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## An Alternative Approach for Evaluating the Efficacy of Potential Biocontrol Agents of Weeds. 1. Inverse Linear Model<sup>1</sup>

DAN J. PANTONE, WILLIAM A. WILLIAMS, and ARMAND R. MAGGENTI<sup>2</sup>

**Abstract.** Methods for evaluating the efficacy of potential classical biocontrol agents were outlined for a model biocontrol agent-weed-crop system. A proposed biocontrol agent (the fiddleneck flower gall nematode), its weed host (coast fiddleneck), and wheat were used as representative organisms. An additive experimental design (inverse linear model) was used. Regression of the reciprocal of the average plant biomass of each species onto the density of itself and the other plant species yielded competitive indices that measure the competitive ability of the plants. The results of 2 yr of field experiments revealed a dramatic change in the competitive interaction between fiddleneck and wheat due to the nematode. During the 1986-87 season in the absence of the nematode, fiddleneck intraspecific competition was 33 times stronger than interspecific competition with wheat. In the presence of the nematode, intra- and interspecific competition of fiddleneck were nearly equal. Only the coefficients that measure interspecific competition changed significantly in the presence of the nematode while the coefficients for intraspecific competition did not. Nomenclature: Coast fiddleneck, *Amsinckia intermedia* Fischer and Meyer #<sup>3</sup> AMSIN; wheat, *Triticum aestivum* L. 'Anza'; fiddleneck flower gall nematode, *Anguina amsinckiae* (Steiner and Scott, 1935) Thorne, 1961.

**Additional index words.** Biological control, competition, interference, nematodes, *Amsinckia intermedia*, *Triticum aestivum*, *Anguina amsinckiae*, AMSIN.

### INTRODUCTION

In the classical biological control of weeds there is so much emphasis on selecting "safe" biocontrol agents of weeds (i.e., those that will not attack cultivated plants) that little attention is given to evaluating the potential effectiveness of an agent (13). Moreover, a scoring system was proposed for determining the relative effectiveness of an agent before introduction and host specificity testing. Candidate agents were rated on a 0 to 6 scale in twelve categories to select those with the greatest potential. The criteria included the type of injury inflicted, phenology of

attack, number of generations, number of progeny per generation, feeding behavior, geographical distribution, and size of the agent. However, these criteria were based totally on observations of the agent, and no need for research on the population ecology of the host plant was suggested.

A critique and revision of this scoring system noted that rating untried agents for efficacy on the basis of the agent's behavior and demography was invalid because it gave unjustifiable rank to untested agents (9). Unfortunately, the revision of the scoring system contained basically the same tactic and failed to propose preintroductory experiments to evaluate the impact of the agent on the population biology of the weed.

Most potential classical biocontrol agents of weeds prove to be ineffective when introduced (21, 23). It would be more efficient to screen potential biocontrol agents for effectiveness before introduction. This approach would allow biological weed control projects to concentrate on clearly effective agents, thereby reducing costs involving introductions and increasing the rate of success. For example, only five agents were effective out of a total of 51 insects that were introduced into Australia to control prickly pear cacti (*Opuntia* spp.) (34). If the 46 ineffective insects were eliminated before introduction, much time would have been saved and costs reduced. Moreover, the risk of the ineffective agents attacking nontarget plants would have been eliminated. Therefore, the approach we are advocating would also make the biocontrol of weeds safer and encourage its use.

With the possible exception of bioherbicides (i.e., inundative releases of plant pathogens), very few biological weed control agents on herbivores cause the direct mortality of mature host plants (2, 11, 12, 14, 32, 33). Once a plant survives the seed and seedling stages, the usual effect of an herbivore is to decrease the size of the plant. If the plant dies, additional factors such as plant competition are usually involved. Relatively moderate levels of herbivory may reduce the prospect for survival of the host plant, and such disturbance can change the species diversity of the plant community (1, 22).

