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Effects of distance to crop rows and to conspecific neighbours on the size of *Brassica napus* and *Veronica persica* weeds

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Abstract

We tested the hypothesis that local competitive conditions are a determinant of the size of individual weeds in cereal crops by investigating the relationship between individual weed size and (a) distance from the crop row and (b) distance to the nearest conspecific neighbour in cereal crops. There were significant but weak effects of distance to rows of summer and winter wheat (*Triticum aestivum*), and distance to conspecific individuals on individuals of two weed species, *Brassica napus* and *Veronica persica*. Our results suggest that local neighbourhood competitive conditions, although detectable, have only limited effects on weed growth. Size-asymmetric competition from the crop population and plasticity in weed growth reduce the importance of a weed individual's exact location relative to crop individuals and to other weed individuals. A static, two-dimensional view of space is not sufficient to describe competitive effects because the third dimension can be the most important in competition, and because many plants can change their locations through plastic growth.

Wir überprüften die Hypothese, dass lokale Konkurrenzbedingungen ein Bestimmungsfaktor für die Größe einzelner Unkräuter in Getreidefeldern sind, indem wir die Beziehung zwischen der individuellen Unkrautgröße und (a) der Distanz zu den Pflanzenreihen und (b) der Distanz zu den nächsten, artgleichen Nachbarpflanzen in Getreidefeldern untersuchten. Es gab signifikante jedoch geringfügige Effekte der Distanz zu den Reihen von Sommer- und Winterweizen (*Tritium aestivum)* sowie der Distanz zu den artgleichen Individuen auf die Individuen von zwei Unkrautarten, *Brassica napus* und *Veronica persica*. Unsere Ergebnisse lassen vermuten, dass Konkurrenzbedingungen in der unmittelbaren Nachbarschaft nur einen begrenzten Effekt auf das Unkrautwachstum haben, auch wenn sie wahrnehmbar sind. Größenasymmetrische Konkurrenz seitens der Getreidepopulation und die Plastizität des Pflanzenwachstums reduzieren die Bedeutung der exakten Position einer einzelnen Unkrautpflanze in Beziehung zu einzelnen Getreide- oder anderen, einzelnen Unkrautpflanzen. Eine statische, zweidimensionale Betrachtung des Raumes reicht nicht aus, um die Konkurrenzeffekte zu beschreiben, weil die dritte Dimension die wichtigste für die Konkurrenz sein kann und weil viele Pflanzen ihre Position durch plastisches Wachstum verändern können.

Key words: crop-weed competition – local competition – nearest neighbour distance – plant spatial arrangement – row spacing

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Introduction

Because plants are rooted and therefore restricted in their movements, plant competition is local (Harper 1977, Stoll & Weiner 2000). Plants interact only with other nearby plants. Many "neighbourhood" models of competition among individual plants assume that the local competitive conditions of an individual plant, such as the number, size and distance of its neighbours, are critical determinants of the individual's experience of competition and therefore growth (Mack & Harper 1977, Weiner 1984, Silander & Pacala 1985, Goldberg 1987). While there has been research on the spatial distribution of weeds within crop fields (e.g. Mortensen et al. 1993, Rew & Cousens 2001), few studies have investigated the role of local neighbourhood competition in crop-weed interactions, and most of these studies have addressed only the effect of individual weeds on crop plant size and yield (Henry & Bauman 1989, Mortensen & Coble 1989).

Crop rows, a ubiquitous but relatively recent feature of modern agriculture, create a specific spatial structure in the field. In a 2-dimensional spatial pattern analysis, rows can be considered very long, narrow clumps, in which crop density is very high in one dimension and very low in the other (Bleasdale 1984, Weiner et al. 2001a). Weeds grow in this crop matrix, and therefore individual weeds may experience large variation in local competitive conditions, depending on their spatial location with respect to the rows and to each other. Crop rows exist in large part because they allow hoeing and harrowing of weeds between the rows (Kepner et al. 1982). But crops compete more effectively against weeds when the crop is sown in a more uniform pattern, rather than in rows (Mohler 2001, Weiner et al. 2001a).

The hypothesis that an individual weed's size is influenced by its spatial location with respect to crop rows has rarely been tested. The biomass of individual *Polygonum convolvulus*, *P. persicaria* and *Stellaria media* plants was negatively related to their distance to the nearest crop plant (Mertens 2002). Distance between *Glycine max* (soybean) and *Xanthium strumarium* (cocklebur) within rows was negatively correlated with the size of individuals of both species (Henry & Bauman 1989). In the present study we test the hypotheses that individual weeds are larger when they germinate (1) between, rather than close to or within, crop rows, and (2) far from, rather then close to, other weed individuals.

