COMPETITION

Dynamics of Competition between Wheat and Oat: I. Effects of Changing the Timing of Phenological Events

Roger D. Cousens,* Allan G. Barnett, and Geoffrey C. Barry

ABSTRACT

Supply and demand for resources change dynamically throughout the growing season. If we are to understand the differences in competitiveness among crop cultivars, we need to study the dynamics of species interactions, not just their outcomes. We examined the temporal patterns in competition between wheat (*Triticum aestivum* L.) and oat (*Avena sativa* L.) in a series of field experiments. The combined effects of shifts in height growth and phenological development were described for monocultures and mixtures by varying the sowing dates of the species. Similar observations were made for oat competing with wheat lines differing in flowering time and for wheat competing with a range of *Avena* taxa. In contrast to earlier work, no reversals of competitive hierarchy were seen during the season. The species that achieved the greater biomass early on remained the better competitor throughout growth. The hypothesis that a delay in emergence will move the timing of such reversals was thus not supported. There were few differences in patterns of the dynamics of competition among *Avena* taxa and no observable differences in competitiveness among wheat lines differing by up to 6 d in flowering date. Overall, the results support the idea that reversals in competitive hierarchy during the season are caused by relative patterns in plant height growth of competitors and may occur only in systems in which competition for light is dominant. Otherwise, an early competitive hierarchy will be maintained throughout the growing season.

Variation in the abilities of crop cultivars to suppress weeds has been the subject of considerable research in recent years (see reviews by Callaway and Forcella, 1993; Lemerle et al., 2001). It is anticipated that farmers will grow competitive genotypes as part of integrated weed management systems (Challaiah et al., 1986; Jordan, 1993; Lemerle et al., 1996). Competitive ability can be assessed in simple screening trials, growing crop cultivars in the presence and absence of weeds and assessing the outcome as crop yield and weed seed production (e.g., Garrity et al., 1992). However, if we can identify plant traits associated with competitiveness, we may be able to breed for competitiveness indirectly by selecting for specific attributes. For example, crop cultivars with long, floppy leaves may compete more effectively for light than those with more erect leaves (Lotz et al., 1991); in the early stages of selection, we might then screen genotype collections for leaf length rather than conducting large, expensive competition experiments.

Joint Cent. for Crop Improvement, Inst. of Land & Food Resour., The Univ. of Melbourne, VIC 3010, Australia. Received 6 Nov. 2002. *Corresponding author (rcousens@unimelb.edu.au).

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

The identification of such traits has usually involved correlation analyses between final yield and morphological descriptors of plants at maturity or at some arbitrary earlier stage (e.g., Reeves and Brooke, 1977; Balyan et al., 1991; Lemerle et al., 1996). Such simple correlations, however, ignore the dynamics of competition. By definition, competition occurs when plants take up resources that are in limited supply. Resources vary in availability throughout the year; different resources will vary in the timing and extent to which they become limiting. For example, competition for nutrients may begin early, whereas water may not become limiting until after anthesis; uptake of a resource early in the season when it is not limited may intensify competition for it much later. Remarkably little attempt, however, has been made to observe the growth dynamics of competing plants. Studies of the growth and development of weeds (e.g., Cousens et al., 1992, 2001; Cousens, 1996a) remain scarce.

Although mere description of growth and development, albeit in detail across time, will not necessarily separate the interacting processes involved in competition, it may generate hypotheses that can be examined in further detailed physiological experiments. In such a study, Cousens et al. (1991) found that wheat and barley (*Hordeum vulgare* L.) initially dominated wild oat (*Avena fatua* L.) during vegetative development, but by physiological maturity, the weed had become equal to or more competitive than the cereals. This reversal in competitive hierarchy became observable at the time when both growth in height and leaf production of the crop ceased. The wild oat continued its reproductive development later and came to over-top the crop. Two alternative hypotheses thus seem plausible explanations for the reversal of competitive hierarchy. First, the reversal may have resulted from the earlier change in wheat from vegetative to reproductive growth. This change in resource partitioning by the crop may result in poorer competitive ability for water and for light as plant tissues senesce. There may also be other changes associated with transfer of resources among different tissues. Second, because the height growth of wild oat continued for longer than wheat, perhaps the late superiority of the weed resulted from a reversal of competitive ability in relation to light. According to the first hypothesis, we would predict that if reproductive development occurs earlier, without a change in relative heights of the species, the reversal of competitive hierarchy would be brought forward as well. According to the

Abbreviations: GDD, growing degree days; RP, relative performance; UK, United Kingdom.

second hypothesis, earlier overtopping by the wild oat, with no change in developmental periods, would bring the reversal of hierarchy forward while if the crop maintains its height advantage throughout growth, it will maintain its competitive advantage.

