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Modelling the combined effect of chemical interference and resource competition on the individual growth of two herbaceous populations

Leticia San Emeterio · Christian Damgaard · Rosa M. Canals

Abstract Resource competition and chemical interference are mechanisms of interaction among plants that may occur simultaneously. However, both mechanisms are rarely considered together when modelling plant growth. We propose a new empirical model that estimates biologically significant parameters on both plant competition and chemical interference. The model is tested with data sets from different density-dependent experiments done with two species (the grass *Lolium rigidum* Gaud. and the legume *Glycine max soya* L.) subjected to a noxious chemical environment when growing (allelochemicals and herbicides, respectively). Hypotheses on the effect of allelochemicals and its interaction with density are tested using maximum likelihood ratio tests in order to ask, for these species, whether chemical interference is playing a significant role in the interactions among plants or on the contrary, whether interactions among plants are sufficiently explained by the resource competition. In all cases a significant interaction between chemicals and density is observed. This interaction is inconsistent with the hypothesis of only resource competition having an influence of plant biomass and suggests a significant density-dependent effect of chemicals on plant growth.

Introduction

Negative interactions among plants can be mediated by resources, competition in the narrow sense, and/or other factors, e.g., allelopathy (Reigosa et al. 1999; Stoll and Weiner 2000). The relative importance of the role played by these different mechanisms of interaction is a controversial question. Since allelopathy and resource competition may act together (Nilsson 1994; Inderjit and del Moral 1997), it is experimentally difficult to distinguish between them, which is a crucial issue in order to understand their relative importance (Weidenhamer 1996; Ridenour and Callaway 2001; Liu et al. 2005).

Most published studies on plant interactions lack specific trials designed to discriminate between resource competition effects and chemical effects. Weidenhamer et al. (1989) proposed an experimental design that allowed to

L. San Emeterio (✉) · R. M. Canals
Departamento de Producción Agraria, Universidad Pública de Navarra, Campus Arrosadía s/n, 31006 Pamplona, Spain
e-mail: leticia.sanemeterio@unavarra.es

C. Damgaard
Department of Terrestrial Ecology, NERI, Velsovej 25, 8600 Silkeborg, Denmark

distinguish allelopathy from resource competition based on the density-dependent nature of the phytotoxic effects. They studied the effect of different concentrations of toxic substances (potential allelochemicals) at different plant densities and proposed that the interaction between phytotoxicity and density could cause a deviation in the predicted decrease in plant size with increasing density. The effect of an allelochemical is stronger at lower plant densities than at higher plant densities due to the dilution of the allelochemical among plants: plants grown at high densities have a smaller amount of allelochemical available per individual plant than plants grown at low densities. Consequently, the maximum plant size may be observed at intermediate plant densities, because plant growth is constrained by phytotoxic effects at low densities, and by resource competition at high densities.

Since resource competition and chemical interference can occur simultaneously, it is important to model the effects of both and, in particular, their interaction. To date, few works on modelling chemical interference among plants have been published. Sinkonnen modelled chemical interference caused by phytochemicals (Sinkkonen 2001) and by decomposing residues (Sinkkonen 2003). These models combined the biological response model based on enzyme kinetics of An et al. (1993) with the "allelochemical dilution hypothesis" of Weidenhamer et al. (1989). However, proposed models focused on the dilution of the toxin with density, overlooking the effect of resource competition on plant growth.

The aim of this research is to model the joint effects of resource competition and chemical interference on plant growth. We propose a new empirical model, which combines a hyperbolic size-density response function with the "allelochemical dilution hypothesis" (Weidenhamer et al. 1989). The hyperbolic size-density response function has been widely used to model plant competition (Firbank and Watkinson 1985; Law and Watkinson 1987) and to estimate the probability of coexistence (Damgaard 1998, 2004). We test the model with data sets on *Lolium rigidum* and soybean (*Glycine max soya*) biomass obtained from different density-dependent experiments. In the first case, experimental data evaluated the effect of *Lolium rigidum* debris on shoot and root biomass of *Lolium rigidum* individuals (Canals et al. 2005). This species has shown an allelopathic and autotoxic potential (San Emeterio et al. 2004) and polyphenolic compounds, such as ferulic and coumaric acids, have been isolated from their leaves, roots and shoots (*data not published*). In the second case, we used data on the effects of the herbicide atrazine on soybean shoot biomass obtained and published by Thijs et al. (1994).