Materials and methods

Winter 1999–2000

Winter wheat (*Triticum aestivum* L. cv Hereward) and our surrogate weed, winter rape (*Brassica napus* L. cv Carola) were planted on 23 September 1999 at the Royal Veterinary and Agricultural University's research farm in Taastrup, Denmark (55°40′N, 12°18′E). The climate is temperate/maritime with a mean temperature of 0 °C in January and 16.5 °C in July, and a mean annual precipitation of 613 mm. The soil is a sandy clay loam typical of eastern Zealand. Summer barley (*Hordeum vulgare* L.) and oats (*Avena sativa* L.) were grown in the preceding year. Wheat was planted in 12.8 cm rows at a density of 449 seeds per square meter. We used a surrogate weed to obtain high weed density across the experimental plot. We chose *B. napus* because it has a high germination percentage and is very competitive. *B. napus* was randomly sown at a density of approximately 200 seeds per square meter by dropping the seeds on the surface from a height of 1 m using a seed drill without coulters and harrowing the soil surface lightly afterwards. Commercial 21-10-3 (N-P-K) fertilizer was applied at the rate of 80 kg ha^{-1} a few weeks after sowing. Two 0.5 m^{-2} subplots were randomly chosen for further study.

Soon after germination, 297 individual *B. napus* plants were marked with a circular metal tag with a numbered strip of white plastic attached to it. Measurements of distance to both rows and to the nearest conspecific neighbour were taken during the winter. Normally measurements to the row were the same as measurements to the nearest crop plant, except in rare cases of gaps in the crop row. Gaps were also noted, and measured. A gap is defined a as space of more that four cm between two adjacent plants within a row. We removed individuals of all other weed species in late winter, again in March, and thereafter as necessary. In early June, each *B. napus* plant was harvested at the soil surface, and height and stem diameter of each plant were measured with a ruler and digital callipers, respectively. Plants were dried for two days in an oven and weighed.

Summer 2000

The above procedure was repeated in a similar spring wheat experiment 200 meters from the first experiment. Planting, marking, and measuring procedures were the same, but the fertilization level was 160 kg ha^{-1}. The wheat cultivar was Jack, and the *B. napus* cultivar Sprinter. We sowed the plots on 12 April 2000, and tagged 190 seedlings 6–8 May. Plants were harvested 7 July.

Winter 2000–2001

Sowing occurred on the 21st of September 2000 and followed the same procedure as the winter of 1999–2000. In this experiment, field-collected *Matricaria perforata* Mérat and *Camelina sativa* (L.) Crantz seed were sown as weeds. We used these species because they are common weeds in cereal crops and were locally abundant in plots neighbouring the first winter experiment. We collected as many seeds as possible of each species, and sowed all of them together in a mixture. Weed seeds were dropped onto the soil surface at the rate of 281 seeds m^{-2} for *Matricaria* and 180 seeds m^{-2} for *Camelina* on the day following sowing of the crop. The density of emerging weeds, including natural weeds, was approximately 200 plants m^{-2} on 24 October. On 16 November, all 164 weeds in the plots were marked. The majority of weeds were *Veronica persica*. *Viola arvensis*, *Poa annua*, *Sonchus asper* and *Lamium purpureum* also appeared, but at densities below 10 plants m^{-2}. We are not sure why the sown weed seeds did not germinate. Individual weed plants were harvested on 7 and 8 June, and measured as in the previous year. For *V. persica*, branch number and maximum axis length were measured. For the other species, only height was measured. All plants were dried and weighed as above.

Statistical analysis

Since distances were measured soon after germination and there was little or no density-dependent mortality, the problem of non-independence of plant size and neighbourhood conditions (Jordan 1989) is avoided. A mixed model analysis of variance was performed to determine if biomass, height, stem diameter, or branch number of the weeds varied with distance to the nearest conspecific neighbour and distance to the nearest row. Formal treatments in the ANOVAs were nearest conspecific neighbour distance, distance to the nearest row, block, gap presence (if included), gap size (if included) and any interaction terms not removed. Biomasses had to be log (summer 2000) or square root (winter 1999–2000, 2000–2001) transformed to achieve homogeneity of variances. Interactions with P > 0.15 were removed from the multiple factor ANOVAs. Plots were considered as random block effects and are not listed in the results. To test for the effects of gaps within the row, the presence versus absence of a gap was added to the ANOVAs. We also looked at the size of gaps as a continuous variable. There was an insufficient range in gap sizes to analyse gap size as an effect in the spring 2001 experiment. For the winter 2000–2001 data, dead plants and non-*V. persica* plants were removed from the analysis. Dead plants were analysed separately (see below), and species other than *V. persica* were removed because there were so few of them. Mortality of *V. persica* was high during the winter of 2000–2001. An unpaired t-test on mortality was performed for both neighbour distance and shortest distance to a row.