Researchers have demonstrated a synergism between plant competition and insect herbivory by *Gastrophysa viridula* Degeer on the weed broadleaf dock (*Rumex obtusifolius* L.) (3). Feeding by the beetle significantly reduced the growth of the weed only when competing plant species were present. Examples of synergisms between herbivores attacking weeds and interspecific plant competition are not limited to arthropods. For example, when skeletonweed (*Chondrilla juncea* L.) infected with a rust (*Puccinia chondrillina* Bubak. and Syd.) was grown in the presence of competing plants, the growth of the weed was reduced more than the additive effects of infection and plant competition would predict (12).

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<sup>3</sup>Letters following this symbol are a WSSA-approved computer code from Composite List of Weeds, Weed Sci. 32, Suppl. 2. Available from WSSA, 309 West Clark Street, Champaign, IL 61820.

Plant competition has been reported as an important factor contributing to the decrease of infected skeletonweed populations in Australia (4, 5, 10, 17). Nematodes have been shown experimentally to shift the competitive balance between plant species. Mixtures of oats (*Avena sativa* L.) and barley (*Hordeum vulgare* L.) grown in a replacement series under controlled environmental conditions were greatly influenced by the oat cyst nematode (*Heterodera avenae* Wollenweber) (30). Oats are susceptible to the nematode while barley is resistant. Oats were the superior competitor in the absence of the nematode. Adding the oat cyst nematode to the system caused the two plant species to compete much more evenly. Interestingly, pure stands of oats were unaffected by the nematode. Much of the evidence that demonstrates that moderate levels of injury by herbivores can shift the competitive balance between plants comes from laboratory experiments. There is a clear need for rigorous field experiments (3).

The dramatic success of the Klamath weed beetle [*Chrysolina quadrigemina* (Suffrian)] as a biocontrol agent of Klamath weed (*Hypericum perforatum* L.) was due in part to interspecific plant competition (16, 18). Leaf-feeding by the beetle decreased the shoot biomass which resulted in plants with smaller root systems. The stunted plants were less able to compete with other species for moisture during summer drought. Over 2 million acres of rangeland were infested with Klamath weed in California, and after the beetle was introduced the weed was reduced by 99% with range forage species becoming ascendant again (20). After the herbivores have reduced the density of the once dominant host plant, they are very likely to be at low densities themselves, and thus the interactions will not be readily apparent from casual observation. For example, if an investigator made observations of the present status of Klamath weed in California without knowing the history of the biocontrol program, it might erroneously be concluded that the Klamath weed beetle is not a significant influence on the plant community and that Klamath weed is not limited by the beetle. Moreover, it might mistakenly be concluded that Klamath weed is a shade-loving species because the beetle controls the weed less effectively in shaded habitats (19). The case history of the Klamath weed beetle illustrates an important point. By observing a potential agent after it has decreased the weed population, it is very difficult to assess the impact of that agent on its weed host or to predict its efficacy as a biocontrol agent. A more powerful method would be to complete controlled experiments involving the impact of the agent on the population biology of the weed.

The fiddleneck flower gall nematode has been proposed as a biological weed control agent of coast fiddleneck (24). This weed can be severely injured by the nematode (25). Nematode galls may form at the stem apex and therefore severely stunt the weed and greatly reduce seed production. Although the nematode needs flowering plants to reproduce, it can feed on and stress fiddleneck seedlings (26).

The major objective of this research project was to provide a conceptual framework for evaluating the efficacy of potential biocontrol agents of weeds by using the fiddleneck

flower gall nematode as a model system. Fiddleneck is an annual and the structure of the fruit (four nutlets) lends itself to an accurate measurement of fecundity. Mature fiddleneck seeds can fall from the plant before harvesting. However, aborted seeds are very small and remain attached. An accurate count of mature seeds can be made by counting the number of fruits (each fruit is composed of four nutlets), multiplying by four, and subtracting the number of aborted seeds. Nematodes appear to be ideal for the population studies we proposed because caging was not needed as with some insects. Contamination of control plots was not a problem in preliminary studies as might have been the situation had a plant pathogen been selected with spores spread by the wind. Additionally, the mode of reproduction of the nematode (galls) allowed the nematode populations to be easily and accurately quantified.

