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Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity

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Summary

1. Recent advances in our understanding of the advantage of initial size in competition among individual plants (size-asymmetric competition) suggest that the potential for many crops to suppress weeds is much greater than generally appreciated. We hypothesize that this potential can be realized if: (i) the crop density is increased significantly and (ii) the crop is regularly (uniformly) distributed in two-dimensional space rather than sown in traditional rows.

2. We tested these hypotheses by sowing four varieties of spring wheat *Triticum aestivum* at three densities (200, 400 and 600 m^{-2}) and in two spatial patterns (normal rows and a uniform grid pattern) in the presence of high weed pressure.

3. There were strong and significant effects of both crop density and spatial distribution on weed growth. Weed biomass decreased with crop density and was 30% lower in the grid pattern.

4. There was a negative linear relationship between above-ground weed biomass in early July and crop yield at harvest, so weed suppression translated directly into yield. The treatment with high crop density and the grid sowing pattern contained 60% less weed biomass and produced 60% higher yield than the treatment closest to normal sowing practices (crops sown in rows at 400 m^{-2}).

5. The results were similar when the experiment was repeated in the following year, even though weed abundance was lower and the weed community was very different. There was 30% less weed biomass and 9% higher yield when the crop was sown in a grid pattern.

6. While weed biomass decreased monotonically with density for all varieties, a significant variety–density interaction suggested that the attributes resulting in good weed suppression at high crop density may not be the same as those most advantageous at low crop density.

7. A more crowded, uniform, distribution of some crops could contribute to a strategy to reduce the use of herbicides and energy-intensive forms of weed control.

Key-words: crop–weed competition, row spacing, size-asymmetric competition, spatial pattern.

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Introduction

There is increasing interest in reducing the use of herbicides in agriculture because of concerns about their environmental effects. Mechanical weed control, the major alternative to herbicide application, also has negative environmental impacts due to energy consumption and additional traffic on fields. There is a great need to develop alternative methods for weed management (Liebman & Gallandt 1997). One idea is the development of cropping systems in which crops themselves are better able to compete with weeds (Harper 1961; Jordan 1993; Mohler 2001). Recent studies on the advantage of initial size in competition among plants suggest that the potential for many crops to suppress weeds themselves is much greater than is

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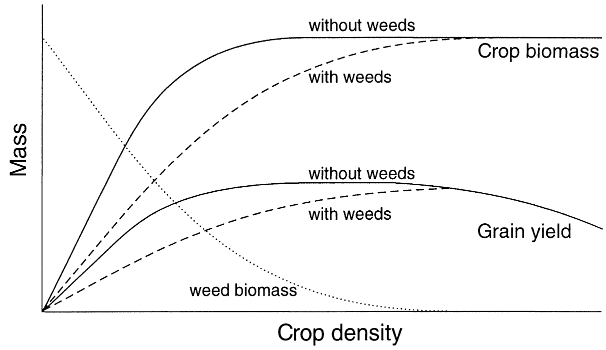

Fig. 1. Theoretical relationship between crop density and yield in the presence and absence of high weed seedling density when the crop seedlings are larger than the weed seedlings. The continuous lines represent density–yield relationships for monocultures (no weeds; Silvertown & Lovett Doust 1993). The dotted lines (with weeds present) are hypothesized.

generally appreciated, but that our current cropping practices do not utilize this potential. Larger plants often have a disproportionate advantage in competition with smaller plants, suppressing the growth of their smaller neighbours, a phenomenon called 'size-asymmetric competition' (Weiner 1990; Schwinning & Weiner 1998). Crop seedlings are usually larger than weed seedlings immediately after germination, so increasing the degree of competitive size-asymmetry in the crop–weed community should benefit the crop at the expense of the weeds. There is evidence that the advantage of size in competition increases with density (Schwinning & Weiner 1998), so weeds should be more suppressed at higher crop densities than at lower densities.

