Dynamics of Competition between Wheat and Oat: II. Effects of Dwarfing Genes

Roger D. Cousens,* Greg J. Rebetzke, and Allan G. Barnett

ABSTRACT

Previous studies in the United Kingdom (UK) and Australia have led to the hypotheses that reversals in competitive hierarchy between wheat (*Triticum aestivum* L.) and oat (*Avena* spp.) could occur only in situations in which (i) there is a reversal in the relative heights of the competitors during the year and (ii) there is strong competition for light. Reversals in competitive hierarchy should not, therefore, occur where the wheat is either taller or shorter than oat throughout growth. We grew near-isogenic lines of wheat for height in monoculture and in replacement mixtures with oat (*A. sativa* L. and *A. strigosa* Schreb.) in 2 yr. In the drier year and with a late-maturing oat cultivar, height of wheat had no influence over its competitive superiority, which was maintained throughout the season. In a somewhat wetter year and with an earlier-maturing oat cultivar, the shortest wheat lines were less competitive than corresponding taller near-isolines. Results were consistent for near-isogenic lines in three contrasting genetic backgrounds. Partial reversals in competitive hierarchy were seen in a late sowing, but these did not correspond with patterns in the relative height growth of the species.

Significant interest is being shown worldwide in the identification of crop cultivars that are able to suppress weed seed production and/or maintain their yield in the presence of weeds (see review by Lemerle et al., 2001). Competitive cultivars will be beneficial in situations where weeds are difficult to control, such as where herbicide resistance has developed or in organic farming systems. Improvements in the competitive ability of cultivars can be achieved through both traditional selection methods and by using modern genetic technologies. It is to be anticipated, however, that the greatest advances will be achieved where we link plant breeding with scientific understanding. For example, considerable genetic improvements in crop establishment under dryland conditions are now being achieved through a detailed understanding of crop physiology (Rebetzke and Richards, 2000). However, our scientific understanding of competitive ability remains poor. Most of our knowledge comes from correlations between competitive outcomes (most often measured at the end of the growing season) and a small number of measured traits (Lemerle et al., 2001). There have been relatively few field studies of weed physiology or of the growth dynamics of competing weeds and crops.

Competition can be highly complex, with different resources becoming limiting at different times in the season and different traits therefore becoming advantageous at different times. The competing species may also have very different phenologies, which are likely to have significant influences over the competitive hierarchies as they develop. Thus, the identification of competitive traits may not be straightforward. One example of such complex dynamics comes from research on wild oat (*Avena fatua* L.) in competition with wheat and barley (*Hordeum vulgare* L.) in the UK, in which Cousens et al. (1991) reported a late reversal of competitive hierarchy between wild oat and both crops. On an individual plant basis, the cereals were initially more competitive, but after crop anthesis, the wild oat became equal to or more competitive than the crops. One explanation was that this might be caused by the relative patterns of resource allocation by the species. It was suggested that if this was the case, by experimentally moving the timing of key developmental stages, the timing of the reversal in competitive hierarchy would also move. In research in Australia with cultivated oat (*A. sativa*) and wheat (Cousens et al., 2003), it was confirmed that small changes in the relative time of emergence (and therefore also of later developmental stages) have a strong influence on the outcome of competition between species of similar height. Differences of a few days in anthesis among lines of a single wheat cultivar had no detectable effect on competition. However, no reversals of competitive hierarchy were found in any of these experiments, either with cultivated oat or with other *Avena* taxa.

An alternative explanation for the reversal of competitive hierarchy in the original UK study (Cousens et al., 1991) was the relative patterns of height development of the competitors. The part played by plant height in competition is well known (Harper, 1977) and has been highlighted in many studies of weed–crop competition, particularly where there are major-gene height differences among the crop genotypes (Lemerle et al., 2001). Taller species will have their leaves higher in the canopy, causing the growth of shorter competitors to be reduced. It is common in experiments on weed–crop competition to measure height of cultivars only at maturity. In some circumstances, however, the species with the height advantage at maturity may not be the taller species throughout growth. A species with short leaves, for example, may be shaded by another species during vegetative growth, but if its reproductive development is initiated earlier and/or its rate of stem extension is greater, it may then become the superior competitor for light. It is therefore necessary to consider the dynamics of height development rather than just final height. In the Cousens et al. (1991) UK study, wild oat plants were indeed initially shorter than the cereals, but stem and

R.D. Cousens and A.G. Barnett, Joint Cent. for Crop Improvement, Inst. of Land and Food Resour., The Univ. of Melbourne, Victoria 3010, Australia; and G.J. Rebetzke, CSIRO Plant Industry, P.O. Box 1600, Canberra, ACT 2601, Australia. Received 6 Nov. 2002 *Corresponding author (rcousens@unimelb.edu.au).

Published in Agron. J. 95:1305–1313 (2003).

677 S. Segoe Rd., Madison, WI 53711 USA

Abbreviations: GDD, growing degree days; LAI, leaf area index; RP, relative performance; UK, United Kingdom.

subsequent canopy extension of wild oat continued longer, leading to later shading by the weed.

Height, however, will only confer a competitive advantage in situations where competition for light is important. This would certainly have been the case in the UK study where stem densities, leaf sizes, and LAI were high. In the Australian study (Cousens et al., 2003), however, water availability was often low, leading to very few tillers, small leaves, high leaf mortality, and low LAI. Competition belowground would have been intense, but the shorter species perhaps would still have received sufficient light. Indeed, the one case in the Australian study where relative heights of the species reversed during growth did not result in a reversal of competitive hierarchy. Hence, we can qualify the proposed mechanism: Reversals of relative height of species during growth can lead to reversals in competitive hierarchy, but this will only occur under conditions in which aboveground competition is intense. If we advance the time at which species' relative heights cross over (without altering other traits), then we should advance the time at which the competitive hierarchy reverses. If species maintain their relative height differential during growth, there should be no reversal of competitive hierarchy.

It is not easy to test these predictions, however, because ideally we require competitors to differ only in the desired traits of height development. Tall and short crop cultivars may differ in many other aspects because they may have very different genetic backgrounds. More meaningful information can be obtained from the comparison of near-isogenic lines differing in particular height genes (Seefeldt et al., 1999). We can use dwarf wheat isolines that remain shorter than oat and tall isolines that are taller than oat throughout growth. Semidwarf isolines may be found that are overtopped by oat later in growth, depending on the characteristics of the oat taxon. Unfortunately, genes affecting plant height may have other pleiotropic effects on growth. For example, dwarfing genes affect coleoptile length, seedling establishment, leaf size, tiller number, harvest index, grain size, and grain mass (Gale and Youssefian, 1985; Richards, 1992; Rebetzke and Richards, 2000). Notwithstanding these limitations, near-isogenic height lines provide the best material available with which to characterize the effects of plant height on competition.

