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Competitive Interactions between Rice and *Caesulia axillaris* or *Echinochloa crus-galli*: A Replacement Series Study

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Abstract

A replacement series study was conducted to evaluate the competition between rice and *Caesulia axillaris* Roxburgh or *Echinochloa crus-galli (L.)* Beauv at two nutrient levels to investigate that how differences in nutrient availability may change the competitive relationship between rice and weeds. Plants were established in mixture proportions of 4:0, 3:1, 2:2, 1:3 and 0:4 (weed: rice) plants pot[-1]. Both weeds were more competitive than rice under high nutrients. *C. axillaris* exhibited higher Relative Yield (RY) as well Aggressivity (Agr) than rice, whereas *E. crus-galli* showed comparable RY but greater competitive ability (Agr) than rice. Further, nutrient stress had different effects on both weeds; although, nutrient stress decreased the competition intensity of *C. axilaris* against rice, it did not change its position in hierarchy (*C. axilaris* dominated rice). Whereas *E. crus-galli* was outcompeted by rice under low nutrient. Thus, our study showed that weeds are better at high nutrient than are the crop. However, the effect of nutrient on weed competitiveness is not straightforward rather it depends on growth traits and nutrient use efficiency of species.

Keywords: Aggressivity; Competitive ability; Replacement series; Rice; Weed

Introduction

Weeds are one of the most important biological constraints in rice production [1,2]. According to study by, rice research directorate, India [3], grain yield losses due to weeds in these rice fields ranged from 15% to 90%. Studies indicate that among grasses *Echinochloa crus-galli* and broad-leaved weeds *Caesulia axillaris* are the most serious weeds of rice under rice–wheat system of the Indian subcontinent [4-6]. *E. crus-galli*, a vigorous C_4 annual species, is one of the world's most serious grassy weed in rice [7,8]. This species is highly competitive, and its morpho-physiological similarities with rice make control measures difficult [9]. Its infestation in the rice field results in the reduced rice tillering, which results in loss of yield [10] because it strongly competes with the rice for soil N by removing up to 80% of it [10,11]. The aggressiveness of *E. crus-galli* is probably due to its efficient C_4 photosynthetic pathway, high nitrogen and water use efficiency [12]. In contrast, *Caesulia axillaris* (pink node flower) is C_3 broad-leaved weed of family Asteraceae. It is an annual weed, with extended emergence period, relatively fast growth and high seed production; in these studies, it reduced the rice yield by 33% [13,14].

Weed management decisions for a particular species can be derived from a detailed knowledge of its biology and competitive ability [15]. Therefore, understanding the relationship between plant traits and competitive ability has emerged as a major research area [16,17]. Such an understanding would provide a better insight into the processes shaping the vigour of weeds. Generally, plant biomass, height and leaf area has been used to provide information on the size and aggressiveness of the plant, which may determine its competitive ability [18]. In recent years, physiological basis for competitive ability offered a powerful means to predict the consequences of competitive interaction. The physiological traits such as Specific Leaf Area (SLA) and photosynthetic rate (A_{area}), are thought to be linked with resource capture and use efficiency [19]. Differential photosynthetic responses to changes in environmental factors such as nutrient, light can affect species aggressivity. However, little is known about the photosynthetic activity of *E. cruss-gali* and *C. axillaris* growing along with rice.

The competitive performance of weeds and crop often depends on environmental conditions [20]. The resources and the fluctuations in their availability can also play a significant role in the competitive ability of species [21,22]. It has been recognized that among the major resources (light, nutrient and water) competition in rice field between weeds and crop are greatest for nutrients [6,14]. Because in tropics, the majority of rice crop grown in lowland areas by transplanting method (rice field is flooded throughout the crop growth period until the grain matuaration), and as summer crop [5,6]. Therefore, in these areas, water and light were never a limiting factor. It has been found that added nutrients increased the competitive ability of weeds more than their crop [23,24]. Conversely, some studies showed that growth of some weed species is decreased while that of the crop is favored under high soil nutrient levels [25,26]. *C. axillaris* and E. cruss-galli are documented as fast growing and nitrophilic species [7]. Singh et al. [27] reported that fertilization increased the biomass of *C. axillaris* and *E. crus-galli* more than that of rice; however, the biomass of same weeds was decreased as compared to the crop at a low dose of N fertilizer. Therefore, it is important to investigate that how

