

Effect of N application on emergence and growth of weeds associated with rice

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Abstract: Study of the effects of added nitrogen (N) on crop and weed growth characteristics is crucial for understanding their relative success when in competition in a mixed stand. We determined photosynthetic capacity (A_{area}), leaf attributes, biomass accumulation and relative growth rate (RGR) of rice and five associated weeds (*Caesulia axillaris*, *Cyperus iria*, *Echinochloa colona*, *Echinochloa crus-galli* and *Fimbristylis miliacea*) at different N input (0, 40 and 120 kg ha⁻¹). We found a clear increase in A_{area} , specific leaf area (SLA), leaf area index (LAI), leaf area ratio (LAR), biomass accumulation and RGR due to N application in all species. Compared to the rice crops, weeds had a higher A_{area} , and showed more efficient biomass gain with increasing N input. Based on morphological and physiological traits, the ranking of responsiveness to added N was *C. axillaris*>*E. crus-galli*>*E. colona* rice>*C. iria*>*F. miliacea*. Across N inputs, LAI showed the maximum relative increase, followed by LAR and A_{area} . Low levels of N inhibited A_{area} and leaf attributes more strongly in *C. axillaris* than in grasses and sedges. *C. axillaris* and *E. crus-galli* appear to be the most competitive and nitrophilic species of those studied in the rice field. LAI is the most important trait, which accounted for the greatest amount of variability in RGR across the N treatment.

Key words: Growth performance, nitrogen, photosynthetic rate, specific leaf area, weeds.

Introduction

The rice–wheat cropping system of the Indo-Gangetic Plains occupies nearly 13.5 million ha area. In India alone, its extent is about 10 million ha (Gupta & Seth 2007). Therefore, this cropping system is the most important one for the food security in the region where rice is a major source of food. However, rice production is seriously constrained by the weed infestation (Subhas & Jitendra 2001). Studies indicate that among grasses *Leptochloa chinensis*, *Echinochloa crus-galli* and *E. colona*, among broad-leaved weeds *Ludwigia parviflora*, *Caesulia axillaris* and *Eclipta prostrata*,

and among sedges *Fimbristylis miliacea*, *Cyperus iria* and *C. diffusa* are the most frequent weeds of rice under rice–wheat system of the Indian subcontinent (Singh *et al.* 2008; Subhas & Jitendra 2001). These weeds are well adapted to the semi-aquatic environment of rice fields, capable of rapid growth and multiplication and are very competitive with crop. Thus, knowledge of weed biology and traits, which favor their success, is desirable for the development of economically and environmentally acceptable weed management systems (Efthimiadou *et al.* 2009; Korres & Fraud-Williams 2002). Understanding the relationship between plant traits and weed impact has emerged as a major

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research area (Navas 2012; Storkey 2004). Such an understanding would provide a better insight into the processes shaping the vigour of weeds and enable the prediction of which species would more likely be serious pests.

Morphological and physiological traits vary in response to different environmental conditions and species relative abundances are controlled by these traits, so that species possessing favorable traits become more abundant (Laliberte *et al.* 2012). In addition, several authors suggested that competitive ability of a species might be related to the functional traits of a species. For instance, competitive success may be enhanced through maximizing photosynthesis (Dur & Goldstein 2001; Feng *et al.* 2007). Species with higher rates of photosynthesis can achieve increased growth rates, biomass accumulation and overall production (Allred *et al.* 2010). Further, specific leaf area (SLA) is found to be a good indicator of many important physiological characteristics including leaf nutrient concentration, photosynthetic capacity, relative growth rate (RGR) and its contributing components (Reich *et al.* 1999; Zhang & Wen 2009). These parameters, along with leaf area ratio (LAR), water use efficiency (WUE) and photosynthetic nitrogen use efficiency (PNUE), are commonly used to explain why and how some plants outperform others (Poorter 1989; Zhang & Wen 2009). Other traits that have also been identified as potential determinants of species success and competitive ability are biomass fractions because the manner in which total biomass is partitioned to different plant parts, influences growth and physiology of an individual (Niklas & Edward 2006; Poorter & Nagel 2000). Differences in these traits are related with the success of plant species thus, we expected that traits, such as biomass allocation to leaves, SLA, and photosynthetic rates, which are indicative of efficient use of resources (Pattison *et al.* 1998), would be greater for a plant possessing a greater degree of competitive ability (Martin & Isaac 2015).

Nitrogen (N) is usually the most limiting among all nutrients due to the larger discrepancy between demand and supply and its crucial role in carbon assimilation and membrane physiology (Martins-Louçao & Lips 2000; Yuan *et al.* 2005). Therefore, N fertilization is widely used to ameliorate soil N availability to enhance plant growth and productivity (Frink *et al.* 1999; Xia & Wan 2008). It has been recognized that among the major plant nutrients, competition between weeds and crop are

greatest for N (Blackshaw *et al.* 2003; Di Tomaso 1995). Weeds not only reduce the amount of N available to crops but the growth of many weeds is also improved by higher soil N levels (Blackshaw *et al.* 2003). Weeds are inherently different in responsiveness to higher soil N levels (Blackshaw *et al.* 2008; Moreau *et al.* 2014). Moreover, the ability to better utilize available N can also provide an advantage in competition for water and light (Di Tomaso 1995). Thus, it is important to understand how different weeds respond to N fertilization under competition and whether crop is a better competitor than weeds at a certain level of N fertilization. For this, functional traits may be useful predictors of the response of weeds to N availability because they represent specific functional adaptations to various environmental constraints (Lavorel & Garnier 2002; Martin & Isaac 2015).

To identify the mechanisms underlying crop–weed competition for N, it is important to quantify the interactive effects of weed interference and N on growth parameters and determine how changes in the functional traits affect competitive success of species. Relative growth rate (RGR), which largely determines the success in fertile and disturbed environment for ruderals, is considered central to understanding the functional ecology of species (Poorter & Remkes 1990; Storkey 2004). High growth rate helps in a rapid completion of the life cycle of ruderals (Poorter & Remkes 1990). This pattern of growth ensures their existence and perennation as the length of the growing season is quite unpredictable due to weed control methods in agro-ecosystem (Hegazy *et al.* 2005). Since variability in growth rate is a function of a number of plant traits with trade-offs with other plant functions (Storkey 2004), it is important to identify key determinants of RGR in agro-ecosystem.

In Asia, limited studies are available on the effect of N fertilization modulating competitive ability of different weed life forms (grasses, sedges and broad-leaved weeds) growing together in rice fields. Therefore, the objective of this research was (i) to understand ecophysiological basis of differences in the response of weeds, and (ii) crop at different N application rates and to identify the traits determining RGR of weeds and rice across the fertilization treatments. In the present study, we hypothesized that the response of the competitive ability of weeds to N may be species specific and related to morphological/physiological traits.

