

Weed shoot morphology effects on competitiveness for light in direct-seeded rice

B P CATON*†, A M MORTIMER*, T C FOIN†, J E HILL*,
K D GIBSON† & A J FISCHER‡

*Crop, Soil, and Water Sciences Division, International Rice Research Institute, Los Baños, Philippines, and

†Agronomy and Range Science Department and ‡Vegetable Crops Department, University of California, Davis, CA 95616, USA

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Summary

The effects of weed shoot morphology on competitiveness for light in rice (*Oryza sativa* L.) have not been well described quantitatively and are difficult to study empirically. A rice:weed model was used to analyse the effects of weed leaf area densities (LAD; $\text{m}^2 \text{m}^{-3}$), leaf angles (as leaf light extinction coefficients, k_{leaf}) and maximum heights (H_m , m) on growth and competition with rice. Weed morphologies were hypothetical but empirically based, as follows: LADs were skewed to the bottom or conical, k_{leaf} values varied from 0.2 (erectophile) to 0.8 (planophile), and H_m values were $0.5H_R$, $1H_R$ and $1.25H_R$, where H_R was rice maximum height. Other parameters were equal to those of rice. Growth and competitiveness were evaluated using mature seed dry weights (g m^{-2}). Short weeds and weeds with conical LADs were weakly competitive, regardless of other traits. For other weed types, interference with rice was positively related to H_m , LAD skewness and more planophile leaves. All three traits were critical determinants of weed interference but no single morphological trait guaranteed competitiveness. All else being equal, weeds with highly skewed LADs produced the most seed dry weight. Planophile leaves were particularly beneficial for short weeds, giving over five times more seed dry weight than erectophile leaves.

Keywords: crop:weed competition, leaf area distribution, height, leaf angle, growth traits.

Introduction

It is well established that weed species vary in their competitive effects on rice (*Oryza sativa* L.) (e.g. Smith, 1988) as in all crops. Although shoot morphologies obviously may differ considerably among weed species, the quantitative effects of this variation on rice:weed competition have not been evaluated precisely. Weeds are often grouped into the categories of grasses, sedges and broad-leaved species as a coarse morphological classification. These types are based on taxon-characteristic features such as monocotyledonous or dicotyledonous leaves,

Correspondence: B P Caton, International Rice Research Institute (IRRI), MCPO Box 3127, Makati City 1271, Philippines.

tillering ability and stem or leaf shape. Despite their familiarity, such general plant descriptions are usually not quantitatively useful and may not describe actual differences. For example, rice and a broad-leaved weed, *Ammannia* spp. (*A. coccinea* Rottb. and *A. auriculata* Willd.; redstem), have similar vertical leaf area distributions (normalized with respect to height) for much of the cropping season (Caton *et al.*, 1999a).

Recently, morphological characteristics of rice and some important rice weeds have been studied in more detail (Breen, 1995; Caton *et al.*, 1997b; Yamasue *et al.*, 1997; B P Caton *et al.*, unpubl. obs.). Using this new and more detailed information, our objective was to examine how weed morphological traits affect their competitiveness for light in direct-seeded rice. Understanding the relative contributions of dynamically changing morphological traits to overall competitiveness is difficult to evaluate by empirical means. For example, it is unclear how one may vary vertical leaf area distributions of weeds in an empirical experiment, while controlling for the effects of other plant growth traits. Modelling approaches are useful for mechanistic analyses such as this because they quantify important interactions. This allows for more direct and detailed analyses of the effects of plant growth traits than can usually be carried out by empirical methods.