altered nutrient availability may change the competitive relationship between rice and weeds and which plant traits are the most important to determine competitive ability of weeds and crop. In order to do so for rice agroecosystem, we designed a replacement series study to elucidate how *C. axillaris* and *E. crus-galli* respond in terms of biomass production and physiological performance, when in competition with rice under different nutrient ability. The objectives of the present study was: (i) to study the responses of *E. crus-galli* and *C. axillaris* (including physiological performance, biomass accumulation and partitioning) and rice to one another, and (ii) to elucidate how nutrient stress alters the competitive performance of the weeds (iii) identification of plant trait associated with competitive ability of plant. We hypothesized that weeds would be more competitive than crop at high nutrient but that the crop would outcompete the weeds under low nutrient conditions.

Materials and Methods

The competitive interference of *Caesulia axillaris* Roxburgh and *Echinochloa crus-galli (L.)* Beauv against rice (BPT var.) was studied in a replacement series in an ambient light-temperature condition (natural weather condition) in the green house at the Botanical Garden of Banaras Hindu University Varanasi, (25˚15′N latitudes and 80˚59'E longitudes) from July to October 2011.

Treatments and experimental design

Treatments comprised growing the test crop (rice) and weeds (*C. axillaris* and *E. crus-galli*) in pure stand and, in mixed cultures; with two strength of nutrient solution *viz.* 50% Hoagland's (HN treatment) and 25% Hoagland's nutrient solution (LN treatment). Hoagland's solutions were prepared according to Arnon and Hoagland [28]. The full strength (l/l) solution has a nitrogen concentration of 3mm $Ca(NO_3)_2.4H_2O$ and 2mm KNO_3. Five planting ratios of the two species used in the study were 4:0, 3:1, 2:2, 1:3 and 4:0. Treatments were replicated five times in a randomized complete block design. For calculations, we report only three replicates for each treatment because some pots were damaged providing a lower number of replicates per treatment. Thus to maintain uniformity, data measured from three replicates. In some mixture proportion where no damage was recorded, we had taken result from all five replicates, but it was not significantly different from the data measured at three replicates. The final sizes of the plants in HN treatments were consistent with the range of sizes observed in the field, suggesting that the nutrient levels were within the range that these species experienced in the field. To ensure that planting density would be enough to result in interference; pilot studies were conducted before deciding to set total plant density in monocultures at four plants pot-1. Species were grown from seeds, collected from a nearby agricultural field. Seeds were germinated on moist filter paper in petridishes at 25˚C before the experiment started germination rates were above 90%. To avoid the replacement series experiment problem of initial size bias [29], all seedlings were used in the experiment of similar size. Plants were grown in plastic pot (20-cm-diam by 18-cm-deep). Each pot was filled to a depth of 15 cm with fine river sand. Sufficient water per day and 100 ml of Hoagland nutrient solution at the interval of three days were provided to assure normal plant growth. Pots were flushed once a month with distilled water to prevent salt accumulation. Supplementary watering without nutrients was applied during the evening. Each pot is covered with

perlite (about 2.0 cm) to reduce the compaction caused by watering and evaporation from soil surface. Pots were re-randomized weekly to avoid the creation of microclimates and species in mixtures were mixed uniformly and distributed equidistantly in the sand.