### MATERIALS AND METHODS

Field experiments were planted in Davis, CA, in early December of 1986 and 1987 and harvested the following May. Nematode galls and fiddleneck seeds used were obtained from a barley field located 5 km south of Morgan Hill, Santa Clara County, California. Fiddleneck seeds were scarified with sandpaper and planted into Yolo fine sandy loam (a fine-silty, mixed, nonacid, thermic Typic Xerorthent) to a depth of approximately 1 cm. Wheat was sown approximately 2 cm deep. Field plots were planted with ratios of 0:20, 0:80, 0:160, 20:0, 20:20, 20:80, 20:160, 80:0, 80:20, 80:80, 80:160, 160:0, 160:20, 160:80, and 160:160 (fiddleneck:wheat densities per m<sup>2</sup>). In addition to the control plots in which no nematodes were present, the above ratios were duplicated and inoculated with approximately 10<sup>6</sup> nematodes per plot which is the equivalent of about 5 nematode galls (8). This was a relatively low rate of inoculation since individual plants at natural sites of infestation are capable of producing an average of 1.6 galls (26). Nematodes were applied to the soil surface immediately following planting. Plot size was 0.5 by 0.5 m with borders extending 1.5 m from the edge of each plot. A completely randomized design was used. A wire mesh fence surrounded the plots to prevent rabbit damage and aerial netting was used as protection from birds. Yield per plant ( $\bar{Y}$ ) was measured as shoot dry weight (g) (biomass), seed number (fecundity), and total seed biomass (g) per plant (seed yield).

Spitters (31) introduced the inverse linear model to evaluate plant competition. Basically, this model involves multiple regressions of the form

$$1/\bar{Y}_f = a_{fo} + a_{ff}d_f + a_{fw}d_w$$

$$1/\bar{Y}_w = a_{wo} + a_{ww}d_w + a_{wf}d_f$$

where  $\bar{Y}_f$  and  $\bar{Y}_w$  are the average-per-plant yields for fiddleneck and wheat, respectively, and  $d_f$  and  $d_w$  are their densities. Unlike substitutive designs, the sum of  $d_f$  and  $d_w$  is not required to be a constant. Intraspecific competition is measured by the partial regression coefficients  $a_{ff}$  and  $a_{ww}$

**Table 1.** Multiple regression analysis of the impact of the nematode and plant density on the reciprocals of the average biomass, fecundity, and seed yield of fiddleneck. Intraspecific competition for fiddleneck is measured by the coefficient  $a_{ff}$  and interspecific competition by  $a_{fw}$ . 1986–87 season.

Yield variable	Treatment	Intercept	$a_{ff}$	$a_{fw}$	$a_{ff}/a_{fw}$	$R^2$
Biomass <sup>a</sup>	Control	-19.9	8.24	0.25*	33.0	0.85
Biomass	Nematode	-47.3	8.76	8.40*	1.04	0.85
Fecundity <sup>b</sup>	Control	-37.1	6.83	1.45*	4.71	0.78
Fecundity	Nematode	-40.5	8.39	6.59*	1.27	0.79
Seed yield <sup>c</sup>	Control	-18.3	2.47	0.37	6.60	0.76
Seed yield	Nematode	-8.30	3.04	1.67	1.81	0.70

<sup>a</sup>Parameter estimates for biomass are  $\times 10^4$ .

<sup>b</sup>Parameter estimates for fecundity are  $\times 10^6$ .

<sup>c</sup>Parameter estimates for seed yield are  $\times 10^3$ .

\*Corresponding coefficients significantly different for the variable due to the impact of the nematode ( $P < 0.05$ ).

while interspecific competition is measured by  $a_{fw}$  and  $a_{wf}$ . Therefore, each fiddleneck plant has an effect on  $1/\bar{Y}_f$  equal to  $a_{ff}/a_{fw}$  wheat plants. In other words, fiddleneck is  $a_{ff}/a_{fw}$  times as aggressive as wheat as a competitor with itself. The coefficient  $a_{fw}$  is defined as the effect on fiddleneck of competition by wheat and  $a_{wf}$  is the effect on wheat of competition by fiddleneck. Similarly,  $a_{ff}$  and  $a_{ww}$  are defined as the effect on fiddleneck and wheat, respectively, of competition by conspecific neighbors.

