RESEARCH PAPER

Ecophysiological characteristics of five weeds and a wheat crop in the Indo-Gangetic Plains, India

VARTIKA SINGH, SWETA GUPTA, HEMA SINGH* and AKHILESH SINGH RAGHUBANSHI
Ecosystems Analysis Laboratory, Banaras Hindu University, Varanasi, India

The objective of this research was to compare selected ecophysiological parameters for a wheat crop found in the Indo-Gangetic Plains of India and its five dominant weeds. The dominant and regionally ubiquitous weeds in the wheat field that was selected for the study were Anagallis arvensis, Chenopodium album, Melilotus albus, Phalaris minor and Rumex dentatus. Taller weeds, such as C. album and P. minor, constituted one group along with the crop, with a low photosynthetic rate, specific leaf area, leaf nitrogen mass basis, chlorophyll content, photosynthetic-nitrogen-use efficiency and leaf area ratio, in comparison to shorter weeds, such as A. arvensis, M. albus and R. dentatus, which formed another group with a high photosynthetic rate, specific leaf area, leaf nitrogen mass basis, chlorophyll content, photosynthetic-nitrogen-use efficiency and leaf area ratio. Interspecific variations in the photosynthetic rate were driven mainly by variability in the specific leaf area and leaf nitrogen content. The taller weeds and the crop had a low specific leaf area later in the season, whereas the smaller weeds had a relatively high specific leaf area, which might be an adaptation to the shaded environment below the canopy. The result indicates that any weed management in the wheat fields of the Indo-Gangetic Plains will need two different approaches because of the different strategies followed by the two weed groups that were identified in the present study.

Keywords: discriminant analysis, Indo–Gangetic Plains, photosynthetic nitrogen use efficiency, Rumex dentatus, wheat field.

Weeds are among the most critical factors affecting the crop yield (Holt & Orcutt 1991) and are responsible for the worldwide productivity decline in various agricultural crops. In India, weeds account for ~37% of the total annual loss of agricultural produce from various pests (Yaduraju 2006). Acting at the same trophic level as the crop, weeds capture the available resources that are essential for crop growth. Thus, leaving weeds uncontrolled will eventually lead to a significant reduction in crop yield and quality. The features that confer competitive superiority to weeds are vigorous shoot and root growth, rapid leaf canopy development, architecture, height, rates of transpiration, photosynthesis and conductance, water use efficiency (Patterson 1995) and high growth rate (Mohler 2001).

Wheat (Triticum aestivum L.) covers ~17% of the total world’s cropped land and contributes 35% of the staple food and 20% of the calories (Chhokar et al. 2006). It is one of the major cereals in India, grown over an area of ~25 million ha (Sharma et al. 2004), and is used as a staple food for a large population (Chhokar et al. 2006). However, weeds are the major constraint in the production of wheat in India as they reduce crop yields by 22.7% (Varshney 2007).

Studies indicate that Phalaris minor Retz, Chenopodium album L., Melilotus indicus L., Avena fatua L., Rumex dentatus L. and Polygonum plebeium R.Br. are the most frequent weeds in irrigated wheat under the rice–wheat system of the Indian subcontinent (Mustafee 1991; Sharma et al. 2004; Tiwari et al. 2007; Vashisht et al. 2008). Phalaris minor Retz. among the grassy weeds and R. dentatus L. among the broad-leaved weeds are of major concern in India (Balyan & Malik 2000; Chhokar...
et al. 2006). The dominance of these two species is influenced by tillage practices as continuous zero-tillage has been shown to lower P. minor incidence and increase the build-up of R. dentatus (Sharma et al. 2004; Tiwari et al. 2007). Alarmingly, P. minor has developed extensive isoproturon resistance due to the latter’s continuous use (Yaduraju 1999; Chhokar et al. 2006). Similarly, C. album L., considered to be among the first five most important weeds in the world, is becoming a serious threat due to the origin of its herbicide-resistant races (Aper et al. 2010).

Singh et al. (2008) discussed the dynamics of the functional groups of weed flora in wheat fields of the Indian Indo-Gangetic Plains on the basis of life form. However, it is necessary to further characterize the weed flora based on their ecophysiological traits that determine their pattern of resource capture and competitive ability. Ecophysiological traits regulate ecosystem processes (Wardle et al. 1998; Díaz et al. 2004), actively influence ecosystem properties, such as resource availability and dynamics, and determine the resource capture ability of any competing species (Kropff et al. 1992). Studies indicate that species with high rates of photosynthesis, transpiration and decomposition have a fast growth rate (Chapin 1993). Similarly, the specific leaf area (SLA) has been shown to correlate positively with traits that allow the plant to acquire external resources rapidly (Poorter & Garnier 1999). According to Storkey (2006), species with a similar ecophysiological profile will have a similar function in terms of competition.

Simulation models have been developed recently in which the mechanisms of interplant competition are described based on plant physiology (see Caldwell et al. 1996). In order to calibrate empirical models of crop yield loss based on relative weed green area to different growing seasons, detailed knowledge of the ecophysiological growth characteristics of weeds and crops is necessary (Storkey 2004). Many of these parameter estimates can vary among crop genotypes, species and cultural practices. The objective of this research was to compare the estimates of selected ecophysiological parameters for a wheat crop and its five dominant weeds that are found in the Indo-Gangetic Plains of India. The area has a tropical monsoonal climate with a cold winter (November to February), a hot summer (April to June) and a warm rainy season (July to September).