Plants were harvested at 70 days after transplantation when physiological maturity achieved in plants. Three replicates were collected for each species in each treatment. Shoots and roots were separated and placed in separate paper bags and transported to the laboratory in ice bags. Harvested plant parts were then dried in an oven at 80˚C for 48 h. From the biomass data, the aggressivity of the species towards each other and relative yield and Relative Yield Total (RYT) of each species combination were computed. Leaf Area (LA) was determined using a leaf area meter (SYSTRONICS, Leaf area meter-211). Specific Leaf Area (SLA) (cm^2 g^{-1}) was calculated as area per unit mass. Leaf Area Ratio (LAR) was calculated as the ratio of leaf area to plant weight. LA, SLA and LAR are widely used variable in comparative plant ecology, because they are associated with many important attributes of plant growth and survival. A superior SLA may increase the capacity of the plant to assimilate CO_2 because more leaves are produced for a given mass of carbon invested in photosynthetic tissues [30,31]; and therefore, provides a higher rate of return on the resources invested when compared to species with a lower SLA. For herbs and grasses, variation in LAR is the key determinant of interspecific variation in RGR [32]. Thus, the more plant invests in leaf area, the higher the total carbon gain and the faster growth will be achieved.

Photosynthetic rate (A_{area}), the plants was measured by LI-6400 gas exchange system (LI-COR, Lincoln, Nebraska, USA) on the upper-most, 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-µmol s^{-1}. Air temperature was 32 ± 0.15˚C and CO_2 concentration was 385±5 µmol CO_2 mol^{-1}. Photosynthetic Active Radiation (PAR) was 1221±36.20 µmol mol^{-1} at the time of experiment. Higher rates of photosynthesis can lead to increased growth rates, biomass accumulation and overall production [33]. Additionally, high carbon gain and growth may confer high competitive ability to species so that they easily out compete the slow growing species by facilitating colonization or resource acquisition [30].

Competition indices

Relative Yield (RY) and Relative Yield Total (RYT):

RY = Yab/Yaa

RYba = Yba/Ybb

In this study, RY and RYT were calculated by whole plant dry weight data. Yab is the total biomass production of species 'a' in a mixture with species 'b' and Yaa is the biomass production of species 'a' in monoculture. Yab/Yaa is relative yield of species 'a' in mixture with species 'b' and vice versa; Yba is the total biomass production for species 'b' in mixture with species 'a', and Ybb is the biomass production of species 'b' in monoculture.

RYT is a measure of resource complementarity. RYT value of 1.0 indicates that the two species have equal demands for the same limiting resources of the environment. A RYT value greater than 1.0

Table 1: Summary (F and P values) of analysis of variance for the effects of species, mixture ratios and nutrient treatments on ecophysiological and biomass partitioning parameters.

	Species ($F_{3,60}$)	Treatment ($F_{1,60}$)	Mixture ($F_{3,60}$)
Leaf Area (LA)	1432***	379***	164***
Specific Leaf Area (SLA)	1548***	87.4***	2.7
Leaf Area Ratio (LAR)	441***	48.4***	1.10
Photosynthetic Rate (A_{area})	20.7***	250.9***	22.2***
Biomass	410.7***	236.5***	193.6***
Root Weight Ratio (RWR)	47.2***	130.0***	0.9
Leaf Weight Ratio (LWR)	21.6***	44.7***	0.9
Relative Yield (RY)	15.02***	19.1***	314.8***
Relative Yield Total (RYT)	14.8***	22.6***	1.3
Aggressivity (Agr)	96.4***	21.8***	126.8***

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

means that, although the species may compete for the same resources, they also make demands on different resources. A RYT value less than 1.0 indicates mutual antagonism [34,35].

In replacement diagrams, actual RY of each species was plotted against the appropriate planting proportion. Expected RY for a species occurs when plants of this species grow equally well in mixture and monoculture. Comparisons of actual RY of each species with their expected RY (diagonal dashed line in replacement diagrams) indicate: (1) competition if the actual RY curve of one species is concave and that of the second convex, (2) niche differentiation if actual RY curves of both species are convex, or (3) mutual antagonism if actual RY curves of both species are concave. If actual RY curves are linear (i.e., do not differ from expected), the ability of one species to interfere with the other is equivalent.

