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Effect of shading on biomass and N mass partitioning in paddy rice seedling through allometric analysis

Zhang Feng [1], LiJie, Wang Xinlin[1]， Mao Wei[1], Zhang Hui[1], Guo Jing[2], Li Jinwen[3]

1Xinjiang Vocation & Technology College of Communications, Urumuqi, China
2Xinjiang Academy of Forestry, Urumuqi 830000， China
3Shanghai Academy of Environmental Sciences, Shanghai, China

Author Contributions:

Conceived and designed the experiments: Zhang Feng, Li Jinwen. Performed the experiments: Zhang Feng, Li Jinwen. Analyzed the data: Zhang Feng, Li Jie, Mao Wei. Wrote the paper: Zhang Feng, Li Jie, Wang Xinlin, Mao Wei. Reviewed and revised the manuscript: Li Jinwen, Zhang Hui, Guo Jing.
All authors have approved the final article, and the authors have declared that no competing interests exist.

Abstract: An allometric analysis of biomass and N mass allocation of rice (*Oryza Sativa* L.) seedlings under non-shading (100% of full sunlight) and shading (30% of full sunlight) were conducted. The allometric exponents or slopes and the intercepts were estimated by the standardized major axis regression. Results indicated that biomass was preferentially allocated to stem along plant ontogeny. Leaves and roots were isometric when rice seedlings were not shaded. More biomass was allocated to leaves and stems when under shading. N mass allocation was also altered by shading. More N mass was allocated to aerial shoot, and accumulated less N mass when plant under shading. Our study revealed that both biomass and N mass were in accordance with the optimal partitioning theory.

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1. Introduction

How plants response to the variation of environmental resources such as light, nutrients, water et al. was a central question in modern plant ecology and evolution. According to the optimal partitioning theory, plants shift more photosynthate to leaf and stem when photosynthetically active radiation (PAR) is more limiting than nutrients, and to root when PAR is less limiting than nutrients (McConnaughay and Coleman, 1999; Aikio, et al., 2009). However, biomass partitioning may change in a predictable way as a function of plant size (total biomass) during plant development, which was dimmed as ontogenetic drift (Evans, 1972). Regardless of the effect of different resources levels, root: shoot ratio of plants gradually decreased with plant development (Gedroc, et al, 1996 and Geng, et al., 2007). To separate the ontogenetic and plastic, allometry, defined as the quantitative relationship between plant size and phenotypic traits, was powerful in summarizing plant development over time and was thus useful for the research on biomass allocation (Poorter et al. 2012). The true plasticity in phenotypic traits, which was adaptive response to environment stress, can be identified through allometric approach (Weiner 2004).

N is vital to photosynthesis, and N concentrations in plant tissues vary considerably as a function of the availability of resources, including light and nutrients. Generally, the N concentration of crops decreased with the accumulation of plant, and an allometric relationship between critical nitrogen uptakes, i.e., the minimum N uptake for achieving the maximum crop biomass could be found in annual crops (Sadras and Lemire, 2014). Highly variable N accrual across most environmental conditions such as light, nutrient, and CO_2 when expressed as a function of time or plant size, but similar patterns of whole-plant N versus non-N biomass accrual over a wide range of environmental conditions(Bernacch et al.,2007).

The in-depth research on biomass allocation of crops was a prerequisite for the development of crop growth simulation model. When different modules of a crop model were framed, the ratios of biomass partition to functional organs need being quantified. Li et al., (2006) developed a model simulating the photosynthate partitioning based on the theory of plant functional equilibrium. Nevertheless, the studies of biomass allocation of cultivated plants were rarely addressed

(Dingkuhn, 1996; Luquet et al. 2005). In most crop models, the biomass partition ratios are generally quantified by empirical equations (Tang, et al., 2009). For example, in a rice (*Oryza Sativa* L.) growth model, the pattern of shoot fraction changing with the physiological development time was well described with a logistic equation (Cao, et al., 2002).

The objective of this study tried to determine how different light treatments resulted in changes of biomass and N mass between different rice organs. We tried to find whether the adjustment of biomass partitioning in rice seedling of under shading, beyond those adjustments that were a consequence of ontogenetic drift, was related to the optimal partitioning theory. Through comparing the allometric relationships between N uptake and non-n biomass, we wanted to find whether N accumulation was changed by shading when compared to the seedlings with the same size.

