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Replacement series analysis of the competitive interaction between a weed and a crop as influenced by a plant parasitic nematode

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Summary – Methods for evaluating the influence of a plant parasitic nematode on plant competition were developed for a nematode-weed-crop system. The interrelationships between the fiddleneck flower gall nematode [*Anguina amsinckiae* (Steiner & Scott, 1935) Thorne, 1961], its weed host, fiddleneck (*Amsinckia intermedia* Fischer & Meyer) and wheat (*Triticum aestivum* L.) were investigated. Replacement series experiments were conducted in a greenhouse with ratios (weed : crop) of 0 : 1, 3 : 1, 1 : 1, 1 : 3, and 1 : 0. Experiments were replicated both in the presence and absence of the nematode. Results showed that the nematode reduced the dry weight of the weed by 25 %, but had no significant effect on the dry weight of the crop. Competitive indices implied that the crop was the dominant competitor both in the presence and absence of the nematode. Measurements of niche differentiation indicated that the two plant species did not fully share the same limiting resources in the absence of the nematode, and that competition for limited resources intensified when the nematode was present.

Résumé – ***Analyse des interactions concurrentielles entre une mauvaise herbe et une culture attaquées par des nématodes, à l'aide de la méthode des séries de substitution*** – Les méthodes permettant d'évaluer les effets de concurrence sont appliquées à un système nématode-mauvaise herbe-culture. Il a été cherché à connaître les relations entre le nématode [*Anguina amsinckiae* (Steiner & Scott, 1935) Thorne, 1961], sa plante hôte (*Amsinckia intermedia* Fischer & Meyer) et le blé (*Triticum aestivum* L.). Des expériences basées sur des séries de substitution sont conduites en serre en considérant des rapports (mauvaise herbe : culture) de 0:1, 3:1, 1:1, 1:3, et 1:0. Ces expériences menées avec et sans nématodes sont répétées deux fois. Les résultats montrent que le nématode réduit de 25 % le poids sec de la mauvaise herbe, mais n'a aucun effet significatif sur le poids sec de la culture. Les indices de concurrence montrent que la culture est le concurrent dominant aussi bien en présence qu'en absence du nématode. Les mesures relatives à la différenciation des niches laissent supposer que les deux espèces végétales ne partagent pas entièrement, en l'absence du nématode, les mêmes ressources limitées et que la concurrence vis-à-vis de ces ressources est accrue en présence du nématode.

Key-words : *Amsinckia intermedia, Anguina amsinckiae, Triticum aestivum,* biological weed control, interference.

De Wit (1960) introduced the replacement series method which incorporates a mathematical approach to interpret the results of plant competition. In this experimental design, the two competing plant species are maintained at one constant overall density while the proportions of the two species are changed (Cousens, 1991). Therefore, one plant species replaces another plant species and hence the term replacement series. The two competing plant species (S_1 and S_2) are grown at proportions z_1 and z_2 where the sum of z_1 and z_2 always equals 1. The two species compete for hypothetical space (Hall, 1974) that includes the sum of all limiting environmental factors (e.g. ground area, water, nutrients, and light). Each plant of s_1 uses b_{11} units of space, and each plant of S_2 uses b_{12} units of the space needed by S_1 (Thomas, 1970). Correspondingly, each plant of S_2 uses b_{22} units of space and each plant of S_1 uses b_{21} units of the space needed by S_2. For proportions z_1 and z_2 with total number of plants N, the total space needed is

$$N(b_{11} z_1 + b_{12} z_2) \quad (1)$$

and

$$N(b_{21} z_1 + b_{22} z_2) \quad (2)$$

for S_1 and S_2, respectively.

Yield is defined as plant shoot biomass. The yields, y_1 and y_2, are proportional to the space occupied by each species and are described by

$$y_1 = m_1 b_{11} z_1 / (b_{11} z_1 + b_{12} z_2) \quad (3)$$

and

$$y_2 = m_2 b_{22} z_2 / (b_{21} z_1 + b_{22} z_2) \quad (4)$$

for S_1 and S_2, respectively, where m_1 and m_2 are constants.