Materials and methods

Data sets

Data were obtained from experiments with two different species, a grass, *Lolium rigidum* Gaud. and a legume, soybean (*Glycine max soya* L.). All experiments were done under controlled conditions and were previously published in Canals et al. (2005) in the case of *Lolium rigidum*, and Thijs et al. (1994) in the case of soybean.

Data on individual shoot and root biomass of *Lolium rigidum* as a function of density and amount of *Lolium rigidum* debris were obtained from pot monocultures sowed in a controlled environment. Monocultures were established at four densities: 1, 2, 4 and 8 plants per 10-cm diameter pot, which corresponded to a density of 127, 255, 510 and 1020 plants m^{-2} respectively. Plants were evenly spaced within the pot. Monocultures were amended with different amounts of debris (a control without residues, and a low, medium and high amount of debris, which corresponded to a field crop residue of about 0, 425, 1250 and 3000 kg DM/ha, respectively). Shoots and roots were harvested 49 days after sowing. The experiment was done in four replicates (for more details see Canals et al. 2005).

Data on individual soybean biomass as a function of neighbour density and concentration of atrazine were obtained from two experiments presented in Figs. 2 and 5 in Thijs et al. (1994). Both experiments had a neighbour-target design

with four densities (3, 6, 9 and 12 neighbour plants per 10-cm diameter pot) and four levels of atrazine (0.0, 0.5, 1.5, and 3.0 mg kg^{-1} solution). In the first experiment, soybean was the target and the neighbour species, and in the second experiment, soybean was the neighbour species and corn was the target species. In both cases the target species was planted in the middle of the pot, and neighbour seedlings were planted evenly around the target individual. Shoots were harvested 29 days after planting. Data were displayed as means of three replicates and no measures of variability were included.

Model

An empirical model, which combines a hyperbolic size-density response function (e.g., Firbank and Watkinson 1985; Law and Watkinson 1987; Damgaard 1998, 2004) with the "allelochemical dilution hypothesis" (Weidenhamer et al. 1989), was used to fit the data from the density-dependent experiments. Previous experience with plant competition models (Damgaard, 1998, 2003, 2004; Damgaard et al. 2002) led us to decide to implement this model among other modelling possibilities.

$$f(x_d, x_a) = \frac{1}{\alpha + \beta x_d} \; \exp(a x_a) \; \exp(-b \, t(x_d) \, x_a) \tag{1}$$

In this model, individual biomass, f, is presented as a function of plant density, x_d, and toxin concentration (amount of debris, x_a). The first factor in the left hand side is a hyperbolic size-density response function, which measures the effect of density, where α and β are parameters that measure the effect of competition.

The middle factor measures the effect of the toxin concentration on individual plant biomass independently of density. If parameter $a = 0$ there is no toxic effect on biomass, if $a > 0$ the effect is stimulatory and, if $a < 0$ the effect is inhibitory.

The last factor measures the interaction between density and toxin concentration, where b measures this interaction effect. A piecewise

function of plant density ($t(x_d)$) was constructed in order to test for the possibility of an optimum plant size at an intermediate density in the presence of the toxin as hypothesised by the "dilution hypothesis":

$$t(x_d) = \begin{cases} T - x_d & x_d < T \\ 0 & 0 < T \le x_d \end{cases} \tag{2}$$

where T measures the density at which the interaction between density and the effect of the toxin disappears as hypothesised in the "dilution hypothesis". When plant density is higher than T, the interaction factor equals one, so there is no interaction effect over that density. It was tested whether this piecewise function (2) fitted better than a simple model of interaction, $t(x_d) = x_d$, that is:

$$f(x_d, x_a) = \frac{1}{\alpha + \beta x_d} \; \exp(a x_a) \; \exp(-b \, x_d \, x_a) \tag{3}$$

If the piecewise function fits significantly better (Eq. 1), the interaction between density and toxin concentration is significant and there is an optimum plant growth at an intermediary density. However, if the simple model of interaction fits significantly better (Eq. 3), there is not an optimum plant growth at an intermediary density, although the interaction may be significant ($b \ne 0$) or not ($b = 0$). In the first case ($b \ne 0$), there is a "dilution" effect, but the interaction effect does not disappear within the density range of the experiment and, therefore, T can not be estimated. In the second case ($b = 0$), the toxin is not "diluted" among plants or there is no phytotoxic effect.