Let us assume that (i) weeds are abundant, (ii) weed seedlings are smaller than crop seedlings, but (iii) weeds have faster growth rates than the crop (Mohler 2001) such that weeds have the potential to grow as large as crop plants by the end of the season, and (iv) the initial size advantage in competition increases with density. The crop fraction of the total (crop + weed) biomass should increase with increasing density, resulting in almost complete weed suppression at very high crop densities (Fig. 1). If effective weed suppression occurs at densities lower than those resulting in substantial yield loss due to competition within the crop population (intraspecific competition), increased crop density could play an important role in weed management. Increasing the crop density will increase the crop fraction of the total biomass, even if competition is not size-asymmetric (Mohler 2001), but a disproportionate decrease in weed biomass due to an increase in crop density, which we call weed suppression, should occur only if competition is size-asymmetric.

Although most studies do show decreased weed biomass at higher crop densities (Wax & Pendelton 1968; Erviö 1972; Mohler 1996; Murphy *et al.* 1996; Doll 1997; Håkansson 1997), the prediction of ever-increasing weed suppression at ever-increasing crop density is not usually observed in crop density studies (Håkansson 1984; Martin, Cullis & McNamara 1987; Teich *et al.* 1993). Theoretical arguments (Fisher & Miles 1973; Grace 1990) and spatially explicit models of plant competition (Miller & Weiner 1989; Bonan 1991) suggest that the ability of crops to suppress weeds at high crop densities may be limited by the spatial distribution of individual crop plants in the field.

In most crop density experiments, the density is altered in only one dimension, by increasing the number of plants sown within each row. Crop rows can be considered very long and narrow clumps, in which the density is very high in one dimension (within the row) and very low in the other dimension (between the rows; Bleasdale 1984). In the absence of weeds, the plasticity of plant growth allows crop plants to grow towards areas of high resource levels (Ballaré 1994; Hutchings & de Kroon 1994), reducing competition within the crop population and capturing the resources in the area between the rows, so the disadvantage of the clumped pattern is relatively small. But in the presence of competition from weeds, increasing the crop density within the rows increases competition within the crop population (intraspecific competition) much more than it increases crop competition with the weeds (interspecific competition). Some of the weeds will be able to 'catch up' in size with the crop plants before they experience competition from the crop (Mohler 1996), and the crop will lose its size advantage. If the crop was distributed in a more regular pattern in two dimensions, such as a simple two-dimensional grid, weed suppression resulting from the crop's initial size advantage should be greatly enhanced. If the crop was distributed in a perfectly uniform pattern, crop plants would begin competing with weed plants sooner, while the crop still had its size advantage, whereas competition among crop plants would be delayed as long as possible (Fisher & Miles 1973). This prediction is supported by studies showing that decreased row spacing, which reduces the degree of 'clumping', usually results in a modest reduction in yield losses due to weeds (Buchanan & Hauser 1980; Patterson *et al.* 1988; Smith *et al.* 1990; Koscelny *et al.* 1991; Forcella, Westgate & Warnes 1992; Malik, Swanton & Michaels 1993; Mohler 2001).

To test the hypotheses that suppression of weeds can be increased greatly by a combination of increased crop density and more uniform spatial distribution, we performed field experiments with spring wheat *Triticum aestivum* L., in which we varied crop density, sowing pattern and variety in the face of high weed pressure.

Methods

We used (i) three crop densities (200, 400 and 600 seeds m^{-2}), (ii) two spatial patterns (normal 12·8-cm rows and a grid pattern) and (iii) four varieties (Baldus, Dragon, Harlekin and Jack). The varieties were chosen to span a wide range of phenotypes among those used in northern European. We modified a precision seed drill (Kverneland Accord Corporation, Soest, Germany) to sow wheat in a grid pattern. This seed drill, which is designed for row crops, uses pneumatic pressure generated by a large fan to attach individual seeds to small holes on rotating disks. The individual seeds are then dropped into the row at a specified spacing. A grid pattern was achieved through narrow row spacings in which the spacing between rows was as close as possible to the precision spacing within the rows for each density. It was not possible to achieve exactly the same inter- and intra-row distance at all three densities. The ratio of inter- to intra-row distance was 3 : 2 for the low and high densities and 1 : 1 for the middle density. We used a standard research seed drill with 12·8-cm row spacing to sow the normal row pattern.