The ratio of b_{11} to b_{12} is defined as the relative crowding coefficient (k_{12}) of S_1 with respect to S_2, while the ratio of b_{22} to b_{21} is termed the relative crowding coefficient (k_{21}) of S_2 with respect to S_1. Therefore,

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$$k_{12} = b_{11}/b_{12} \quad (5)$$

and

$$k_{21} = b_{22}/b_{21} \quad (6)$$

If the two plant species have equal competitive abilities, k_{12} and k_{21} will both equal 1.0. Alternately, if the competitive ability of S_1 is greater than that of S_2, k_{12} will be greater than 1.0, and if S_1 is less competitive than S_2, k_{12} will be less than 1.0. Of particular interest is the case where two plant species are competing for the same space and $b_{11} = b_{21}$ and $b_{22} = b_{12}$; in this special case, $k_{12} = 1/k_{21}$.

Substituting k_{12} and k_{21} into equations 3 and 4,

$$y_1 = m_1 k_{12} z_1/ (k_{12} z_1 + z_2) \quad (7)$$

and

$$y_2 = m_2 k_{21} z_2/ (k_{21} z_2 + z_1) \quad (8)$$

which is the final form of the model. In the case of a monoculture of S_1, $z_1 = 1.0$ and $z_2 = 0$. Substituting these values into equation (7), it can be seen that m_1 is the yield of S_1 in monoculture. Likewise, it can shown that m_2 is the yield of S_2 in monoculture.

The extent to which two plant species avoid competition for the same limited resource is sometimes referred to as resource complementarity (Snaydon, 1991) or niche differentiation (Spitters, 1983). Those species which are most similar and compete for the same resources in the same manner would be expected to have little niche differentiation. The relative yield (RY) and the relative yield total (RYT) can be used to quantify niche differentiation (de Wit & van den Bergh, 1965). The RY is calculated by the equations

$$RY_1 = y_1/m_1 \quad (9)$$

and

$$RY_2 = y_2/m_2 \quad (10)$$

for S_1 and S_2, respectively. The RYT is the sum of the two relative yields and is calculated by the expression

$$RYT = RY_1 + RY_2 \quad (11)$$

RYT values of 1.0 indicate that the two plant species are making demands on identical resources and compete fully (Trenbath, 1974). Values greater than 1.0 indicate some niche differentiation is occurring and the two species compete partially (Snaydon & Satorre, 1989), while values less than 1.0 imply the two species are mutually antagonistic (Harper, 1977).

Plant parasitic nematodes have been shown to shift the balance between two interacting plant species (Sibma *et al.,* 1964). Mixtures of oats (*Avena sativa* L.) and barley (*Hordeum vulgare* L.) grown in replacement series were greatly influenced by the oat cyst nematode (*Heterodera avenae* Wollenweber). Oats are susceptible to the nematode while barley is resistant. When the nematode was absent, oats yielded more than barley, and the relative crowding coefficient was 6 for oats with respect to barley. However, when the oat cyst nematode was present, the situation was much more balanced and the relative crowding coefficient was 1.3. Moreover, the nematode did not reduce the yield of oats in pure stands.

Pantone *et al.* (1989) investigated the influence of the fiddleneck flower gall nematode, *Anguina amsinckiae* (Steiner & Scott, 1935) Thorne, 1961, on plant competition between fiddleneck, *Amsinckia intermedia* Fischer & Meyer, a weed, and wheat, *Triticum aestivum* L. in field studies. The nematode is very host specific and only attacks species within the genus *Amsinckia* (Pantone, 1987). However, they used the inverse linear model (Spitters, 1983) instead of the replacement series design and the model of de Wit (1960). A dramatic decrease in the competitive ability of the weed was observed in the presence of the nematode. The index that measured interspecific competition of wheat with respect to fiddleneck increased 33-fold in nematode inoculated plots. Although fiddleneck was the dominant competitor in the absence of the nematode, when the nematode was present the two plant species competed nearly equally. In addition, some measurements of niche differentiation decreased greatly in nematode infested plots, indicating that the intensity of plant competition increased.