A model was used in this study to examine relationships amongst three important quantitative traits influencing competitiveness: (1) vertical leaf area distributions, (2) leaf angles and (3) maximum plant heights. The effects of plant height on competition for light are well known (e.g. Berkowitz, 1988). Leaf angle specifies the orientation of leaves to incoming radiation and, therefore, strongly affects light capture (Loomis & Williams, 1969). Leaf angles were quantified as leaf light extinction coefficients (k_{leaf}), which vary from erectophile (nearer to 0) to planophile (nearer to 1). Leaf angle is not the only factor that determines k_{leaf} , but is probably the most important (Loomis & Williams, 1969). Vertical leaf area distributions are often described by leaf area density (LAD; $\text{m}^2 \text{m}^{-3}$). LADs may strongly affect competition (Caldwell, 1987) but have only recently been measured for direct-seeded rice and some associated weeds. B P Caton *et al.* (unpubl. obs.) found in a temperate system that *Scirpus mucronatus* L. (ricefield bulrush) had conical LAD, whereas rice and *Echinochloa oryzoides* (Ard.) Fritsch. (early watergrass) LADs were skewed to the bottom. Yamasue *et al.* (1997) found similar results for rice and *E. phyllopogon* (Stapf.) Koss (late watergrass) in transplanted rice. Broad-leaved weeds also have bottom-skewed LADs, such as those of *Sagittaria montevidensis* Cham. & Schlecht. (California arrowhead) (Breen, 1995) and *Ammannia* spp. (Caton *et al.* 1999a), although the LAD shapes differ.

The model used in the analysis was DSRICE1 (Caton *et al.*, 1999c), which simulates rice and weed growth and direct competition for light in temperate, direct-seeded systems. Competition for light was simulated between rice and hypothetical weeds for all possible combinations of LAD, leaf angle and maximum plant height, but no other differences. This was carried out for standard environmental and management conditions of direct-seeded rice in California. Weed competitiveness was evaluated using rice yields and weed seed dry weights at maturity.

Materials and methods

Simulation model

DSRICE1 was developed to analyse integrated weed management strategies in direct-seeded rice systems (Caton *et al.*, 1999c). It runs on a daily time step, uses daily maximum and minimum

temperatures and solar radiation as inputs, and requires management specifications for flooding and seeding dates, water depth, light extinction coefficient of water, cultivar, weed species and weed density. DSRICE1 simulates direct competition for light, based on the vertical distributions of live and dead shoot material (leaves and stems) and associated light extinction coefficients. Photosynthesis is separately integrated over leaf angles, canopy height and diurnal temperatures. Plant height growth in the model is a function of thermal units (TU, d °C), not dry weight accumulation. Height is a tabular function until 200 d °C and a logistic function thereafter, with parameters for height gain rate and maximum height.

In validation tests the model simulated rice growth in monoculture accurately, including water depth effects on early season growth (Caton *et al.*, 1999b). DSRICE1 simulated competition with *Ammannia* spp. and *E. oryzoides* – two very different weed species – well for continuously flooded fields (Caton *et al.* 1999a). The model version used in this study differed only in the use of rice growth parameters for weeds, and coding to allow different morphological traits to be easily changed from treatment to treatment.

Specification of weed morphological traits

In this study, it was not our intent to simulate real rice:weed interactions but to assess the effects on rice:weed competition for light of three morphological traits over their likely ranges. While it was important for the tested values of the traits to be realistic, it was also critical to eliminate other differences. Hence, all weed growth parameters besides the traits below were identical, and for simplicity were equal to those of rice (Caton *et al.*, 1999c).

The maximum height of cv. M-202 is about 0.95 m (Caton *et al.*, 1999c). Three relative maximum weed heights were used in this study: $1H$, $1.25H$ and $0.5H$, where H is the maximum plant height of rice. These values were consistent with common rice weeds. Hereafter, $1.25H$ weeds are considered tall and $0.5H$ weeds short.

Also, k_{leaf} values of 0.2, 0.4, 0.6 and 0.8 were tested, which represent reported ranges. For rice and *E. oryzoides*, k_{leaf} varies from 0.4 to 0.6 over the season (Kropff & Lotz, 1993). Caton *et al.* (1999a) used $k_{\text{leaf}} = 0.8$ for *Ammannia* spp., and we believe $k_{\text{leaf}} = 0.2$ accurately described the very erect, narrow foliage of *S. mucronatus*.