MATERIALS AND METHODS

The study was conducted from December 2008 to April 2009 at the research farm of the Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India. The farm (25°15′N, 80°59′E) was situated 76 m a.s.l. The annual rainfall at the study site averages 1100 mm, of which >85% falls during the rainy season from the south-west monsoon. The details of the rainfall and temperature conditions of the area are given in Figure 1. The soil is alluvial, well-drained, pale brown, silty loam, Inceptisol with a neutral reaction and is low in available N and K (Singh et al. 2011).

Experimental design

The experiment was set in a completely randomized block design with three replicate plots (each

---

Fig. 1. Mean daily temperature and rainfall during the study period (2008–2009) at Banaras Hindu University, Varanasi, India. (□), Rainfall; (●), temperature.
Kundan variety is a high-yielding (4.0–4.5 t ha\(^{-1}\)), semidwarf variety of wheat. Its life cycle continues for ≤125–130 days after sowing (DAS). These fields had been subjected to the same treatments, as described below, for the past 12 years and followed a rice–wheat–fallow crop rotation. The fertilizer application of NPK followed the regional practices. The basal treatments of KCl and P\(_2\)O\(_5\) were applied at the rate of 80 and 40 kg ha\(^{-1}\), respectively, P\(_2\)O\(_5\) being applied in the form of single superphosphate and KCl being applied in the form of potash at the time of sowing. Nitrogen was applied as urea at the rate of 120 kg N ha\(^{-1}\) in three split doses. The first dose of urea (40 kg N ha\(^{-1}\)) was applied at the time of sowing; other two doses (40 kg N ha\(^{-1}\)), were applied to top dressing during the active tillering (30 DAS), and flowering stages (60 DAS) of wheat, respectively. In order to avoid water shortages until harvest, the plots were surface-irrigated weekly.

The weeds were allowed to develop in the wheat plots without physical and chemical control.

The weed composition was analyzed by using two 50 cm × 50 cm randomly placed quadrats in five wheat fields of the study area. For each weed species, the Importance Value Index (IVI) was calculated as the sum of the relative values of frequency, density and dominance. Based on this analysis, five dominant weeds were selected for the study; namely, Anagallis arvensis, C. album, Melilotus albus, P. minor and R. dentatus. (Table 1). Other authors also have reported that these are the most important weeds in the Indo-Gangetic Plains, in terms of ubiquitous dominance and crop damage (Mustafee 1991; Sharma et al. 2004; Tiwari et al. 2007; Vashisht et al. 2008).

Phalaris minor Retz. (littleseed canarygrass) is an annual exotic and the most noxious weed of wheat in a rice–wheat system over an area of ~10 million ha in India. The plant height approaches ≤100 cm; at maturity, P. minor inflorescences can be taller than the dwarf wheat varieties. Chenopodium album (common lambsquarter) is a fast-growing, broad-leaved winter weed of the family Chenopodiaceae, reaching heights of ≤150 cm. Rumex dentatus L. is a small-seeded, broad-leaved weed of wheat, commonly known as “toothed dock” or “jungali palak”, growing to a maximum length of ~12 cm; however, after flowering, it produces a slender, erect stem ≤70–80 cm in height. Melilotus albus (sweet clover) is a dicot legume, reaching 10–50 cm in height. Anagallis arvensis is a dicot, annual or perennial plant, reaching ~30 cm in height.

Monitoring of the physiological and leaf traits

Naturally occurring weed populations in the wheat plots were used for monitoring of the traits. Data on the physiological traits of wheat and its weeds were collected at the grain maturation stage of wheat (75 DAS). At the time of the experiment, R. dentatus, M. albus and A. arvensis were in the flowering stage; however, >50% of the populations of P. minor and C. album had started fruiting. Therefore, for convenience, only those plants of P. minor and C. album that had started fruiting were used. Three individuals per species from each of the three plots were selected for the experiment. The uppermost, youngest, fully grown and apparently healthy leaf from each individual on sunny days between 08.00 hours and 11.00 hours local time was used for the experiment.

The photosynthetic rate (A), stomatal conductance (gs) and transpiration rate (E) of the plants were measured with a gas exchange system (LI-6400; LI-COR, Lincoln, NE, USA). The rates were determined at, or near, light-saturating conditions (mean photosynthetically active radiation: 1305.2 ± 64 μmol m\(^{-2}\) s\(^{-1}\)). The flow rate was maintained at 500 μmol s\(^{-1}\). During the measurement, the air temperature was 29.3°C ± 0.6°C and the leaf temperature was 28°C. The vapor pressure deficit, based on the measured leaf temperature, varied by 2.3 ± 0.05 kPa. The relative humidity ranged from 35% to 38% and the CO\(_2\) concentration was 380 ± 5 μmol CO\(_2\) mol\(^{-1}\). The leaves were held in the chamber until the photosynthesis values became constant. The water use efficiency (WUE) was calculated as the ratio of A/E. The photosynthetic nitrogen-use efficiency (PNUE) was calculated as the ratio of A to leaf N concentration per unit area.