In this study, we compared the dynamics of competition between cultivated oat and different wheat isolines varying in plant height. We also varied the intensity of competition for sunlight by supplying additional water through irrigation.

MATERIALS AND METHODS

The field site used for this experiment was the Wimmera Research Station, in northwestern Victoria, Australia. A description of the site is given by Cousens et al. (2003). Long-term average annual rainfall for the site is 419 mm. Growing season rainfall (June–November) was 190 mm in 1999 and 195 mm in 2000 compared with the long-term average of 250 mm. In 1999, the site received less than half the long-term monthly averages in June, July, and September while in 2000, monthly rainfall was well below average in June and August. Areas were cultivated before sowing to produce a fine seedbed. A commercial fertilizer was applied (13.6 kg N ha^{-1}, 11.6 kg P ha^{-1}, and 9.3 kg S ha^{-1}) at sowing in both years.

In all experiments, plots were 3.2 by 1.2 m arranged in a randomized complete block design. The number of wheat cultivars and the oat taxon, along with the number of replicates, varied among experiments and are given below. In each experiment, there were monocultures of wheat and oat, plus a single mixture consisting of equal proportions at the same total plant density as monocultures, i.e., a replacement-series design. In mixtures, different species were sown alternately within rows, and these positions were staggered in adjacent rows (giving a checkerboard layout). Seeds were sown individually by hand to a depth of approximately 5 cm using a specially made planting device. Spacing was 15 cm between rows and 5 cm between plants within rows. This gave a density of approximately 133 plants m^{-2}. Fungicides and insecticides were sprayed as required to control diseases and insect damage. Other weeds were removed by hand throughout the growing season.

There were three experiments as follows:

Competition between Wheat Height Isolines and *Avena strigosa* cv. Saia

In this experiment, conducted in 1999, we compared growth of three wheat height isolines in competition with *A. strigosa*. This oat taxon was used because of its late pattern of height development (Cousens et al., 2003). Near-isogenic height lines of the wheat cultivar Maringa have been used extensively in scientific studies (e.g., Miralles and Slafer, 1997; Miralles et al., 1998). We obtained lines supposedly containing the following dwarfing genes: *Rht-B1b* (*Rht1*), *Rht-D1b* (*Rht2*), both *Rht-B1b* and *Rht-D1b* (*Rht1+2*), *Rht-B1c* (*Rht3*), and the tall Maringa (*rht*) parental line. Preliminary experiments in plant pots showed that the allele composition of each line was unreliable: Three lines were therefore chosen to represent tall (*rht*), semidwarf (*Rht-B1b* or *Rht-D1b*), and dwarf statures (*Rht3*). Seeds of all lines were passed through sieves to obtain seed of similar size. Each line and the oat (*A. strigosa*) cultivar Saia were sown in monocultures and in mixtures of the two species. *Avena strigosa* was chosen in preference to the wild oat weed to ensure reliability of emergence, minimal variation in growth rate, and synchronous development. The experiment was sown from 8 to 10 June 1999. There were three replicate blocks of each treatment.

Competition between Wheat Height Isolines and *Avena sativa* cv. Vasse

In this experiment, conducted in 2000, we grew three wheat height isolines from each of three genetic backgrounds in competition with cultivated oat. Because the three backgrounds differed in height even in the absence of dwarfing genes, we hoped to establish a range of different patterns of relative height development of competing species. The same tall, semidwarf, and dwarf lines of Maringa were used as in 1999. We also included two other sets of near-isogenic lines developed by Richards (1992). The KCD lines were derived from crosses between Kalyansona (*Rht*1) and Chenab 70 (*Rht2*); the APD lines were from crosses of Arz (*Rht1*) and Pato Argentino (*Rht2*). Lines contained zero, one (either *Rht1* or *Rht*2), or two (*Rht1*+2) height-reducing alleles. The experiment was sown on 5 to 7 June 2000. All other details were the same as for the previous experiment.

Effect of Irrigation on the Competitiveness of Wheat Height Isolines with *Avena sativa* cv. Vasse

In this experiment, conducted in 2000, we compared competition under rainfed and irrigated conditions. Irrigation was intended as a way of increasing the intensity of competition for light. Because the experiment was sown later than the previous experiment, yet was adjacent to it, this study could also be used to compare the effects of sowing date on the interaction between height line and competition. Only the three Maringa height near-isolines were included. Irrigated plots were separated physically from rainfed plots and were therefore analyzed as separate experiments. Plots were sown from 14 to 17 August. Irrigation supplemented rainfall from the four- to five-leaf stage of wheat onwards. If rainfall in the previous week was less than 25 mm, sufficient water was applied to bring the total amount of water (rainfall + irrigation) to at least 25 mm. A total rainfall equivalent of 165 mm was added in this way.

Sampling Procedures

Seedling emergence, defined as the stage when the coleoptile tip first became visible, was recorded daily in a 1-m^2 permanent quadrat within each monoculture. Recording ceased when there was no further emergence on five consecutive dates. The few gaps where no seedling emerged were left unfilled. Five adjacent plants of each species were sampled from every plot at frequent intervals to grain maturity, starting from a randomly selected end of each plot. Within each plot, the two outside rows were left intact, and two rows were left between sampling dates. Each plant was measured at its highest point without disturbing the canopy and was then removed. The number of live tillers was counted on each plant. Green leaf area was measured using a LI-COR (Lincoln, NE) LI-1300 area meter, and plant dry weight (material above the crown node only) was recorded after drying at 80°C for 48 h. Grain at maturity was threshed by hand and weighed; 1000-grain weight and harvest index were determined. Growing degree days (GDD) were calculated above a base temperature of 0°C.

Data Analysis

All measured variables were examined within a sample date by analysis of variance for a randomized complete block design, using the Minitab (State College, PA) statistical package. Means were compared using the least significant difference for the appropriate a priori contrasts. After anthesis and where the attribute had reached an asymptote (determined by eye), data were combined across the last three sample dates to achieve greater precision in comparisons of treatments. There was no indication that any data transformation was required. For each date, the relative performance (RP) of each species was calculated as the mean value of the measured attribute in mixture divided by its mean value in monoculture. Thus, if growth in mixture is unaffected by the identity of the neighboring species, RP will maintain a value of 1.0; if species B has a larger effect on A than A does on itself, then the RP of A will fall below 1.0, and so on. Thus, we can plot the time course of competitive hierarchy of the two species. A disadvantage is that statistical analysis of RP is difficult. However, where the plant attribute (such as mass) differs significantly between mixture and monoculture, the RP can be considered to differ from unity.