One researcher used the reciprocals of the variances as weights because of the heterogeneity of errors involved in estimating the competition coefficients (31). The variance of the dependent variable ( $1/\bar{Y}$ ) increases at higher densities, and therefore using the reciprocals of the variance of the dependent variable as weights maintains homogeneity. Simply stated, the variance of the yield ( $\bar{Y}$ ) decreases as the

**Table 2.** Multiple regression analysis of the impact of the nematode and plant density on the reciprocals of the average biomass, fecundity, and seed yield of fiddleneck. Intraspecific competition for fiddleneck is measured by the coefficient  $a_{ff}$  and interspecific competition by  $a_{fw}$ . 1987–88 season.

Yield variable	Treatment	Intercept	$a_{ff}$	$a_{fw}$	$a_{ff}/a_{fw}$	$R^2$
Biomass <sup>a</sup>	Control	54.3	10.1	6.43*	1.57	0.75
Biomass	Nematode	530	5.95	9.29*	0.64	0.81
Fecundity <sup>b</sup>	Control	-20.6	16.7	9.84**	1.70	0.59
Fecundity	Nematode	1362	6.48	19.7**	0.33	0.41
Seed yield <sup>c</sup>	Control	48.8	5.75	3.52**	1.63	0.53
Seed yield	Nematode	756	0.86	7.85**	0.11	0.20

<sup>a</sup>Parameter estimates for biomass are  $\times 10^4$ .

<sup>b</sup>Parameter estimates for fecundity are  $\times 10^6$ .

<sup>c</sup>Parameter estimates for seed yield are  $\times 10^3$ .

\*Corresponding coefficients significantly different for the variable due to the impact of the nematode ( $P < 0.05$ ).

\*\*( $P < 0.01$ ).

**Table 3.** Multiple regression analysis of the impact of the nematode and plant density on the reciprocals of the average biomass, fecundity, and seed yield of wheat. Intraspecific competition for wheat is measured by the coefficient  $a_{ww}$  and interspecific competition by  $a_{wf}$ . 1986–87 season.

Yield variable	Treatment	Intercept	$a_{ww}$	$a_{wf}$	$a_{ww}/a_{wf}$	$R^2$
Biomass <sup>a</sup>	Control	-7.20	4.97	16.4**	0.30	0.86
Biomass	Nematode	-90.2	5.81	8.09**	0.72	0.72
Fecundity <sup>b</sup>	Control	21.8	2.28	19.3	0.12	0.40
Fecundity	Nematode	-58.4	4.41	7.92	0.56	0.74
Seed yield <sup>c</sup>	Control	6.30	0.56	5.26	0.11	0.39
Seed yield	Nematode	-21.3	1.31	2.16	0.61	0.74

<sup>a</sup>Parameter estimates for biomass are  $\times 10^4$ .

<sup>b</sup>Parameter estimates for fecundity are  $\times 10^5$ .

<sup>c</sup>Parameter estimates for seed yield are  $\times 10^3$ .

\*\*Corresponding coefficients significantly different for the variable due to the impact of the nematode ( $P < 0.01$ ).

**Table 4.** Multiple regression analysis of the impact of the nematode and plant density on the reciprocals of the average biomass, fecundity, and seed yield of wheat. Intraspecific competition for wheat is measured by the coefficient  $a_{ww}$  and interspecific competition by  $a_{wf}$ . 1987–88 season.