Aggressivity (Agr): It is an index for the measure of the intensity of plant competition. It is used by McGilchrist & Trenbath [36] for
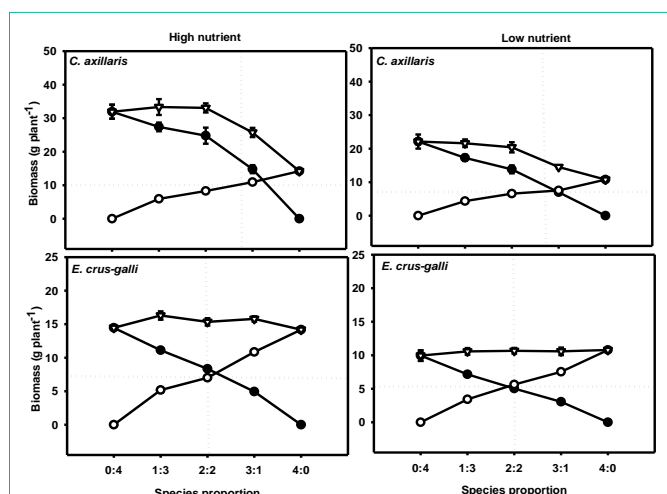

Figure 1: Biomass production of the *C. axillaris* (●), *E. crus-galli* (●), rice (O) and total biomass per pot (∇) at different mixture ratios under High Nutrient (HN), and Low Nutrient (LN) treatments. Vertical lines are standard errors. Two straight lines in each frame indicate the theoretically expected responses for two equally competitive species, which intersect at the point of equivalency, Harper [51].

the first time. Gain or loss of biomass due to interspecific competition was determined by calculating Aggressivity (Agr) for each species. A dominant species will have a higher aggressivity index than a dominated species [37].

$$Aab = (Yab/Yaa \times Zab) - (Yba/Ybb \times Zba)$$

Where Yab, Yba, Yaa, and Ybb are as defined in previous equation. Zab and Zba are sown proportions of crop "a" and "b" in the mixture. If Aab=0, both species are equally competitive, and if Aab is positive then species 'a' is the dominant species, while a negative value for Aab means that 'a' is the dominated species and *vice versa*.

Statistical analysis

An analysis of variance (Procedures in SPSS 17.0) was used to partition the main effects of species, mixture ratios, nutrient level. RY and RYT from each mixed culture were compared to the value of 1.00 using t-tests (P=0.05). The data were log-transformed before analysis to normalize statistical distributions and meet with the assumptions of the ANOVA.

Results

Biomass production

ANOVA indicated that species, nutrient treatment and the mixture proportion had significant effects on plant biomass. A summary of the analysis of variance of the effects of species, nutrient level, mixture ratio is presented in (Table 1).

In monoculture, *C. axillaris* had significantly greater biomass than rice at the end of the experiment, and biomass production per pot of *C. axillaris* was greater than that of rice by 125 % under High Nutrient (HN) treatment, and 105 % under Low Nutrient (LN) treatment (Figure 1). However, *E. crus-galli* had almost similar biomass to rice. Nutrient stress had great negative effect on biomass production of all studied species. Compared with the HN treatment, LN treatment decreased the DW of *C. axillaris* by 44%, *E. crus-galli* by 45% and rice by 32%, respectively (Figure 1). Lines with constant slopes would present equal competition between species across all ratios, resulting in an intersection point of the two curves at the 2:2 ratio. As shown in (Figure 1) the plot of *C. axillaris* and rice interaction did not intersect at the 2:2 ratio, indicating frequent occurrence of interspecific competition where growth of rice was restrained in the mixtures. However, the plot of *E. crus-galli* and rice showed almost constant slope and intersect at the 2:2 ratio, reveals that relative gain in biomass of one species in a mixture was equal to loss in a biomass of other species. Consequently, the sum of biomass of *E. crus-galli* and rice at each proportion was similar to that of each species grown in monoculture. It implies that both species are equivalent in competitiveness (i.e. rice could be substituted for *E. crus-galli* or *E. crus-galli* for rice on an equal basis, with a similar effect on biomass production).