The experiment was sown on 23 April 1998 at the Royal Veterinary and Agricultural University's research farm in Taastrup, Denmark (55°40′ N, 12°18′ E). The soil is a sandy clay loam typical of eastern Zealand. The climate is temperate/maritime with a mean temperature of 0 °C in January and 16·5° in July, and a mean annual precipitation of 613 mm. Plots were 1·66 × 10·0 m, and there were four replicates blocks. To provide high weed pressure, spring rape *Brassica napus* L. was dropped onto the soil surface at a rate of 200 m^{-2}, harrowed lightly and rolled immediately after the crop was sown. The plots were fertilized at the rate of 80 kg N ha^{-1} 2 weeks after sowing. We counted crop and weed emergence within single, randomly placed, 0·25-m^2 quadrats on 5 May. We measured the total biomass of weeds at the approximate maximum (6–10 July 1998) by harvesting, drying and weighing all above-ground weed biomass within a single randomly placed 0·25-m^2 quadrat in each plot. At maturity in early October, the crop was harvested and grain yield determined after cleaning.

The experiment was repeated in the following year (sown 23 April 1999), with the medium and high densities increased to 450 and 720 m^{-2}, respectively. The ratio of inter- to intra-row distance in the grid pattern was 1 : 1 for the low density, 4 : 5 for the medium and 5 : 4 for the high density. The germination of our surrogate weed, *B. napus*, was much lower in 1999 than in 1998 due to several weeks of dry weather immediately after sowing, but naturally occurring weeds, especially *Chenopodium album* L. and several *Polygonum* species, were abundant. The number of crop seedlings in one randomly placed 0·25-m^2 quadrat per plot was counted in one block on 15 May. Above-ground weed biomass in two randomly placed 0·25-m^2 quadrats was harvested in each plot in early July. The wheat was harvested at maturity in mid-September.

Results

1998

The overall emergence rate for the wheat was 85%, with significant varietal differences (Baldus, 79%; Dragon, 87%; Harlekin, 91%; Jack, 82%; MS = 585, $F = 4·8$, $P = 0·005$) and no effects of the other factors. The number of *B. napus* seedlings m^{-2} was normally distributed with a mean of 146 and a standard deviation of 35, with no significant effects of any of the factors. Although several naturally occurring weed species appeared, *B. napus* comprised 93% of the total weed biomass harvested.

We observed significant and strong effects of both crop density and sowing pattern on weed biomass in 1998 (Table 1). Weed biomass was, on average, 30% lower in the grid sowing pattern (Fig. 2). There was a negative linear relationship between weed biomass in July and yield at harvest (Fig. 3a). In the high density grid pattern, weed biomass was 60% lower (Fig. 2) and grain yield 60% higher (Fig. 4) than in the treatment corresponding to normal sowing practices (400 seeds m^{-2}, sown in rows).

Although the weed biomass decreased monotonically with density for all varieties, there was a highly significant interaction between density and variety (Table 1 and Fig. 5). There were no other significant or near-significant interactions.

Table 1. ANOVA on total above-ground dry mass of weeds m^{-2} in the two experiments; 1999 data log-transformed. Interactions with $P > 0·1$ are removed from the analyses

Source	d.f.	MS	*F*-value	*P*-value
(a) 1998				
Sowing density	2	142437	56·53	< 0·001
Sowing pattern	1	135060	53·60	< 0·001
Variety	3	12957	5·14	0·003
Block (random effect)	3	13703	5·44	0·002
Density × Variety	6	13682	4·82	< 0·001
Residual	80	2519		
(b) 1999				
Sowing density	2	1·397	167·11	< 0·001
Sowing pattern	1	0·531	63·62	< 0·001
Variety	3	0·022	2·68	0·052
Block (random effect)	3	0·068	8·16	< 0·001
Density × Variety	6	0·017	2·06	0·067
Residual	80	0·008		