Yield variable	Treatment	Intercept	$a_{ww}$	$a_{wf}$	$a_{ww}/a_{wf}$	$R^2$
Biomass <sup>a</sup>	Control	-83.3	9.24	21.0**	0.44	0.81
Biomass	Nematode	-38.0	11.7	8.18**	1.43	0.96
Fecundity <sup>b</sup>	Control	-138	9.24	26.0**	0.36	0.67
Fecundity	Nematode	-0.83	11.0	10.1**	1.09	0.84
Seed yield <sup>c</sup>	Control	-48.0	3.48	8.50*	0.41	0.57
Seed yield	Nematode	-7.87	4.55	3.18*	1.43	0.87

<sup>a</sup>Parameter estimates for biomass are  $\times 10^4$ .

<sup>b</sup>Parameter estimates for fecundity are  $\times 10^5$ .

<sup>c</sup>Parameter estimates for seed yield are  $\times 10^3$ .

\*Corresponding coefficients significantly different for the variable due to the impact of the nematode ( $P < 0.05$ ).

\*\*( $P < 0.01$ ).

**Table 5.** Resource partitioning between fiddleneck and wheat.

Yield variable	Treatment	$(a_{ff}/a_{fw})/(a_{wf}/a_{ww})$	
		1986–87	1987–88
Biomass	Control	9.90*	0.69
Biomass	Nematode	0.75	0.92
Fecundity	Control	0.57	0.61
Fecundity	Nematode	0.71	0.36
Seed yield	Control	0.73	0.67
Seed yield	Nematode	1.11*	0.16

<sup>a</sup> $(a_{ff}/a_{fw})/(a_{wf}/a_{ww})$  greater than 1.0 indicates significant resource partitioning.

## RESULTS AND DISCUSSION

yield increases, and consequently plants with larger yields are weighted more in the regression. All regressions in this study were weighted regressions in which the yield was used as the weight variable. If the yields are proportional to the reciprocals of the error variances, then the best linear unbiased estimators are the weighted least squares estimates (35).

Regressions for nematode-treated plots were compared to untreated plots using a general linear model (29). A dummy variable was used to indicate the presence or absence of the nematode, and F-tests of regressions of the pooled data indicated if the parameter coefficients were significantly different due to the presence of the nematode (6, 36). The partitioning of resources was analyzed by using the double ratio  $(a_{ff}/a_{fw})/(a_{wf}/a_{ww})$  which ranks the relative strengths of intraspecific and interspecific competition. Values greater than one indicate significant niche differentiation (28, 31). By using the inverse linear model it was possible to analyze some of the interactions between stress induced by the nematode and competition.

Results reveal a dramatic change in the competitive interaction between fiddleneck and wheat due to the introduction of nematodes and show some interesting general patterns. For example, the coefficients that measure interspecific competition ( $a_{fw}$  and  $a_{wf}$ ) were significantly affected by the nematode while the coefficients for intraspecific competition ( $a_{ff}$  and  $a_{ww}$ ) were not (Tables 1, 2, 3, 4). Since the nematode does not attack wheat, it would not be expected that intraspecific competition ( $a_{ww}$ ) for wheat would be affected, and our results support this hypothesis. Moreover,  $a_{fw}$  increased with the nematode and  $a_{wf}$  decreased in each case. Correspondingly, the ratio that measures the relative competitive ability of fiddleneck compared to wheat ( $a_{ff}/a_{fw}$ ) decreased in the presence of the nematode, while the competitive ability of wheat ( $a_{ww}/a_{wf}$ ) increased. Fiddleneck was 33 times as strong a competitor with itself as was wheat with fiddleneck with respect to biomass during the 1986–87 season in the absence of the nematode ( $a_{ff}/a_{fw}$ , Table 1). That