RESULTS

Competition between Wheat Height Isolines and *Avena strigosa* cv. Saia

The oat cultivar used in 1999 was shorter than all wheat height isolines throughout much of plant development, only *telescoping* its stems as the wheat was reaching maturity (Fig. 1). The dwarf line produced significantly less grain yield in monoculture than the taller lines; number of grains per head, 1000-grain weight, and harvest index were also reduced (Table 1). All three wheat isolines produced significantly ($P < 0.05$) more biomass in mixture than in monoculture from 500 GDD onwards (Fig. 2a). Similar effects were seen for leaf area and tiller number (data not shown). In contrast, oat produced a greater mean biomass in monoculture than any mixture from 1200 GDD onwards, but this was significant ($P < 0.05$) only for some isolines and at some sample dates (Fig. 2b). Grain yield and number of heads per plant for wheat were significantly greater in mixture than in monoculture. Temporal patterns of RP were similar among the three isolines (Fig. 3) although the response of the semidwarf line to oat was somewhat less than for the other lines. Wheat quickly became the superior competitor and maintained this throughout growth.

Competition between Wheat Height Isolines and *Avena sativa* cv. Vasse

The oat cultivar used in 2000 showed a pattern of height development similar to all three wheat height near-isolines although it was similar in its final height to the dwarf lines of Maringa and KCD (Fig. 4). APD was shorter than equivalent height lines of Maringa and KCD and also achieved its maximum height later during development. The wheat backgrounds also differed in various other traits when growing in monoculture. For example, Maringa produced the largest number of tillers while APD produced the fewest. APD also produced smaller biomass and grain yield (Table 2) despite having

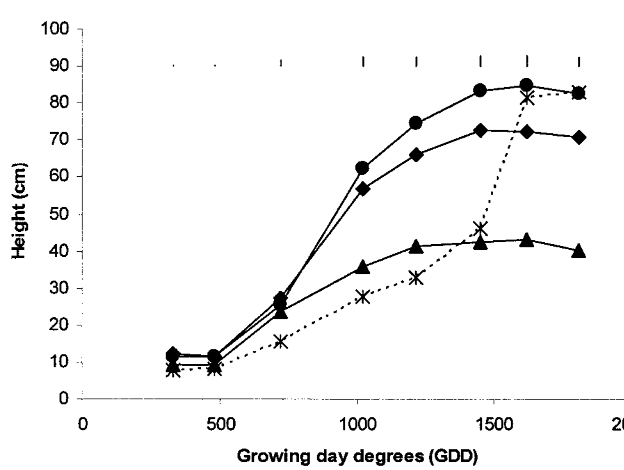

Fig. 1. Height of oat [*Avena strigosa* cv. Saia] (*) and three near-isogenic height lines of wheat cultivar Maringa in 1999. Symbols indicate the wheat height line: ● = tall, ◆ = semidwarf, and ▲ = dwarf. Vertical bars indicate the standard error within a sample date.

Table 1. Components of yield and other parameters for three wheat height near-isolines of wheat cultivar Maringa and oat in 1999.

	Final height	1000-grain weight	Heads per plant	Grains per head	Grain yield per plant	Plant mass	Harvest index
	cm	g			g	g	%
Wheat							
Tall—monoculture	78.7	39.9	1.53	19.7	1.20	3.47	34.6
Tall—mixture	76.3	36.5	2.47	21.3	1.81	5.39	32.8
Semidwarf—monoculture	63.0	32.8	1.73	22.2	1.25	3.77	33.2
Semidwarf—mixture	67.3	34.5	2.00	20.2	1.41	4.10	34.6
Dwarf—monoculture	38.0	19.6	1.87	16.0	0.61	2.60	22.8
Dwarf—mixture	38.3	26.9	2.33	17.9	1.10	3.73	30.2
SE	2.52	2.08	0.19	1.24	0.15	0.57	1.62
P for:							
Height line	*<0.001*	*<0.001*	*NS*	*<0.05*	*<0.01*	*NS*	*<0.001*
Mixture vs. monoculture	*NS*	*NS*	*<0.01*	*NS*	*<0.01*	*<0.05*	*NS*
Interaction	*NS*	*0.08*	*NS*	*NS*	*NS*	*NS*	*<0.05*
Oat							
Monoculture	76.3	–	1.87	–	–	2.86	–
Mixture—tall wheat	76.2	–	1.47	–	–	1.67	–
Mixture—semidwarf wheat	70.1	–	1.64	–	–	1.63	–
Mixture—dwarf wheat	72.2	–	1.93	–	–	2.19	–
SE	4.0	–	0.27	–	–	0.33	–
P	*NS*	–	*NS*	–	–	*NS*	–