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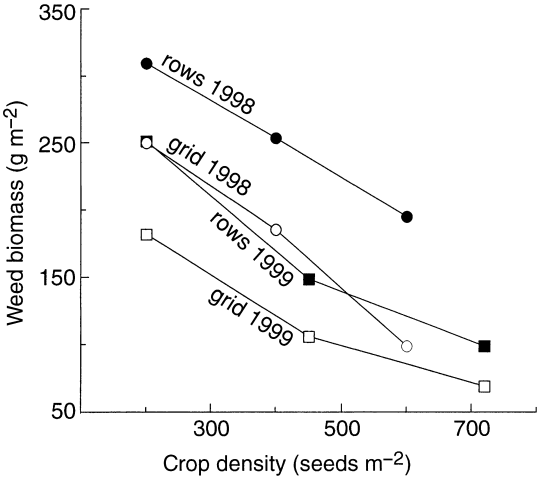

Fig. 2. Relationship between sowing density and weed biomass for spring wheat *Triticum aestivum* grown in two spatial patterns (filled symbols, rows; empty symbols, grid pattern) at three densities over 2 years (circles, 1998; squares, 1999) in the presence of high weed pressure.

1999

In the second year, the overall emergence of wheat was 85%. There was significantly higher emergence in the grid pattern (MS = 569, $F = 8{\cdot}2$, $P = 0{\cdot}01$) but no effect of density or variety on emergence. Because of the poor *B. napus* germination, the weed community was very different from the previous year, with a much longer period of weed emergence, lower total weed abundance, and greater species diversity. This resulted in a very different distribution of total weed biomass, which required log-transformation to achieve homogeneity of variances. Despite these differences, the overall results were similar to the previous year (Table 1 and Fig. 2). There were large effects of both crop density and sowing pattern on weed biomass, with 30% less weed biomass (Fig. 2) and 9% greater yield (Fig. 4) in the grid pattern compared with the row pattern. The negative relationship between weed biomass in July and yield at harvest was almost as strong as in 1998, but the range of weed biomass was lower (Fig. 3b).

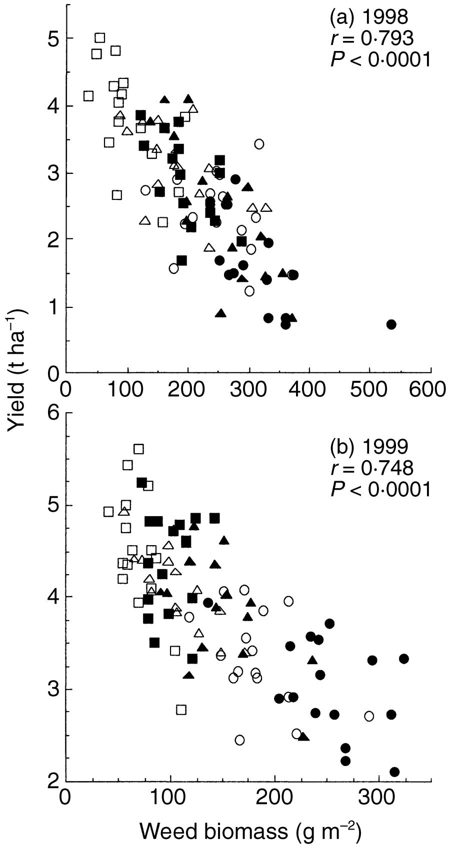

Fig. 3. Relationship between weed biomass in early July and grain yield of spring wheat *Triticum aestivum* in 1998 and 1999 (circles, low crop density; triangles, medium density; squares, high density; filled symbols, crop sown in rows; empty symbols, crop sown in a grid pattern).

In 1999 the interaction between density and variety was only marginally significant (Table 1). Again, there were no other significant or near-significant interactions.

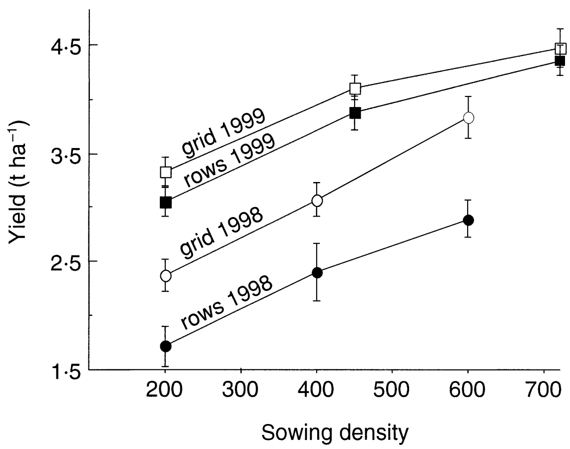

Fig. 4. Grain yield as a function of the sowing density for spring wheat *Triticum aestivum* grown in two spatial patterns (filled symbols, rows; empty symbols, grid pattern) at three densities over 2 years (circles, 1998; squares, 1999) in the presence of high weed pressure. Bars represents 1 SE. The effect of sowing density and pattern are highly significant ($P < 0{\cdot}001$) in both years.