Relative Yield (RY) and Relative Yield Total (RYT)

Relative Yield (RY) differed significantly among treatment, mixture proportion and species; however, RYT varied only in treatment and species (Table 1). The replacement diagram illustrated in Figure 2 is interpreted based on the shape of the curves derived from the dry weight of each species. Actual RY of *C. axillaris* was significantly higher than expected in each proportion under HN
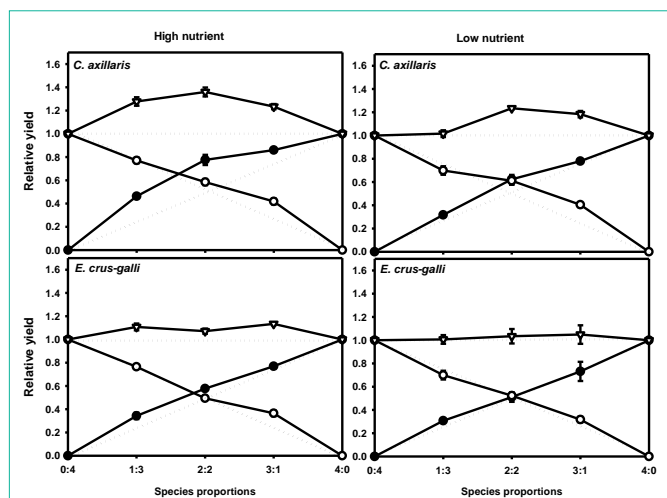
Figure 2: Replacement series diagrams illustrating mean ± SE relative yield of *C. axillaris* (●), *E. crus-galli* (●), rice (O) and relative yield total (∇) as a function of species proportions. The diagonal dashed lines are the expected relative yields when plants of a species grow equally well in mixture and in monoculture of *C. axillaris*, *E. crus-galli* and rice under different nutrient treatments.

Figure 3: Leaf area of *C. axillaris* (●), *E. crus-galli* (●), rice (O) and total leaf area per pot (∇) at different mixture ratios under High Nutrient (HN), and Low Nutrient (LN) treatments. Vertical lines are standard errors. Two straight lines in each frame indicate the theoretically expected responses for two equally competitive species, which intersect at the point of equivalency, Harper [51].

Table 2: Aggressivity (mean ± SE) of *C. axillaris* (CA), *E. crus-galli* (ECg), when grown with rice at different mixture ratios under different nutrient treatments.

	CA × Rice		ECg × Rice	
Weed:rice ratio	HN	LN	HN	LN
3 : 1	2.15 ± 0.09	1.93 ± 0.02	1.94 ± 0.08	1.68 ± 0.12
2 : 2	0.55 ± 0.03	0.03 ± 0.01	0.17 ± 0.06	-0.03 ±0.01
1 : 3	-0.92 ± 0.07	-1.15 ± 0.14	-1.95 ± 0.02	-1.79 ± 0.12

Table 3: Specific Leaf Area (SLA; cm^2 g^{-1}) and Leaf Area Ratio (LAR; cm^2 g^{-1}) of *C. axillaris* (CA), *E. crus-galli* (ECg) and rice at different mixture ratios under High Nutrient (HN) and Low Nutrient (LN) treatment.

Traits	SLA		LAR	
Treatments	HN	LN	HN	LN
$CA_{monoculture}$	324 ± 1.2	318 ± 1.8	87 ± 17.1	70 ± 4.7
CA_3: $Rice_1$	325 ± 0.8	317 ± 2.5	80 ± 3.9	73 ± 4.8
CA_2: $Rice_2$	330 ± 7.5	322 ± 1.5	77 ± 11.6	68 ± 3.3
CA_1: $Rice_3$	318 ± 1.8	319 ± 1.6	75 ± 8.9	67 ± 7.1
$Rice_{monoculture}$	170 ± 1.5	166 ± 0.2	35 ± 5.8	28 ± 3.9
$Rice_3$: CA_1	170 ± 0.8	168 ± 1.5	39 ± 1.6	29 ± 2.8
$Rice_2$: CA_2	171 ± 1.8	165 ± 1.0	35 ± 2.6	27 ± 3.5
$Rice_1$: CA_3	170 ± 0.7	164 ± 1.3	41 ± 7.5	21 ± 1.3
$ECg_{monoculture}$	144 ± 5.0	126 ± 1.7	23 ± 1.4	18 ± 3.3
ECg_3: $Rice_1$	133 ± 1.4	127 ± 1.1	23 ± 1.5	19.9 ± 4
ECg_2: $Rice_2$	129 ± 1.5	128 ± 1.0	21 ± 3.0	18 ± 2.3
ECg_1: $Rice_3$	128 ± 0.2	131 ± 1.1	22 ± 1.3	16 ± 3.7
$Rice_3$: ECg_1	170 ± 0.9	168 ± 1.5	34 ± 2.4	29 ± 5.3
$Rice_2$:ECg_2	172 ± 1.1	165 ± 0.6	38 ± 2.8	28 ± 3.7
$Rice_1$:ECg_3	171± 2.4	163 ± 1.0	37 ± 3.0	32 ± 4.9