Nagamine and Maggenti (1980) proposed the fiddleneck flower gall nematode as a biological weed control agent of the weed, fiddleneck. Researchers have investigated various aspects of the host-parasite biology and the host range of the nematode (Steiner & Scott, 1934; Godfrey, 1940; Pantone *et al.,* 1985, 1987; Pantone & Womersley, 1986; Pantone, 1987); however, only one previous series of experiments has been performed to assess the efficacy of this proposed biocontrol agent (Pantone *et al.,* 1989). The objective of the present study was to use the replacement series experimental design and the de Wit model to further evaluate the influence of the fiddleneck flower gall nematode on weed-crop competition.

Materials and methods

Fiddleneck seeds were scarified with a fine forceps and planted into Yolo Fine Sandy Loam (a fine-silty, mixed, nonacid, thermic Typic Xerorthent) to a depth of 1 cm in 30-cm diameter by 40-cm deep pots. Seeds of wheat (cv. Yecora Rojo) were sown approximately 3 cm deep. Replacement series were planted with mixed species ratios of 1:1, 1:3 and 3:1 and in monocultures at a constant overall density of 24 plants per pot for all treatments (a total of five seedling combinations). Six replicates of each combination were controls grown without nematodes and six were inoculated with approximately 250 000 nematodes per pot, which is the equivalent of about 1.4 nematode galls. All pots were arranged in a randomized complete block design. The initial photoperiod was 12 h, and the temperature was constant at

15 °C. After 65 days, the daylength was increased to 16 h to stimulate flowering and maturation. The soil was not supplemented with fertilizer and was watered as needed. Plants matured at approximately the same time, and were harvested after 110 days. All specimens were dried at 60 °C, and the shoot dry weight was measured for both plant species. In addition, the number of nematode galls produced per plant was recorded.

Although computer programs are available for the analysis of replacement series experiments, a general nonlinear regression program (Anon., 1988) was used for all regressions. This approach has similar performance and provides additional statistics (Larsen & Williams, 1988). Nonlinear regressions were performed for controls and nematode-treated plots for both species according to the de Wit model equations. Using equations [7] and [8], the unknown parameters k_{fw}, k_{wf}, m_f, and m_w were estimated for both the nematode-treated and untreated replacement series where f (fiddleneck) represented species 1, and w (wheat) represented species 2. Parameters were estimated by the multivariate secant method of Ralston and Jennrich (1978). Parameters for the nematode-treated and untreated controls were compared using t tests (Zar, 1974). The relative yield total (Harper, 1977) was calculated for each replacement series to estimate the degree of niche differentiation between plant species.

Results and discussion

Anguina amsinckiae decreased the yield of fiddleneck both in monocultures and mixed stands (Fig. 1; Table 1). Wheat yields remained the same, and no corresponding increase in the yield of wheat was measured as the yield of fiddleneck decreased. When the nematode was absent, the yield of fiddleneck in monocultures (m_f) was 51.04 g, compared to 38.17 g in nematode treatments. The shift of the fiddleneck replacement series by the nematode treatment corresponded to an average decrease ($P < 0.05$) of 12.87 g (25 percent) for monocultures. Despite this, values of the relative crowding coefficients indicated that the presence of the nematode did not significantly increase the competitive ability of wheat as in other experiments (Pantone *et al.*, 1989). Wheat was the dominant competitor in all treatments with k_{wf} values of 5.80 and 3.63 in the controls and nematode-treatments, respectively (Table 1). Relative crowding coefficients for fiddleneck with respect to wheat (k_{fw}) were 0.62 in the absence of the nematode and 0.69 in the presence of the parasite. Since the relative crowding coefficients for fiddleneck with respect to wheat (k_{fw}) were less than 1.0, it is implied that the yield of fiddleneck was more sensitive to interspecific competition than intraspecific competition. High relative crowding coefficient values for wheat with respect to fiddleneck suggest that wheat was aggressive in both the presence and absence of the nematode.