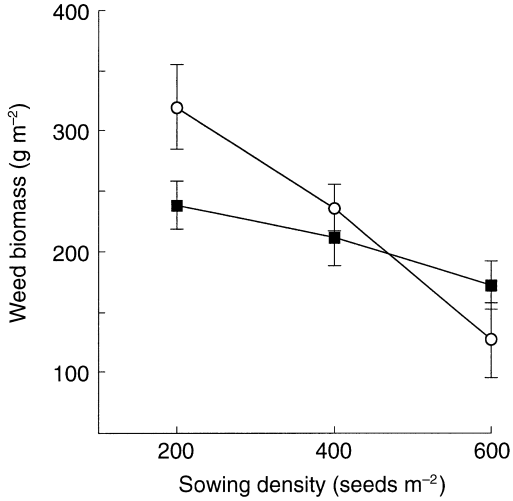

Fig. 5. Weed biomass as a function of crop sowing density for two of the varieties of spring wheat *Tritium aestivum*, Jack (open circles) and Harlekin (closed squares), in the 1998 experiment. Bars represents ± 1 SE. Harlekin was the best competitor with weeds at the lowest crop density and the worst at the highest density, while Jack was the best at the highest crop density and worst at the lowest.

Discussion

Numerous studies have investigated the effects of crop density and/or row spacing on yield losses due to weeds (reviewed by Mohler 2001). While increased crop density almost always results in reduced weed growth, most studies do not find large enough effects to justify significant increases in crop density in the field. With very few exceptions (Malik, Swanton & Michaels 1993), decreased row spacing results in only a modest reduction in weed biomass and weed losses. This could be because (i) decreased row spacing alone does not represent a large enough increase in spatial uniformity, or (ii) the crop did not have a sufficient initial size advantage, or (iii) competition was not very size-asymmetric.

The size-asymmetry of competition may help to explain the large variation in the results of the numerous studies on crop density, sowing pattern and weed losses. Recent studies on size-asymmetric competition suggest that increased crop density and spatial uniformity can be expected to have large effects on weed growth when (i) the crop has a significant initial size advantage over the weeds when competition begins, and (ii) when competition for light is important enough to structure competitive interactions (Schwinning & Weiner 1998). The first of these criteria implies that in cases where weeds emerge much earlier than the crop and/or have an equal or greater initial size (e.g. weeds emerging from rhizomes or roots, or crops with very small seeds), weed suppression through increased crop density and spatial uniformity will probably not be successful. The second criterion suggests that when below-ground competition dominates crop–weed interactions (e.g. in dryland farming or under very low nutrient levels), we would expect competition to be more size-symmetric (Schwinning & Weiner 1998), thus reducing the potential for weed suppression by crops. Also, some crops (e.g. onions) have almost no ability to compete for light because of their growth form, even if they have a size advantage. There are many crops and environments that do meet the criteria outlined above.

Size-asymmetric competition appears to be primarily due to competition for light, which is a 'one-sided' interaction in that higher leaves shade lower leaves, but not vice versa (Weiner 1990; Schwinning & Weiner 1998). Even if the crop's spatial distribution does not affect its total leaf area index (LAI), rows will result in much more spatial variation in the distribution of this LAI than a uniform distribution of the crop. Early in the growing season, row sowing results in high LAI in and near the rows, and little or no leaf area halfway between the rows. The reduced spatial variation in LAI in a uniform pattern means that the ground will be covered sooner when the crop is uniformly distributed, and this was noticeable in our experiments. Because of the exponential nature of light extinction within canopies (Monsi, Uchijima & Oikawa 1973), a uniform pattern should also result in a reduction in the total amount of light reaching the ground. If the extinction of light through a shaded leaf is the same as that of an unshaded leaf, then the absolute amount of light removed by a shaded leaf will be less than that of an unshaded leaf. Thus, the maximum total shading for a given LAI should occur when this LAI is distributed as uniformly as possible.