whereas actual RY of rice did not differ from expected with the exception of 1:3 ratio. The plot of RY data of *C. axillaris* and rice intersect at the left of the 2:2 mixture (Figure 2), indicating that *C. axillaris* was a better competitor of resources than rice. Conversely, under LN the lines intersect almost at the point of equivalency (2:2 mixture ratios) of the expected yield, demonstrating that the weed and rice have a relatively similar interspecific effect on biomass production of one another.

Actual RY of *E. crus-galli* and rice, when grown together, were not significantly differ from expected values in each mixture proportion under LN treatment. However, it was little higher from expected values in *E. crus-galli* under HN treatment. The plot of RY data of *E. crus-galli* and rice intersected almost at the point of equivalency in both nutrient treatments, indicating that both species were equally competitive for resources.

Mixtures were over yielding i.e. RYT was higher than 1.0 under HN regardless of weed species. Whereas, under low nutrient, RYT was near unity for *E. crus-galli* and rice mixture while significantly higher than 1 for *C. axillaris* and rice mixture except in the 1:3 mixture ratio (weed:rice).

Competitive ability

Aggressivity (Agr) an index to calculate competitive ability, differed significantly between species and nutrient treatments (Table 1). *C. axillaris* and *E. crus-galli* had a positive and rice a negative aggressivity with the exception at 1:3 (weed: rice) planting ratio,
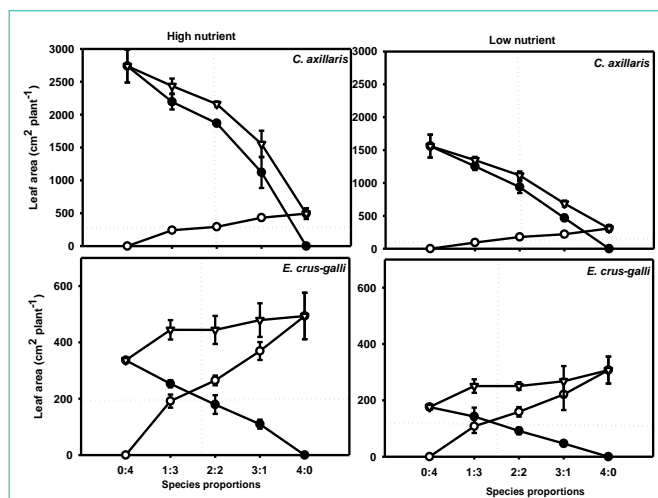
suggesting that both weeds were dominant and rice the subordinate species under high nutrient treatment (Table 2). Aggressivity of *C. axillaris* was greater than that of *E. crus-galli* under both nutrient treatments. Aggressivity values of *C. axillaris* and *E. crus-galli* declined as its density decreased in the mixture, and were negative at the weed: crop planting ratio of 1:3. Low nutrient significantly reduced the aggressivity values of both weeds and even negative value observed for *E. crus-galli* at 2:2 ratio (Table 2).