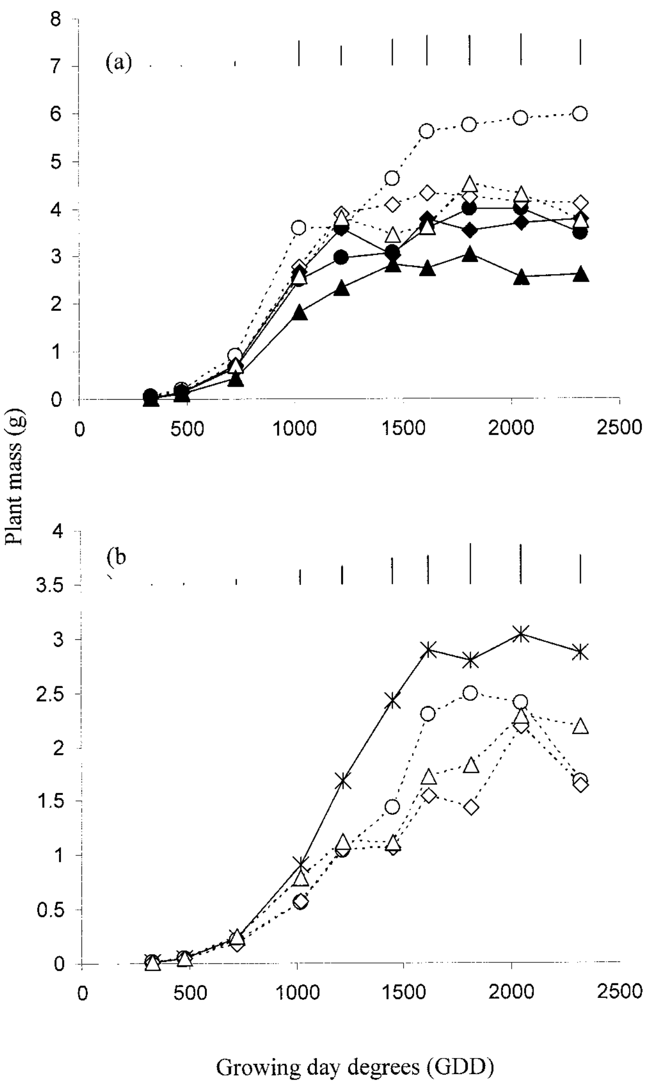

Fig. 2. Biomass over time for (a) wheat cultivar Maringa and (b) oat (*Avena strigosa* cv. Saia) in monoculture (solid lines and solid symbols) and replacement mixtures (dotted lines and open symbols) in 1999. Symbols indicate the wheat height line used: ● = tall, ◆ = semidwarf, and ▲ = dwarf; oat monoculture is shown by *. Vertical bars indicate the standard error within a sample date.

the highest harvest index. Highest harvest indices were commonly achieved by the shortest height lines.

All three dwarf wheat isolines, when grown in mixture, grew poorly when compared with monoculture though the corresponding growth of oat was affected little in mixture (Table 2 and Fig. 5). On average, wheat produced less grain and fewer heads per plant in mixture than in monoculture. There was no significant influence of wheat line on the sizes of oat plants at maturity (Table 3). The onset of competitive superiority of oat over wheat (as indicated by the point of divergence of their RP lines) varied among the three genetic backgrounds (Fig. 5.). For KCD, wheat and oat were almost equal competitors throughout growth. For APD, oat tended to be more competitive than wheat from about 800 GDD onwards, with oat being most dominant over the dwarf isoline. For Maringa, the dwarf isoline was again the least competitive, being suppressed by oat, whereas the semidwarf was slightly more competitive than oat (only significant at one sample date) and the tall isoline was not significantly different in mixture than monoculture.

Effect of Irrigation on the Competitiveness of Wheat Height Isolines with *Avena sativa* cv. Vasse

Irrigation had no obvious effect on plant height of either species in the later sowing date in 2000 (Table 4). However, wheat growing in monoculture under irrigation tended to produce heavier plants with more stems, heavier grains, and greater harvest index, leading to greater grain yields than under dryland conditions. Similarly, oat plants also tended to be larger under irrigation (Table 5).

Under both dryland and irrigated conditions, dwarf isolines in monoculture produced plants with lower biomass, fewer heads, and lower grain yield than the taller isolines (Table 4). Mean grain size also tended to be reduced for dwarf isolines, but this was not significant. Under irrigation, harvest index was significantly higher in the dwarf isoline.

Wheat plant mass, grain yield, and heads per plant

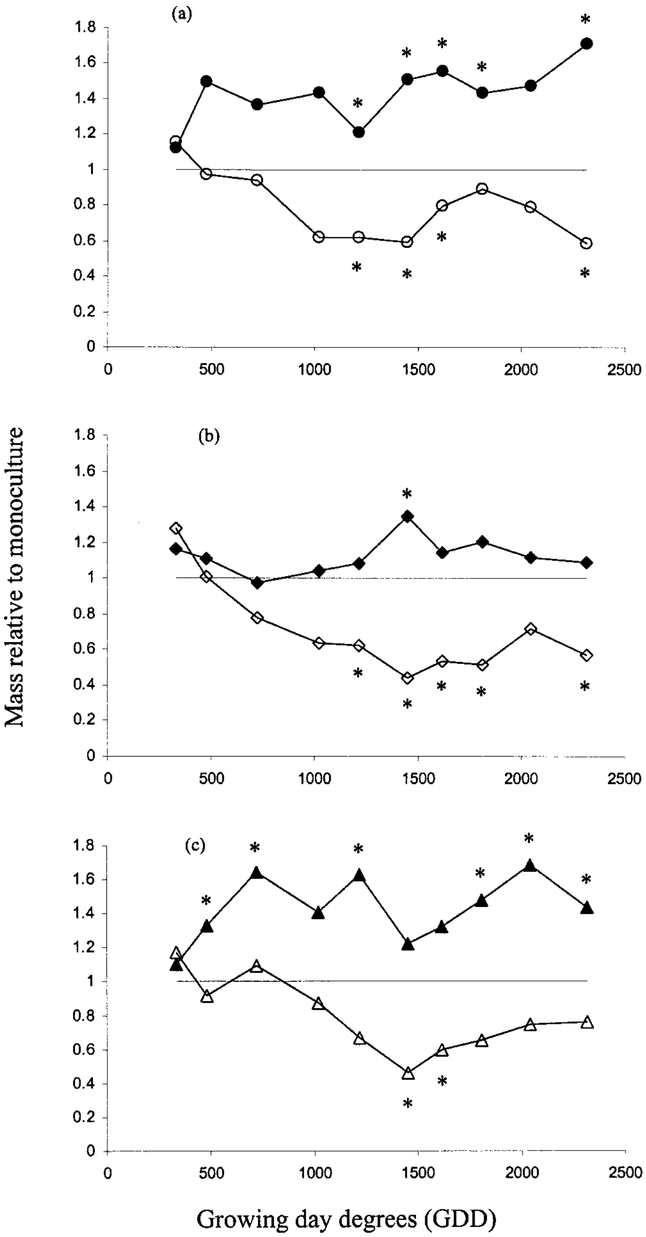

Fig. 3. Relative performance, as measured by the ratio of plant mass in mixture to plant mass in monoculture, for oat [*Avena strigosa* cv. Saia] (○, ◇, and △) and three height lines of wheat cultivar Maringa in 1999: tall (●), semidwarf (◆), and dwarf (▲). The horizontal line indicates the expected value for equal mass in mixture and monoculture. Asterisks indicate those observations for which mixture biomass significantly differs from monoculture ($P <$ 0.05), i.e., relative performance is significantly different from 1.0.

