leaf area, and it has been well documented that leaf photosynthesis is positively related to specific leaf weight in rice (Peng, 2000). Consistently, in this study, Yuxiangyouzhan had higher specific leaf weight and consequently higher net photosynthetic rate than Huanghuazhan. This might be partly attributed that higher specific leaf weight resulted in higher leaf chlorophyll and soluble protein contents. In addition, similar with the pattern of seed reserve mobilization during germination and heterotrophic growth, Yuxiangyouzhan allocated more dry matter to shoot but less to root during early autotrophic growth than Huanghuazhan. This might also be partly responsible for the strong seedling vigor in Yuxiangyouzhan, and is in agreement with that reported by Asch et al. (1999). In this regard, it is suggested that too high levels of root biomass would not necessarily promote shoot growth because it consumes assimilates produced by the shoot (Yang et al., 2012). The energy used to produce root biomass is as twofold as that used to produce shoot biomass (Passioura, 1983). Based on this, the notion of root growth redundancy has been raised, namely: a too great root system could result in invalid consumption of energy and could be unfavorable to shoot growth (Cai et al., 2003; Tabata et al., 2008; Wang et al., 2004). These highlight the need for greater fundamental understanding of the physiological processes governing assimilate partitioning during early growth stages in rice cultivars with superior early vigor.

Taken together, our results indicate that Yuxiangyouzhan has both superior seed and seedling vigor. The former is attributed to the low mechanical strength of seed hull, high conversion efficiency of seed reserve, and high mobilization of seed reserve to plumule, while the latter is due to large leaf area, high leaf photosynthetic capacity, and high partitioning of dry matter to shoot. The results of this study enrich the physiological understanding of superior early vigor in rice. Moreover, there is an interesting result that the differences in early vigor-related morphological and physiological traits between Yuxiangyouzhan and Huanghuazhan are larger in our current study than in our previous study (Huang et al., 2012). This might be related to the different seed sources in two studies. The seeds used in the current and previous studies were collected in early rice-growing season in Bingyang (a location in South China) and in single rice-growing season in Changsha (a location in Yangtze River basin), respectively. The temperature during the grain-filling period in early rice-growing season in Bingyang was generally higher than that in single rice-growing season in Changsha. It has been well documented that the effect of high temperature on amylose content in rice is cultivar dependent (Resurreccion et al., 1977; Zhong et al., 2005). Under high temperature, amylose content increases or remains unchanged for cultivars with higher amylose content but decreases for cultivars with lower amylose content. Therefore, the difference in seed amylose content between Yuxiangyouzhan and Huanghuazhan might be larger in our current study than in our previous studies. This might be partially responsible for the larger differences in early vigor-related morphological and physiological traits between Yuxiangyouzhan and Huanghuazhan in the present study than in the previous study because, as mentioned above, seed amylose content is an important physiological trait related to early vigor. These suggest that further studies are required to determine the environmental effects on early seed vigor in rice. However, there are limitations in our study that must be acknowledged. Firstly, since the study was conducted under laboratory and pot conditions, the results are not necessarily applicable to natural growing conditions, especially the adverse growing conditions such as cold, drought, and salt. Secondly, because our study covers only the comparison of two cultivars and some important tests in relation to seed vigor (including cold germination, accelerated aging, and electrical conductivity) are not done in the study, we cannot draw a general conclusion on the morphological and physiological factors contributing to early vigor in rice. Thirdly, we did not determine the yield attributes of the two cultivars with different early vigor in this study, and thus it is unable to draw useful information on the role of early vigor in yield formation in rice. Therefore, further studies involving more environments, cultivars, and tests are needed to generate more conclusive results.

Author contributions

Conceived and designed the experiments: MH, LJ, and YZ. Performed the experiments: MH, RZ, JC, and FC. Analyzed the data: MH. Contributed reagents/materials/analysis tools: MH, RZ, JC, and FC. Wrote the paper: MH.

Disclosure statement

No potential conflict interest was reported by the authors.

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