It is not easy to test these predictions, however, due to the close association of height growth and phenological development. Comparisons of cultivars varying in final height or time of maturity will confound these traits with many other attributes as a result of their differing genetic backgrounds. There are three other ways in which we can manipulate patterns of height and phenological development, but these too are not without their problems. First, we can stagger the sowing dates of the species. By doing this, we change the relative timing of height development (without greatly affecting final heights), but at the same time, we also alter the relative phenological development of the species. Second, we can compare competition with the weed among near-isogenic crop lines differing in height. Such genetic resources are widely available but have seldom been used in the study of weed–crop competition (though see Seefeldt et al., 1999). Third, we can compare competition with the weed among near-isogenic crop lines differing in flowering date. Fewer lines are available for this, and the differences in flowering time are not large. There is also the problem that near-isogenic lines do not differ only in the traits desired but almost inevitably are accompanied by pleiotropic effects on other plant characteristics (Gale and Youssefian, 1985; Richards, 1992)

Hence, there is no totally unambiguous way to distinguish between the alternative hypotheses of (i) relative patterns of resource allocation vs. (ii) relative height development in the changeover in competitive hierarchy among species. However, if we use all three experimental approaches, it is likely that we will be able to gain considerable insights into competitive interactions. In this first paper, we describe the effects on growth and development of varying the relative times of sowing wheat and oat as well as from competition with three lines of a single wheat cultivar differing in flowering time. We also varied the weed genotype to determine the likelihood that any differences between this and the previous study were caused by the species of oat used. In the second paper (p. 1305–1313 of this issue), we will report on the effects of variation in height development on competition by using wheat lines containing different dwarfing genes.

MATERIALS AND METHODS

The field site was the Wimmera Research Station, Dooen (300 km west-northwest of Melbourne, 36°39′ S, 142°16′ E) in northwestern Victoria, Australia. The soil type is a Haploxerert vertisol, and the average annual rainfall is 419 mm. In the year before the experiments, the 1998 area had been sown to chickpea (*Cicer arietinum* L.), whereas the 1999 area had been sown to canola (*Brassica napus* L.) the previous year and the 2000 area had previously grown a field pea (*Pisum sativum* L.) crop. Rainfall for all 3 yr was below average, with a growing season rainfall of 285 mm in 1998, 189 mm in 1999, and 235 mm in 2000. Areas were cultivated before sowing to produce a fine seedbed, and a commercial fertilizer was applied (13.6 kg N ha^{-1}, 11.6 kg P ha^{-1}, and 9.3 kg S ha^{-1}).

In all experiments, plots were 3.2 by 1.2 m arranged in randomized complete block designs. The number of wheat cultivars and oat taxa, along with the number of replicates, varied among experiments, as described below. In each experiment, there were monocultures of wheat and oat, plus mixtures consisting of equal proportions at the same total plant density as the monocultures, i.e., each experiment incorporated 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.

Five experiments were conducted as follows:

Effects of Timing of Emergence

In two similar experiments conducted in consecutive years, we examined the effect of varying the relative time of emergence of species on the dynamics of competition. Wheat cultivar Tatiara (an awnless biscuit cultivar) and oat cultivar Vasse were sown in monocultures and in mixtures. *Avena sativa* was chosen rather than a real weed to ensure reliability of emergence, minimal variation in growth rate, and synchronous development. In the first experiment, in 1998, oat was sown at the same time as the wheat (4 June) or on 7 July. In the second experiment, in 1999, the wheat was sown on 7 June and oat on 7 June, 16 June, 24 June, 5 July, and 12 July. In 1998, there were four replicates, whereas there were three replicates in 1999.

Effects of Different *Avena* Taxa

In a single experiment, we examined the effect of choice of oat taxon on the dynamics of competition. This was because previous work in the United Kingdom (UK) (Cousens et al., 1991) had used *A. fatua*, whereas in this work in Australia, we mostly used cultivated oat. The same wheat cultivar (Tatiara) as in the previous experiments was grown in replacement series with *A. sativa* L. cv. Vasse (a short-strawed cultivar), *A. strigosa* Schreb. cv. Saia (a tall cultivar), and the two species of wild oat common in crop fields in Australia [*A. fatua* L. and *A. sterilis* subsp. *ludoviciana* (Durieu) M. Gillet & Magne]. Both species of wild oat had been collected from the same field at Wongan Hills, Western Australia. One replicate was sown per day, from 12 to 14 June 2000.