Growth attributes

We observed significant species, mixture and nutrient treatment effects on LA; however, LAR and SLA showed only species and

Figure 4: Photosynthetic rate of *C. axillaris* (●), *E. crus-galli* (●) and rice (O) at different mixture ratios under High Nutrient (HN), and Low Nutrient (LN) treatments. Vertical lines are standard errors. Two straight lines in each frame indicate the theoretically expected responses for two equally competitive species, which intersect at the point of equivalency, Harper [50].
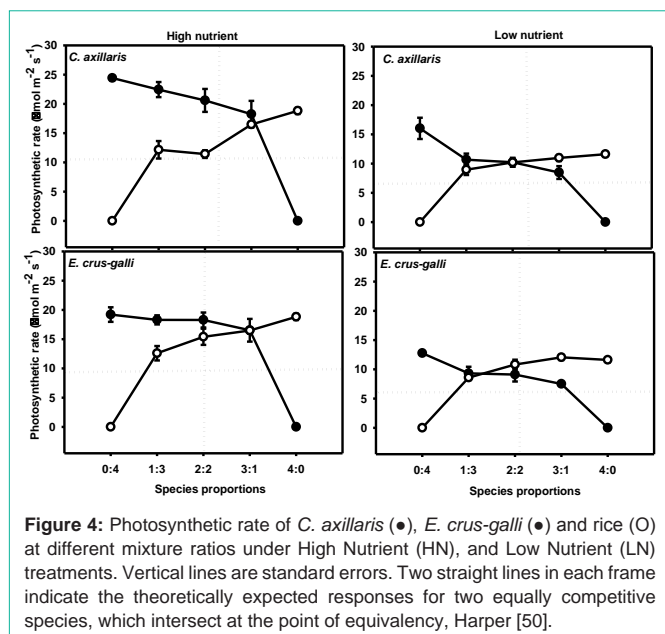
treatment effects (Table1). *C. axillaris* showed greater LA, SLA and LAR than rice in mixture; however, *E. crus-galli* exhibited less LA, SLA and LAR as compared to rice in mixture under both nutrient treatments (Table 3).

Leaf area of the both weeds declined linearly as the number of rice plant increased in the pot. In *C. axillaris*, the decrease in LA in mixture with rice than monoculture was higher in low nutrient (43%) as compared to high nutrient (36%), while *E. crus-galli* showed almost similar decrease in both nutrient treatments. The plot of LA of rice and *C. axillaris* intersects at the right of the point of equivalence i.e. at 3:1 planting ratio (rice: *C. axillaris*) in both nutrient treatments (Figure 3), again showing the dominance of *C. axillaris* in the mixture. However, the plot of *E. crus-galli* and rice intersect close to the 2:2 ratio in both nutrient treatments.

Physiological attributes

Species, treatment and mixture significantly influenced photosynthetic rate (A_{area}) (Table 1). Both weeds showed higher A_{area} as compared to rice in mixture under HN. Under LN, Aarea of *C. axillaris* reduced but were never lower than rice; however, *E. crus-galli* exhibited lower A_{area} than that of rice (Figure 4). Both weeds showed larger reduction in A_{area} under LN, while rice showed greater decrease under HN treatment. The step-wise multiple regressions revealed that among the growth attributes and biomass accumulation, Leaf Area (LA) had the largest influence on competitive ability (Agr) of plants. It was observed that the variation in LA accounted for 54.5% variation in Agr. The final model was Agr = −0.22LA + 0.74 (R^2 = 0.54 P = 0.04).

Discussion

The species with the greater competitive ability is usually termed as dominant species or superior competitor, and has a greater ability to acquire resources and to occupy the superior ecological niche [38]. Positive Agr value indicates increased ability for competition; therefore, *C. axillaris* and *E. crus-galli* were more competitive and rice was less competitive when grown in equal proportion. However, data on the relative yield reveals that *C. axillaris* was a superior

competitor when grown in mixture with rice while, there was equal competition between *E. crus-galli* and rice. Therefore, more than one approach for determining competitiveness is required. Interspecific competition was greater at HN than LN treatment, which suggests that the intensity of competition enhanced with increasing resource availability [39]. Further, the result indicated greater competitive ability of *C. axilaris* than *E. crus-galli* with rice. Rapid development due to superior growth traits of *C. axillaris* at early growth stages was likely to responsible for its competitive advantage. The nutrient stress did change the competition intensity between *C. axilaris* and rice, but did not change the position in hierarchy i.e. *C. axilaris* holds a competitive advantage over rice. Conversely, the value of aggressivity for *E. cruss-galli* was negative, implies that it was dominated by rice in pot. One feasible explanation for the reduced competitiveness of *E. cruss-galli* in low nutrient may be that *E. cruss-galli* competitiveness is highly dependent on nitrogen as also found in the study of Holm et al. [7].

