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John L. Lindquist

University of Nebraska-Lincoln, jlindquist1@unl.edu

Martin Kropff

University of Minnesota

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Author(s): John L. Lindquist and Martin J. Kropff

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Applications of an Ecophysiological Model for Irrigated Rice (*Oryza sativa*)-*Echinochloa* Competition¹

JOHN L. LINDQUIST and MARTIN J. KROPFF²

Abstract. A simulation model of rice-barnyardgrass competition for light was used for two management applications. First, simulations using 47 weather data sets from four locations in Asia were conducted to evaluate the influence of weather variation on single year economic threshold densities of barnyardgrass. Second, rapid leaf area expansion and leaf area index were evaluated as potential indicators of improved rice competitiveness and tolerance to barnyardgrass. Influence of weather variation on single year economic thresholds was small under the assumption that competition was for light only. Increasing early leaf area expansion rate reduced simulated barnyardgrass seed production and increased single year economic thresholds, suggesting that the use of competitive rice cultivars may reduce the need for chemical weed control. The model predicted that rice leaf area index 70 to 75 d after planting was a good indicator of early leaf area expansion rate. **Nomenclature:** Barnyardgrass, *Echinochloa crus-galli* (L.) Beauv., #³ ECHCG; rice, *Oryza sativa* L. 'IR72.'

Additional index words. Economic threshold, integrated weed management, weed ecology, IPM, weed-crop interference, ECHCG.

INTRODUCTION

World rice production must be increased by as much as 67% to feed the projected human population in 2025 (8). Weed competition reduces current rice production by an estimated 25% (18). *Echinochloa* species are among the most severe weeds in irrigated rice crops and most rice producers rely on hand weeding for control. Owing to high costs or lack of available labor and herbicides, a need for alternative weed management strategies exists. Integration of cultural weed management practices may be utilized effectively in many rice growing areas. Development of appropriate cultural practices requires a quantitative understanding of weed-crop interference relationships and factors that alter them (13).

Empirical weed-crop interference models (e.g., 4, 15) are commonly used to quantify competitive relationships and predict

yield loss. These empirical relationships show considerable variation among years and locations (1, 21), presumably due to variation in weather and other environmental factors. A number of simulation models have recently been developed to quantitatively describe mechanisms of inter-plant competition based on fundamental plant physiology (6, 12, 16, 20, 22, 23). These ecophysiological models may be utilized to evaluate the relative importance of weather, year, and location variability in weed-crop interference relationships.

Improved cultivar competitiveness and tolerance to weeds have been suggested as methods of reducing the negative influence of weeds on crop yield (2, 5, 9). Improved rice competitiveness may benefit management by reducing weed reproductive output. Because fewer seeds are produced, the influence of barnyardgrass on rice yields in subsequent years should be reduced. Improved tolerance to weeds aids management by reducing the impact of each weed on crop yield, resulting in an increase in the number of barnyardgrass plants needed to cause economic damage (i.e., economic threshold weed density would increase). Ecophysiological models may be used to generate hypotheses regarding which plant characteristics confer improved competitiveness or tolerance in crops.

An ecophysiological model (INTERCOM) was developed for rice-barnyardgrass competition for light in well-fertilized high-yielding irrigated rice ecosystems (12). Kropff et al. (17) evaluated INTERCOM performance using data from an experiment with irrigated direct seeded rice and barnyardgrass. Dry matter production, leaf area development, and yield were simulated accurately for all treatments. Further tests of model performance were made using eight data sets collected over a wide range of environments. Direct seeded or transplanted rice yield loss resulting from barnyardgrass interference was predicted accurately by the model (92% of variation accounted for) over a wide range of competition situations (14).

In this study, INTERCOM was used to examine two applications for an integrated weed management program. Objectives were to evaluate the influence of weather variation and improved early leaf area growth rate on simulated rice-barnyardgrass competition and on single year economic threshold densities of barnyardgrass.

MATERIALS AND METHODS

Model overview. Details of INTERCOM structure have been described elsewhere (12). Required model inputs include daily weather data (maximum and minimum temperature, global radiation, and rainfall), site latitude, plant density, planting date, and a number of species-specific parameters.

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²Former Grad. Res. Asst., Dep. Agron. Plant Gen., Univ. Minnesota, St. Paul, MN 55108 and Systems Agron., International Rice Research Institute, P.O. Box 933, 1099, Manila, The Philippines. Present address of authors: Dep. Agron., Univ. Nebraska, Lincoln NE 68583-0915; Dep. Theor. Prod. Ecol., Wag. Agric. Univ., Bornsesteeg 65, 6708 PD Wageningen, Netherlands and the Institute for Agrobiological and Soil Fertility Research, P.O. Box 14, 6700 AA, Wageningen, Netherlands.