The harvested plants were separated into the roots, stems, leaves and inflorescences. The leaves were separated into green and senesced leaves and the leaf area measurements were made on the green leaves with a leaf area meter (211; Systronics, Dubai, United Arab Emirates). The plant parts then were oven-dried to a constant weight at 70°C for 48 h. The specific leaf area (SLA) (the abbreviations are listed in Table 2) was calculated as the area per unit mass, while the leaf area ratio (LAR) and leaf mass ratio (LMR) were calculated as the ratio of leaf area and total plant weight and leaf mass to total plant weight, respectively.

The relative growth rate (RGR) and net assimilation rate (NAR) were determined by using the following expression (Evans 1972; Hunt & Cornelissen 1997):

$$RGR = \frac{(\ln W_f - \ln W_i)/(T_f - T_i)}$$

© 2015 Weed Science Society of Japan
Table 1. Relative frequency (RF), relative density (RD), relative dominance (RA) and Importance Value Index (IVI) of the dominant weed species that were found in the wheat agroecosystem under study on different days after sowing (DAS)

| Species                  | 25 DAS       | 60 DAS       | 90 DAS       | 105 DAS       |
|--------------------------|--------------|--------------|--------------|--------------|
|                          | RF | RD | RA | IVI | RF | RD | RA | IVI | RF | RD | RA | IVI | RF | RD | RA | IVI |
| Phalaris minor           | 11.1 | 26.1 | 20.2 | 57.4 | 9.6 | 19.2 | 16.2 | 45.0 | 9.3 | 21.3 | 17.9 | 48.5 | 11.4 | 23.6 | 18.4 | 53.4 |
| Melilotus albus          | 10.6 | 14.6 | 11.9 | 37.1 | 9.6 | 21.9 | 18.5 | 50.0 | 9.3 | 17.7 | 14.9 | 41.9 | 11.4 | 19.2 | 14.9 | 45.5 |
| Chenopodium album        | 10.6 | 22.7 | 18.0 | 51.3 | 9.6 | 15.1 | 12.7 | 37.4 | 8.2 | 16.1 | 15.1 | 39.4 | 9.5 | 15.8 | 14.3 | 39.6 |
| Anagallis arvensis       | 7.4  | 5.2  | 6.0  | 18.6 | 8.8 | 5.7  | 5.3  | 19.7 | 9.3 | 6.6  | 5.5  | 21.5 | 7.6  | 5.0  | 5.9  | 18.5 |
| Rumex dentatus           | 5.5  | 4.3  | 4.9  | 14.8 | 4.8 | 8.4  | 7.1  | 20.3 | 4.7 | 5.9  | 6.2  | 16.8 | 7.6  | 6.1  | 7.4  | 21.1 |
| Alternanthera sessilis   | 6.9  | 4.0  | 4.9  | 15.8 | 6.8 | 3.8  | 4.5  | 15.1 | 8.6 | 6.8  | 6.3  | 21.7 | 6.7  | 3.7  | 4.9  | 15.3 |
| Solanum nigrum          | 4.1  | 1.9  | 3.8  | 9.9  | 8.4 | 3.7  | 3.5  | 15.6 | 8.6 | 3.9  | 4.1  | 16.6 | 7.6  | 6.1  | 6.0  | 19.7 |
| Polygonum barbatum       | 4.6  | 2.0  | 3.3  | 9.9  | 6.8 | 3.2  | 3.8  | 13.8 | 8.2 | 5.0  | 4.7  | 18.0 | 8.1  | 5.3  | 5.9  | 19.3 |
| Vicia hirsuta           | 7.4  | 3.3  | 3.8  | 14.5 | 4.8 | 2.1  | 3.4  | 10.3 | 6.6 | 3.7  | 4.4  | 14.8 | 7.6  | 4.4  | 5.1  | 17.1 |
| Cyperus spp.            | 6.9  | 4.2  | 4.8  | 15.9 | 4.8 | 3.8  | 5.5  | 14.0 | 4.7 | 2.6  | 3.9  | 11.2 | 6.2  | 3.7  | 4.7  | 14.6 |
| Melilotus indicus        | 5.5  | 3.3  | 4.1  | 12.9 | 4.0 | 2.5  | 4.6  | 11.1 | 5.8 | 2.7  | 3.7  | 12.3 | 4.3  | 2.4  | 3.0  | 9.8  |
| Vicia sativa           | 4.6  | 2.1  | 3.5  | 10.3 | 8.0 | 4.3  | 4.4  | 16.7 | 3.5 | 1.5  | 3.6  | 8.7  | 2.9  | 1.1  | 2.3  | 6.2  |
| Dianthus annulatum      | 5.1  | 2.0  | 3.4  | 10.5 | 5.6 | 2.4  | 3.5  | 11.5 | 4.3 | 2.0  | 3.6  | 9.9  | 3.8  | 1.6  | 2.6  | 8.0  |
| Lathyrus sp.            | 4.6  | 2.0  | 3.8  | 10.4 | 4.4 | 1.7  | 3.1  | 9.2  | 5.1 | 2.5  | 3.8  | 11.4 | 2.4  | 0.9  | 2.4  | 5.7  |
| Cynodon dactylon       | 5.1  | 2.4  | 3.5  | 10.9 | 4.4 | 2.1  | 3.8  | 10.3 | 3.9 | 1.5  | 2.1  | 7.5  | 2.9  | 1.1  | 2.3  | 6.3  |
Here, \( W_2 \) is the total plant weight at time \( T_2 \), \( W_1 \) is the total plant weight at time \( T_1 \), \( \Delta A_2 \) is the total leaf area at time \( T_2 \) and \( \Delta A_1 \) is the total leaf area at time \( T_1 \). For the present study, the \( T_1 \) and \( T_2 \) measurements were at 45 and 75 DAS, respectively.