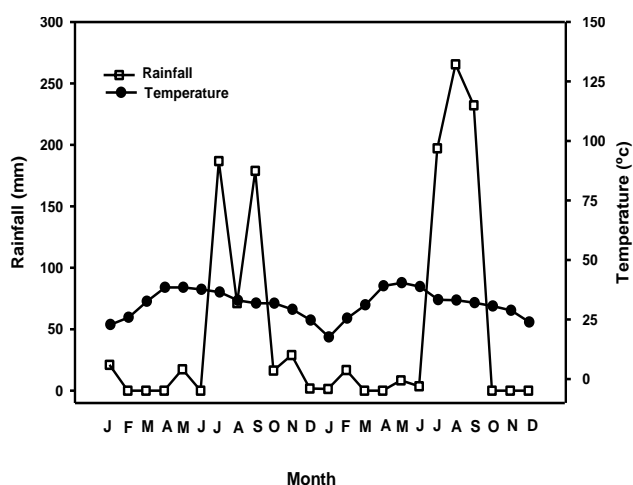


Fig. 1. Mean daily temperature and rainfall during the study period (2009–2010) at Banaras Hindu University, Varanasi, India.

Materials and methods

Site Description

The study was conducted from July to November of 2009 and 2010 at the Research farm of the Institute of Agricultural Sciences, Banaras Hindu University, Varanasi. The farm is located at 25°15'N latitude and 80°59'E longitude and is situated 76 m above the mean sea level. The area is a part of Indo-Gangetic Plains having tropical monsoonal climate. The year is divisible into a cold winter (November to February), a hot summer (April to June) and a warm rainy season (July to September). The annual rainfall averages 1100 mm, of which more than 85% falls during the rainy season from the southwest monsoon. The details of rainfall and temperature conditions of the area are given in Fig. 1. The soil is alluvial, well drained, pale brown, silty loam, incept sol with a neutral reaction, and is low in available nitrogen and potassium (Singh *et al.* 2011)

The weeds

A reconnaissance survey of the entire farm area for weed composition and literature search for the weeds of rice (*Oryza sativa* L.) field in the Indo-Gangetic Plains indicated five dominant weeds *Caesulia axillaris* Roxburgh, *Cyperus iria* L., *Echinochloa colona* (L.) Link, *Echinochloa crus-galli* (L.) Beauv and *Fimbristylis miliacea* (L.) Vahl.

These weeds were selected for the present study.

E. colona (jungle rice) and *E. crus-galli* (barnyard grass) are C₄ grasses and are among the world's most serious weeds (Rao *et al.* 2007). Both species are highly competitive and their morpho-physiological similarities with rice make control measures difficult (Galon & Agostinetto 2009). *F. miliacea* (grass like fimbry) is annual C₄ sedge, which grows in clumps of erect stems. It is a very serious weed in the rice fields of southern and eastern Asia (Begum *et al.* 2006). *C. iria* (rice flat-sedge) is annual, tufted C₄ sedge, and a major weed of lowland rice throughout the world (Holm *et al.* 1991). *C. axillaris* (pink node flower), a member of family Asteraceae, is an erect annual broad-leaved weed and well known weed of rice (Subhas & Jitendra 2001). In the present research farm, height of *E. crus-galli* ranged from 92–110 cm, *E. colona* 50–60 cm, *F. miliacea* 55–70 cm, *C. iria* 55–60 cm and *C. axillaris* 80–95 cm (Singh 2012).

Experimental design and procedures

For the field experiment, nine plots (each 5 m × 3 m) were established in an extensive rice field in which rice-wheat-fallow crop sequence was practiced from past 12 years. Strips of 1 m separated each plot from the other. Transplanting of 21 days old rice seedlings (var. BPT) was done on puddled soil on 6 July and 22 July for the first (2009) and the second year (2010) of the study, respectively, with a spacing of 30 × 15 cm. It is a high-yielding (5.5–6.5 tones ha⁻¹); dwarf to medium variety of rice (plant height up to 100 cm), life cycle continues up to 140–150 days after sowing (DAS). Weeds were allowed to develop in rice plots without physical and chemical control. Weeds emerged around 15 days after transplantation. Plots were kept flooded (5–10 cm) throughout the crop growth period until the grain maturation. The three N application rates selected were 0 (control), 40, and 120 kg N ha⁻¹ (treatments termed as N₀, N₁ and N₂, respectively). The 120 kg N ha⁻¹ rate represented applied N that would meet the recommended rate for rice field of the area. The plots were arranged in a randomized block design with three plots per treatment. N was applied in the form of urea (46% N); half of which was applied at the time of rice transplantation by uniform broadcasting and the remaining half when active tillering was detectable. All treatments received the basal treatment of KCl

Table 1. Effects of N supply on biomass and density of weeds and rice at different growth stages. Values are mean of two-year \pm SE.

	Harvest date	Biomass (g plant ⁻¹)			Density (plant m ⁻²)		
		N0	N1	N2	N0	N1	N2
<i>C. axillaris</i>	4 WAT	0.46 \pm 0.02	0.59 \pm 0.03	0.76 \pm 0.05	22	25	32
	8 WAT	2.17 \pm 0.15	2.34 \pm 0.24	3.97 \pm 0.54	28	32	49
<i>C. iria</i>	4 WAT	0.94 \pm 0.18	1.21 \pm 0.12	1.61 \pm 0.34	26	29	36
	8 WAT	1.36 \pm 0.12	1.47 \pm 0.15	1.88 \pm 0.22	20	18	22
<i>E. colona</i>	4 WAT	1.73 \pm 0.18	1.80 \pm 0.2	2.34 \pm 0.17	27	29	34
	8 WAT	1.98 \pm 0.14	2.59 \pm 0.10	3.22 \pm 0.30	16	20	22
<i>E. crus-galli</i>	4 WAT	1.98 \pm 0.28	2.88 \pm 0.26	3.45 \pm 0.21	28	30	43
	8 WAT	6.78 \pm 0.72	7.36 \pm 0.43	11.44 \pm 0.90	27	38	58
<i>F. miliacea</i>	4 WAT	0.92 \pm 0.11	0.59 \pm 0.08	1.09 \pm 0.20	27	30	34
	8 WAT	1.44 \pm 0.24	1.36 \pm 0.20	1.77 \pm 0.29	28	34	36
Rice	4 WAT	7.35 \pm 0.67	7.63 \pm 0.58	10.07 \pm 0.67	18	18	19
	8 WAT	23.65 \pm 1.64	25.23 \pm 1.48	33.94 \pm 1.13	18	18	18

(potash) and P₂O₅ (single superphosphate) at the rate of 60 kg ha⁻¹. P₂O₅ and KCl were broadcasted before puddling. These rates of application and timings correspond to those commonly followed by farmers in transplanted rice of the area.

Plants were sampled thrice during the growth period of rice: i.e. (i) at the time of active tillering of rice, four weeks after transplantation (WAT), (ii) at the time of anthesis (eight WAT), and (iii) at senescence (12 WAT). Only *C. axillaris* and *E. crus-galli* were present at all sampling dates, however, *C. iria*, *E. colona* and *F. miliacea* were absent at 12 week sampling because they completed their lifecycle by that time. Therefore, data for only two sampling dates (four WAT and eight WAT) are considered.