Effects of Timing of Anthesis

In two similar experiments conducted in consecutive years, we examined the effects of timing of reproductive development on the dynamics of competition. Three lines of the wheat cultivar Gamenya differing in flowering date were grown in replacement series with oat cultivar Saia (in 1999) or with cultivar Vasse (in 2000). Sowing dates were 11 and 12 June 1999 and 1 and 2 June 2000. There were three replicates. This cultivar was not bred for local conditions and was thus not used in the other experiments.

Sampling Procedures

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. (There is no reason to expect that emergence would be any different in the mixture plots.) 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 measured 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 from daily maximum and minimum air temperatures above a base temperature of 0°C. Temperatures were recorded at an automatic weather station, approximately 500 m away.

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 data transformations were 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 other species, RP will maintain a value of 1.0; if species B has a greater effect on A than A does on itself, then the RP of A will fall below 1.0, and so on. [Relative performance is simply double the relative yield, which is calculated on a unit area basis (Harper, 1977).] Thus, we can plot the time course of competitive hierarchy between 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. It should be mentioned that the replacement-series design has received much criticism from some researchers (e.g., Snaydon, 1994; Gibson et al., 1999). The design is, however, entirely valid for the above purpose (Cousens, 1996b, 2000; Hoffman and Buhler, 2002) because it merely reports the effect of neighbor type on plant stature at the experimental density; no inferences are made about resource partitioning among species, the amounts of inter- and intraspecific competition, or the resulting long-term population dynamics.

RESULTS

Effects of Timing of Emergence

When the two species were sown at the same time in 1998, the biomass growth of oat was significantly less in mixture than in monoculture (Fig. 1). Wheat perhaps grew marginally better in mixture than in monoculture although the difference was mostly not significant. Hence, competition between the two species was somewhat one-sided. After the fourth sample date (approximately when the maximum number of tillers had been produced), the RP of wheat in mixture was consistently >1, whereas for oat, it was consistently <1 (Fig. 2a). There was no suggestion of a reversal of competitive hierarchy during the season; variation within the graphs is partly the result of sampling error. At maturity, there were few significant differences in yield components of wheat (Table 1) or size parameters of oat (Table 2). The one exception was that significantly fewer oat panicles were produced in mixture.

When oat was sown 33 d after wheat, its growth was suppressed considerably, whereas the wheat became considerably larger in mixture than in monoculture (Fig. 1). The response of wheat demonstrates that stands were dense enough for competition to occur within 85 d (570 GDD) of emergence. These trends can also be seen