³Letters following this symbol are WSSA-approved computer code from Composite List of Weeds, Revised 1989. Available from WSSA, 1508 West University Ave., Champaign, IL 61821-3133.

The model simulates competition for light, based upon the profile of absorbed photosynthetically active radiation (PAR)⁴ in the canopy and the photosynthesis-light absorption response curve of individual leaves. The quantity of PAR absorbed by each species is a function of the amount and distribution of photosynthetic area (leaves, stems, reproductive organs) within the canopy and the light extinction coefficient. The photosynthesis-light response curve is defined using a saturation function with the maximum value determined by the nitrogen content of leaves.

For both rice and barnyardgrass distribution of photosynthetic area within the canopy is assumed to be parabolic with a peak area at 50% of plant height. This assumption is supported by the data of Noda et al. (19). Height growth of each species occurs independently of species interaction and is simulated as an empirical function of accumulated growing degree days (GDD)⁴.

Gross CO₂ assimilation is integrated over canopy height. Net CO₂ assimilation is determined by subtracting maintenance and growth respiration from gross CO₂ assimilation. Daily dry matter growth increase is calculated from net CO₂ assimilation rate and then partitioned to the roots, stems, leaves, and reproductive organs based upon empirically derived allocation functions. Dry matter loss rates are determined empirically and imposed on the growth increment of each organ group as a function of phenological stage of development.

Influence of weather variation on simulated rice-barnyardgrass competition. The influence of annual weather variation on rice-barnyardgrass competition was examined by repeatedly simulating direct seeded (300 plants m⁻²) rice yield loss across a range of barnyardgrass densities (0, 5, 10, 20, 40, 60, 80, 150, 200, or 300 plants m⁻²). Both rice and barnyardgrass were set to emerge on the same day. Parameter estimates used in simulations were identical to those used by Kropff et al. (17) when evaluating model performance. Forty-seven weather data sets from four locations across Asia were used in these simulations. Date (Julian day) of seeding varied across sites depending on seasonality of the weather (Table 1). Cousens' hyperbolic yield loss equation (4) was fit to the pooled simulated data. Estimates of the I⁴ coefficient from Cousens' equation were used in calculating single year economic thresholds (ET⁴, 3, 24):

$$ET = \frac{C}{Y \cdot P \cdot I \cdot H} \quad [1]$$

where C is total cost of herbicide and its application (\$ ha⁻¹), Y is weed free crop yield (kg ha⁻¹), P is crop price (\$ kg⁻¹), I is proportional yield loss as weed density approaches zero (4), and H is herbicide efficacy (proportion of plants killed).

Coefficients used to calculate ET are often determined empirically and used deterministically (as if they were true con-

⁴Abbreviations: ET, single year economic threshold; GDD, growing degree days; I proportional yield loss as weed density approaches zero; LAI, leaf area index; PAR, photosynthetically active radiation; RGRL, relative leaf area growth rate from emergence until total canopy LAI reaches 1.0.

Table 1. Weather data bases used in rice-barnyardgrass competition simulations.

Location of station	Years available	Julian date of planting
Beijing, China	1980 to 1988	145
KhonKaen, Thailand	1975 to 1988	45
Aduturai, India	1980 to 1992	45
Los Banos, Philippines	1980 to 1990	45

stants). A coefficient estimate and its standard error may be used to determine ET stochastically and provide information about the variability of weed threshold levels. The estimate of I and its standard error obtained from fitting Cousens' equation to the simulated data in Figure 1 were used to evaluate the influence of weather variability on single year economic threshold populations of barnyardgrass. Values of I are assumed to be normally distributed and therefore may be randomly generated using the Box-Muller algorithm (10). This method was used to generate 1000 estimates of I. ET was then calculated iteratively for each I, holding all other coefficients constant to values shown in Table 2.

Influence of early leaf area growth rate on rice competitiveness and tolerance. INTERCOM was used to evaluate the influence of improved early leaf area growth rate on rice competitiveness and tolerance. In the model, expansion of leaf area index (LAI)⁴ is determined using an exponential growth function until total canopy LAI reaches 1.0. Following this early growth period, the model simulates growth and competition as described in the model overview section. The exponential growth function consists of a single coefficient that defines relative leaf area growth rate (RGRL⁴, LAI GDD⁻¹, 12).

The model was used to determine whether variation in RGRL would influence simulated barnyardgrass panicle biomass at maturity and the yield loss-weed density relationship. Six rice-

Figure 1. Simulated rice yield loss (YL)-barnyardgrass density (D) relationship using 47 weather data sets from four locations in Asia. Coefficient estimates for Cousens' equation were $I = 1.16 \pm 0.01$, $A = 102.31 \pm 0.54$ ($n = 470$).