Results

Winter 1999–2000

There was large variation in the measured parameters in all years and for both species (Table 1). The distance to the nearest conspecific neighbour had a highly significant effect on the mass of *B. napus* plants (Fig. 1, Table 2), and the distance to the nearest row was marginally significant (Fig. 2, Table 2). The results were similar for *B. napus* diameter. Nearest conspecific neighbour and distance to a row had significant effects (Table 2). There were no significant interactions. There were no significant effects on plant height.

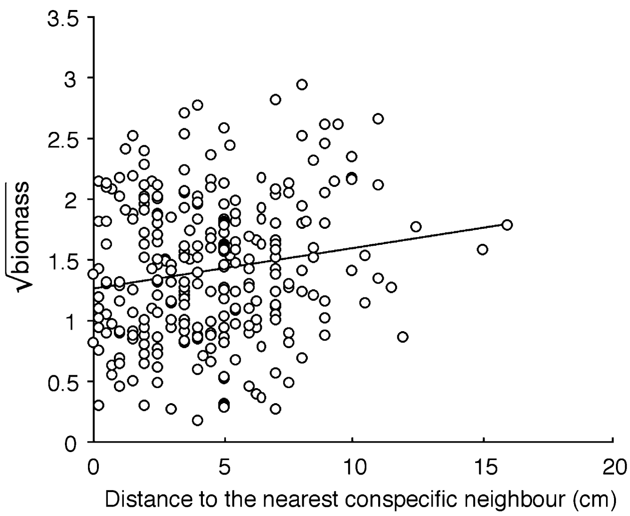

Fig. 1. Square root of biomass of individual *Brassica napus* weeds versus their distance to the nearest conspecific neighbour in the winter 1999–2000 experiment. N = 297; r^2 = 0.05; P = 0.002.

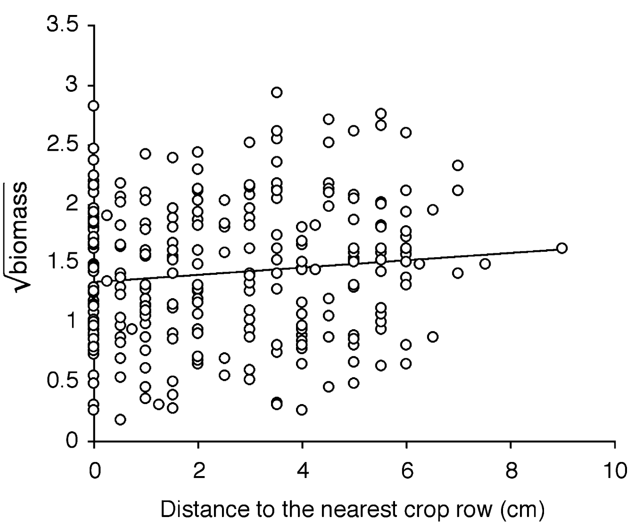

Fig. 2. Square root of biomass of individual *Brassica napus* weeds versus distance to the nearest cereal row in the winter 1999–2000 experiment. N = 297; r^2 = 0.07; P = 0.05.

Summer 2000

There were no significant effects of distance to crop row or to conspecific neighbour on biomass (Table 2). There was a significant interaction between neighbour distance and row distance on diameter on *B. napus* biomass (Table 2). There were no significant effects of distance to row or distance to nearest conspecific neighbour on *B. napus* height (Table 2).

Table 1. Means ± standard deviations (untransformed) of plant weight, height, diameter (*Brassica napus*) and branch number (*Veronica persica*). Variables were transformed in the analyses.