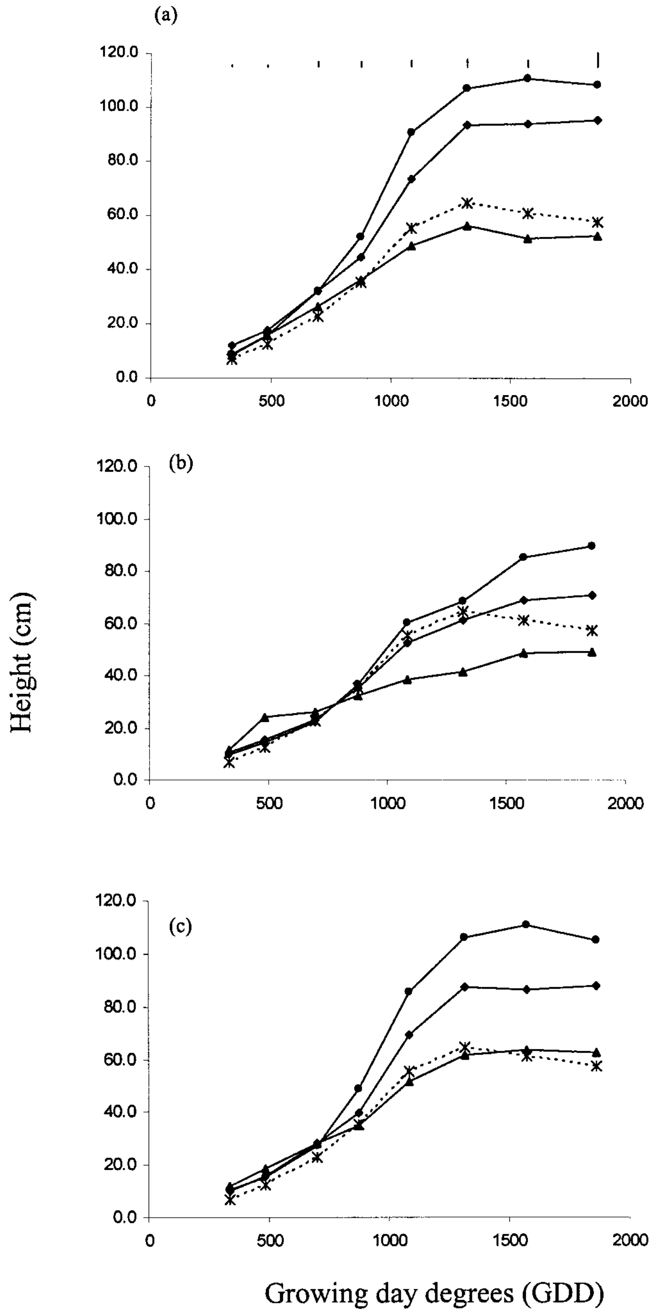

Fig. 4. Height of oat [*Avena sativa* cv. Vasse] (*) and three near-isogenic height lines of (a) wheat cultivar Maringa, (b) APD, and (c) KCD in 2000. Symbols indicate the wheat height line: ● = tall, ◆ = semidwarf, and ▲ = dwarf. Vertical bars indicate the standard error within a sample date.

were, with one exception (tall, dryland), reduced by growing in mixture (Table 4). Oat plants tended to be smaller when growing with the tall isoline, but this was not significant (Table 5). Time courses of RP showed divergence (i.e., the establishment of competitive superiority) after about 800 GDD in all cases except for the tall line under dryland conditions (Fig. 6). In that case, wheat was the better competitor after 1500 GDD. For the two shorter-height lines, there was a tendency for this competitive superiority to decrease toward maturity under both irrigation regimes. In one case (semidwarf, dryland), there appeared to be a reversal of the competitive hierarchy, with wheat being the better competitor until the final two harvests (although this was not significant). With irrigation, oat plants tended to be more competitive than wheat, regardless of the height of the wheat line. However, in dryland conditions, the taller wheat lines tended to compete equally with oat.

Comparisons among Experiments

There were a few differences among experiments in environmental conditions and field procedures that are

Table 2. Components of yield and other parameters for wheat height near-isolines in 2000.

	Final height	1000-grain weight	Heads per plant	Grains per head	Grain yield per plant	Plant mass	Harvest index
	cm	g			g	g	%
Maringa							
Tall—monoculture	94.1	35.6	3.20	23.4	2.69	9.89	27.0
Tall—mixture	88.5	34.8	3.13	22.9	2.51	9.00	27.7
Semidwarf—monoculture	81.0	30.9	3.07	24.4	2.07	6.56	31.5
Semidwarf—mixture	94.8	27.1	3.20	27.4	2.20	9.01	25.8
Dwarf—monoculture	52.4	31.5	3.53	25.8	2.76	7.80	35.4
Dwarf—mixture	45.3	30.1	3.60	17.2	1.74	4.35	39.6
APD							
Tall—monoculture	89.5	32.4	2.33	28.8	2.01	5.80	34.7
Tall—mixture	85.2	30.0	1.73	33.9	1.77	4.94	35.5
Semidwarf—monoculture	69.1	32.1	2.00	31.4	2.00	5.56	36.9
Semidwarf—mixture	72.3	32.2	1.80	33.7	1.92	4.91	39.2
Dwarf—monoculture	49.3	25.4	1.80	36.1	1.66	4.24	39.1
Dwarf—mixture	47.7	24.6	1.20	32.2	0.93	2.13	43.4
KCD							
Tall—monoculture	105.4	32.3	2.93	30.0	2.87	10.65	26.7
Tall—mixture	100.5	39.9	2.73	25.0	2.18	10.59	21.2
Semidwarf—monoculture	87.9	35.4	2.93	30.6	3.15	9.80	32.2
Semidwarf—mixture	73.5	35.4	2.40	38.1	2.73	8.67	31.1
Dwarf—monoculture	62.5	38.9	2.87	25.7	2.82	8.28	33.8
Dwarf—mixture	61.9	35.5	2.20	33.1	2.59	7.05	37.0
SE	6.13	3.97	0.26	5.55	0.37	1.08	1.96
***P* for:**							
Height line	*<0.001*	*0.09*	*<0.001*	*NS*	*<0.01*	*<0.001*	*<0.001*
Monoculture vs. mixture	*NS*	*NS*	*<0.05*	*NS*	*<0.05*	*NS*	*NS*
Interaction	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

worthy of further exploration. Maringa was sown in all experiments, but plants were notably smaller in 1999 than in 2000. Plants of *A. strigosa* in 1999 were also smaller than in similar experiments in 2000 (Cousens et al., 2003). This probably reflects the low rainfall of 1999 during early growth, particularly in July and September.