When weed pressure is high, reduced weed biomass translates directly into yield (Christensen 1995; Lemerle *et al*. 1996). By the end of the growing season most of the available resources were consumed, so there was a simple negative linear relationship between yield and weed biomass when weed pressure was high (Fig. 3). Even though the effects of crop density and sowing pattern on weed biomass were very similar in both years, the effects of increased weed suppression on yield were smaller in the second year, when weed biomass was lower and yield was less limited by weeds. The effects of both crop density and sowing pattern on yield were highly significant in both years, however.

A critical aspect of the ability of a crop to produce high yields after suppressing weeds at high density is the shape of the simple density–yield curve (Fig. 1). If harvestable yield decreases steeply above the optimum (weed-free) density, then the densities required for weed suppression may give only low yields. If the density–yield curve is relatively flat, as it is for many cereal crops, then these higher densities can be used for weed suppression.

The significant interaction between density and variety means that varieties that perform best in the face of high weed pressure at low crop density may not be those that perform best at high density. In the first year there was a suggestion of a trade-off in the ability to compete with weeds at high and low density: the variety that performed best at high density was the one that performed worst at low density, while the best at low density performed worst at high density (Fig. 5). The existence of such a trade-off would suggest that we cannot simply talk about 'competitive varieties', but it raises the theoretical possibility of developing 'high density' varieties for increased weed suppression at high density. Even if this hypothesized trade-off is supported in future studies, it remains to be seen if the potential gains in weed suppression could justify such a breeding strategy. In the second year, with lower, more diverse, weed pressure and log-normal distributions, the interaction between variety and density was only marginally significant.

Greatly increased suppression of weeds by some crops through increased density and more uniform sowing distributions can play an important role in a comprehensive strategy (Liebman & Gallandt 1997) for reducing the use of herbicides and energy-intensive forms of weed control. We call for the development of 'high density cropping systems' in which competition among plants in the field is seen as something to be influenced and directed, not, as in the conventional view, something to be avoided.

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References

Ballaré, C.L. (1994) Light gaps: sensing the light opportunities in highly dynamic canopy environments. *Exploitation of Environmental Heterogeneity by Plants* (eds M.M. Caldwell & R.W. Pearcy), pp. 73–110. Academic Press, San Diego, CA.

Bleasdale, J.K.A. (1984) *Plant Physiology in Relation to Agriculture*. Macmillan Press, London, UK.

Bonan, G.B. (1991) Density effects on the size structure of annual plant populations: an indication of neighbourhood competition. *Annals of Botany*, **68**, 341–347.

Buchanan, G.A. & Hauser, E.W. (1980) Influence of row spacing on competitiveness and yield of peanuts (*Arachis hypogaea*). *Weed Science*, **28**, 401–409.

Christensen, S. (1995) Weed suppression ability of spring barley varieties. *Weed Research*, **35**, 241–247.

Doll, H. (1997) The ability of barley to compete with weeds. *Biological Agriculture and Horticulture*, **14**, 43–51.

Erviö, L.-R. (1972) Growth of weeds in cereal population. *Journal of the Scientific Agricultural Society of Finland*, **44**, 19–27.

Fisher, R.A. & Miles, R.E. (1973) The role of spatial pattern in the competition between crop plants and weeds. A theoretical analysis. *Mathematical Biosciences*, **18**, 335–350.

Forcella, F., Westgate, M.E. & Warnes, D.D. (1992) Effect of row width on herbicide and cultivation requirements in row crops. *American Journal of Alternative Agriculture*, **7**, 161–167.

Grace, J.B. (1990) On the relationship between plant traits and competitive ability. *Perspectives in Plant Competition* (eds J. Grace & G.D. Tilman), pp. 51–65. Academic Press, New York, NY.