Six samples (two per plot) were randomly collected on each sampling date for each species in each treatment. The mean of the two samples per plot was used in analysis (i.e. 3 replicates per treatment per species). Roots were sampled by monoliths of 15 \times 15 \times 15 cm dimensions. Monoliths were washed with fine jet of water using mesh screens. The plant components were placed in separate paper bags and transported to the laboratory in ice bags. The ratio of biomass of each plant component to total biomass yielded leaf weight ratio [LWR]; stem weight ratio [SWR]; root weight ratio [RWR]; flower weight ratio [FWR]. In grasses and sedges, the whole of the inflorescence was measured for FWR. Leaf area was determined

using a leaf area meter (SYSTRONICS, Leaf area meter-211); the leaves and other plant parts were oven dried at 70 °C for 48 h to obtain the dry mass. Specific leaf area (SLA) (cm² g⁻¹) was calculated as area per unit mass. Leaf area index (LAI) was calculated as one-sided area of leaf per unit ground surface area and leaf area ratio (LAR) was calculated as the ratio of leaf area to plant weight. Same plant was used for measurements of biomass fractions, SLA, LAR, LAI and RGR at each harvest. Relative growth rate (RGR) and net assimilation rate (NAR) were determined using following expression: (Hunt & Cornelissen 1997).

$$\text{RGR} = (\ln W_2 - \ln W_1) / (T_2 - T_1) \quad \text{NAR} = (\ln LA_2 - \ln LA_1) / (LA_2 - LA_1) \times (W_2 - W_1) / (T_2 - T_1)$$

Where W₁ = dry weight of the plants at four weeks after transplanting (t₁), W₂ = dry weight at eight weeks after transplanting (t₂). LA₂ is total leaf area at time T₂, and LA₁ is total leaf area at time T₁. For density weeds and rice were harvested close to the ground from three locations in each plot using quadrats (50 \times 50 cm). Samples were separated by species, individuals per species were counted and biomass was estimated after drying at 70 °C for 48 h.

Physiological attributes were directly measured in the field from six plants (i.e. two per plot) per species per treatment on each sampling date. Photosynthetic rate (A_{area}), conductance (gs) and transpiration rate (E) of the plants were measured simultaneously by LI-6400 gas exchange system

(LI-COR, Lincoln, Nebraska, USA) on the uppermost, fully expanded and apparently healthy leaves from each individual on sunny days in natural light condition between 0800 and 1100 hours local time. Flow rate was maintained at $500 \mu\text{mol s}^{-1}$. Air temperature was $32 \pm 0.15 \text{ }^\circ\text{C}$, relative humidity ranged from 35–40% and CO_2 concentration was $385 \pm 5 \mu\text{mol CO}_2 \text{ mol}^{-1}$. Photosynthetic active radiation (PAR) was $1221 \pm 36.20 \mu\text{mol mol}^{-1}$ at the time of experiment. Water use efficiency (WUE) was calculated as the ratio of photosynthetic rate (A_{area}) to transpiration rate (E). Photosynthetic nitrogen use efficiency (PNUE) was calculated as the ratio of A_{area} to leaf nitrogen concentration per unit area (Pons & Westbeek 2004). PNUE was calculated only at eight WAT. Physiological traits were measured for only five species (*C. axillaris*, *C. iria*, *E. colona*, *E. crus-galli* and rice) while the same in *F. miliacea* could not be measured because of too narrow leaves.

Chemical analysis

Dried leaf material was used to determine the organic N concentration according to Kjeldahl method (Jackson 1958). For each species, leaves from the same plot were mixed into one sample per plot. Thus, there were three samples for each species in each treatment. Analysis was done at eight WAT in both the years. Leaf nitrogen concentration per unit area (LNCA) was calculated as the ratio of leaf nitrogen concentration (g g^{-1}) to SLA.

Statistical analysis

The trait values of each species in three plots were considered as replicates for one treatment. Finally, at the end of 2 years the total number of data points for morphological traits and RGR was 216 ($n = 3 \text{ replicates} \times 6 \text{ species} \times 3 \text{ treatment} \times 2 \text{ sampling dates} \times 2 \text{ years}$). While the same in the case of physiological traits was 180 ($n = 3 \text{ replicates} \times 5 \text{ species} \times 3 \text{ treatment} \times 2 \text{ sampling dates} \times 2 \text{ years}$). The effect of treatments on species, year and various eco physiological traits were analyzed by multivariate ANOVA. Two-tailed Pearson's correlation coefficients among traits were calculated to observe the relationships among these variables. A stepwise multiple regression was performed to identify the best predictor of RGR. All the statistical analyses were performed using SPSS software (ver. 16).

Results

Weed emergence and biomass

N application significantly affected weed emergence (represented here by density); number of weed plants per m^2 increased with N addition, highest densities were observed for *E. crus-galli*. Analysis of variance showed that biomass is significantly influenced by N application (treatment), species, year and their two-way interactions except for species \times year and time \times year interactions (Table 2). Averaged over the two years, biomass of weeds and crop increased concomitantly with nitrogen supply at all sampling intervals (Table 1). Maximum increase in biomass due to increased N supply was observed in *C. axillaris* followed by *E. crus-galli* (Fig. 2). *E. colona* and *C. iria* showed the least effect of N on biomass (Fig. 2).

Biomass partitioning and dry matter allocation

Significant effects of species and time were observed on all biomass partitioning parameters. However, the effect of year and treatment were only significant for RWR and LWR (Table 2). Most of the dry matter in the investigated weeds was allocated at the vegetative stage to the leaves, followed by stems and roots (Fig. 3). The leaf fraction generally decreased over time, as the plants invested more in other organs like roots, flowers and stems. Maximum RWR and LWR were observed in *C. axillaris* followed by *E. crus-galli*, while highest SWR was found in rice followed by *E. crus-galli* (Fig. 3). RWR decreased with increased N application rate; *C. axillaris* exhibited the maximum decrease (38%) in RWR with increasing N rate followed by *C. iria* (17%) and *E. crus-galli* (16%) (Fig. 2). In *E. colona* and *F. miliacea*, N application did not result in decrease of RWR. Highest relative increase in LWR in N2 over N0 treatments was found in *C. axillaris* (33%) and *E. crus-galli* (31%) (Fig. 2).

Relative growth rate and net assimilation rate

The relative growth rate (RGR) significantly differed among species, treatments and years while their interactions were not significant (Table 2). In both the years, *C. axillaris* exhibited the highest RGR, whereas the lowest values were recorded for *F. miliacea* and *C. iria* (Fig. 4). N application enhanced the growth rate of all species; particularly

Table 2. Summary of ANOVA (F values) for leaf attributes and biomass fractions of weeds and rice.