Statistical procedures

In order to fit the model to the data, an error term was included in Eq. 1 and 3. Data on individual shoot and root biomass of *Lolium rigidum* were Box-Cox transformed ($\lambda_1 = -2$, $\lambda_2 = 1$). After transformation, the residuals were approximately normally distributed and with homogeneous variance. Data on shoot biomass of soybean needed no transformation. The likelihood function of a

normal distribution was used to perform likelihood ratio tests by a standard hierarchical procedure (Damgaard 1998). So we assessed first, whether the piecewise function (2) fitted better than the simple model of interaction (Eq. 3); second, whether parameter b was significantly different from zero, i.e., whether there was a significant interaction between phytotoxicity and density; and third, whether parameter a was significantly different from zero, i.e., whether there was a significant phytotoxic effect independent on density. The existence of a significant interaction between phytotoxicity and density, inconsistent with the predicted biomass decrease with increasing density, would suggest that chemical interference plays a significant role and therefore, that resource competition is not the only factor affecting plant biomass.

Results

The empirical chemical interference model fitted the data on *Lolium rigidum* shoot and root biomass from the density-dependent experiments judging by a comparison between observed and predicted values ($r^2 = 0.96$ for individual shoot biomass, Table 1, Fig. 1; and $r^2 = 0.77$ for individual root biomass, Table 2, Fig. 2). The parameters that measure competition were estimated as $\alpha = 1.87$, $\beta = 0.008$ for shoot biomass and $\alpha = 9.48$, $\beta = 0.0224$ for root biomass. The piecewise $t(x_d)$ function fitted better than the simple interaction model (Eq. 3) for both shoot and root data sets, b was significantly different from zero ($b = 2.33 \cdot 10^{-6}$ and $4.17 \cdot 10^{-6}$, for shoot an root biomass, respectively) and the effect of the amount of debris independent on density, measured by a, was not significant ($a = 0$, Table 3). A significant interaction effect between density and amount of *Lolium rigidum* debris was predicted to occur below 200 plants m^{-2} for shoots, and 190 plants m^{-2} for roots ($T = 200$ and 190, respectively). The prediction was in agreement with the experimental observation since, at the highest amount of debris, the maximum plant size occurred at 200 plants m^{-2} (Table 3).

Regarding soybean data sets, the empirical model fitted the data on soybean biomass

obtained from the Thijs' target-neighbour experiments. See Figs. 3 and 4 for a graphical comparison between observed and predicted values ($r^2 = 0.80$ and 0.93, respectively). The parameters that measure competition were estimated as $\alpha = 0.91$, $\beta = 0.11$ and $\alpha = 0.96$, $\beta = 0.21$ for data with soybean and corn as target species, respectively. The effect of concentration of atrazine and its interaction with density was significant along the density range of the experiment, since a and b were significantly different from zero ($a = -0.34$ and -0.57; and $b = -0.03$ and -0.04, for soybean and corn as target species, respectively) and the simple model fitted better than the piecewise $t(x_d)$ function (Table 3).

Discussion

The empirical model has proved a powerful tool for the analysis of chemical interference in density-dependent experiments. The model is adequate to analyse chemical interference in general (phytotoxic effects of any toxic substance), and particularly allelopathy, if we assume that the amount of decomposing residues is directly proportional to the allelochemical concentration. The model is appropriate when the response curve has its maximum size at intermediate densities. However, it would need modification to include more complex responses to allelochemical concentration such as the saw tooth curves described by Reigosa et al. (1999) and to account for changes in biomass allocation.