Year	N	Weight (g)	Height (cm)	Diameter (mm)	Branch number
1999	297	2.21 ± 1.76	73.95 ± 25.51	4.48 ± 1.67	
2000	190	1.24 ± 2.11	37.70 ± 16.34	3.05 ± 1.10	
2001	91	0.52 ± 0.36	36.61 ± 15.59		2.30 ± 1.49

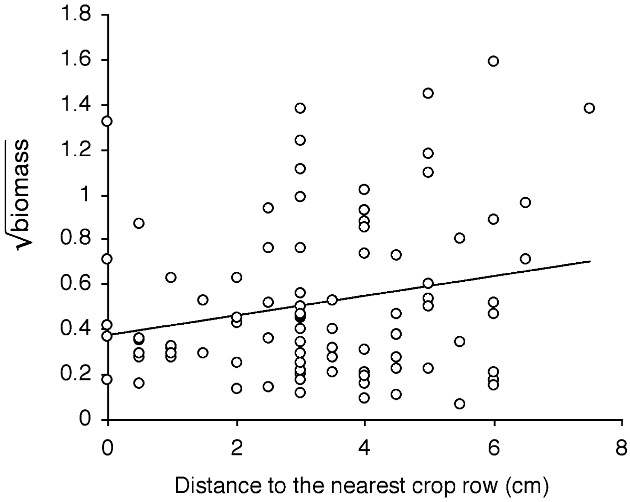

Fig. 3. Square root of biomass of individual *Veronica persica* weeds versus their distance to the nearest cereal row in the winter 2000–2001 experiment. N = 91; r^2= 0.03; P = 0.014.

Table 2. Summary of statistical tests of the effects of distance to crop rows and distance to nearest conspecific neighbour on different measures of weed size. If not listed, interaction terms were not significant (P > 0.15) and were removed from the model. R = distance to the nearest row; N = distance to nearest conspecific neighbour. Block effects, which were included in the analyses, are not shown.

Season	Weed	Measure of size	Effect	SS	df	P value	Adjusted r^2
Winter 1999–2000	*B. napus*	Biomass	R	1.15	1	0.051	0.06
			N	3.22	1	0.001	
			Resid	117.24	293		
		Diameter	R	19.51	1	0.006	0.08
			N	22.61	1	0.003	
			Resid	753.88	293		
		Height	R	928.4	1	0.23	ns
			N	1879.0	1	0.09	
			Resid	188820.1	293		
Summer 2000	*B. napus*	Biomass	R	0.35	1	0.24	0.11
			N	0.88	1	0.06	
			Resid	43.60	172		
		Diameter	R	0.18	1	0.68	0.105
			N	0.71	1	0.41	
			R x N	5.37	1	0.03	
			Resid	198.70	184		
		Height	R	0.1	1	0.98	0.09
			N	863.2	1	0.06	
			Resid	45107.1	185		
Winter 2000–2001	*V. persica*	Biomass	R	0.326	1	0.01	0.06
			N	0.05	1	0.35	
			Resid	4.30	84		
		Branch number	R	18.10	1	0.004	0.09
			N	2.19	1	0.30	
			Resid	166.21	81		
		Length	R	101.5	1	0.52	ns
			N	153.5	1	0.43	
			Resid	20524.5	84		

Winter 2000–2001

Only 40% of the marked *V. persica* individuals survived the winter. The plants that survived and those that died did not have significantly different distances to conspecific neighbours (mean difference = 0.016 cm; Table 2) or to crop rows (mean difference = 0.113 cm; Table 2) when compared by a t-test.

The distance to the closest row had a significant effect on the mass of *V. persica* plants (Table 2), although the combined model had an adjusted r^2 of only 0.06. The distance to the nearest conspecific neighbour did not have a significant effect. Row distance also had a significant effect on branch number (Table 2). Nearest conspecific neighbour distance did not have a significant effect on *V. persica* biomass. There were no significant interactions. Neither of the factors had a significant effect on individual height.

Effect of gaps in crop rows

The presence of a nearby gap in the row had an effect on weed diameter ($r^2 = 0.12$, SS = 5.05, DF = 1, P = 0.03) in the summer of 2000, but did not otherwise have significant effects on weed biomass, height, diameter, or branch number. Gap size had no significant effect on any measure of plant success.

Discussion

Although effects of distance to the nearest crop row and distance to the nearest conspecific neighbour could be detected and were statistically significant, they were weak, accounting for relatively little of the variation in individual weed size in the field. No effect of the presence or size of gaps in the crop row could be detected. The weak effect of distance to crop row and nearest neighbour distance, and the absence of any effect of crop row gaps on individual weed size suggest that neighbourhood conditions at the most local level are not critical in comparison with other factors affecting individual weed size in the field. There are several possible explanations for the weakness of these effects:

The first possible explanation is simply that competition in this system is weak. This possibility can be rejected because, in the absence of the crop or at very low crop densities, individuals of both these weed species are many times larger than under these field conditions (Weiner et al. 2001a, von Wettberg & Weiner, unpublished data).