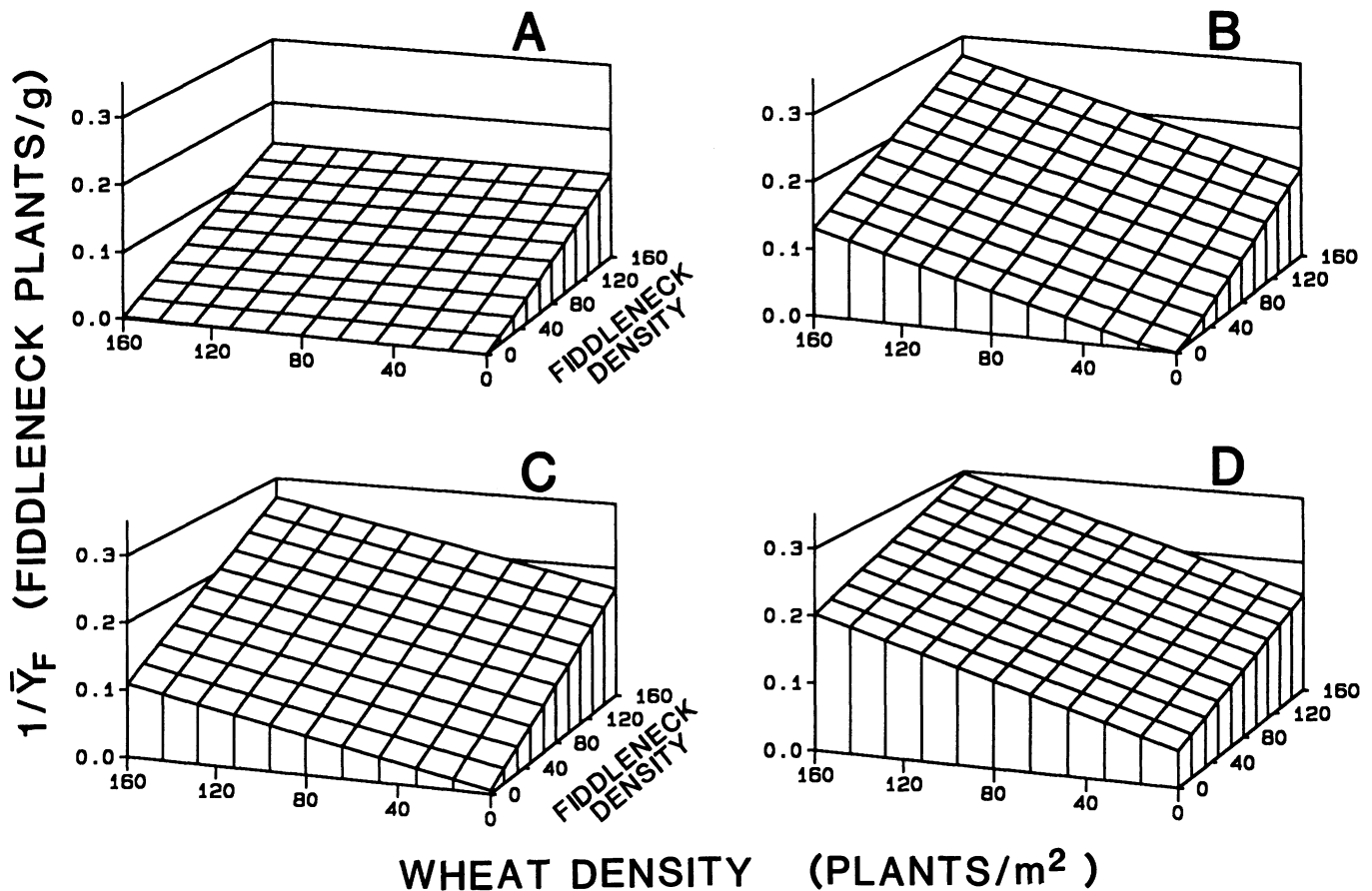


Figure 1. Multiple regression planes demonstrating the combined effects of fiddleneck density and wheat density on the reciprocal of the mean biomass per fiddleneck plant. A and B are the 1986–87 season controls and nematode treatments, respectively. C and D are the 1987–88 season controls and nematode treatments, respectively.

is, it took 33 wheat plants to have the same impact on fiddleneck biomass as would one fiddleneck plant. The effect of wheat on the biomass of fiddleneck was almost identical to the effect of fiddleneck on itself in the presence of the nematode ( $a_{ff}/a_{fw} = 1.04$ ). Similarly, adding one wheat plant had the same effect on wheat as adding 0.30 ( $a_{ww}/a_{wf}$ ) fiddleneck plants in the controls, whereas in nematode-treated plots one wheat plant had an effect equal to 0.72 fiddleneck plants.