The RYT gives an accurate assessment of the greater biological efficiency in competitive situation [40]. The RYT value of mixtures in HN treatment were greater than 1.0, regardless of the planting ratio and weed type, indicating that while the two species competed for resources, but complementary facilitation dominated over the competitive interference. Moreover, RYT values higher than 1.0 and lower than 2.0 indicate that resource complementarity and competition interference between the crop and weeds occurred at the same time [41]. Other studies on crop and weed mixtures have also attributed values of RYT > than 1 [42-44]. The mixture of *E. crus-galli* and rice showed RYT close to one (> 1.2) in HN and equal to 1 in LN (Figure 2), which showed that both the species required the same limiting resources for successful growth. It could be possibly due to the similarity in their growth habit, rooting architecture, shoot and leaf morphology as both species in mixture belong to same life form (grasses). Usually, species with similar growth habits could make similar demands on the limited resource for growth, but the differences in their efficiency in utilization of these resources makes them a better competitor [45]. Further, values of RYT always greater than 1 in *C. axilaris*-rice mixture, implies that the crop exploited the resources somewhat differently than did *C. axilaris*, probably, due to different rooting depths between the two species as both species belongs to distinct life form.

Understanding of the trait-specific growth parameters aids the explanation of potential mechanisms by which resource exploitation can provide competitive ability [46]. Several traits are known to be affect biomass accumulation and thereby competitive ability *viz.* RGR, A_{area}, SLA and LA [46,47]. There was considerable variation among the three species for each growth traits; *C. axilaris* showed significantly higher values of SLA, LA and Aarea, among all. This result is consistent with the results of competitive indice, where *C. axilaris* exhibited highest value of Agr. In this instance, the high competitive ability (Agr) of *C. axilaris* observed in this study can be explained in terms of its prolific rooting system [27], which enables to capture more of soil water and nutrients. In addition, high LA and SLA enables it to produce more assimilates by providing greater surface area for photosynthesis which translated into high RGR. Moreover, although *E. crus-galli* had relatively comparable biomass and relative yield in the mixture with rice under HN, it exhibited

greater competitive ability than rice. Therefore, it can be speculated that comparatively higher photosynthetic rate than rice could be responsible for its increased competitive potential. Conversely, despite of relatively similar biomass to rice, these traits were lower in LN treatment, which results in negative Agr than rice. This result supports the view of Weigelt et al. [48], who reported that competitive strength of a species could be determined through species-specific traits and biomass allocation strategies.

Stepwise multiple regressions were performed to determine which growth parameter influenced the aggressivity most. In this study, stepwise regression picked up LA as the most important trait, which accounted for the greatest amount of variability in Agr, emphasizing the role of leaf area in determining the competitive potential of rice and weeds across the gradients of nutrient availability. Rapid leaf area development in plants is beneficial for light competition [1]; in addition, high leaf area contributes to competitiveness by increasing growth rate, which resulted in rapid biomass accumulation of the plant [1,49,50]. However, leaf area could explain only 54.5% variability in Agr, indicating that other traits, not studied by us are also important in modulating the competitive ability of weeds and rice.

Conclusion

This study showed that nutrient availability had different effects on the different species. *C. axilaris* was the superior competitor than rice at both higher and lower nutrient levels. Although nutrient stress decreased the competition intensity of *C. axilaris* against rice, it did not change its position in the hierarchy. Unlike *C. axilaris*, *E. crus-galli* performed poorly in nutrient stress conditions (as shown by the competitive indices) and was outcompeted by rice. Thus, our study is consistent with the hypothesis that weeds are better at high nutrient than are the crop. However, contrary to our expectations, the low nutrient had little effect on *C. axilaris* competitiveness; only *E. crus-galli* showed a decrease in competitiveness. Thus, it appeared that the effect of nutrient on weed competitiveness is not straightforward rather it depends on growth traits and nutrient use efficiency of species.

Acknowledgement

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