	LAI	LAR	SLA	LMR	RWR	SWR	FWR	Biomass	RGR
Species (F _{5,144})	1511**	2993**	3765**	96.64**	137.58**	223.53**	613.98**	820.74**	37.46**
Treatment (F _{2,144})	360.67**	243.14**	284.56**	4.08*	11.84**	2.31	2.34	67.41**	26.38**
Time (F _{1,144})	16.69**	3916**	2245**	254.65**	339.50**	257.25**	220.01**	719.11**	-
Year (F _{1,144})	23.94	19.35**	14.28**	17.42*	0.49	0.39	4.7514	24.05*	4.56*
Species×Treatment (F _{10,144})	103.95**	48.92**	134.98**	5.71*	6.05*	1.23	3.41*	35.88**	0.53
Species × Time (F _{5,144})	47.14**	105.10**	299.32**	2.61	19.88**	12.66**	477.4**	94.77**	-
Species × Year (F _{5,144})	3.03*	18.53**	1.46	7.43**	5.30**	1.80	0.65	4.08*	1.23
Treatment × Time (F _{2,144})	7.67*	17.47**	3.07*	1.52	1.14	0.88	2.92	0.45	-
Treatment × Year (F _{2,144})	7.67*	17.47**	3.07*	0.34	0.31	0.45	12.19**	10.50**	0.15
Year × Time (F _{1,144})	23.35**	53.91**	6.28*	5.85*	11.12*	0.71	8.80*	0.80	-

**Significant at $P < 0.01$ level, * significant at $P < 0.05$ level.

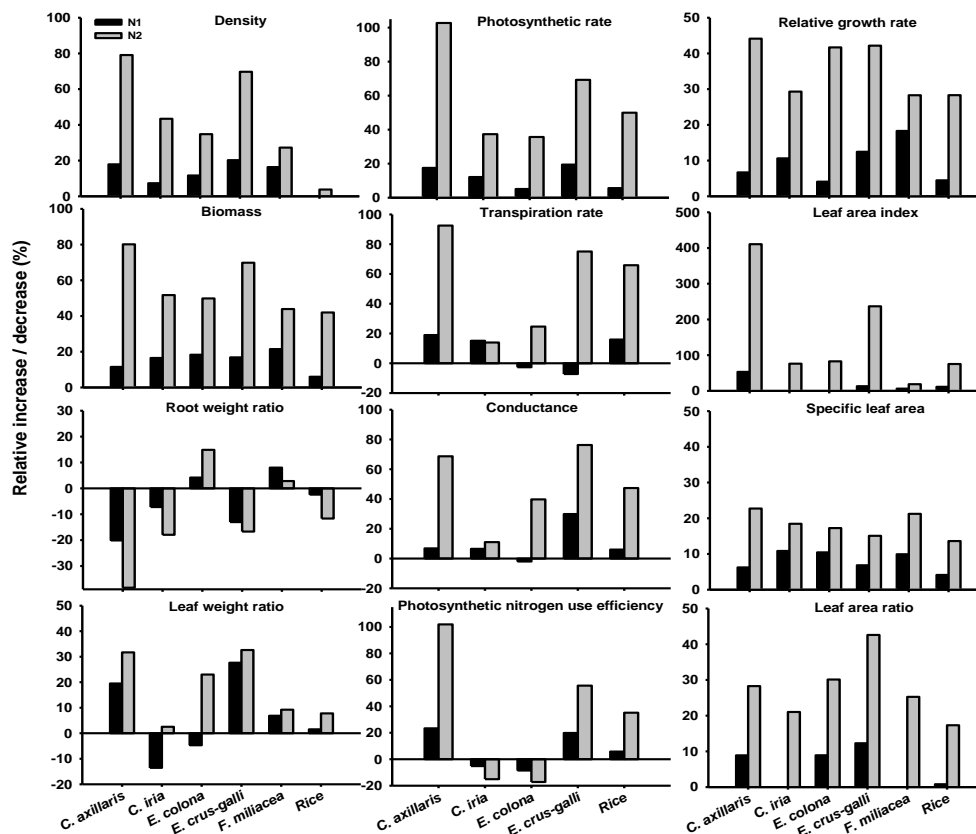


Fig. 2. Relative increase/decrease (%) in biomass, density, root weight ratio (RWR), leaf weight ratio (LWR), physiological traits, relative growth rate (RGR) and leaf attributes of weeds and rice in N1 and N2 treatments over N0 treatments. Data are mean of four and eight weeks.

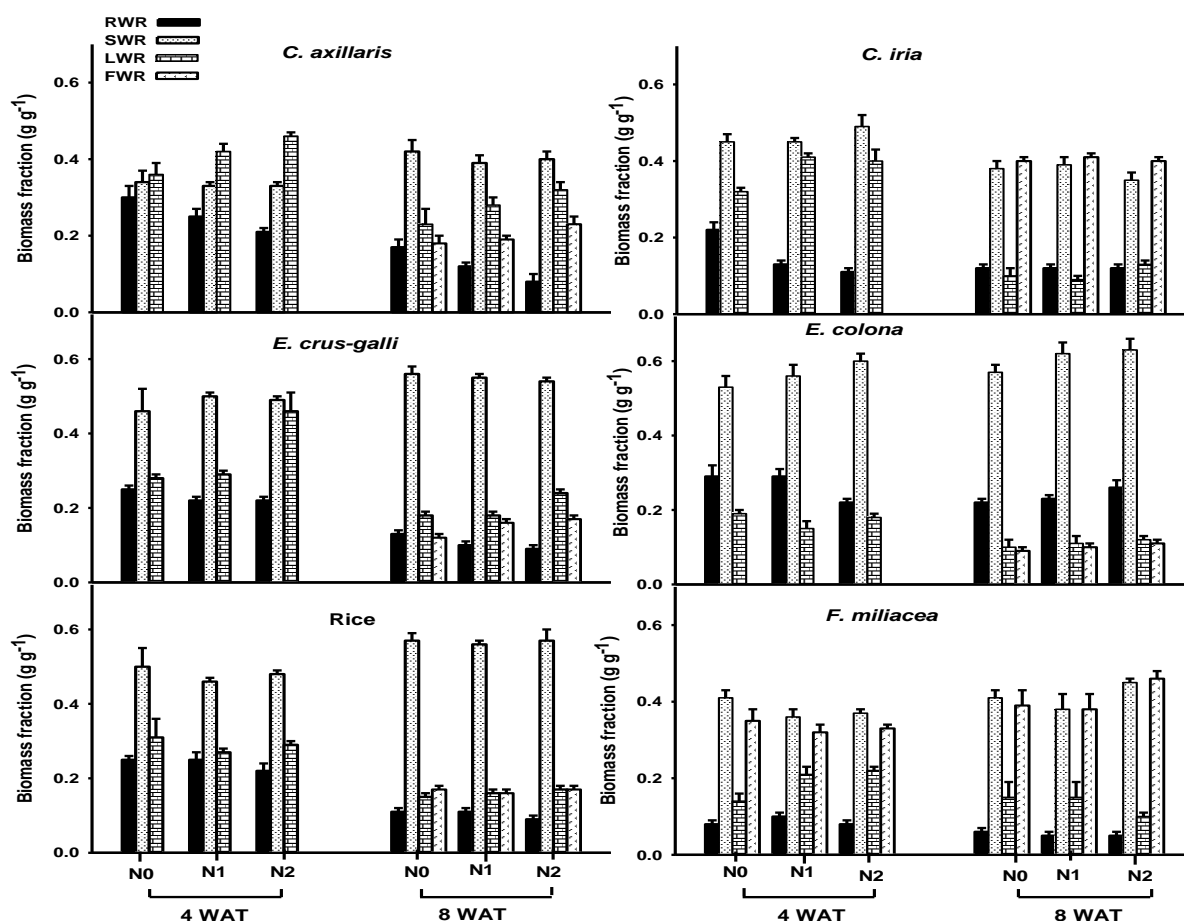


Fig. 3. Dry matter allocation at the different growth stages of the weeds and rice at different nitrogen application rate. Values are mean of two-year \pm SE.