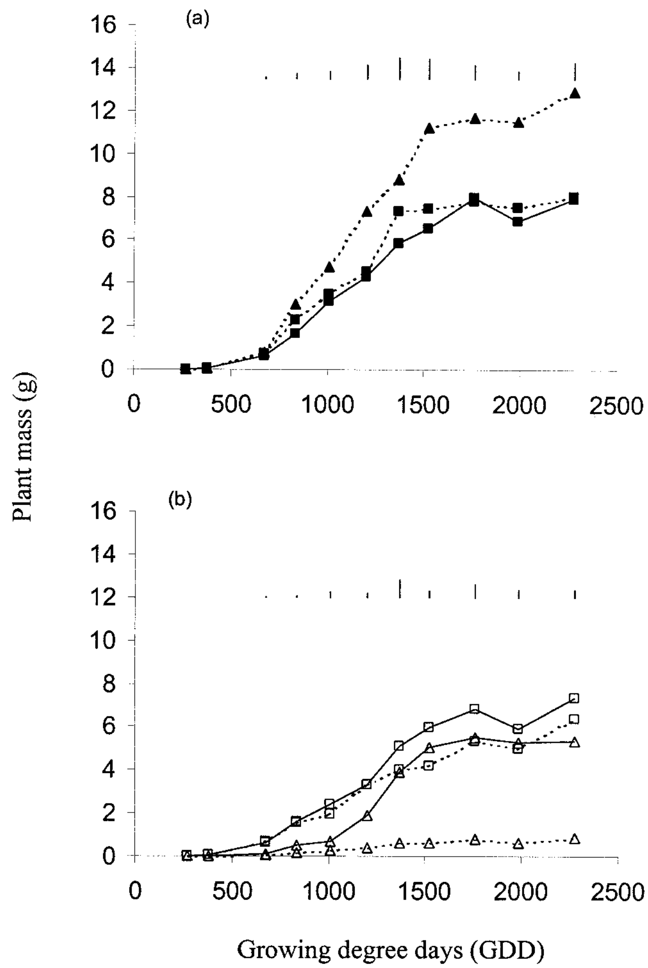

Fig. 1. Growth curves for (a) wheat cultivar Tatiara and (b) oat (*Avena sativa* cv. Vasse) grown in monocultures (solid lines) and mixtures (dashed lines) in 1998. The two species were sown either at the same time (■, □) or with oat sown 33 d after the wheat (▲, △). Growing degree days are calculated from the day of sowing and are above a base temperature of 0°C. Vertical lines show standard errors for each sample date.

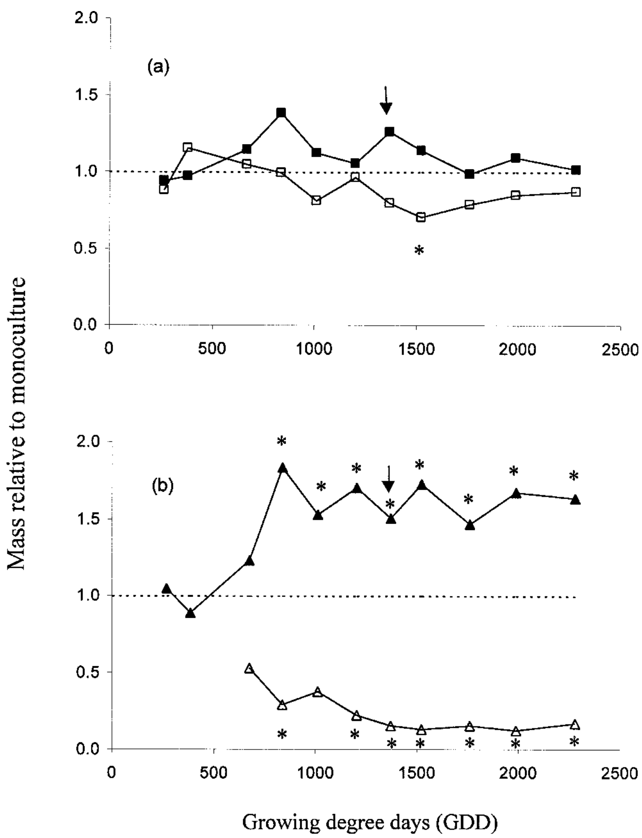

Fig. 2. Time courses of relative mass for (a) wheat cultivar Tatiara and oat (*Avena sativa* cv. Vasse) sown together and (b) oat sown 33 d after wheat in 1998. Wheat is shown as solid symbols and oat as open symbols. Arrows indicate dates of anthesis for wheat. Relative mass is defined as the mean mass of an individual plant of the *target* species in mixture divided by its mean mass in monoculture. See text for interpretation of values of relative performance, such as that calculated using plant mass. An asterisk by a symbol indicates that the plant mass in mixture was significantly different ($P < 0.05$) than in monoculture (i.e., relative mass differed from 1).

in the time courses of RP (Fig. 2b); the patterns were similar whether RP was expressed as biomass, leaf area, or tiller number. Again, the competitive hierarchy was established by the time of maximum tiller number, and the values of RP changed little thereafter. Competition had little effect on plant height, with the exception of

Table 2. Oat attributes for the two timing-of-emergence experiments.

	Final height	Panicles per plant	Plant mass
	cm		g
1998			
Monoculture (0)†	58.7	1.80	7.32
Mixture (0)	59.1	1.43	6.39
Monoculture (+33)	50.1	1.63	5.31
Mixture (+33)	33.6	0.98	0.87
SE	2.52	0.146	0.405
P for:			
Time of sowing	*<0.001*	*0.06*	*<0.001*
Monoculture vs. mixture	*<0.05*	*<0.01*	*<0.001*
Interaction	*<0.01*	*NS*	*<0.05*
1999			
Monoculture (0)	38.0	2.13	3.81
Mixture (0)	38.8	1.76	2.59
Monoculture (+9)	40.9	2.00	4.14
Mixture (+9)	37.7	1.42	2.36
Monoculture (+17)	38.4	1.85	3.28
Mixture (+17)	38.7	1.27	2.50
Monoculture (+28)	38.0	1.85	2.94
Mixture (+28)	29.8	1.27	1.28
Monoculture (+35)	34.5	2.15	2.96
Mixture (+35)	21.5	1.18	0.75
SE	1.68	0.194	0.468
P for:			
Time of sowing	*<0.01*	*NS*	*<0.05*
Monoculture vs. mixture	*<0.01*	*<0.001*	*<0.001*
Interaction	*<0.01*	*NS*	*NS*