2. Materials and Methods

2.1 Experiment Design

A potted experiment was conducted at the greenhouse from May to July in 2013, and the rice cultivator of Xiushui 63 was selected. According to previous measurements, the root length of Xiushui 63 was less than 40 cm. Therefore, for the unlimited growth of rice roots, plastic pots with depth of 0.5m and diameter of 0.4m were chosen and filled with sieved soil. The soil organic matter and total N contents is 40.50 g kg^{-1} and 4.2 g kg^{-1} respectively. Rice seeds were sown into the pots on May 5, and 5 homogeneous seedlings were retained in each pot before the shading treatment began. Half of the pots randomly selected, and were covered by black nylon mesh. The PAR above pots was measured by external quantum sensor of a gas analyzer (Li-6400. Licor, USA). The PAR above shaded pots was approximate 30%-40% of that above non-shading pots. There were totally 36 replicates for shading and non-shading treatments respectively.

2.2 Measurements

Rice plants were sampled at an interval of about 10 days on days after sowing 20. The precise measurement of root biomass was a difficult task. In order to completely gather entire plant roots, the pots were cleaved and roots with soil were taken out. Soil adhering to roots, especially to the lateral roots, was carefully washed away by water. Plants were divided into root, stem and leaf. As the plant was in vegetative stage, there was no spike appearing. Each part was over-dried to a constant weight 70°C. After weighting, samples were frozen by liquid nitrogen and grounded into fine power. The C and N contents were determined by elemental analyzer (Vario EL III, Germany) with double replicates. The N mass was calculated by multiplying biomass and N concentration for each part. Non-N biomass of the seedling was equal to total biomass minus N mass.

2.3 Statistics

Allometric relationships between traits were exponential relationships described by the following equation:

$$y = \beta x^{\alpha} \qquad [1]$$

$$\ln(y) = \beta + \alpha \ln(x) \qquad [2]$$

where x (root biomass, root N mass, total N mass) and y (stem, leaf biomass, shoot N mass, non-N biomass) were the two traits, α was the scaling coefficient (slope) and β was a regression constant (intercept) (Warton et al. 2006). The allometric exponents or slopes and the intercepts were estimated by the standardized major axis regression (SMA; SMATR Version 2.0; Warton et al., 2006) on ln transformed data. The numerical values of α were compared to determine if they were consistent with an isometric relationship, i.e. α=1.0, which was taken as the null hypothesis.

3. Result

Biomass allocation between different organs

Bomass partitioning between leaves and roots were almost isometric when the rice grown without shading, and the regression slope (0.99) was not significantly different from 1(P=0.552, Table 1). When the seedlings were under shading, the allocation pattern were allometric (*slope*=1.07, significantly different from 1, P=0.002). In the shading treatment, the allometric regressions lay above that of the non-shading treatment (Fig. 1a). Slopes of the two regressions were significantly different from each other (test statistic=7.932, P=0.006). For a given root biomass, the rice seedlings allocated more biomass to leaves when the rice seedlings were under shading (Fig.1a).

The slopes of regressions of ln (stem biomass) on ln (root biomass) or ln (leaf biomass) under shading or non-shading treatments were all significantly higher than 1(P<0.001), as this value was outside the 95% confidence interval (CI, Table 1). The slopes of regressions of ln (stem biomass) on ln (root biomass were not changed by shading (test statistic=0.169, P=0.687, Table 1), but the intercepts of the 2 regressions were significantly different from each other (P<0.001). In the shading treatment, the allometric regressions lay above that of the non-shading treatment (Fig. 1b). For the same root size, more biomass was allocated to stems when plant seedling was under shading (Fig.1b). Shading significantly lowered the regression slope of allometric relationship between stem biomass and leaf biomass (test statistic=22.731, P=0.001). For a given stems size, more biomass were allocated to leaves when plant seedlings were under shading (Fig.1c).

N allocation between root and shoot and N accumulation

The allocation of N between roots and shoots (including leaves and stems) were allometric. Regression slope of ln (shoot N mass) on ln (leaf N mass) under shading and non-shading were 1.121 and 1.198 respectively, and both were significantly higher than 1(*P*=0.002, 0.009 respectively, Table 2). Shading didn't alter the slopes of the 2 regressions (test statistic=0.116, *P*=0.742). In shading treatment, the regression lay above that of the non-shading treatment (Fig. 2a), with intercepts of the 2 regressions significantly different from each other(*P*<0.001). Comparing at the same root N mass, rice seedlings allocated more N to shoot when under shading.