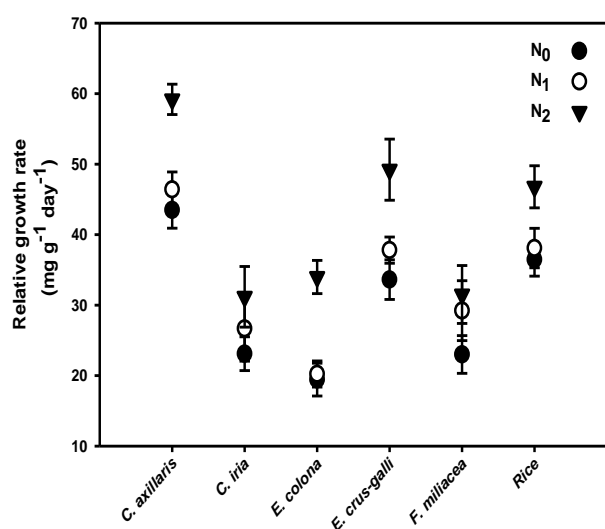


Fig. 4. Relative growth rate (RGR) of the weeds and rice at different nitrogen application rate. Values are mean of two-year \pm SE.

of *C. axillaris*, *E. crus-galli* and *E. colona* (Fig. 2). Similar to RGR, N addition also increased the NAR significantly in all species (Fig. 5) and RGR and NAR were positively related ($RGR = 10.62 + 4930 \text{ NAR}$, $R^2 = 0.62$, $P < 0.001$).

Physiological attributes

Significant effect of species, treatment and time except year were observed for A_{area} (Table 3). Two-way interactions were also significant except species \times year. *C. axillaris* showed highest A_{area} in N2 and N1 treatments at all sampling dates followed by *E. crus-galli* (Fig. 6). Photosynthetic rate, transpiration rate and g_s of all species showed a positive response to N treatment (Fig. 6). The maximum relative increase in A_{area} and transpiration rate (E) under N2 treatment compared to N0 was in *C. axillaris* while in the case of stomatal conductance (g_s), *E. crus-galli* exhibited maximum relative increase (Fig. 2).

Table 3. Summary of ANOVA (F values) for physiological attributes of weeds and rice.

	A _{area}	gs	E	WUE	PNUE
Species (F _{4,120})	57.79**	281.37**	202.98**	232.46**	212.37**
Treatment (F _{2,120})	203.28**	69.15**	72.85**	0.52	95.83**
Time (F _{1,120})	356.08**	173.82**	7.90*	243.02**	-
Year (F _{1,120})	3.55	11.03*	35.60**	27.84**	0.19
Species × Treatment (F _{8,120})	7.27**	3.51*	8.62**	4.94*	51.59**
Species × Time (F _{4,120})	14.81**	7.87**	25.90**	14.93**	-
Species × Year (F _{4,120})	1.56	3.13*	14.77**	18.47**	1.90
Treatment × Time (F _{2,120})	6.57*	0.98	2.93	0.36	-
Treatment × Year (F _{2,120})	5.27*	0.45	1.60	1.78	4.40*

** Significant at $P < 0.01$ level, * significant at $P < 0.05$ level.

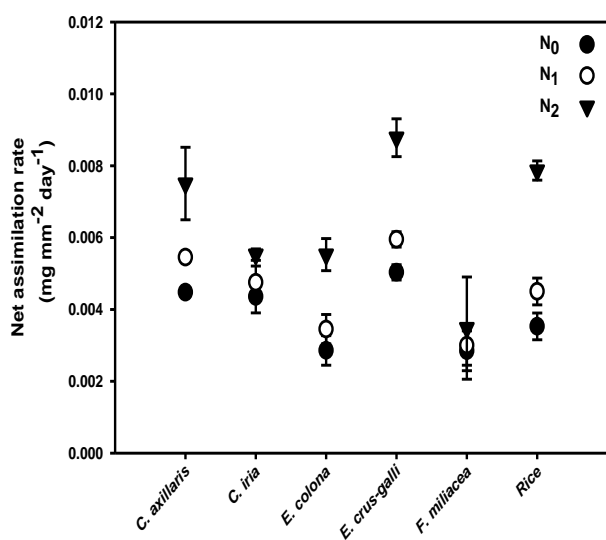


Fig. 5. Net assimilation rate (NAR) of the weeds and rice at different nitrogen application rate. Values are mean of two-year \pm SE.

Further, species, year and time effects were also significant for water use efficiency (WUE) but the treatment effect was not significant (Table 3). Over the growing season, highest WUE was recorded in *E. crus-galli* followed by *E. colona* and lowest in *C. axillaris* (Fig. 6).

Species and treatment effects were significant for PNUE (Table 3). Across the species and treatment, its value ranged from 81.25 to 268.71 $\mu\text{mol mol}^{-1} \text{s}^{-1}$ (Fig. 7). *C. axillaris* exhibited highest PNUE in all treatments. PNUE increased with increasing N level in *C. axillaris*, *E. crus-galli* and rice, while decreased with increasing N level in *C. iria* and *E. colona*. *C. axillaris* exhibited 102% increase in N2 over N0 treatment, whereas *E. crus-*

galli and rice showed 55% and 35% increase, respectively, in N2 as compared to N0 treatment (Fig. 2).

Leaf attributes

Year, species, time and treatment significantly influenced the leaf attributes (SLA, LAR, LAI; Table 2). Two-way interactions were also significant for all leaf attributes. SLA and LAR were greatest in *C. axillaris* at all treatments and at all sampling dates (Table 4). *C. axillaris* showed highest LAI in N2 treatment followed by rice, whereas rice exhibited maximum LAI in N1 and N0 treatments (Table 4). SLA and LAR at four WAT was highest for all species and treatments and then declined rapidly, while maximum LAI was observed at eight WAT in all species. The highest relative increase in leaf traits due to N addition was observed in LAI (410% in *C. axillaris* and 237% in *E. crus-galli*) followed by LAR and SLA (Fig. 2).