The plant height was measured from the base of the plant to the tip of the longest leaf. For this, five healthy plants were selected from each population (wheat + weeds) at the grain maturation stage of wheat. The ANOVA was used to infer species differences in the observed ecophysiological parameters and a range test was used for the pairwise multiple comparisons (Holm–Sidak method). A discriminant analysis was used to group species based on their studied ecophysiological traits. A discriminant analysis was carried out with SPSS by entering the independents together and setting all group prior probabilities as equal. A within-group covariance matrix was used. A univariate Anova’s Box’s M and unstandardized function coefficients were the requested output. A path analysis was done by using AMOS 16.0 software (Arbuckle 2007), which implements the general approach to data analysis known as “structural equation modeling”, also known as “analysis of covariance structures”, or “causal modeling”.

### RESULTS

The respective mean heights of wheat, \( P. \) minor, \( C. \) album, \( R. \) dentatus, \( M. \) albus and \( A. \) arvensis were \( 105 \pm 1, 100 \pm 0.4, 109 \pm 2.5, 68 \pm 1, 41 \pm 1.5 \) and \( 29 \pm 1 \) cm at the grain maturation stage of wheat. The ANOVA showed significant differences in the plant height of various species (\( F_{5,34} = 542.45, P \leq 0.001 \)).

In the present study, the SLA values across the species varied from 17.79 to 24.54 \( \text{m}^2 \text{kg}^{-1} \) (Table 3). The differences in the mean values of SLA among the species were statistically significant (\( F_{3,38} = 16.007, P \leq 0.001 \)). However, the pairwise multiple comparisons showed that, based on their SLA values, the species could be divided into two groups: \( M. \) albus, \( A. \) arvensis and \( R. \) dentatus in the high-SLA group and wheat, \( P. \) minor and \( C. \) album in the low-SLA group. The species with a higher SLA also had a higher LNCm (Table 3) and total chlorophyll content (Table 3).

The total chlorophyll content in the leaves of the species differed significantly (\( F_{5,48} = 16.36, P < 0.001 \)). The pairwise multiple comparison indicated that the level of chlorophyll in wheat and the weeds was the same, except for \( M. \) albus, which had the highest value of chlorophyll among all the species under study. As a result of a positive relationship (\( R^2 = 0.72, P = 0.03 \)) between the SLA and the LNCm, the leaf N content on an area basis became almost similar for the weeds. Although the crop (wheat) had a significantly lower

© 2015 Weed Science Society of Japan
Table 3. Comparative growth performance of wheat and its weeds in terms of specific leaf area (SLA), leaf area ratio (LAR), relative growth rate (RGR), net assimilation rate (NAR), leaf mass ratio (LMR) and physiological traits

| Characteristic | Anagallis arvensis | Chenopodium album | Melilotus albus | Phalaris minor | Rumex dentatus | Wheat |
|----------------|-------------------|------------------|----------------|---------------|---------------|-------|
| SLA (m² kg⁻¹)  | 22.48 ± 0.65b     | 18.75 ± 0.69a    | 24.54 ± 0.97b  | 17.65 ± 0.16a | 22.21 ± 1.00b | 17.79 ± 0.52a |
| LAR (m² kg⁻¹)  | 9.19 ± 0.96c      | 2.95 ± 0.41ab    | 8.59 ± 1.32c   | 6.95 ± 2.50bc | 7.43 ± 3.17bc | 1.11 ± 0.08a |
| RGR (mg mg⁻¹ per day) | 0.068 ± 0.006a | 0.10 ± 0.007a | 0.081 ± 0.004a | 0.069 ± 0.011a | 0.090 ± 0.005a | 0.076 ± 0.004a |
| NAR (mg mm⁻² per day) | 0.003 ± 0.004a | 0.012 ± 0.003b | 0.005 ± 0.001a | 0.005 ± 0.002a | 0.003 ± 0.001a | 0.014 ± 0.003c |
| LMR (%)        | 0.27 ± 0.04b      | 0.14 ± 0.02ab    | 0.25 ± 0.03b   | 0.17 ± 0.04ab | 0.14 ± 0.04ab | 0.08 ± 0.03a |
| LNCₙ (%)       | 5.65 ± 0.05a      | 4.38 ± 0.02b     | 6.07 ± 0.02c   | 4.87 ± 0.05d  | 5.60 ± 0.01a  | 3.19 ± 0.01e |
| LNCₙ (g m⁻²)   | 2.52 ± 0.07c      | 2.34 ± 0.12b     | 2.47 ± 0.02bc  | 2.76 ± 0.03c  | 2.52 ± 0.08c  | 1.79 ± 0.04a |
| Chlorophyll (mg g⁻¹) | 1.39 ± 0.02b    | 1.18 ± 0.06ab    | 1.81 ± 0.06c   | 1.07 ± 0.07a  | 1.41 ± 0.04b  | 1.18 ± 0.11ab |
| A (μmol m⁻² s⁻¹) | 13.13 ± 0.24d    | 7.67 ± 0.37b     | 14.88 ± 0.19e  | 5.78 ± 0.37a  | 10.75 ± 0.54c | 5.47 ± 0.31a |
| gₜ (mol H₂O m⁻² s⁻¹) | 0.21 ± 0.01b     | 0.19 ± 0.04ab    | 0.38 ± 0.03c   | 0.10 ± 0.01a  | 0.54 ± 0.04c  | 0.11 ± 0.01ab |
| E (mmol H₂O m⁻² s⁻¹) | 10.25 ± 0.38c   | 7.42 ± 1.03b     | 14.20 ± 0.89d  | 4.03 ± 0.19a  | 12.31 ± 0.77c | 3.99 ± 0.30a |
| WUE (μmol mol⁻¹) | 1.29 ± 0.03ab    | 1.20 ± 0.17ab    | 1.09 ± 0.09ab  | 1.43 ± 0.04b  | 0.90 ± 0.07a  | 1.4 ± 0.24c |
| PNUE (μmol mol⁻¹ s⁻¹) | 73.05 ± 0.68d   | 45.92 ± 4.03b    | 84.18 ± 1.45e  | 29.30 ± 2.10a | 59.65 ± 4.73c | 42.77 ± 3.26b |