Håkansson, S. (1984) Row spacing, seed distribution in the row, amount of weeds – influence on production in stand of cereals. *Weeds and Weed Control. 25th Swedish Weed Conference*, Vol. 1, pp. 17–34. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Håkansson, S. (1997) Competitive effects and competitiveness in annual plant stands. I. Measurement methods and problems related to plant density. *Swedish Journal of Agricultural Research*, **27**, 53–73.

Harper, J.L. (1961) Approaches to the study of plant competition. *Mechanisms in Biological Competition* (ed. F.L. Milthorpe), Vol. 15, pp. 1–39. Cambridge University Press, Cambridge, UK.

Hutchings, M.J. & de Kroon, H. (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. *Advances in Ecological Research*, **25**, 159–238.

Jordan, N. (1993) Prospects for weed control through crop interference. *Ecological Applications*, **3**, 84–91.

Koscelny, J.A., Peeper, T.F., Solie, J.B. & Solomon, S.G. (1991) Seeding date, seeding rate, and row spacing affect wheat (*Triticum aestivum*) and cheat (*Bromus secalinus*). *Weed Technology*, **5**, 707–712.

Lemerle, D., Verbeek, B., Cousens, R.D. & Coombes, N.E. (1996) The potential for selecting wheat varieties strongly competitive against weeds. *Weed Research*, **36**, 505–513.

Liebman, M. & Gallandt, E.R. (1997) Many little hammers: ecological management of crop–weed interactions. *Ecology in Agriculture* (ed. L.E. Jackson), pp. 291–343. Academic Press, San Diego, CA.

Malik, V.S., Swanton, C.J. & Michaels, T.E. (1993) Interaction of white bean (*Phaseolus vulgaris* L.) cultivars, row spacing, and seeding density with annual weeds. *Weed Science*, **41**, 62–68.

Martin, R., Cullis, B. & McNamara, D. (1987) Prediction of wheat yield loss due to competition by wild oats (*Avena* spp). *Australian Journal of Agricultural Research*, **38**, 487–499.

Miller, T.E. & Weiner, J. (1989) Local density variation may mimic effects of asymmetric competition on plant size variability. *Ecology*, **70**, 1188–1191.

Mohler, C.L. (1996) Ecological bases for the cultural control of annual weeds. *Journal of Production Agriculture*, **9**, 468–474.

Mohler, C.L. (2001) Enhancing the competitive ability of crops. *Ecological Management of Agricultural Weeds* (eds M. Liebman, C.L. Mohler & C.P. Staver), in press. Cambridge University Press, Cambridge, UK.

Monsi, M., Uchijima, Z. & Oikawa, T. (1973) Structure of foliage canopies and photosynthesis. *Annual Review of Ecology and Systematics*, **4**, 301–328.

Murphy, S.D., Yakubu, Y., Weise, S.F. & Swanton, C.J. (1996) Effect of planting patterns and inter row cultivation on competition between corn (*Zea mays*) and late emerging weeds. *Weed Science*, **44**, 856–870.

Patterson, M.G., Walker, R.H., Colvin, D.L., Wehtje, G. & McGuire, J.A. (1988) Comparison of soybean (*Glycine max*)–weed interference from large and small plots. *Weed Science*, **36**, 836–839.

Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size-asymmetry in competition among plants. *Oecologia*, **113**, 447–455.

Silvertown, J. & Lovett Doust, J. (1993) *Introduction to Plant Population Biology*, 3rd edn. Blackwell Science, London, UK.

Smith, B.S., Murray, D.S., Green, J.D., Wanyahaya, W.M. & Weeks, D.L. (1990) Interference of three annual grasses with grain sorghum (*Sorghum bicolor*). *Weed Technology*, **4**, 245–249.

Teich, A.H., Smid, A., Welacky, T. & Hamill, A. (1993) Row spacing and seed-rate effects on winter wheat in Ontario. *Canadian Journal of Plant Science*, **73**, 31–35.

Wax, L.M. & Pendelton, J.W. (1968) Effect of row spacing on weed control in soybeans. *Weed Science*, **15**, 462–465.

Weiner, J. (1990) Asymmetric competition in plant populations. *Trends in Ecology and Evolution*, **5**, 360–364.

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