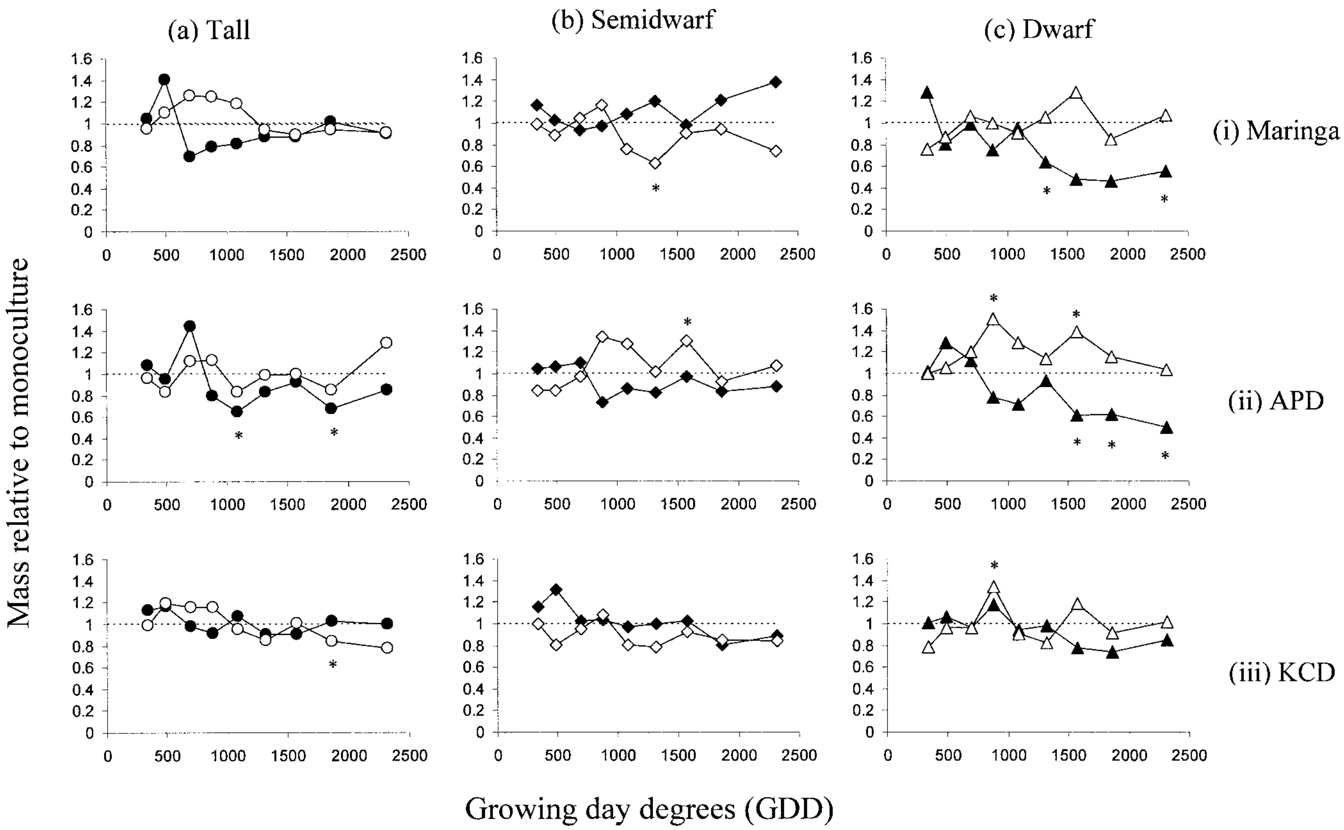

Fig. 5. Relative performance, as measured by the ratio of plant mass in mixture to plant mass in monoculture, for oat (*Avena sativa* cv. Vasse) and three height lines of wheat cultivar Maringa (row i), APD (row ii), and KCD (row iii) in 2000: tall (column a), semidwarf (column b), and dwarf (column c). Solid symbols refer to wheat and open symbols to oat. The horizontal line indicates the expected value for equal mass in mixture and monoculture. Asterisks indicate those observations for which mixture biomass significantly differs from monoculture ($P < 0.05$), i.e., relative performance is significantly different from 1.0.

Table 3. Final harvest parameters for oat competing with wheat height near-isolines in 2000.

		Final height	Heads per plant	Plant mass
		cm		g
Monoculture		57.6	2.07	9.09
Mixture with:				
Maringa	tall	62.5	1.87	8.31
	semidwarf	58.9	1.67	6.70
	dwarf	52.0	1.67	9.76
APD	tall	62.9	1.87	11.71
	semidwarf	61.3	1.60	9.75
	dwarf	60.4	1.80	9.38
KCD	tall	74.9	1.60	7.09
	semidwarf	72.2	1.93	7.65
	dwarf	72.9	1.53	9.23
SE		7.76	0.21	1.29
P		*NS*	*NS*	*NS*

Plants had very few fertile tillers and little green leaf area at anthesis. As a result, competition for light would have been much less than in a year of average to high rainfall. It is possible that site conditions could have had some influence as a neighboring field was used in 1999: The soil type was very similar, but the weed population appeared to be considerably higher (though these were controlled). The competitive superiority of wheat in 1999, compared with the superiority of oat in 2000, appears to be due to the oat taxon used in that year. In other experiments (Cousens et al., 203), *A. strigosa* cv. Saia was a poorer competitor than *A. sativa* cv. Vasse.

DISCUSSION

In a previous paper (Cousens et al., 2003), we proposed that the relative heights of competitors will only be an important factor in competition when aboveground competition for light is strong. Moreover, reversals in competitive hierarchy during the season would only occur in those situations if they were driven by relative patterns of height growth. Increases in the availability of water and/or nutrients would thus both increase the sensitivity of competition to plant height and make reversals of competitive hierarchy more likely. No evidence was found to support the alternative hypothesis that reversals in competitive hierarchy are driven by patterns of phenological development (Cousens et al., 2003).

In the present paper, in a very dry year and with a late-maturing oat cultivar, we found that three wheat height isolines performed similarly under competition; there were no reversals of competitive hierarchy even when (for the semidwarf and dwarf cultivars) the wheat was *overtaken* in height later in the season. Wheat was more competitive than oat in the dry year. In a slightly wetter year with an earlier-developing/larger-leaved oat cultivar, whether sown early or late and whether under natural rainfall or with supplementary irrigation, oat was competitively superior to very short dwarf wheat lines. Competitiveness among taller wheat height lines

Table 5. Final harvest parameters for oat competing with height near-isolines of wheat cultivar Maringa in 2000, sown late under dryland conditions or with supplementary irrigation.