Values are the mean ± one standard error. The values in rows with different letters are significantly different from each other (Tukey’s Honestly Significant Difference test at \( P < 0.05 \)).

A, photosynthetic rate; E, transpiration rate; gₜ, stomatal conductance; LNC, total nitrogen content; PNUE, photosynthetic nitrogen-use efficiency; WUE, water use efficiency.
LNC, than the weeds, its LNP was many times higher than that of the weeds (Table 3).

In this study, the RGR of the different species did not vary significantly (Table 3). However, the NAR was the most for wheat and the least for A. arvensis and R. dentatus, while the LAR was at its maximum for A. arvensis and its lowest for wheat (Table 3). Significant variations in the LMR among the species was observed ($F_{3,48} = 4.73$, $P = 0.001$). Wheat had significantly lower LMR values, compared to A. arvensis and M. albus, while all the other species under study had similar values (Table 3).

The ANOVA showed a statistically significant difference in A between the various species ($F_{5,48} = 123.08$, $P < 0.001$); however, the range test indicated that the values of A were the same for wheat and P. minor. The higher-SLA group species also had higher rates of A (Table 3). g s varied significantly among the species ($F_{5,48} = 42.35$, $P < 0.001$): R. dentatus had the highest level of conductance, whereas P. minor and wheat had the lowest values. E varied significantly ($F_{5,48} = 40.37$, $P < 0.001$): the values were highest for M. albus and R. dentatus and lowest for wheat (Table 3). The highest WUE values were observed for wheat and P. minor and the lowest for R. dentatus ($F_{5,48} = 3.79$, $P = 0.006$).

Figure 2 shows the result of the discriminant analysis that was used to group the species on the basis of the ecophysiological parameters that were measured in the present study. The analysis revealed two distinct groups: (i) A. arvensis, M. albus and R. dentatus, with a high SLA, leaf N and chlorophyll content; and (ii) C. album, P. minor and wheat, with a low SLA, leaf N and chlorophyll content. Photosynthetic rate (A) in the first group of species was significantly higher, compared to the second group. The proportion of variance represented by the first axis of the discriminant analysis was 0.96. A stepwise multiple regression identified photosynthesis as the most significant predictor of the first discriminant axis. Apart from the discriminators used for analysis, E, g s and WUE were members of the second group of predictors, which correlated significantly with the canonical discriminant functions. The first discriminant axis was also significantly correlated with the LAR and LMR. There was a negative correlation between the scores of discriminant axis 1 and the NAR. The second axis was explained mainly by variations in the chlorophyll content, but the inclusion of the SLA and photosynthesis in the model significantly improved the relationship.

**DISCUSSION**

The results that were obtained in this study have led to a functional grouping of weeds of wheat fields based on the ecophysiological traits that determine their pattern of resource capture ability in space and time. Species within the same group were similar in terms of their morphology, as well as physiology, and adopted similar strategies for growth and reproduction. Taller weeds, such as C. album and P. minor, constituted one group along with the crop, having a low A, SLA, LNC, chlorophyll, PNUE and LAR in comparison to the shorter weeds, such as A. arvensis, M. albus and R. dentatus, which formed another group with a high A, SLA, LNC, chlorophyll, PNUE and LAR. This might be related to their shorter life span compared to taller weeds, which emerge with the crop (Om et al. 2004; Singh 2012) and continue till crop harvest. Although the shorter weeds emerge later in the season and complete their life cycle early, for their survival they have to face intense competition from the crop and taller weeds, particularly for light. Therefore, a high SLA, PNUE, LNC and other supporting traits ensure their survival. Besides this, these traits also provide the smaller weeds with a benefit during light competition. Although being tall is beneficial for light competition, it demands a cost for plants. According to Nagashima and Hikosaka (2011), as the plant’s height increases, its need to invest biomass more than proportionately in the stem to support its own weight increases, which in turn reduces the fraction of leaf mass in the plant and thus C gain. However, a smaller plant increases its biomass allocation to the green parts and increases its SLA and other leaf traits, which

![Fig. 2. Canonical discriminant functions of five weeds and wheat on the basis of their ecophysiological traits. Aa, Anagallis arvensis; Ca, Chenopodium album; Mi, Melilotus albus; Pm, Phalaris minor; Rd, Rumex dentatus; Ta, wheat.](image-url)
results in increased light acquisition efficiency (intercepted photon flux per unit aboveground mass) (Kamiyama et al. 2010).