The coefficients of determination ( $R^2$  values) indicate that shoot biomass was the best indicator of plant competition and seed yield was the poorest. Spitters (31) stated that it is better to use shoot biomass to measure plant competition than the yield of any other plant part, because biomass production has a linear relationship with the uptake of the limiting resource.

The intercept estimates the reciprocal of the yield of an isolated plant, and the larger the intercept, the smaller the maximum yield (31, 27). Therefore, a negative intercept is not logical and is caused by the sensitivity of the model to random errors (31). Our estimates of the intercept are of

limited utility because they are outside the data range of the regressions. A better estimate of the intercept could be made if observations at very low densities were incorporated into the experiment.

The ratio  $a_{ff}/a_{fw}$  was consistently lower in the 1987–88 season for each variable and  $a_{ww}/a_{wf}$  was higher than in 1986–87 (Tables 1, 2, 3, 4). Therefore, wheat was more competitive during year 2. This could be due to warmer temperatures during seedling establishment in the 1987–88 season. In competition experiments in Australia (7), fiddleneck was reported to have an optimum growth temperature that is much lower than that for wheat.

Using the results in Tables 1, 2, 3, 4, yields can be predicted at a given density. For example, in the 1986–87 season using the median plant density of 80 plants per square meter for both fiddleneck and wheat, fiddleneck will yield approximately 15 g per plant in the absence of the nematode and 7.5 g if the nematode is present (a 50% decrease). Correspondingly, wheat yields about 5.9 g in the controls and 9.8 if the nematode is present (a 66% increase).