Table 2. Variables used to calculate the single season economic threshold (ET) in equation [1].

Variable name	Value ^a
Herbicide cost (C, \$ ha ⁻¹)	24.14
Weed free crop yield (Y, kg ha ⁻¹)	4000
Crop price (P, \$ kg ⁻¹)	0.198
Yield loss (I, % weed ⁻¹)	1.16 (0.01)
Herbicide efficacy (H)	0.90
Economic threshold (ET)	2.93 (0.02)

^aData provided by K. Moody at IRRI. Values in parentheses are $\pm$ one standard deviation.

^bButachlor (*N*-(butoxymethyl)-2-chloro-*N*-(2,6-diethylphenyl)acetamide) at 1 kg ha⁻¹.

barnyardgrass mixture treatments were simulated for each of six RGRL values (0.005, 0.007, . . . 0.015 LAI °C⁻¹ d⁻¹). Each RGRL value represents a hypothetical rice cultivar. Direct seeded rice density was assumed constant at 300 plants m⁻².

Barnyardgrass density treatments of 0, 10, 20, 40, 80, and 300 plants m⁻² were set to emerge simultaneously with the crop. Simulated output included weed panicle biomass at maturity and crop yield, from which yield loss was determined. Cousens' equation was fit to simulated yield loss-barnyardgrass density relationships obtained for each RGRL value. Resulting estimates of *I* were used to calculate ET deterministically.

To determine the best time during the growing season that leaf area should be measured to obtain maximum differences among genetic lines, rice leaf area index was simulated for five rice RGRL values (0.005, 0.007, 0.009, 0.011, and 0.015 LAI °C⁻¹ d⁻¹). Direct seeded rice density was 300 plants m⁻² and barnyardgrass, emerging simultaneously with the crop, was simulated at 10 and 300 plants m⁻². Simulated LAI over time was compared among the five RGRL values.

RESULTS AND DISCUSSION

Influence of weather variation on simulated rice-barnyardgrass competition. Ninety-nine percent of the total variation in simulated yield loss across weather conditions was explained by barnyardgrass density based on the least squares best fit of Cousens' equation (Figure 1). These simulated data suggest that environmental variation resulting from weather alone has little influence upon the competitive relationship between rice and barnyardgrass. In this version of INTERCOM, changes in total incident radiation (e.g., due to cloud cover) would influence each species only through their photosynthesis-light response curves and rate of development (a function of GDD). Kropff et al. (11) conducted sensitivity analyses on INTERCOM and found that the coefficients defining the photosynthesis-light response curve had little impact on crop yield loss. Since competition is for light only, it is not surprising that weather variation had little impact on simulated rice-barnyardgrass interference relationships. Hill et al. (7) compiled irrigated rice barnyardgrass interference data from seven experiments conducted at four locations (Japan, Philippines,

Arkansas, and California) and found that yield loss relationships varied little across environments.

Single year economic threshold values calculated using 1000 randomly generated values of *I* ranged from 2.86 to 3.01 plants m⁻², with a mean $\pm$ standard deviation of 2.93 ± 0.02 plants m⁻². The impact of variation in *I* on ET densities of barnyardgrass was minimal because the estimated standard error of *I* was very small. Estimates of *I* obtained from fitting Cousens' equation to observed data will have a much larger standard errors (e.g., 21) due to random and experimental error, and microenvironmental heterogeneity within an experiment. Methods of evaluating risk associated with yield loss predictions and herbicide application recommendations need to be more fully developed and incorporated into bioeconomic decision aid models and other applied integrated weed management programs.

Influence of early leaf area growth rate on rice competitiveness and tolerance. INTERCOM predicts that an increased RGRL will negatively affect barnyardgrass panicle biomass at maturity (Figure 2). However, the relative effect varies as a function of weed density; the relationship is nearly linear when weed density is high and strongly curvilinear at low weed densities. These results suggest that increasing early leaf area expansion may improve rice competitiveness by reducing barnyardgrass seed production. However, because some seeds are always produced, further research is needed to determine the effect of increased crop competitiveness on long-term weed population dynamics.

Simulated rice yield loss as a function of barnyardgrass density decreases dramatically as rice RGRL increases (Figure 3). Estimates of *I* from simulated yield loss relationships in Figure 3 are lower when rice RGRL is high (Table 3), suggesting that rapid leaf area expansion will improve rice tolerance to barnyardgrass competition. Single year economic threshold densities of barnyardgrass calculated deterministically, using estimates of *I* shown in Table 3, range from 0.13 to 13.4 plants m⁻². The impact of even small increases in RGRL may result in

Figure 2. Simulated mature barnyardgrass panicle biomass as a function of rice early leaf area expansion rate (RGRL) over five weed densities.