The biological significance of the competition parameters has been broadly described (Mead 1970; Seber and Wild 1989). In the absence of a toxin, $1/\alpha$ measures the individual biomass at low plant densities and $1/\beta$ measures the asymptotic value of biomass per area at high plant densities. However, in the presence of a toxin, the individual biomass at low plant densities decreases with increasing toxicity, becoming a deficient measure of individual biomass. On the contrary, if the toxin is "diluted" among neighbour plants, $1/\beta$ can estimate the asymptotic value of biomass per area at high density, since this value is independent on toxicity once a certain density is reached. This density is

Table 1 Observed and predicted values of *Lolium rigidum* individual shoot biomass as a function of *Lolium rigidum* density and amount of *Lolium rigidum* debris

Debris	Density (plants m^{-2})							
	127		255		510		1,020	
	obs	pred	obs	pred	obs	pred	obs	pred
0	0.34 ± (0.04)	0.34	0.27 ± (0.02)	0.25	0.18 ± (0.01)	0.16	0.10 ± (0.01)	0.10
454	0.33 ± (0.09)	0.31	0.25 ± (0.02)	0.25	0.16 ± (0.01)	0.16	0.11 ± (0.02)	0.10
1500	0.23 ± (0.02)	0.26	0.22 ± (0.05)	0.25	0.16 ± (0.01)	0.16	0.08 ± (0.01)	0.10
3000	0.22 ± (0.10)	0.20	0.26 ± (0.01)	0.25	0.17 ± (0.04)	0.16	0.09 ± (0.01)	0.10

Debris, amount of *Lolium rigidum* debris in kg ha^{-1}; obs, average and 95% confidence interval; pred, predicted value from the model when $\alpha = 1.87$, $\beta = 0.008$, $a = 0$, $b = -2.33 \times 10^{-6}$, $T = 200$

Fig. 1 Predicted individual shoot biomass of *Lolium rigidum* as a function of *Lolium rigidum* density and amount of *Lolium rigidum* debris. $\alpha = 1.87$, $\beta = 0.008$, $a = 0$, $b = 2.33 \times 10^{-6}$, $T = 200$ (Eq. 1 model). Black points are the observed values and big black points are the media
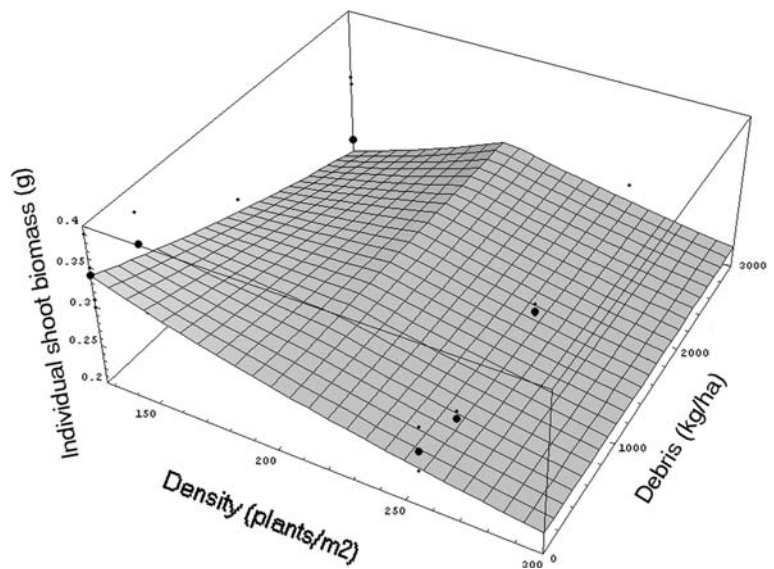

Table 2 Observed and predicted values of *Lolium rigidum* individual root biomass as a function of *Lolium rigidum* density and amount of *Lolium rigidum* debris