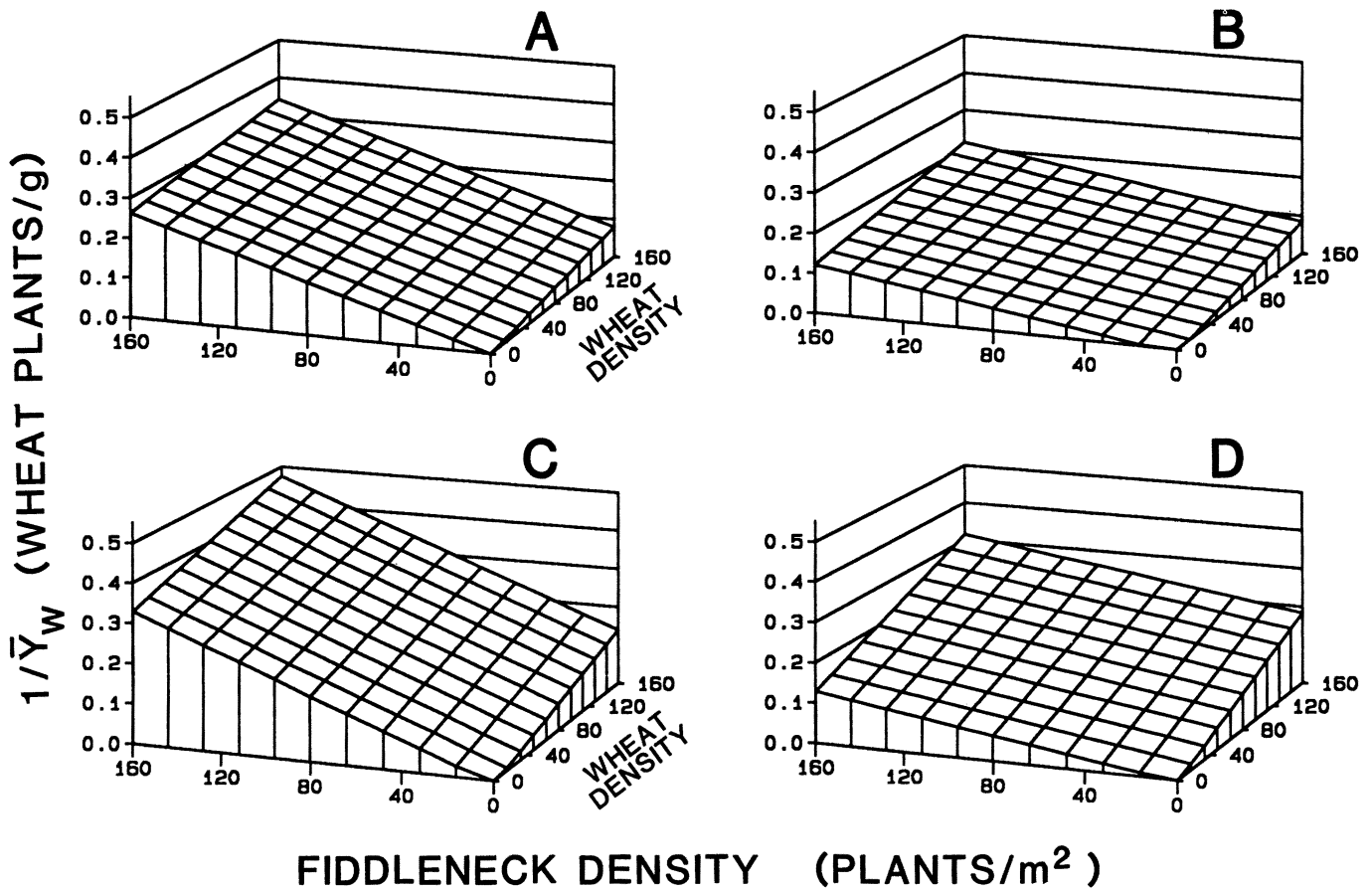


Figure 2. Multiple regression planes demonstrating the combined effects of wheat density and fiddleneck density on the reciprocal of the mean biomass per wheat plant. A and B are the 1986–87 season controls and nematode treatments, respectively. C and D are the 1987–88 season controls and nematode treatments, respectively.

A three-dimensional plot demonstrates the combined effects of fiddleneck and wheat on the reciprocal yield of fiddleneck (Figure 1). The slope of the regression plane indicates that wheat had little impact on fiddleneck yield during year 1. Competition was primarily intraspecific. However, adding the nematode decreased the competitive ability of fiddleneck, and the slope of the regression plane due to wheat density was increased. Similarly, the slope of the plane due to fiddleneck density on the reciprocal yield of wheat was decreased by the nematode (Figure 2).

When intraspecific competition exceeds interspecific competition,  $a_{ff}/a_{fw}$  is greater than  $a_{wf}/a_{ww}$ , and the double ratio  $(a_{ff}/a_{fw})/(a_{wf}/a_{ww})$  is greater than unity. Moreover, when the double ratio exceeds one, the two species are only partially restricted by the same resource. This is referred to as resource partitioning or niche differentiation (28, 31). In general, the double ratio  $(a_{ff}/a_{fw})/(a_{wf}/a_{ww})$  was not greater than one (Table 5), indicating that potential for resource partitioning was primarily low for these two plant species under the conditions tested. The prominent exception to this pattern was in the 1986–87 season when the double ratio was 9.9 for the biomass controls. This ratio was 0.75 in the presence of the nematode, demonstrating that the capacity of niche differentiation greatly decreased when the nematode was present.

Currently, a typical biological weed control program costs more than \$2 million and takes 20 yr to complete (15). Unfortunately, the majority of biological weed control projects end in failure, and only 30% are successfully completed (21, 23). Clearly a new approach to biocontrol is needed. These experiments demonstrate how the inverse linear model can be used to assess the impact of herbivores on the population ecology of competing plant species. This technique could increase our basic understanding of how stress induced by herbivores and plant competition affects the population biology of plants. It has been proposed that as more insects and pathogens are established on the target weed, stress on the weed increases and that successful biological control occurs gradually (15). However, in the vast majority of biological control projects, success was due to a single agent (21, 23). Therefore, the key to successful biocontrol might be to find that one agent which will be efficacious, and the methodology outlined in this paper provides a means by which potential weed biocontrol agents can be screened and ranked for efficacy.

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