We performed multiple regression to identify the most significant predictor of RGR, LAI among the morphological and PNUE among the physiological traits had the largest influence on RGR in N2 plots. It was observed that the variation in LAI alone accounted for 80% variation in RGR, and LAI and PNUE together explained 91% variation in RGR. The final model was $\text{RGR} = 31.53 + 0.59 \text{ LAI} + 0.44 \text{ PNUE}$ ($R^2 = 0.91$). However, in N1 and N0 plots, RGR was governed only by morphological traits. In N1 plots, LAI alone explained 63% variation in RGR while LAR in combination with LAI explained 84% variation in RGR. In N0 plots, also SLA and LAI were the most significant predictors of RGR. The regression models were:

Table 4. Effects of N supply on leaf attributes at the different growth stages of the weeds and rice. Values are mean of two-year \pm SE.

	Harvest date	Leaf N (%)			LAI			SLA (cm ² g ⁻¹)			LAR (cm ² g ⁻¹)		
		N0	N1	N2	N0	N1	N2	N0	N1	N2	N0	N1	N2
<i>C. axillaris</i>	4 WAT	—	—	—	0.35 \pm 0.13	0.73 \pm 0.13	1.31 \pm 0.13	836 \pm 5	894 \pm 6	958 \pm 5	427 \pm 1	489 \pm 1	429 \pm 1
	8 WAT	3.02 \pm 0.10	3.28 \pm 0.05	4.32 \pm 0.15	0.58 \pm 0.08	0.69 \pm 0.10	3.45 \pm 0.25	333 \pm 7	348 \pm 7	451 \pm 12	77 \pm 4	100 \pm 3	165 \pm 10
<i>C. iria</i>	4 WAT	—	—	—	0.03 \pm 0.00	0.05 \pm 0.00	0.05 \pm 0.00	145 \pm 2	152 \pm 1	167 \pm 2	32 \pm 1	28 \pm 0.55	37 \pm 0
	8 WAT	1.11 \pm 0.07	1.52 \pm 0.06	2.37 \pm 0.07	0.06 \pm 0.00	0.07 \pm 0.00	0.13 \pm 0.01	110 \pm 12	143 \pm 2	147 \pm 2	12 \pm 1	15 \pm 1	17 \pm 1
<i>E. colona</i>	4 WAT	—	—	—	0.05 \pm 0.01	0.06 \pm 0.01	0.07 \pm 0.01	189 \pm 1	206 \pm 1	214 \pm 1	29 \pm 0	28 \pm 1	53 \pm 0
	8 WAT	1.12 \pm 0.06	1.46 \pm 0.03	2.31 \pm 0.09	0.10 \pm 0.01	0.09 \pm 0.05	0.21 \pm 0.01	138 \pm 2	155 \pm 2	169 \pm 2	17 \pm 1	21 \pm 1	25 \pm 1
<i>E. crusgalli</i>	4 WAT	—	—	—	0.32 \pm 0.02	0.36 \pm 0.03	0.83 \pm 0.02	229 \pm 1	233 \pm 1	258 \pm 1	50 \pm 0	48 \pm 0	62 \pm 0
	8 WAT	1.43 \pm 0.04	1.57 \pm 0.06	2.25 \pm 0.17	0.69 \pm 0.06	0.77 \pm 0.08	2.55 \pm 0.12	160 \pm 3	189 \pm 6	229 \pm 7	22 \pm 1	32 \pm 1	41 \pm 2
<i>F. miliacea</i>	4 WAT	—	—	—	0.02 \pm 0.00	0.04 \pm 0.13	0.05 \pm 0.00	150 \pm 0.3	165 \pm 0.3	180 \pm 0.3	31 \pm 0.2	29 \pm 0	40 \pm 0
	8 WAT	1.00 \pm 0.08	1.34 \pm 0.07	1.58 \pm 0.03	0.14 \pm 0.01	0.13 \pm 0.00	0.14 \pm 0.00	132 \pm 5	145 \pm 5	178 \pm 5	15 \pm 1	17 \pm 1	19 \pm 1
Rice	4 WAT	—	—	—	1.01 \pm 0.13	0.88 \pm 0.13	1.44 \pm 0.13	233 \pm 1	240 \pm 2	252 \pm 1	64 \pm 0.1	69 \pm 0	73 \pm 0
	8 WAT	1.83 \pm 0.05	2.23 \pm 0.05	2.90 \pm 0.16	1.28 \pm 0.07	1.15 \pm 0.10	2.61 \pm 0.16	167 \pm 3	176 \pm 4	203 \pm 1	29 \pm 1	25 \pm 2	36 \pm 2

For N1 treatment; $RGR = 24.34 + 0.62LAI + 0.48LAR$ ($R^2 = 0.84$)

For N0 treatment; $RGR = 20.74 + 0.67SLA + 0.55LAI$ ($R^2 = 0.86$)

Discussion

Effects of N on weed emergence and biomass partitioning

Increased N fertilization enhanced the number of weed plants per unit urea as N fertilizer may play an important role in breaking dormancy of weed species (Agenbag & De Villiers 1989). Sweeney *et al.* (2008) also reported that N applications increased weed growth, though no differences were found in Italian ryegrass emergence dynamics with different N application regimes (Scursoni *et al.* 2012). In the present study, N addition did not equally benefit all weeds; highest changes in density with N addition occurred in *C. axillaris* and *E. crus-galli*.

N fertilization significantly affected the RWR and LWR in all species. RWR decreased by increasing N fertilization while LWR showed an opposite trend. Under low N supply, plants partition a large proportion of assimilates to roots (Boussadia *et al.* 2010; Remans *et al.* 2006), so that with greater root mass and volume more nitrogen can be acquired and N concentration in new leaves can be optimized (Barker *et al.* 2006). However, the larger investment in roots comes at the expense of leaf growth (low LWR) (Bonifas & Lindquist 2006), which subsequently limits the relative growth rate.

Effects of N addition rates on ecophysiological attributes

Leaf N content of all species significantly increased with increasing N addition (Table 4). The amount of N present in leaves represents the degree of fertility of the soil in which a plant is growing (Roche *et al.* 2004; Sabate *et al.* 1995) and leaf photosynthesis is largely determined by leaf N content. Therefore, N shortage results in a significant decrease in A_{area} in all species as more than half of the total leaf N is allocated to the photosynthetic apparatus (Boussodia *et al.* 2010; Makino & Osmond 1991). N stress results in reduced carboxylation efficiency by Rubisco together with a decrease in the ability to regenerate RuBP; this will lead to low daily rate of photosynthesis (Cabrera-Bosqueta *et al.* 2009). However, effect of N was not similar across species; maximum decrease in A_{area} in N0 plot as compared to N2 plots was found in *C. axillaris* followed by *E.*

crus-galli while *C. iria* and *E. colona* showed comparatively smaller decrease.

Gas exchange parameters such as conductance (gs) and transpiration rate (E) showed marked decrease due to less available N. Decline in gs with decreasing N availability and significant relationships between A_{area} and gs (Table 5) suggested that stomatal responses affected by N availability, may reduce the supply of CO₂ to the intercellular spaces and thereby A_{area} (Chen *et al.* 2005). Plants grown in low N have low E as compared to high N plants because transpiration rates are influenced by stomatal behavior and gs (Xie & Luo 2003), thus a decrease in gs leads to a reduction in E (Patane 2011).