LAD profiles in the analysis were either bottom skewed or conical. LADs were further described with the fraction of total leaf area in the top half of the plant (F_{top}). Measured values of F_{top} for rice and *E. oryzoides* were both about 0.70, whereas that for *S. mucronatus* (conical) was at most 0.35 (B P Caton *et al.*, unpubl. obs.). Measured F_{top} of *Ammannia* spp. is similar to that of rice (Caton *et al.*, 1999a), but that for *S. montevidensis* is 0.90, as most of its leaves are clustered at the top of the plant (Breen, 1995). Thus, three LAD variations were tested: bottom-skewed with $F_{\text{top}} = 0.70$ and 0.90, and conical with $F_{\text{top}} = 0.35$ (Fig. 1a).

Simulation specifications

Analyses reflected environmental conditions and cultural practices for temperate rice production in the Sacramento Valley, California. Long-term data for daily maximum and minimum temperatures (30 year; 1968–97) and solar radiation (15 year; 1983–97) were used (available at <http://www.ucipm.ucdavis.edu>). Rice (cv. M-202, semi-dwarf, Japonica type) density was 250 plants m^{-2} and weed density was 50 plants m^{-2} . Flooding occurred on 15 May, and seeding was 3 days later, giving weeds a 2-day growth advantage (see Caton *et al.*, 1999a). Water depths were

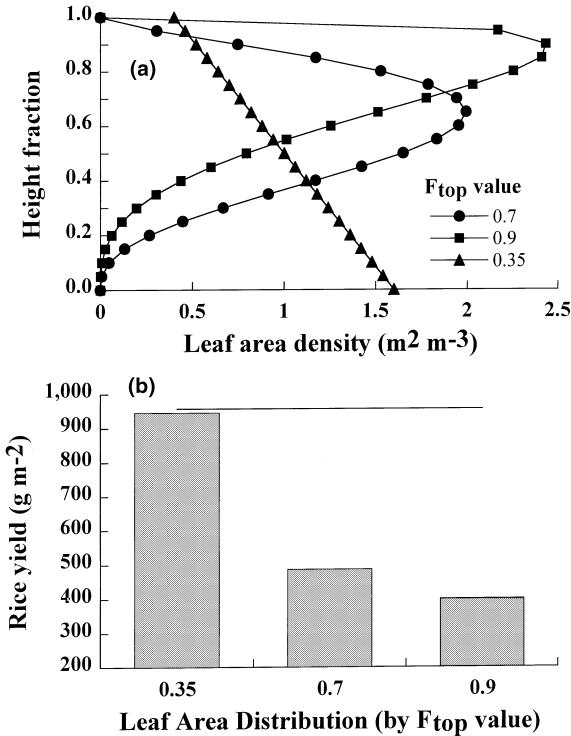


Fig. 1 Leaf area densities (LAD) of weeds and their simulated effects on competition with rice. (a) LADs based on empirical measurements of rice and weeds in California and Japan (see text). F_{top} is the fraction of leaf area in the top half of the plant. For each curve total LAI = 1. (b) Simulated rice yields (140 days after seeding) in competition with weeds having skewed or conical distributions. Data are presented for tall weeds with $k_{\text{leaf}} = 0.6$. The solid line indicates weed-free rice yield.

0.1 m until 60 days after seeding (DAS), and 0.2 m thereafter, and the light extinction coefficient of water was 3.0 (Caton *et al.*, 1999c). Effects on simulated rice and weed seed dry weights at 140 DAS were evaluated.

Results

The simulation results revealed that four patterns were evident for interference with rice: (1) weeds with conical distributions minimally affected rice yields (Fig. 1b), regardless of height or k_{leaf} value (not shown); (2) interference was positively related to height (Fig. 2a), so short weeds were not very competitive, regardless of LAD or k_{leaf} ; (3) all else being equal, $F_{\text{top}} = 0.90$ was more competitive than $F_{\text{top}} = 0.70$ within bottom-skewed LADs (Fig. 2a and b); and (4) greater k_{leaf} (more planophile leaves) increased interference (Fig. 2b). The effects of LAD skewness and k_{leaf} were both enhanced in weeds which were taller than rice, through positive feedback on growth which increased the competitive asymmetry between the weed and rice.