Debris	Density (plants m^{-2})							
	127		255		510		1020	
	obs	pred	obs	pred	obs	pred	obs	pred
0	0.0760 ± (0.0138)	0.0810	0.0790 ± (0.0148)	0.0657	0.0593 ± (0.0054)	0.0477	0.0380 ± (0.0109)	0.0308
454	0.0856 ± (0.0396)	0.0719	0.0660 ± (0.0252)	0.0657	0.0457 ± (0.0137)	0.0477	0.0288 ± (0.0085)	0.0308
1,500	0.0521 ± (0.0107)	0.0545	0.0425 ± (0.0109)	0.0657	0.0459 ± (0.0095)	0.0477	0.0227 ± (0.0067)	0.0308
3,000	0.0359 ± (0.0200)	0.0366	0.0667 ± (0.0077)	0.0657	0.0556 ± (0.0209)	0.0477	0.0231 ± (0.0067)	0.0308

Debris, amount of *Lolium rigidum* debris in kg ha^{-1}; obs, average and 95% confidence interval; pred, predicted value from the model when $\alpha = 9.48$, $\beta = 0.0224$, $a = 0$, $b = -4.17 \times 10^{-6}$, $T = 190$

estimated by T and may be a function of toxin concentration, i.e., T may be expected to increase with increasing toxin concentration. Thus, T is a measure of the density at which optimal plant size at the highest toxin concentration is observed: plant biomass is limited by phytotoxicity below this density, and by resource competition above this density.

Fig. 2 Predicted individual root biomass of *Lolium rigidum* as a function of *Lolium rigidum* density and amount of *Lolium rigidum* debris. $\alpha = 9.48$, $\beta = 0.0224$, $a = 0$, $b = 4.17 \ 10^{-6}$, $T = 190$ (Eq. 1 model). Black points are the observed values and big black points are the media

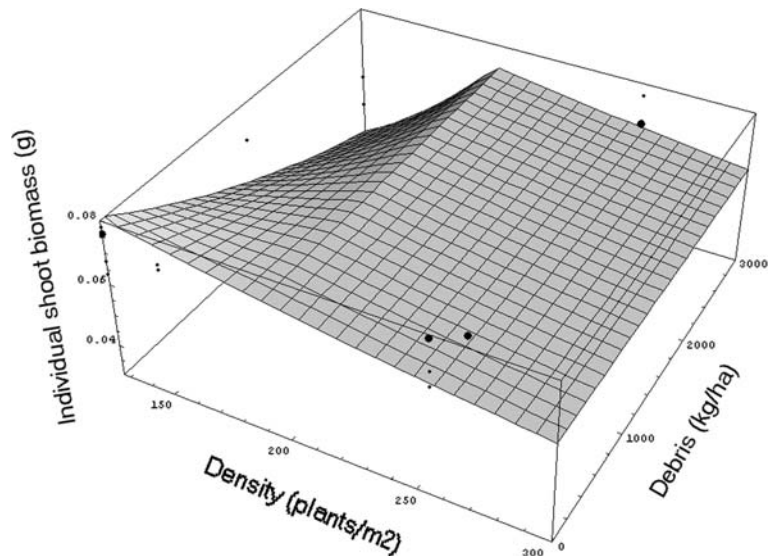**Table 3** Likelihood ratio tests of hypothesis on chemical interference model

	H_0	H_1	H_2 ($b = 0$)	H_3 ($a = 0$)
Lolium rigidum shoot biomass (Canals et al. 2005)[a]				
l	122.72	115.22	115.02	122.41
d.f.		1	2	1
P		0.0001	0.00045	0.436
Lolium rigidum root biomass (Canals et al. 2005)[b]				
l	173.57	168.58§	168.2	172.60
d.f.		1	2	1
P		0.0016	0.0047	0.1636
Soybean biomass with soybean as a target (Thijs et al. 1994, Fig. 2)[c]				
l	34.38	34.38	25.89	16.89
d.f.		1	1	1
P		0.9997	0.00003	$3.33 \ 10^{-9}$
Soybean biomass with corn as a target (Thijs et al. 1994, Fig. 5)[d]				
l	24.83	24.83	15.33	10.16
d.f.		1	1	1
P		≈ 1	0.000012	$5.75 \ 10^{-8}$