Figure 3. Simulated rice yield loss as a function of barnyardgrass density over six RGRL values. Lines show best fit of Cousens' equation to each simulated data set.

a relatively large increase in ET and a reduced need for chemical control.

These relationships suggest that rapid leaf area expansion may be an excellent indicator of rice competitiveness and tolerance. However, determination of the relative leaf area growth rate requires repeated measurements of leaf area early in the growing season. This is impractical for a breeder evaluating large numbers of genetic lines. Recent reports suggest that a measure of crop canopy area or leaf area index early in the growing season may be a sufficient indicator of crop competitiveness or tolerance (2, 5, 9).

Plots of simulated leaf area index as a function of days after planting suggest that maximum differences in rice LAI (among hypothetical lines) in the presence of barnyardgrass occurred 70 to 75 d after planting, regardless of RGRL value (Figure 4). At moderate weed density (10 plants m^{-2}), maximum differences in rice LAI occurred at low RGRL values (0.005 to 0.007 $LAI\ ^{\circ}C^{-1}\ d^{-1}$). However, at high weed density (300 plants m^{-2}), maximum differences in LAI occurred when RGRL values were higher (0.011 to 0.015 $LAI\ ^{\circ}C^{-1}\ d^{-1}$, Figure 4). These results suggest that both time of sampling and weed density maintained during a breeding trial may have an important influence upon whether

Figure 4. Simulated rice leaf area index (LAI) as a function of days after planting (DAP) for five RGRL values. Barnyardgrass emerged simultaneously with the crop at 10 (a) and 300 (b) plants m^{-2} .

significant differences in leaf area index will be detected among genetic lines.

The RGRL values used for rice in these simulations were chosen to create a range of early leaf area growth rates. Field measured RGRL values used to simulate our growth experiments were 0.009 and 0.012 $LAI\ ^{\circ}C^{-1}\ d^{-1}$ for rice and barnyardgrass, respectively. Values reported for other species range from 0.0085 to 0.019 $LAI\ ^{\circ}C^{-1}\ d^{-1}$ (12). We assume that genetic variation in rice RGRL is sufficiently wide that values used in these simulations are potentially real.

INTERCOM predicts that as RGRL is increased, rice yield also increases (Table 3). Since changes in biomass allocation patterns among hypothetical genotypes are not considered in the model, an increase in yield can only occur if total above ground biomass is increased. In practice, some genetic lines of rice are likely to have very high values of RGRL accompanied by a reduction in harvest index, particularly if the increase in leaf area expansion results from a tradeoff in the fraction of biomass being allocated to the leaves versus other organs. This would result in

Table 3. Influence of rice RGRL on estimated value of I obtained from fitting Cousens' equation to simulated yield loss in Figure 3, economic threshold (ET) densities of barnyardgrass using [1], and simulated weed-free rice yield.

RGRL	I	ET	Yield
$LAI\ ^{\circ}C^{-1}\ d^{-1}$	% yield loss	plants m^{-2}	kg ha^{-1}
0.005	27.47	0.13	6361
0.007	3.50	0.97	6769
0.009	1.16	2.92	6931
0.011	0.55	6.21	7000
0.013	0.32	10.75	7037
0.015	0.25	13.44	7029

a line that is highly tolerant to weeds but does not yield well under high input conditions. Breeders must therefore be wary of undesirable traits associated with high rice RGRL. Jordan (9) suggested that breeding for competitiveness and tolerance traits is not likely to occur until the benefits are shown to be greater than the potential costs. Such a breeding effort may be most appropriate for low input cropping systems, crop production situations where herbicides are unavailable or very costly, or where the probability of ground water contamination is high. Field research is needed to evaluate real gains in competitiveness and tolerance among cultivars varying in RGRL.

This version of INTERCOM assumes high soil nutrient and water concentrations, and therefore only simulates competition for light. The competitive relationships examined in this study would change considerably under conditions where more than one resource is limiting or where light is not the most limiting resource. Traits that confer improved competitiveness and tolerance in a light-limiting system may be ineffective or even detrimental in a moisture- or nitrogen-limiting system. Knowledge of the most limiting resource in a given environment and the response of both crop and weed to that resource in limited supply is extremely important for the identification of traits conferring competitiveness and tolerance in other cropping systems. Versions of INTERCOM that simulate competition for light, water, and soil nitrogen are currently under development.

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