The correlation between rice yields and weed seed dry weights was high ($r = -0.93$, Fig. 3a), but one interesting trend was noted. For tall weeds with bottom-skewed LADs, those with $F_{\text{top}} = 0.9$ (line of points from 3 to 4 in Fig. 3a) reduced rice yields by only about 15% more than weeds with $F_{\text{top}} = 0.7$ (points 1–2 in Fig. 3a), but produced 50% more seed dry weight on average. The effect of k_{leaf} on seed dry weight of short weeds was even greater: those with $k_{\text{leaf}} = 0.8$ produced 5.6 times more seed dry weight than those with $k_{\text{leaf}} = 0.2$ (Fig. 3b).

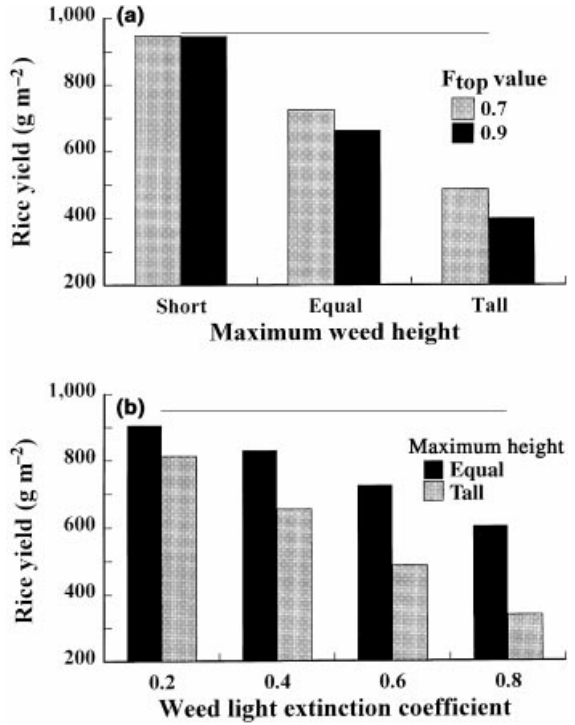


Fig. 2 Effects of (a) maximum heights and (b) leaf light extinction coefficients (k_{leaf}) of weeds on simulated rice yields. (a) Effects of weed maximum heights. Data presented for weeds with bottom-skewed LADs and $k_{leaf} = 0.6$. (b) Effects of weed k_{leaf} values from very erect (0.2) to nearly horizontal (0.8). Data presented for weeds with skewed LAD, $F_{top} = 0.70$. The solid lines in each graph indicate weed-free rice yield.

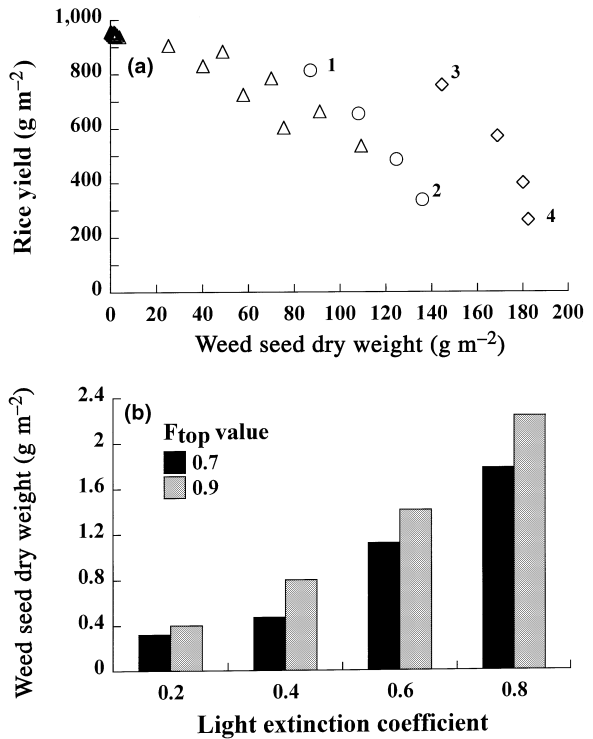


Fig. 3 (a) Relationship between simulated values of weed seed dry weight and rice yields, and (b) effects of leaf light extinction coefficients (k_{leaf}) of short weeds on seed dry weights. Labelled points in (a) are discussed in the text.