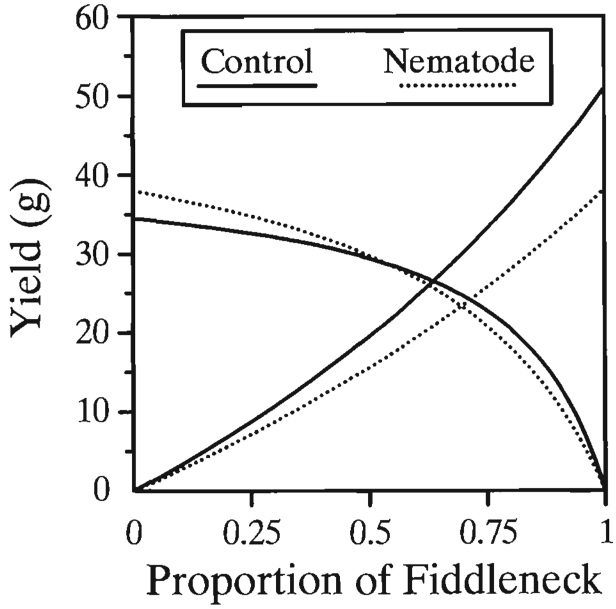

Fig. 1. *The yield of fiddleneck and wheat in replacement series experiments with and without inoculations of the fiddleneck flower gall nematode. The two lines (solid and dashed, respectively) which are 0.0 when the proportion of fiddleneck is 0.0 refer to fiddleneck (controls and nematode-inoculated, respectively). The other two lines refer to wheat.*

Table 1. *De Wit model parameters for the fiddleneck-wheat replacement series. Yields of monocultures (± standard error) are indicated by* m_f *and* m_w *for fiddleneck and wheat, respectively. The relative crowding coefficients (± standard error) for fiddleneck with respect to wheat and wheat with respect to fiddleneck are denoted by* k_{fw} and k_{wf}, respectively.

	Monoculture yield (g)		Relative crowding coefficients	
Treatment	m_f	m_w	k_{fw}	k_{wf}
Control	51.04* ± 4.01	34.52 ± 2.90	0.62 ± 0.16	5.80 ± 3.71
Nematode	38.17* ± 4.28	38.02 ± 3.66	0.69 ± 0.15	3.63 ± 2.13

* Control and nematode treatments signficantly different ($\alpha = 0.05$).

Relative yield totals for the replacement series were found to be greater than 1.0 at all mixed ratios, and reached a maximum value of approximately 1.3 for untreated mixtures and 1.2 for mixtures infested with nematodes (Fig. 2). The high *RYT* values, which exceeded 1.0, also imply that fiddleneck and wheat were able to avoid interpecific competition to a certain extent. High *RYT* values suggest that the interacting plants were using different strategies to exploit limiting resources and that niche differentiation occurred. With respect to plant stature, fiddleneck differs from wheat in that it remains in a rosette stage until it matures and flowers. Moreover,

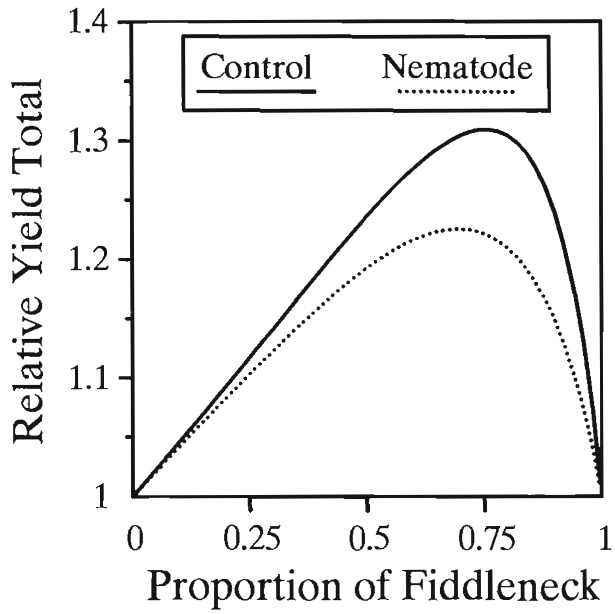

Fig. 2. *The Relative Yield Total (RYT) of fiddleneck and wheat with and without inoculations of the fiddleneck flower gall nematode.*