Literature is equivocal about the effect of N on WUE. Increment in WUE due to N addition is reported in many studies (Caviglia & Sadra 2001; Nielsen & Halvorson 1991), on the other hand, Lu *et al.* (2005) reported a decrease in WUE with increasing N supply. In our study, the effect of N addition on WUE depends on plant species investigated. WUE increased significantly with increasing N level in *C. iria*, no effect was observed in *C. axillaris*, *E. colona* and rice, and negative effect in *E. crus-galli*. Species differences in response to N supply indicate that N impacts are not straightforward and plants control WUE by physiological and morphological processes in a very complex manner (Brueck & Senbayram 2009). Further, substantial differences in PNUE were recorded among the species. Rice, *C. axillaris* and *E. crus-galli* showed an increase in PNUE with N addition rate. Opposite to this, *C. iria* and *E. colona* showed a decrease in PNUE with increasing N availability. Hence, *C. iria* and *E. colona* showed an improvement of the N budget in its leaves under N limiting condition and might therefore be better adapted to N shortage. Cabrera-Bosqueta *et al.* (2009) also reported an increase in PNUE with decreasing soil N.

Among leaf attributes, LAI was affected most severely by N supply (Fig. 2). Under low N condition, the decrease in LAI can be explained by either a reduction in interception of photosynthetic active radiation (PAR) as a consequence of a reduction in the leaf expansion rate or due to higher rate of loss of senescent leaves (Colnenne *et al.* 2002; Lemaire *et al.* 2008). It has been found that in fertilized plots, plants tend to have thinner and less dense leaves (Knops & Reinhart 2000). Consistent with this we found that SLA was significantly higher in N2 plots than in N1 and N0 plots, but the relative increase was lower as compared to other

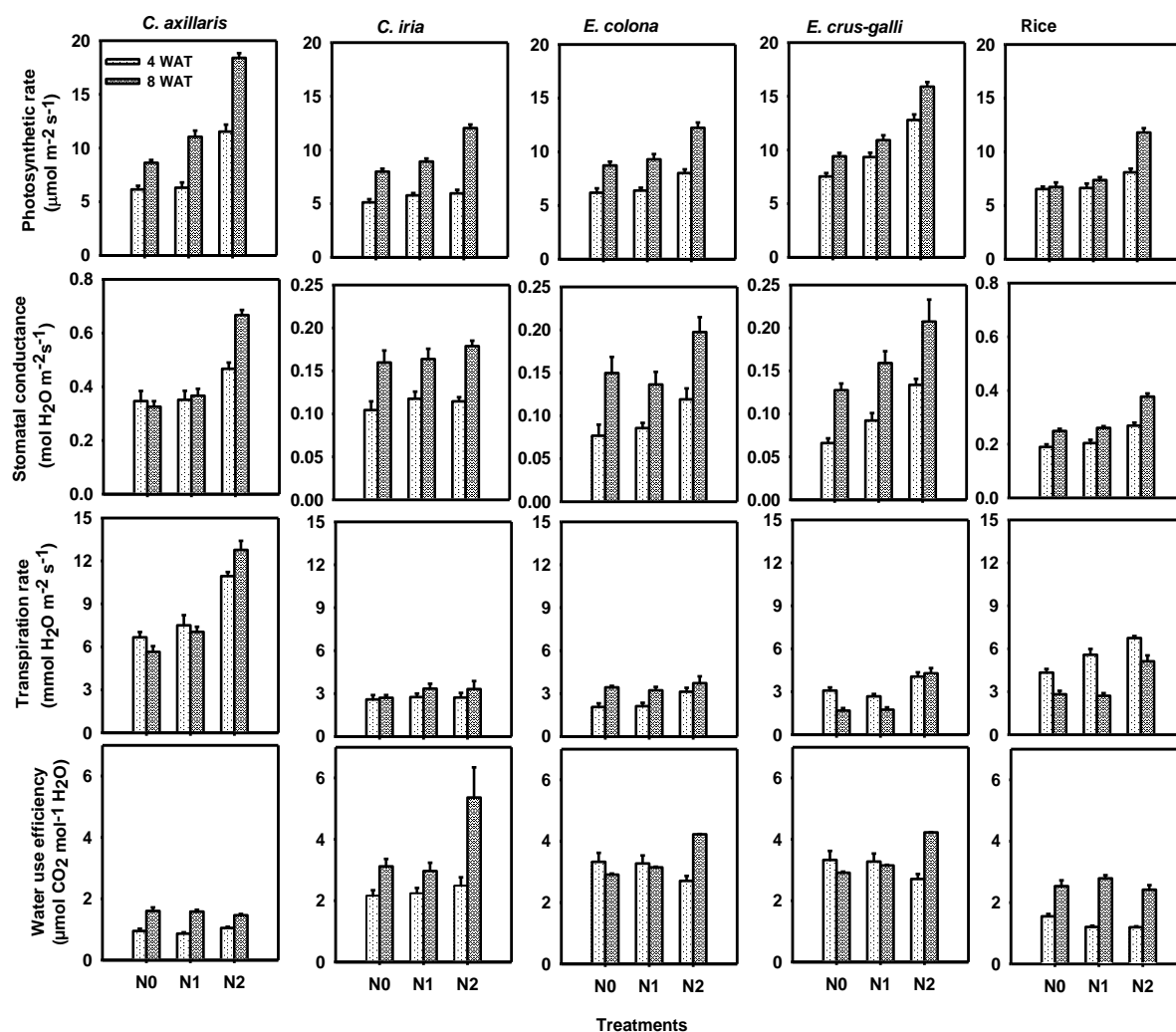


Fig. 6. Effects of nitrogen (N) application on leaf photosynthetic rate (A_{area}), stomatal conductance (g_s), transpiration rate (E) and water use efficiency of weeds and rice measured at different weeks after the rice transplantation. Values are mean of two-year \pm SE.

leaf traits (Fig. 2). Poorter *et al.* (2012) also observed that the effect of N fertilization on SLA is less strong than on biomass allocation and leaf expansion. Further, LAR also varied substantially due to N application in all species. The drastic reduction in LAR (leafiness) observed under low N for most species, could be a consequence of either a decline in LWR, which in turn represents a higher proportion of assimilates allocated to stem growth and/or decline in SLA (Lemaire *et al.* 2008). A significant positive relation between LAR, LWR and SLA support this conclusion (Table 5).

Growth Performance

On account of both the morphological and physiological traits, *C. axillaris* and *E. crus-galli*

were the most efficient weeds with high relative growth rates (RGR) leading to their dominant status. On the other hand *E. colona*, *C. iria* and *F. miliacea* exhibited lower growth performance among all weeds, assuming subordinate status. Ability of a plant to capture resource more rapidly and efficiently than other would provide a higher competitive ability. For majority of species this ability can be described by functional traits such as LAI, SLA, LAR, PNUE, A_{area} , RGR etc. (Dinkguhn *et al.* 1999; Ewe & Sternberg 2003; Lemaire 2001). Better use of nutrients (high PNUE and photosynthetic rate) in combination with high resource capture ability (LAI, SLA and LAR) enables the dominant species (*C. axillaris* and *E. crus-galli*) to grow fast and outcompete the sub-

Table 5. Correlation matrix of ecophysiological traits of rice and its weeds.