Discussion

These results illustrated that weed competitiveness for light is improved by being taller, having a more skewed vertical leaf area distribution (greater F_{top}) and having more planophile leaves (greater k_{leaf}). Overall weed competitiveness for light, however, was determined by interactions between morphological traits. For example, tall weeds were less competitive if they also had a conical LAD or erect leaves (low k_{leaf}). Likewise, weeds with very planophile leaves (i.e. $k_{\text{leaf}} = 0.8$) were less competitive if they had conical LADs or were short. Therefore, weed competitiveness for light was a function of the combined morphological traits.

Our analysis was similar to that carried out by Graf *et al.* (1990), although their model simulated competition for both light and nitrogen in transplanted rice. They compared observational and simulated data for competition with functional groups of weeds (Cyperaceae, Graminae and Dicotyledoneae). Those groups were further divided into tall or small classes, with separate parameters for density, seed dry weight and leaf area duration. However, the weed groups had common values (with rice) for k_{leaf} (0.6) and LADs (bottom skewed with $F_{\text{top}} = 0.75$). Our analysis extended that of Graf *et al.* (1990) in considering k_{leaf} values and more realistic LADs, and by simulating all possible combinations of these parameters.

These results have implications for the competitiveness of actual rice weeds. For example, short weeds and weeds with conical LADs were not competitive with rice, regardless of leaf angle. The evidence supports the hypothesis that short weeds in rice are weakly or non-competitive, such as *S. montevidensis* (Breen, 1995) and *Heteranthera limosa* (Sw.) Willd. (ducksalad) (Smith, 1988). When competition for resources other than light is unimportant, weeds such as *S. montevidensis* may not even need to be controlled (K D Gibson *et al.*, unpubl. obs.).

Less is known about competition from weeds with conical LADs, but it seems reasonable to assume that they will be weakly or even non-competitive unless that disadvantage is overcome by some other means. Other physiological growth traits (e.g. photosynthetic rates), or high densities resulting from high reproductive rates may enable greater growth and, thus, more interference with rice growth. The latter may explain why Graf *et al.* (1990) found that tall cyperaceous competitors were most important, as that class had a density about 17 times greater than that of tall graminoid weeds (hence, 3.4 times as much starting dry weight). Another possibility is that such weeds affect rice through mechanisms for which DSRICE1 does not account, such as below-ground competition for nutrients or space (e.g. Gibson *et al.*, 1999), although Graf *et al.* (1990) found that competition for light was most important. Such inferences can only be settled with much-needed data on rice:weed competition. It should also be noted, however, that such weeds may co-occur with rice through alternative methods of minimizing competition. Nevertheless, weeds that are short or have conical LADs probably have a severe disadvantage competing for light in a rice canopy, and therefore a relatively small direct impact on yield losses.

One practical application of these results may be for the evaluation of potential interference from weeds in field situations. Scouted weeds could be scored for morphological traits that are more, equal, or less competitive than the crop. This score would measure the likelihood for interference with the crop. In the simplest scenario, the results here suggested that rice weeds could be broadly classed as competitive and non-competitive based on whether they were short or have conical LADs. In more complex scenarios a range of scores would be generated. The exact use of such information would depend on the study objectives, but it may help target potentially troublesome species for further research and exclude species that seem unlikely to

cause problems. In this case, while weed heights and leaf angles are easily observed, evaluating LAD will be more difficult because it is not as visually apparent and few weed LADs have been described. Other relevant characters such as weed leaf area duration relative to the crop may also be added. It is important to note that the approach depends on identification of important competitive processes and traits, and that it may overlook non-competitive weeds which reduce crop quality or interfere with management operations (e.g. drying and harvesting).