The direct and indirect effects of the SLA, LAR, LMR and leaf chlorophyll content on the photosynthesis of the two identified groups, as derived from a path analysis, are shown in Figure 3. The study indicates that the SLA and LAR together were able to influence photosynthesis in the group 1 species (A. arvensis, M. albus and R. dentatus), which had a high SLA, leaf N and chlorophyll content. However, the LMR, by modulating the chlorophyll content, influenced the photosynthesis of the group 2 species (C. album, P. minor and wheat), which had a low SLA, leaf N and chlorophyll content. Any change in the SLA relates to actual changes in the leaf structure and chemical composition. A lower SLA could be associated with slower intercellular diffusion of CO₂ (Parkhurst 1994; Hikosaka et al. 1998; Poorter & Evans 1998) or with greater internal shading of chloroplasts by attenuating photons passing through the lamina (Terashima & Hikosaka 1995), either of which could decrease the A of a leaf. The SLA is also associated with N allocation to photosynthesis (Poorter & Evans 1998). The N allocation to carboxylation and bioenergetics increases with an increasing SLA (Hikosaka et al. 1998; Onoda et al. 2004). Hikosaka et al. (1998) also found that the SLA is positively correlated with the fraction of leaf N in ribulose-1,5-bisphosphate carboxylase (RuBisCO), a key enzyme of photosynthesis. This is because of the fact that ~60% of the leaf soluble proteins consist of RuBisCO, which is often regarded as the most limiting factor for biomass production (Evans & Seemann 1989; Takashima et al. 2004). Other studies also demonstrate that increasing leaf N parallels increasing investment in photosynthetic compounds (thylakoid proteins, enzymes of the Calvin cycle (Onoda et al. 2004; Takashima et al. 2004; Harrison et al. 2009; Hikosaka & Shigeno 2009).

Interspecific variations in A were driven mainly by variability in the SLA, leaf N content and chlorophyll content (Hikosaka 2010). Considering all the species, the SLA, chlorophyll and LNCₘ were positively correlated with A (Fig. 4). High-SLA species might allocate a lower fraction of leaf N to cell walls, leaving more N for photosynthesis, as compared with low-SLA species, and have a higher PNUE (Poorter & Evans 1998). This is evident by the fact that the high-SLA species in this study had a high PNUE ($R^2 = 0.96$, $P = 0.002$). Similarly to the present study, A has been positively correlated with LNCₘ and SLA in many studies (Poorter et al. 1990; Hikosaka 2010). According to Reich et al. (1999), these patterns are common to all species because significant N per unit mass accumulation would be required in the leaves to achieve a high A.

The variation in the LAR is largely determined by the variation in the SLA (Poorter & Remkes 1990; Atkin et al. 1996). In this study, the LAR and SLA were positively related ($R^2 = 0.56$, $P = 0.08$). According to Storkey (2005), at the lower light levels early in the season, species with a high SLA have a high RGR. As the light intensity increases, however, it becomes more advantageous to have a lower SLA to increase the capacity of individual leaves to absorb light. This will be more important for the taller species and there appears to be a general trade-off between plant height later in the season and the SLA (Storkey 2005). This also was observed in the study, as the taller weeds (C. album and P. minor) and the crop (wheat) had a low SLA later in the season. Plants with internodes, such as Chenopodium and many

\[
\begin{align*}
\text{Group 1} & \\
\text{SLA} & \rightarrow A_{\text{max}} \\
\text{LAR} & \rightarrow A_{\text{max}} \\
\text{LMR} & \rightarrow A_{\text{max}} \\
\text{Chlorophyll} & \rightarrow A_{\text{max}} \\
\text{Group 2} & \\
\text{SLA} & \rightarrow A_{\text{max}} \\
\text{LAR} & \rightarrow A_{\text{max}} \\
\text{LMR} & \rightarrow A_{\text{max}} \\
\text{Chlorophyll} & \rightarrow A_{\text{max}}
\end{align*}
\]

Fig. 3. Path analysis of five weeds and wheat on the basis of their ecophysiological traits. A, photosynthetic rate; LAR, leaf area ratio; LMR, leaf mass ratio; SLA, specific leaf area.
grasses, have been shown to display a very rapid (within minutes) increase in the rate of elongation growth of the stems after initiation of a simulated shade treatment (see references in Martínez-García et al. 2010). These alterations are accompanied by changes, including a reduced chlorophyll content, hyponastic leaves, increase in apical dominance (leading to reduced branching in dicots and tillering in grasses) and acceleration of flowering (Casal et al. 1990; Kebrom & Brutnell 2007). Also in this study, C. album, P. minor and wheat had a lower chlorophyll content, compared to A. arvensis, M. albus and R. dentatus.