		Final height	Heads per plant	Plant mass
		cm		g
Irrigation				
Monoculture		53.8	4.40	9.06
Mixture with:	tall wheat	52.2	3.33	8.45
	semidwarf wheat	51.9	3.67	8.72
	dwarf wheat	49.3	3.33	9.47
SE		1.15	0.34	0.82
P		*NS*	*NS*	*NS*
Dryland				
Monoculture		53.9	3.27	8.10
Mixture with:	tall wheat	42.6	2.38	5.29
	semidwarf wheat	48.0	3.33	8.66
	dwarf wheat	49.7	3.33	8.55
SE		0.84	0.44	1.54
P		*<0.01*	*NS*	*NS*

Table 4. Components of yield and other parameters for three wheat height near-isolines of wheat cultivar Maringa in 2000, sown late under dryland conditions or with supplementary irrigation.

	Final height	1000-grain weight	Heads per plant	Grains per head	Grain yield per plant	Plant mass	Harvest index
	cm	g			g	g	%
Irrigated							
Tall—monoculture	84.2	20.0	5.40	34.1	3.62	12.85	28.7
Tall—mixture	91.6	23.7	3.60	32.3	2.74	9.03	30.5
Semidwarf—monoculture	83.5	18.6	3.80	35.2	2.54	7.96	32.2
Semidwarf—mixture	78.9	20.9	3.40	31.6	2.32	7.11	32.4
Dwarf—monoculture	47.5	18.0	3.27	33.2	1.98	5.87	33.8
Dwarf—mixture	44.8	16.7	2.47	37.3	1.61	4.78	34.2
SE	2.33	1.88	0.53	4.00	0.56	1.86	1.14
P for:							
Height line	*<0.001*	*NS*	*<0.05*	*NS*	*0.094*	*<0.05*	<0.01
Mixture vs. monoculture	*NS*	*NS*	*<0.05*	*NS*	*NS*	*NS*	NS
Interaction	*0.068*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Dryland							
Tall—monoculture	88.7	19.6	3.47	30.9	2.04	7.44	27.5
Tall—mixture	89.6	17.8	3.97	35.8	2.46	8.87	27.7
Semidwarf—monoculture	75.7	18.8	3.53	31.9	2.14	7.11	30.0
Semidwarf—mixture	75.9	17.6	2.87	33.7	1.70	5.55	30.3
Dwarf—monoculture	43.5	16.6	2.80	29.9	1.40	4.65	29.8
Dwarf—mixture	41.6	14.6	2.40	24.9	0.90	3.50	25.5
SE	3.30	1.74	0.36	3.86	0.30	0.91	1.51
P for:							
Height line	*<0.001*	*NS*	*<0.05*	*NS*	*<0.05*	*<0.01*	*NS*
Mixture vs. monoculture	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Interaction	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

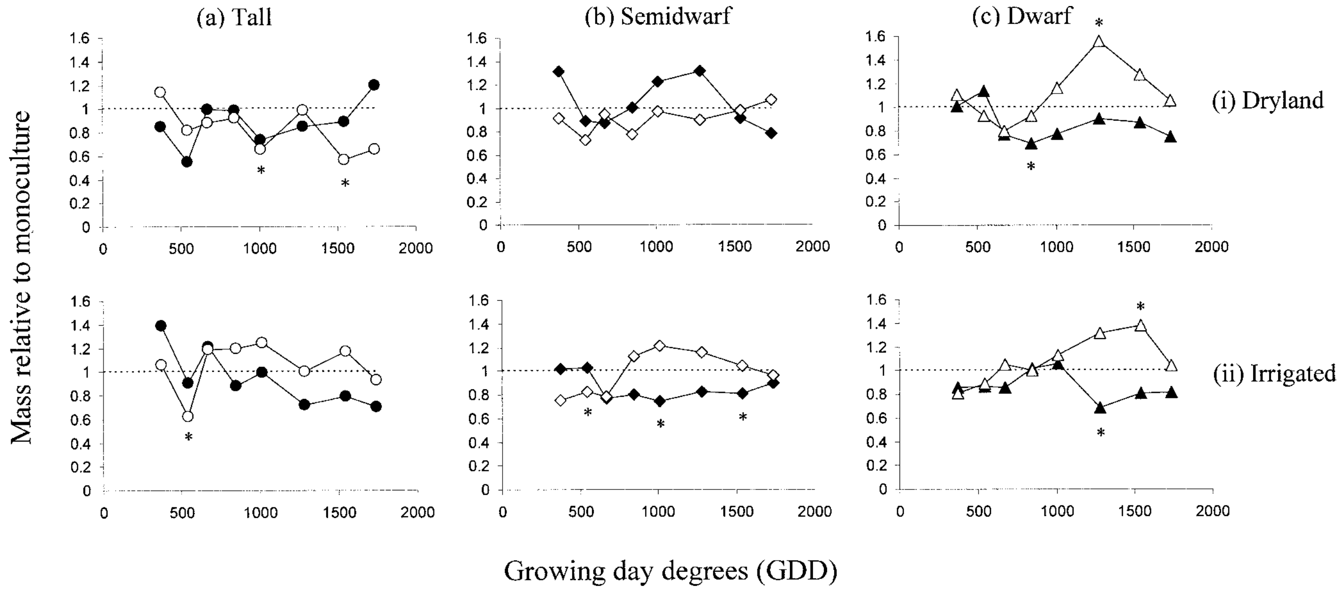

Fig. 6. Relative performance, as measured by the ratio of plant mass in mixture to plant mass in monoculture, for oat (*Avena sativa* cv. Vasse) and three height lines of wheat cultivar Maringa sown late in 2000 under dryland conditions (row i) or supplemented by irrigation (row ii): tall (column a), semidwarf (column b), and dwarf (column c). Solid symbols refer to wheat and open symbols to oat. The horizontal line indicates the expected value for equal mass in mixture and monoculture. Asterisks indicate those observations for which mixture biomass significantly differs from monoculture ($P < 0.05$), i.e., relative performance is significantly different from 1.0.

and oat varied among wheat genetic backgrounds and experiments, but oat and wheat tended to have similar effects on each other.

These experimental results thus support the hypothesis that height will only be important when there is more intense competition for light. Seefeldt et al. (1999) also found that the percentage yield loss of a dwarf (*Rht1*+*Rht2*) line was greater than that of taller lines while the reduction of weed seed production was greatest for taller lines. Comparisons among crop cultivars often (but not always) find that competitiveness is correlated with height (Lemerle et al., 2001). To a certain extent, the strength of such correlations will depend on whether the cultivars included in the experiment differ in major, or only minor, height genes. Studies of cultivar competitiveness have usually been conducted under conditions that are either of reasonable rainfall or are well watered. We are not aware of any studies of the competitiveness of height lines that have been undertaken under low rainfall conditions.