A second possible explanation for the weak effect of near neighbours is that our measures of local competition are too crude: distance to the row and to the nearest other weed individual do not provide a good enough description of the local neighbourhood. Studies that best account for plant size as a function of neighbourhood conditions usually include information on the number or size or distance of all neighbours within a certain area (Mack & Harper 1977, Weiner 1984, Silander & Pacala 1985). While this criticism may be valid for the distance to the nearest weed neighbour, in this crop-row system our other two independent variables, distance to the nearest crop row and the presence of a gap in the row near the subject plant, will be highly correlated with more detailed measures of the local crowding. We would expect a strong signal from these two variables if local neighbourhood conditions were important determinants of weed size in this system.

The third and most likely explanation for the weakness of the effects of near neighbours is that the crop in our experiments is larger than the weeds, and competition between crop and weed is often "size asymmetric" (Weiner 1990, Weiner et al. 2001a). Simple neighbourhood analyses work best when competition is size-symmetric (Thomas & Weiner 1989, Stoll et al. 1994). This is because when competition is highly size-asymmetric, an individual's exact location relative to other individuals becomes less important for its performance than whether or not it is larger than its neighbours (Hara & Wyszomirski 1994, Weiner et al. 2001b). Under size-asymmetric competition the vertical dimension of plant competition for light becomes more important than the horizontal dimensions. The crop generates a partially shaded environment determined by its own growth form, density and spatial pattern. If the crop plants are generally larger than the weeds, the exact location of a weed within this crop matrix may not be critical. The spatial pattern of the crop is very important in creating the competitive environment in which weeds grow at a larger scale, but within this environment a weed's two-dimensional location has only minor effects.

The role of asymmetric competition from the crop in reducing the importance of a weed's location relative to the crop is consistent with the result that *B. napus* size appeared to be more sensitive to the proximity of a single conspecific neighbour than to the proximity of the crop row. While this could reflect niche differences between crop and weed species, such that intraspecific competition is stronger than interspecific competition, it is more likely to occur because conspecifics will tend to be of similar size. This will make competition from conspecifics more symmetric, and therefore more sensitive to distance.

The row distances used in this experiment are typical in Denmark when hoeing is not performed. If the distance between rows was much larger, allowing for much more variation in row-weed distance and generating a less uniform environment around the crop, effects of distance to the row are likely to have a stronger effect. This may explain why somewhat stronger effects of distance to the nearest crop plant on weed size were found in experiments that included very wide row spacings (Mertens 2002).

In the spring 2000 experiment there was a significant interaction between distance to the row and distance to the nearest neighbour on *B. napus* diameter, such that plant size increased with distance to a row only if a plant was relatively distant from a conspecific neighbour. Similarly, distance to a conspecific neighbour only had an effect on plants that were relatively far from a row. Thus, effects of proximity of a conspecific neighbour and a crop row were less than additive. Since the effect of neighbours on individual plants is often hyperbolic (Weiner 1984, Silander & Pacala 1985, Stoll & Weiner 2000), the reduction in size due to neighbours is smaller for each additional neighbour. It is therefore easier to detect a difference between no neighbours and one neighbour than between one and two neighbours.

Proximity to the closest conspecific neighbour appears to have a negative effect on the size of *B. napus* plants, but not on *V. persica*. During the winter experiment with *B. napus*, plant size, measured as dry weight or stem diameter, decreased with decreasing distance to a conspecific neighbour. In the summer experiment there was an interaction between the distance to a conspecific neighbour and the distance to the crop row. Our inability to detect an effect of neighbours on *V. persica* may have been because *V. persica* occurred at a lower density, which could have reduced the presence of intraspecific competition. It is also possible that neighbour distance has less effect on *V. persica* size than on *B. napus* size because of the difference in growth form between the two species. The sprawling form of *V. persica* may make it more able to avoid the competitive effects of neighbours through plasticity in growth form and direction (Hutchings & de Kroon 1994). One would expect that that a plant's "original" location, i.e. where the plant emerges from the soil, is a less accurate descriptor of a procumbent plant's location than that of an upright plant.

Plant height was unaffected by any of our measures of local crowding. Height is known to be the measure of plant size that is least sensitive to competition (Lanner 1985, Nagashima & Terashima 1995). Many plants grow to the same height over a wide range of densities at the expense of diameter and biomass. Some species, such as *V. persica*, have a procumbent growth form, and in this case height is not a very informative aspect of plant size. Such species do not compete with wheat for light, but grow away from neighbours to avoid being shaded (Hutchings & de Kroon 1994).

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