Species that are adapted to a shaded environment below the canopy are characterized by a high SLA late in the season. The shorter weeds (A. arvensis, M. albus and R. dentatus) in this study had a relatively high SLA. The plants with a high RGR tended to have a high NAR and LAR. However, in this study, the NAR and LAR were negatively correlated (Fig. 5). The variation in the LAR was related mainly to the variation in the SLA and, to a lesser extent, to that of the LMR. This negative correlation between the LAR and the NAR might be related to the negative correlation between the NAR and the SLA (Villar et al. 1998). An inverse relationship between the LAR and the NAR also was reported by Poorter and Remkes (1990) and Meziane and Shipley (1999).

© 2015 Weed Science Society of Japan
ACKNOWLEDGMENT

Funding support from the Ministry of Environment and Forests, Government of India, New Delhi, is acknowledged.

REFERENCES

Aper J., De Riek J., Mechant E., De Cauwer B., Bulcke R. and Reheul D. 2010. The origin of herbicide-resistant Chenopodium album: analysis of genetic variation and population structure. Weed Res. 50, 235–244.

Arbuckle J.L. 2007. AMOS 16 User's Guide. AMOS Development Corporation, Spring House, PA.

Arnon D.I. 1949. Copper enzymes in isolated chloroplasts. I. Polyphenoloxidase in B. vulgaris. Plant Physiol. 24, 1–15.

Atkin O., Botman B. and Lambers H. 1996. The causes of inherently slow growth in alpine plants: an analysis based on the underlying carbon economies of alpine and lowland Poa species. Funct. Ecol. 10, 698–707.

Balyan R.S. and Malik R.K. 2000. New herbicides for Jangali Palak (Rumex retroflexus L.). Indian J. Weed Sci. 32, 86–88.

Caldwell R.M., Pachepsky Y.A. and Timlin D.J. 1996. Current research status on growth modeling in intercropping. In: Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics (ed. by Ito O., Johansen C., Adu-Gyamfi J.J., Katayama K., Kumar Rao J.V.D.K. and Rego T.J.). Japan International Centre for Agricultural Sciences, Tsukuba, 617–635.

Caal J.J., Whitelam G.C. and Smith H. 1990. Phytochrome effects on the relationship between chlorophyll and steady-state levels of thylakoid polypeptides in light-grown tobacco. Plant Physiol. 94, 370–374.

Chapin F.S. 1993. Functional role of growth forms in ecosystem and global processes. In: Scaling Physiological Processes: Leaf to Globe (ed. by Field C.B.). Academic Press, London, 287–312.

Chihokar R.S., Sharma R.K., Chauhan D.S. and Mongia A.D. 2006. Evaluation of herbicides against Phalaris minor in wheat in north-western Indian plains. Weed Res. 46, 40–49.

Díaz S., Hodgson J., Thompson K., Cabido M., Cornelissen J.H.C., Jalili A. et al. 2004. The plant traits that drive ecosystems: evidence from three continents. J. Veg. Sci. 15, 295–304.

Evans G.C. 1972. The Quantitative Analysis of Plant Growth. University of California Press, Berkeley, CA.

Evans J.R. and Seemann J.R. 1989. The allocation of protein nitrogen in the photosynthetic apparatus: costs, consequences and control. In: Photosynthesis (ed. by Briggs W.R.), Alan R. Liss, New York, 183–205.

Harrison M.T., Edwards E.J., Farquhar G.D., Nicotra A.B. and Evans J.R. 2009. Nitrogen in cell walls of sclerophyllous leaves accounts for little of the variation in photosynthetic nitrogen use efficiency. Plant Cell Environ. 32, 259–270.

Hikosaka K. 2010. Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species. Plant Biotechnol. 27, 223–229.

Hikosaka K., Hanba Y., Hirose T. and Terashima I. 1998. Photosynthetic nitrogen-use efficiency in leaves of woody and herbaceous species. Funct. Ecol. 12, 896–905.

Hikosaka K. and Shigeno A. 2009. The role of Rubisco and cell walls in the interspecific variation in photosynthetic capacity. Oecologia 160, 443–451.

Holt J.S. and Orcutt D.R. 1991. Functional relationships of growth and competitiveness in perennial weeds and cotton (Gossypium hirsutum L.). Weed Sci. 39, 575–584.

Hunt R. and Cornelissen J. 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol. 135, 395–417.

Kamayama C., Oikawa S., Kubo T. and Hikosaka K. 2010. Light interception in species with different functional groups coexisting in moorland plant communities. Oecologia 164, 591–599.

Kebrom T.H. and Brutnell T.P. 2007. The molecular analysis of the shade avoidance syndrome in the grasses has begun. J. Exp. Bot. 58, 3079–3089.

Kroöff M., Spitters C., Schnieders B., Joenje W. and Groot W. 1992. An eco-physiological model for interspecific competition, applied to the influence of Chenopodium album L. on sugar beet. II Model evaluation. Weed Res. 32, 451–463.

Martínez-García J.F., Galstyan A., Salla-Martret M., Cifuentes-Esquível N., Gallelli M. and Bou-Torrent J. 2010. Regulatory components of shade avoidance syndrome. Adv. Bot. Res. 53, 65–116.