Reversals of height advantage were seen for dwarf and semidwarf wheat in 1999 (Fig. 1) and for dwarf Maringa, dwarf KCD, and semidwarf APD in 2000 (Fig. 4: in all three cases, the changes in height advantage were only marginal). However, late reductions of competitive superiority, as shown by the RP in mixture, were apparent (but not significant) only for the semidwarf Maringa height line under dryland conditions when sown late (Fig. 6). The hypothesis that reversals of competitive hierarchy occur when there is a reversal of height advantage during growth is not supported. However, it is still possible that the effect might occur in situations where the changeover in relative heights is greater. The hypothesis that reversals of competitive dominance will be more apparent under the most intensive aboveground competition is also not supported. Again, it is possible that the treatments included in this study were not sufficiently different: The effect may occur under conditions that lead to an even greater LAI, such as higher plant densities and greater fertilizer application. Hence, we must conclude that the reasons for late reversals in competitive hierarchy between wheat and oat in some experiments remain unclear.

While the competitive environment of late-sown plants was modified by a single irrigation regime, a more comprehensive series of water and nutrient additions for midseason sowings could lead to greater clarity. Such experiments have been conducted previously for weeds in additive experimental designs (e.g., Mortensen and Coble, 1989) but not with respect to the temporal development of competitive effects. Moreover, most conclusions concerning the temporal effects of weeds are drawn indirectly from the effects of time of weed removal on crop yield (Zimdahl, 1999). If we aim to develop an understanding of weed–crop competition that is as soundly based as our understanding of crop growth, we need to take a more physiological approach to the study of weeds and take the appropriate measurements.

Presence of the *Rht-B1b* and *Rht-D1b* dwarfing genes is associated with concomitant reductions in leaf area early in the season (Richards, 1992; Rebetzke and Richards, 1999). This reduction has been observed previously for the Maringa (Keyes and Paolillo, 1989) and KCD and APD (Richards, 1992) height near-isolines used in the current study. Other dwarfing genes are available that reduce plant height, reducing plant lodging and increasing grain yield (e.g., *Rht4*, *Rht8*, and *Rht12*) but do not reduce leaf area or shorten coleoptile length (Rebetzke and Richards, 2000). Indeed, presence of these gibberellin-responsive dwarfing genes enables selection of wheat with even greater leaf area development early in the season (Botwright et al., 2003).

Wheat with greater early vigor is likely to have greater water use efficiency in environments where a large component of total water use is soil evaporation (López-Castañeda and Richards, 1994). For example, soil evaporation can be as high as 50% of total water use in Mediterranean environments where crops are largely reliant on in-season, or current, rainfall. A number of studies have also identified greater vigor to be important in competition with weeds early in the season (e.g., Lemerle et al., 2001). Studies are currently underway (e.g., Watt et al., 2001) to identify the extent to which greater leaf area development through use of alternative dwarfing genes can affect increases in root growth and subsequent competition for water and nutrients.

ACKNOWLEDGMENTS

We thank M.D. Gale for access to his Maringa material and Michael Mackey of the Australian Winter Cereals Collection, Tamworth, NSW.

REFERENCES

Botwright, T.L., G.J. Rebetzke, R.A. Richards, and A.G. Condon. 2003. Effect of GA-sensitive semidwarf *Rht* genes on cellular dimensions in wheat. Ann. Bot.

Cousens, R.D., A.G. Barnett, and G.C. Barry. 2003. Dynamics of competition between wheat and oats. I. Effects of changing the timing of phenological events. Agron. J. 95:(this issue).

Cousens, R.D., S.E. Weaver, T.D. Martin, A.M. Blair, and J. Wilson. 1991. Dynamics of competition between wild oats (*Avena fatua* L.) and winter cereals. Weed Res. 31:203–210.

Gale, M.D., and S. Youssefian. 1985. Dwarfing genes in wheat. p. 1–35. *In* G.E. Russell (ed.) Progress in plant breeding. Volume 1. Butterworths, London.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Keyes, G.J., and D.J. Paolillo. 1989. The effects of dwarfing genes *Rht*1 and *Rht*2 on cellular dimensions and rate of leaf elongation in wheat. Ann. Bot. 64:683–690.

Lemerle, D., G.S. Gill, C.E. Murphy, S.R. Walker, R.D. Cousens, S. Mokhtari, S.J. Peltzer, R. Coleman, and D.J. Luckett. 2001. Genetic improvement and agronomy for enhanced wheat competitiveness with weeds. Aust. J. Agric. Res. 52:527–548.

López-Castañeda, C., and R.A. Richards. 1994. Variation in temperate cereals in rainfed environments: III. Water use and water-use efficiency. Field Crops Res. 39:85–98.

Miralles, D.J., S.D. Katz, A. Colloca, and G.A. Slafer. 1998. Floret development in near isogenic wheat lines differing in plant height. Field Crops Res. 59:21–30.

Miralles, D.J., and G.A. Slafer. 1997. Radiation interception and radiation use efficiency of near-isogenic wheat lines with different height. Euphytica 97:201–208.

Mortensen, D.A., and H.D. Coble. 1989. The influence of soil water content on common cocklebur (*Xanthium strumarium*) interference in soybeans (*Glycine max*). Weed Sci. 37:76–83.

Rebetzke, G.J., and R.A. Richards. 1999. Genetic improvement of early vigour in wheat. Aust. J. Agric. Res. 51:235–245.

Rebetzke, G.J., and R.A. Richards. 2000. Gibberellic acid-sensitive dwarfing genes reduce plant height to increase kernel number and grain yield of wheat. Aust. J. Agric. Res. 51:235–245.

Richards, R.A. 1992. The effect of dwarfing genes in spring wheat in dry environments: I. Agronomic characteristics. Aust. J. Agric. Res. 43:517–527.

Seefeldt, S.S., A.G. Ogg, Jr., and Y. Hou. 1999. Near-isogenic lines for *Triticum aestivum* height and crop competitiveness. Weed Sci. 47:316–320.

Watt, M., J.A. Kirkegaard, S. Simpfendorfer, G.J. Rebetzke, and M.E. McCully. 2001. Variation in wheat genotypes to no-till farming—responses to soil biology and structure. p. 424–425. *In* Proc. Int. Soc. of Root Res. (ISRR) Symp., 6th, Nagoya, Japan. 11–15 Nov. 2001. Jpn. Soc. for Root Res., Nagoya, Japan.

Zimdahl, R.L. 1999. Fundamentals of weed science. 2nd ed. Academic Press, San Diego.