the root systems of the two species differ greatly. Fiddleneck is a tap-rooted plant, while wheat has a diffuse root system typical of grasses. The opportunity for fiddleneck and wheat to differ in resource exploitation and utilization appears to be great, but would be expected to be somewhat limited under greenhouse conditions as compared to the field. The decrease of the *RYT* in the presence of the nematode implies that niche differentiation decreased and that the nematode decreased the potential for the two plant species to avoid competition by exploiting resources differently.

The results of this experiment differ markedly from the replacement series experiments reported by Sibma *et al.* (1964). In the oat cyst nematode experiment, pots were inoculated with 500-600 nematodes per 200 ml of soil. Under this inoculum level, the oat cyst nematode only reduced yields of oats grown in mixed stands and did not reduce the yield of oats in pure stands as did the fiddleneck flower gall nematode in the present experiment. Although both the oat cyst and the fiddleneck flower gall nematodes are plant parasitic nematodes, fundamental differences exist in their host-parasite biology. The oat cyst nematode is a cyst forming nematode that attacks the roots of its host, while fiddleneck flower gall nematode is only known to attack above-ground plant parts. In the case of oat cyst nematode, Sibma *et al.* (1964) attributed the absence of any apparent nematode damage in pure stands to the presence of sufficient roots to extract water and nutrients from the soil; apparently, adequate roots remained to compensate for any nematode damage. The fiddleneck flower gall nematode, however, feeds directly on the meristems of the shoot (Godfrey, 1940; Pantone & Womersley, 1986), and damage by the nematode to meristematic tissues may stunt shoot growth and not be compensated. The results of the present experiment indicated that nematode damage to fiddleneck can occur independently of interspecific competition which differs from the oat cyst nematode damage to oats.

Although the overall results of the present greenhouse study are similar to the previous field studies of Pantone *et al.* (1989) in that the nematode reduced the biomass of fiddleneck, many important differences exist. For example, the field study indicated that fiddleneck was the dominant competitor in the absence of the nematode, whereas relative crowding coefficients from the greenhouse study indicated that wheat dominated the interaction. Moreover, in the field studies the competitive indices for wheat increased with nematode treatments and correspondingly so did wheat yields in mixed stands. In the present study, no increases in relative crowding coefficients or yields could be demonstrated for wheat (Table 1). Overall, the effects of the nematode in the previous field experiments were much more dramatic than in the present greenhouse study, and results indicate that greenhouse studies of nematode impacts on plant competition should be interpreted with caution. Differences in soil moisture levels and light intensities could contribute to the observed differences between greenhouse and field studies.

Out of a total of 360 fiddleneck plants, only nine galls were produced in this greenhouse study. This output was equivalent to 0.4 galls per pot compared to an inoculation rate of 1.4 galls. This incidence of gall formation was much lower than that observed in the field where a natural fiddleneck population averaged 2.4 galls per plant (Pantone & Womersley, 1986). The formation of dew under field conditions may provide conditions more favorable for nematode invasion during floral development. In addition, light intensity might influence floral development and subsequent nematode gall formation. It is unclear to what extent the presence of galls is associated with nematode damage, and feeding by the nematodes on seedlings may be more damaging than the formation of nematode galls.

In summary, the techniques outlined provide a method for quantifying the impact of plant parasitic nematodes on weed-crop competition under greenhouse conditions. Moreover, these methods may provide insights into the mechanisms by which herbivores and pathogens influence their hosts.

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