N and non-N biomass accumulations of rice seedlings under shading or non-shading conditions were shown in Fig. 2b. For the same non-N biomass, the accumulation of N was lower when the rice seedlings are under shading (Fig 2b). The slopes of regressions of ln (non-N biomass) on ln (N mass) of rice seedlings under shading and non-shading were 1.092 and 1.116 respectively, not statistically different from each other (test statistic=1.073, *P*=0.286, Table 2), but statistically different from 1(*P*<0.001). The regression line of shading treatment was above that of the non-shading treatment (Fig. 2b), with intercepts of the two regressions significantly different from each other (*P*<0.001).

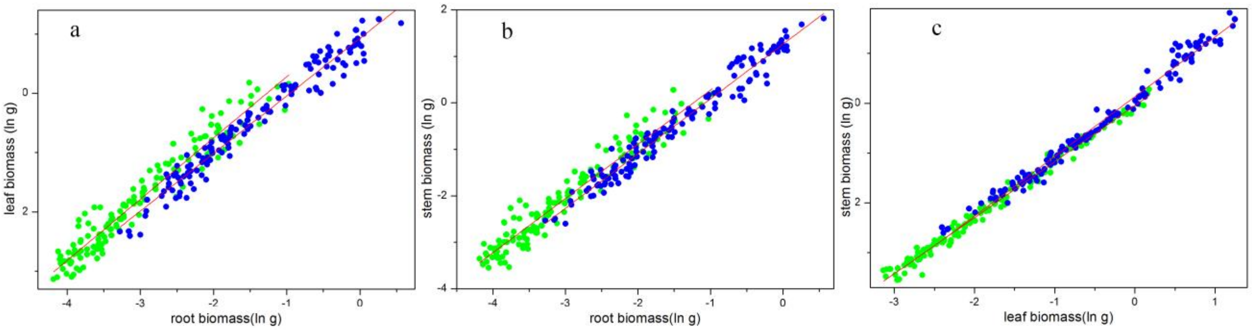

Figure 1. Ln (leaf biomass)-ln (root biomass) relationship (a), ln (stem biomass)-ln (root biomass) relationship (b), and ln (stem biomass)-ln (leaf biomass) relationship (c) of rice (*Oryza Sativa* L.) seedlings under shading (green) and non-shading (blue). Parameters fit by the standardized major axis are given in Table 1.

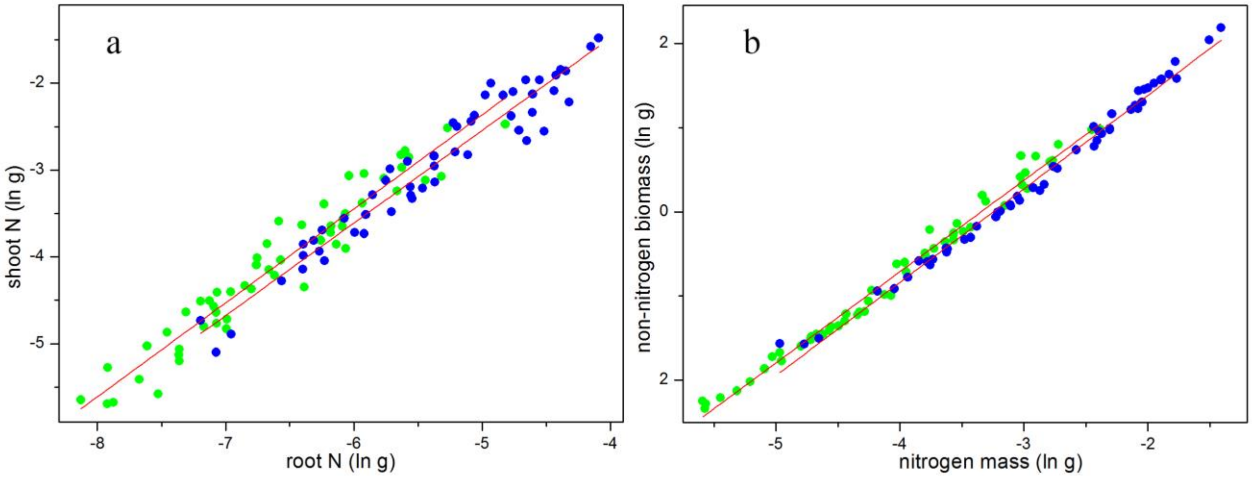

Figure 2. Ln (shoot N mass)- ln (root N mass) relationship (a), and ln (non-nitrogen biomass)-ln (N mass) relationship (b) of rice (*Oryza Sativa* L.) seedlings under shading (green) and non-shading (blue). Parameters fit by the standardized major axis are given in Table 2.