[a] H_0: $\alpha = 1.89$, $\beta = 0.0008$, $a = -1.89 \ 10^{-5}$, $b = 2.05 \ 10^{-6}$, $T = 200$; H_1: $\alpha = 2.22$, $\beta = 0.0069$, $a = -9.22 \ 10^{-5}$, $b = -4.77 \ 10^{-8}$; H_2: $\alpha = 2.31$, $\beta = 0.0066$, $a = -7.54 \ 10^{-5}$, $b = 0$, $T = 200$; H_3: $\alpha = 1.87$, $\beta = 0.008$, $a = 0$, $b = 2.33 \ 10^{-6}$, $T = 200$

[b] H_0: $\alpha = 9.31$, $\beta = 0.02$, $a = -3.65 \ 10^{-5}$, $b = 1.58 \ 10^{-6}$, $T = 282$; H_1: $\alpha = 10.42$, $\beta = 0.016$, $a = -1.76 \ 10^{-4}$; $b = -1.11 \ 10^{-7}$; H_2: $\alpha = 11.04$, $\beta = 0.014$, $a = 1.34 \ 10^{-4}$, $b = 0$, $T = 282$; H_3: $\alpha = 9.48$, $\beta = 0.022$, $a = 0$, $b = 4.18 \ 10^{-6}$, $T = 190$

[c] H_0: $\alpha = 0.90$, $\beta = 0.11$, $a = 0.036$, $b = 0.04$, $T = 9.89$; H_1: $\alpha = 0.91$, $\beta = 0.11$, $a = -0.34$, $b = -0.03$; H_2: $\alpha = 1.14$, $\beta = 0.059$, $a = -0.15$, $b = 0$; H_3: $\alpha = 1.43$, $\beta = 0.04$, $a = -0.15$, $b = 0$

[d] H_0: $\alpha = 0.96$, $\beta = 0.21$, $a = 0.53$, $b = 0.03$, $T = 27.51$; H_1: $\alpha = 0.96$, $\beta = 0.21$, $a = -0.57$, $b = -0.04$; H_2: $\alpha = 1.29$, $\beta = 0.15$, $a = -0.31$, $b = 0$; H_3: $\alpha = 1.84$, $\beta = 0.089$, $a = 0$, $b = 0.038$

d.f., number of parameters fixed by the hypothesis; l, Value of the maximized likelihood function; P, probability of the hypothesis being correct assuming a chi-square distribution for the test ratio; H_0, full model hypothesis (Eq. 1); H_1, Simple interaction model (Eq. 3); b, interaction effect parameter; a, concentration effect parameter