	RGR	A _{area}	gs	E	WUE	PNUE	SLA	LAR	LAI	BM	RWR
A _{area}	0.70**										
gs	0.68**	0.31									
E	0.76**	0.55**	0.90**								
WUE	-0.35	0.03	-0.68**	-0.69**							
PNUE	0.55**	0.85**	0.43*	0.55**	0.04						
SLA	0.71**	0.40*	0.96**	0.87**	-0.54**	0.55**					
LAR	0.68**	0.34	0.97**	0.85**	-0.55**	0.49**	0.99**				
LAI	0.82**	0.68**	0.47**	0.70**	-0.37*	0.50**	0.46*	0.42*			
BM	0.21	-0.06	-0.19	-0.02	-0.16	0.28	0.278	0.29	0.51**		
RWR	-0.26	-0.27	-0.01	-0.17	-0.08	-0.15	-0.01	-0.01	-0.37*	-0.14	
LWR	0.77**	0.42*	0.70**	0.65**	-0.22	0.51**	0.78**	0.77**	0.60**	0.01	-0.24

** Significant at $P < 0.01$, * significant at $P < 0.05$.

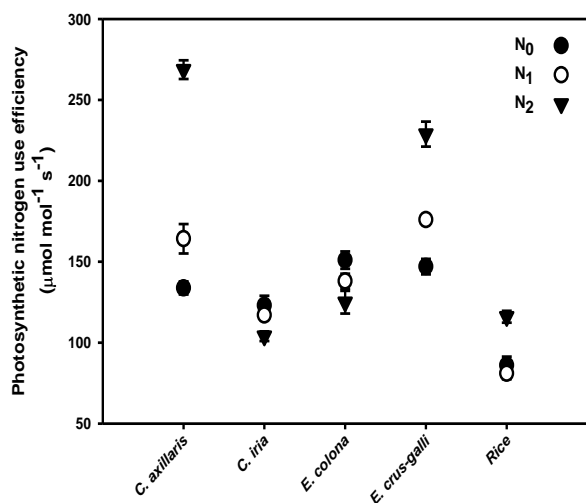


Fig. 7. Photosynthetic nitrogen use efficiency (PNUE) of the weeds and rice at various nitrogen levels. Values are mean of two-year \pm SE.

ordinate species due to resource preemption. This will lead to higher biomass production and consequently to a higher competitive ability for light and nutrients than other species.

According to Wilson and Tilman (1991), N is often limiting at low rates of N supply, but light would more likely be limiting at high rates of N supply. Therefore, it appears that the differences in the response of weeds to increased N supply might be due to a direct effect of N availability on growth traits or due to indirect effects of larger crop canopy. A larger crop canopy intercepts more light and

reduces the light availability at soil level. Therefore, short height species are deprived of light and unable to respond to increase in N supply. Weeds with height almost similar to that of the rice viz. *C. axillaris* and *E. crus-galli* were not shaded out and were able to take advantage of the increased nitrogen supply as height facilitate light capture and thereby confer competitive ability (Funk *et al.* 2016).

In N₁ and N₀ plots, there was relatively low variation in growth traits of weed plants as well as in biomass and density per m². The dominant weeds still had higher LAI, PNUE, A_{area}, RGR and biomass per unit area, but the differences between dominant and subordinate species were lower than that at high nitrogen supply. Because low resource system supports lower growth rates, less aboveground biomass and provides less shading, this leads to lower intensities of competition (Negreiros *et al.* 2014; Wilson & Tilman 1991).

All growth parameters, except for WUE, had significant positive relationship with RGR (Table 5). However, biomass accumulation was only related with LAI, which showed that improved interception of radiation is the main driving force for the enhancement in plant biomass production (Latiri-Souki *et al.* 1998). When stepwise multiple regressions was performed for N₂ plots with RGR as the dependent variable and growth attributes as independent variables, LAI among morphological and PNUE among physio-logical traits were selected by the model. Variability in LAI accounted for 80% variability in RGR. Light is reported to be the primary resource for which weeds compete in

high N-input cropping system (Sinoquet & Caldwell 1995; Wilson & Tilman 1991). The growth parameter critical to the competition for light is LAI, which determine the intensity of competition for light among individual plants (Lemaire 2001) and largely responsible for high photosynthesis in crowded stands (Hikosaka *et al.* 1999). A high photosynthetic rate results in greater growth rate; it has been assumed that the growth rate was about half of photosynthesis (Hikosaka *et al.* 1999; Kirschbaum 2011). According to Hikosaka *et al.* (1999), differences in LAI among species makes competition more asymmetric in crowded stand, which is consistent with our study, where large differences in LAI as well as in A_{area} , biomass accumulation and RGR were observed among weeds. Among physiological traits, PNUE together with LAI explained 91% variability in growth rate. In dense stands, plant growth is determined not only by resource acquisition but also by the efficiency of resource use, because resources obtained are not always used with the same efficiency by different plants (Hikosaka *et al.* 1999). Therefore, high N use efficiency gives the species an advantage to assimilate more C at given N investment, which invariably enhances the growth rate. On the other hand, in N1 and N0 plots, only morphological traits (LAI, SLA and LAR) govern the variability in RGR. This showed that in low resource system, resource acquisition traits are more important for increasing growth rates.

Among all weeds, *C. axillaris* exhibited maximum increase in physiological and leaf traits due to N addition followed by *E. crus-galli*. *C. axillaris* partitioned most of its resources to green parts, which is highly sensitive to nitrogen availability (Cechin & Fumis 2004). In addition, Radin (1983) found that broad-leaved species were more vulnerable to N limitation than graminaceous plants. Among grasses, *E. crus-galli* is the most responsive to nitrogen and can remove up to 80% of the nitrogen from the soil (Holm *et al.* 1991). Our study showed that both of the above weeds are much vigorous in high nitrogen condition and are nitrophilic in nature. In contrast, N application had comparatively little effect on rice and sedges. The ranking of responsiveness to added N was *C. axillaris*>*E. crus-galli*>*E. colona*>rice>*C. iria*>*F. miliacea*. It is important that in low N treatments, rice may be able to withstand weed interference better than in high nutrient conditions. Thus, the study suggests that if the weed assemblage consists of species which are highly responsive to N, then fertilizer management

strategies to favour crops over weeds deserve greater attention. The response of weeds to N could be identified by measuring functional traits among which LAI, PNUE and SLA are the key determinants for predicting competitive potential (in terms of growth rate) of species. Superior performance of *C. axillaris* in the field indicates that in coming years this weeds may be a greater threat to irrigated rice-wheat cropping system compared to the current major grassy weed *E. crus-galli*. Further, high responsiveness of *C. axillaris* to nitrogen makes it more serious in high N input conventional cropping systems. Therefore, for the management of weeds, high N application should be avoided in the area where the incidence of *C. axillaris* weeds is high.

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