Table 1. Regression parameter estimates (standardized major axis regression) of ln (stem and leaf biomass) on ln (root and leaf biomass) of rice (*Oryza Sativa* L.) under shading and without shading.

y	*x*	**treatment**	*n*	**slope**	**95% CI of slope**	**intercept**	r^2
Stem	Root	shading	143	1.211	(1.158-1.266)	1.574	0.928
		non-shading	140	1.198	(1.161-1.235)	1.292	0.967
Leaf	Root	shading	143	1.070	(1.025-1.117)	1.423	0.932
		non-shading	140	0.990	(0.958 -1.022)	0.954	0.962
Stem	Leaf	shading	143	1.132	(1.113 -1.152)	-0.0366	0.989
		non-shading	140	1.210	(1.185-1.236)	0.137	0.984

Table 2. Regression parameter estimates (standardized major axis regression) of ln (shoot N mass, non-N biomass) on ln (root N mass, total N mass) of rice (*Oryza Sativa* L.) seedlings under shading and without shading. CI was confidence interval.

y	*x*	**treatment**	*n*	**slope**	**95% CI of slope**	**intercept**	r^2
Shoot N mass	Root N mass	shading	55	1.121	(1.044-1.205)	3.305	0.932
		non-shading	52	1.102	(1.026-1.184)	2.981	0.936
Non-N biomass	N mass	shading	55	1.092	(1.058-1.126)	3.658	0.987
		non-shading	52	1.116	(1.086-1.147)	3.621	0.955

4. Discussion

Our results indicated that rice seedlings showed obvious ontogenetic drift in stems allocation, no matter grown under shading or non-shading conditions. Allometric analysis indicated that biomass was priorly allocated to stem along the whole ontogenetic trajectory of rice seedlings in vegetable stage (slopes of regressions of stem vs leaves or roots significantly >1, $P<0.001$). Stems were the organ in which panicle primordium developed. The rice seedlings probably allocated more biomass to stem for the preparation of reproducing, that is to say, acting as the sink of carbohydrates. Therefore, the authors supposed that the allometry of stems vs leaves or roots could attributed to the sink effect. The leaves and roots were almost isometric when the plants grown without shading, which could be attributed to the equilibrium of plant internal C to N. The biological molecule in plant has a specific stoichiometry. Though plants consist of kinds of molecules whose relative abundances change over ontogeny, the general argument might still hold (Shipley and Meziane, 2002). The isometric relationship between leaves and roots probably was due to kept the stoichiometric equilibrium of C and N uptakes.

Shading significantly altered the intercept of allometric regressions of ln (stem biomass) on ln (root biomass). The main hypothesis was probably related to the role played by the stems in the mechanical support of leaves for C fixation (Normand *et al*., 2008), and due to stems contained chlorophyll could also assimilate tiny C. Therefore, it was believed that when under shading, more proportion of carbohydrates was allocated to stems, not only for assisting leaves to capture more C, but also for fixing C itself. The slopes variation of allometric regression of stems vs leaves indicated much more biomass was allocated to leaves when plant under shading. The present study was in accordance with the optimal allocation theory, which was supported by the variation of slopes or intercepts of the allometric regression of leaves vs root and stems. Taking into account the sink effect of stems, it could be concluded that priority of biomass allocation of rice seedlings was: stems>leaves=roots when the plants were non-shading, and shifted to stems>leaves>roots when under shading.

Besides biomass allocation, the allocation of N between roots and the aerial shoots are also allometric. More N mass was allocated to shoots when plant was under shading. The N mass was closely related to chlorophyll, which assimilated C in leaves. Allometric analysis indicated that to cope shading, both biomass and N mass were allocated to aerial shoot to captured more C. The slopes of regressions of ln (non-N biomass) on ln (N mass) statistically different from 1(1.092 and 1.116 for shading and non shading respectively), indicating the N concentration was diluted by biomass. It was worthwhile to notice that the shading significantly altered the N mass *vs* biomass allometry. For a given plant size, the rice accumulated less N when the light was limited.

5. Conclusions

Biomass allocation of rice seedlings under different PAR treatments can have both plastic and ontogenetic components. The biomass was priorly allocated to stem during over plant ontogeny. Shading significantly altered both biomass and N allocation through allometric analysis. Rice plant seedlings accumulated less N mass when under shading comparing at the same plant size. Our results indicated that biomass and N allocation were consistent with the optimal partitioning theory.

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