Morphology is not the only determinant of weed competitiveness, and morphological and physiological traits other than those studied here are likely to contribute to weed interference with rice. Moreover, many life history traits affect the overall fitness of a weed for a given cropping system, and these may or may not affect competitiveness (Cousens & Mortimer, 1995). One such factor may be morphological plasticity, which many weeds possess (Baker, 1965; Schlichting, 1986). For the traits examined here, plasticity in weed plant height seems most important in rice (Caton *et al.*, 1997a; B P Caton *et al.*, unpubl. obs.). However, plasticity in LAD (McLachlan *et al.*, 1993) and in leaf angles (i.e. solar tracking or heliotropism) (e.g. Regnier & Harrison, 1993) may also be important in some situations. Whenever plasticity reduces weed mortality, shifts shoot areas higher in the canopy, or otherwise increases resource capture, it will certainly increase interference. However, morphological plasticity may also act in ways that do not increase competition. For example, plants may avoid shading by flowering (and senescing) early. Through such phenotypic modifications or avoidance of competition, some weeds may persist in cropping systems without appreciably affecting crop yields. Approaches that develop understanding of the interactions of life history, physiological and morphological traits in governing crop:weed dynamics will be valuable in designing better integrated weed management programmes.

Canopy specifications in these simulations were kept simple to facilitate comparisons, but some canopy development processes are more dynamic. For example, leaf angles may change during the season (Kropff & Lotz, 1993) and LADs for rice and weeds vary in response to tillering and senescence over the growing season (B P Caton *et al.*, unpubl. obs.). Whether patterns of leaf:stem:root partitioning – assumed here to be invariable – are generally related to shoot morphology seems potentially more important. Such information may help to improve understanding of relationships between morphology, physiology and competitiveness.

Although results indicated that precise quantification of shoot morphological traits will be needed for accurate predictions of competition for light between rice and weeds, the qualitative patterns that emerged were perhaps of more interest. One notable example was the large benefit to short weeds of having planophile leaves, especially in combination with a highly skewed LAD. We cannot be certain from these results alone that the morphology of short rice weeds is related to their fitness or persistence, but that particular life form is abundant in California rice fields. We identified at least six common examples among important rice weeds: *S. montevidensis*, *H. limosa*, *Alisma plantago-aquatica* L. (common waterplantain), *Echinodorus cordifolius* (L.) Griseb. (burhead), *Potamogeton* spp. (pondweeds), *Monochoria vaginalis* (Burm. f.) Kunth (monochoria), and perhaps *Bacopa* spp. (waterhyssops) (Bayer & Hill, 1992). In contrast, short weeds with erect leaves or less skewed LADs seem much less common; the only obvious example is *Eleocharis* spp. (spikerushes) – sedges with a maximum height of about 0.5 m. This seems deserving of further research because the pattern appears to match field observations. We feel that the qualitative results of this analysis should be robust for situations in which competition is primarily for light.

To conclude that placing leaves higher in the canopy and decreasing leaf angles increases weed or plant competitiveness for light in general may seem too obvious. We argue, however, that this

model analysis quantified and confirmed what ‘conventional wisdom’ or common sense has only suggested. It also went beyond empirical studies in which the effects of only one or two of these traits were analysed for very few species (e.g. McLachlan *et al.*, 1993). This modelling approach was an efficient means to quantitatively evaluate multiple traits across many species or plant types, which is perhaps impossible in an empirical study because of the difficulty of designing appropriate treatments and controls. Also, the effects of single traits on competitiveness were more intuitive than the demonstration that competitiveness was ultimately determined by interactions between traits. Prior to the Green Revolution, similar model analyses were critical for understanding crop production in monoculture (Loomis & Williams, 1969). As more weeds are studied in detail, models will be critical tools for analysing the differences in morphological and physiological traits that are likely to be found, and more importantly their interactive effects on growth and competition.