Fig. 3 Predicted Soybean individual biomass as a function of density and atrazine concentration, $\alpha = 0.91$, $\beta = 0.11$, $a = -0.34$, $b = -0.03$ (Eq. 3 model). Black points are the observed values
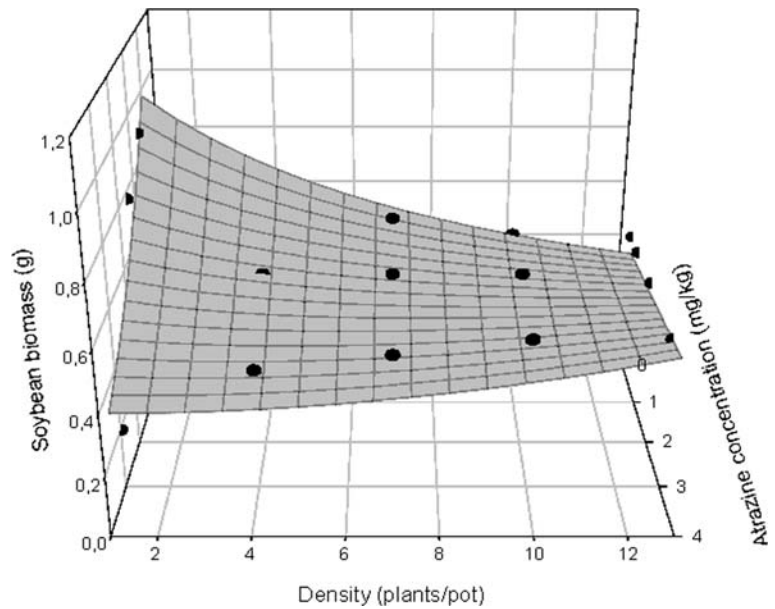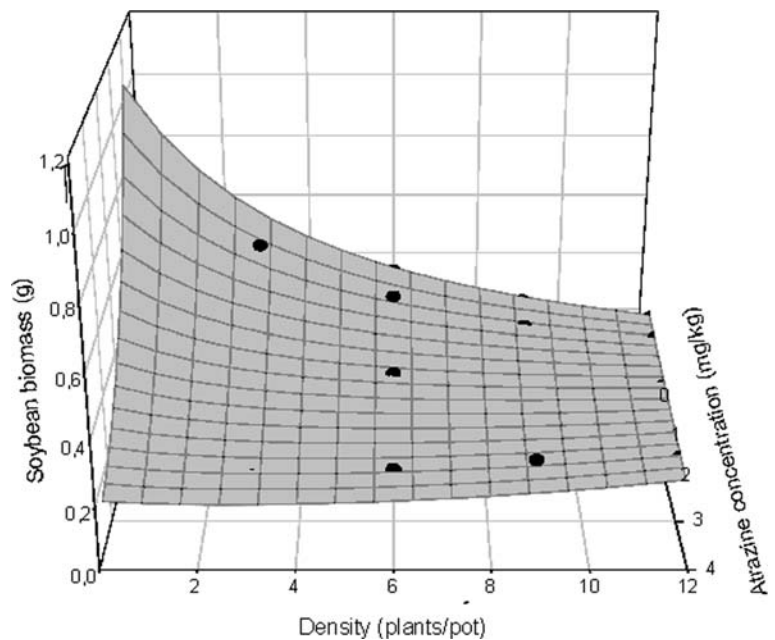
Fig. 4 Predicted Soybean individual biomass as a function of neighbour density and atrazine concentration with corn as target species, $\alpha = 0.96$, $\beta = 0.21$, $a = -0.57$, $b = -0.04$ (Eq. 3 model). Black points are the observed values

In the case of *L. rigidum* data sets, the model estimated that the optimal root and shoot size at the highest amount of debris was reached at a density of 190 plants m^{-2} for roots and 200 plants m^{-2} for shoots. A decrease of individual biomass was observed bellow and above this density. However, the model did not account for a trend towards a greater root biomass among plants growing at higher density and with increased

levels of debris (255 plants m^{-2} and 3000 kg ha^{-1} versus 127 plants m^{-2} and 1500 kg ha^{-1}, for instance; Table 2). This trend, an increase in resource allocation to roots in individuals growing in the presence of a competitor, is consistent with previous works on plant competition and resource allocation (Bloom et al. 1985; Craine 2006).

In the case of soybean we could not observe an optimum size at intermediate densities, but we

found a significant interaction between atrazine concentration and plant density: at high concentrations of atrazine there was an increase of individual biomass with density (Fig. 3). Residue experiments have been criticized since the incorporation of debris into the soil can stimulate microbial growth and reduce available nutrients, causing a decrease in plant biomass (Harper 1977). However, neither the maximum individual biomass at intermediate densities (Fig. 1, 2) nor the increase of individual biomass with density (Fig. 3) can be explained by resource competition, instead, it can be explained by the "dilution hypothesis". At high densities, the effect of the toxin is diluted among plants, therefore the individual biomass increases with density when plants grow at high toxic concentrations. In both plant species, a positive, facilitative, neighbour effect was found among individuals: at high toxin concentrations, the presence of neighbours allows plants to produce more biomass until certain density (T) is reached, then, resource competition balances positive effects.

In stressful habitats, positive neighbour effects are an important mode of plant interaction (Stoll and Weiner 2000). This phenomenon has been described for different habitats such as arid systems (Maestre et al. 2003), wetlands (Callaway and King 1996) and salt marshes (Bertness and Shumway 1993; Hacker and Bertness 1995; Huckle, et al. 2002). Although mechanisms of facilitation are different, under toxic stresses positive neighbour effects may balance negative effects on individuals.

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