Meziane D. and Shiple B. 1999. Interacting components of interspecific relative growth rate: constancy and change under differing conditions of light and nutrient supply. Funct. Ecol. 13, 611–622.

Mohler C.L. 2001. Enhancing the competitive ability of crops. In: Ecological Management of Agricultural Weeds (ed. by Liebman M., Mohler C.L. and Staver C.P.). Cambridge University Press, Cambridge, 269–321.

Mustafee T.P. 1991. Weed problems in wheat and their control in the Indian subcontinent. Trop. Pest Manag. 37, 245–251.

Nagashima H. and Hikosaka K. 2011. Plants in a crowded stand regulate their height growth so as to maintain similar heights to neighbors even when they have potential advantages in height growth. Ann. Bot. 108, 207–214.

Om H., Kumar S. and Dhiman S.D. 2004. Biology and management of Phalaris minor in rice–wheat system. Crop Prot. 23, 1157–1168.

Onoda Y., Hikosaka K. and Hirose T. 2004. Allocation of nitrogen to cell walls decreases photosynthetic nitrogen-use efficiency. Funct. Ecol. 18, 419–425.

Parkhurst D. 1994. Diffusion of CO2 and other gases inside leaves. New Phytol. 126, 449–479.

Patterson D. 1995. Effects of environmental stress on weed–crop interactions. Weed Sci. 43, 483–490.

Poorter H. and Evans J. 1998. Photosynthetic nitrogen-use efficiency of species that differ inherently in specific leaf area. Oecologia 116, 26–37.
Poorter H. and Garnier E. 1999. Ecological significance of inherent variation in relative growth rate and its components. In: *Handbook of Functional Plant Ecology* (ed. by Pugnaire F.I. and Valladares F.). Marcel Dekker, New York, 81–120.

Poorter H. and Remkes C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83**, 553–559.

Poorter H., Remkes C. and Lambers H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.* **94**, 621–627.

Reich P.B., Ellsworth D.S., Walters M.B., Vose J.M., Gresham C., Voin J.C. et al. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**, 1955–1969.

Sharma R.K., Babu K.S., Chhokar R.S. and Sharma A.K. 2004. Effect of tillage on termites, weed incidence and productivity of spring wheat in rice–wheat system of North Western Indian plains. *Crop Prot.* **23**, 1049–1054.

Singh A., Sharma G.P. and Raghubanshi A.S. 2008. Dynamics of the functional groups in the weed flora of dryland and irrigated agroecosystems in the Gangetic plains of India. *Wheat Biol. Manag.* **8**, 250–259.

Singh H., Pathak P., Kumar M. and Raghubanshi A.S. 2011. Carbon sequestration potential of Indo-Gangetic agroecosystem soils. *Trop. Ecol.* **52**, 223–228.

Singh V. 2012. Ecological analysis of plant functional traits in agroecosystem (PhD thesis). Banaras Hindu University, Varanasi, India.

Storkey J. 2004. Modelling seedling growth rates of 18 temperate arable weed species as a function of the environment and plant traits. *Ann. Bot.* **93**, 681–689.

Storkey J. 2005. Modelling assimilation rates of 14 temperate arable weed species as a function of the environment and leaf traits. *Weed Res.* **45**, 361–370.

Storkey J. 2006. A functional group approach to the management of UK arable weeds to support biological diversity. *Weed Res.* **46**, 513–522.

Takashima T., Hikosaka K. and Hirose T. 2004. Photosynthesis or persistence: nitrogen allocation in leaves of evergreen and deciduous *Quercus* species. *Plant Cell Environ.* **27**, 1047–1054.

Terao H. and Hikosaka K. 1995. Comparative ecophysiology of leaf and canopy photosynthesis. *Plant Cell Environ.* **18**, 1111–1128.

Tiwari S.K., Singh S.K. and Pandey S. 2007. Combined influence of tillage and herbicide application on weed dynamics and yield of wheat under rice–wheat system. *Plant Arch.* **7**, 319–320.

Vashisht R., Sangwan N. and Solanki Y.P.S. 2008. Weed flora of wheat in Jhajjar district of Haryana in three different crop rotations. *Res. Crops* **9**, 563–565.

Villar R., Veneklaas E.J., Jordano P. and Lambers H. 1998. Relative growth rate and biomass allocation in 20 Aegilops (Poaceae) species. *New Phytol.* **140**, 425–437.

Wardle D.A., Barker G.M., Bonner K.I. and Nicholson K.S. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *J. Ecol.* **86**, 405–420.

Wright I. and Westoby M. 2000. Cross-species relationships between seedling relative growth rate, nitrogen productivity and root vs leaf function in 28 Australian woody species. *Funct. Ecol.* **14**, 97–107.

Yaduraju N.T. 1999. Control of herbicide resistant Phalaris minor: need for a sound weed management system. *Pestology* **23**, 264–266.

Yaduraju N.T. 2006. Herbicide resistant crops in weed management. In: *Proceedings of the Golden Jubilee National Symposium on ‘Conservation Agriculture and Environment’* (Varanasi, India, October 23–26 2006). Banaras Hindu University, Varanasi, 297–298.

© 2015 Weed Science Society of Japan