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References

- BAKER HG (1965) Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (eds HG Baker & GL Stebbins), 147–168. Academic Press, New York, USA.
- BAYER DE & HILL JE (1992) Weeds. In: *Integrated Pest Management for Rice* (eds ML Flint & BPO Ohleneger), Vol. Publication 3280, 32–55. University of California Statewide Integrated Pest Management Project, Division of Agriculture and Natural Resources, Oakland, California, USA.
- BERKOWITZ AR (1988) Competition for resources in weed-crop mixtures. In: *Weed Management in Agroecosystems: Ecological Approaches* (eds MA Altieri & M Liebman), 89–119. CRC Press, Boca Raton, Florida, USA.
- BREEN JL (1995) *The design, parameterization and validation of CANWER, a model to simulate biomass development, shading, tillering and yield of direct-seeded rice in competition with broadleaf weeds*. PhD Thesis, University of California, USA.
- CALDWELL MM (1987) Plant architecture and resource competition. In: *Potentials and Limitations of Ecosystem Analysis* (eds ED Schulze & H Zwolfer), Ecological Studies 61, 164–179. Springer-Verlag, New York, USA.
- CATON BP, FOIN TC, BREEN JL & HILL JE (1997a) Phenotypic plasticity among weeds of direct-seeded rice in California. In: *Proceedings Sixteenth Asian-Pacific Weed Science Society Conference* (ed. A Rajan), 42–45. Malaysian Plant Protection Society, Kuala Lumpur, Malaysia.
- CATON BP, FOIN TC & HILL JE (1997b) Phenotypic plasticity of redstem (*Ammannia* spp.) in competition with rice. *Weed Research* **37**, 33–38.
- CATON BP, FOIN TC & HILL JE (1999a) A plant growth model for integrated weed management in direct-seeded rice: III. Interspecific competition for light. *Field Crops Research* **63**, 47–61.
- CATON BP, FOIN TC & HILL JE (1999b) A plant growth model for integrated weed management in direct-seeded rice: II. Validation testing of water-depth effects and monoculture growth. *Field Crops Research* **62**, 145–155.
- CATON BP, FOIN TC & HILL JE (1999c) A plant growth model for integrated weed management in direct-seeded rice: I. Development and sensitivity analyses of monoculture growth. *Field Crops Research* **62**, 129–143.
- COUSENS R & MORTIMER AM (1995) *Dynamics of Weed Populations*. Cambridge University Press, New York, USA.

- GIBSON KD, FOIN TC & HILL JE (1999) The relative importance of root and shoot competition between water-seeded rice and *Echinochloa phyllopogon*. *Weed Research* **39**, 181–190.
- GRAF B, GUTIERREZ AP, RAKOTBE O, ZAHNER P & DELUCCHI V (1990) A simulation model for the dynamics of rice growth and development: II. The competition with weeds for nitrogen and light. *Agricultural Systems* **32**, 367–392.
- KROPFF MJ & LOTZ LAP (1993) Eco-physiological characterization of the species. In: *Modelling Crop–Weed Interactions* (eds MJ Kropff & HH van Laar), 83–104. CAB International, Wallingford, UK.
- LOOMIS RS & WILLIAMS WA (1969) Productivity and the morphology of crop stands: patterns with leaves. In: *Physiological Aspects of Crop Yield* (eds JD Eastin, FA Haskins, CY Sullivan & CHM van Bavel), 27–51. American Society of Agronomy, Crop Science Society of America, Madison, Wisconsin, USA.
- MCLACHLAN S, TOLLENAAR M, SWANTON C & WEISE S (1993) Effect of corn-induced shading on dry-matter accumulation, distribution, and architecture of redroot pigweed (*Amaranthus retroflexus*). *Weed Science* **41**, 568–573.
- REGNIER EE & HARRISON SK (1993) Compensatory responses of common cocklebur (*Xanthium strumarium*) and velvetleaf (*Abutilon theophrasti*) to partial shading. *Weed Science* **41**, 541–547.
- SCHLICHTING CD (1986) The evolution of phenotypic plasticity in plants. *Annual Reviews of Ecology and Systematics* **17**, 667–693.
- SMITH RJ, Jr (1988) Weed thresholds in Southern U.S. rice, *Oryza sativa*. *Weed Technology* **2**, 232–241.
- YAMASUE Y, MURAYAMA H, INOUE H, MATSUI T & KUSANAGI T (1997) Productive structures of rice and *Echinochloa oryzicola* Vasing. in mixed stands. *Journal of Weed Science and Technology* **42**, 357–365.