† Number in parentheses indicates sowing date difference in days relative to wheat.

late-sown oat (Fig. 3). There was no obvious effect of competition on plant phenological development in either species.

By maturity, the largest proportional effects on wheat from a 33-d delay in sowing of oat was seen in the number of heads per plant and number of grains per head (Table 1), with no significant effect on the mean grain size. The mean number of oat panicles per plant was also reduced under competition, from 1.63 to 0.98 (i.e., no fertile tillers in mixture) when oat was sown late (Table 2).

When both species were sown on the same date in 1999, wheat grew significantly less well in mixture than in monoculture (Fig. 4). This suppression of wheat by oat started quite abruptly and at an early date (Fig. 5a); it was consistent across all replicates. Whereas wheat emerged 3 d ahead of oat in 1998, it emerged 1 d later than oat in 1999 (Table 3). Also in 1999, in monoculture,

Table 1. Components of wheat yield and other parameters for the two timing-of-emergence experiments.

	Final height	1000-grain weight	Heads per plant	Grains per head	Grain yield per plant	Plant mass	Harvest index
	cm	g			g	g	%
1998							
Monoculture	80.6	41.19	2.33	26.38	2.512	7.91	31.90
Mixture (oat at same time)	77.7	39.59	2.45	25.48	2.468	8.03	30.63
Mixture (oat + 33 d)	82.1	39.72	3.43	32.02	4.338	12.92	33.27
SE	1.48	0.464	0.190	1.726	0.366	0.800	1.965
P	*NS*	*0.09*	*<0.05*	*0.07*	*<0.05*	*<0.01*	*NS*
1999							
Monoculture	54.5	43.40	1.71	22.04	1.628	4.59	35.71
Mixture (oat same time)	46.3	44.47	1.27	13.23	0.729	2.01	36.40
Mixture (oat + 9 d)	49.1	40.97	1.56	16.96	1.101	2.76	40.24
Mixture (oat + 17 d)	52.5	44.98	2.00	20.50	1.743	6.07	32.02
Mixture (oat + 28 d)	54.5	42.94	3.00	20.90	2.661	8.08	33.43
Mixture (oat + 35 d)	57.0	42.60	2.91	26.75	3.238	8.12	39.87
SE	1.97	0.832	0.203	0.877	0.159	0.638	2.81
P	*<0.05*	*NS*	*<0.001*	*<0.001*	*<0.001*	*<0.001*	*NS*

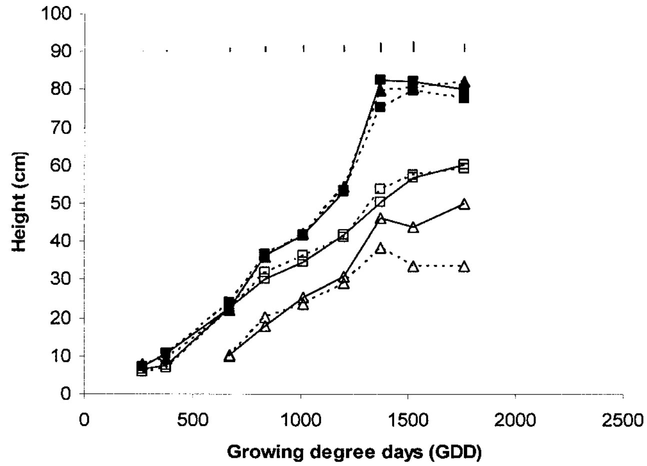

Fig. 3. Growth in height of wheat cultivar Tatiara (closed symbols) and oat (*Avena sativa* cv. Vasse—open symbols) in monoculture (solid lines) and mixtures (dashed lines) in 1998. The two species were either sown at the same time (■, □) or with oat sown 33 d after the wheat (▲, △). Vertical lines show standard errors for each sample date.

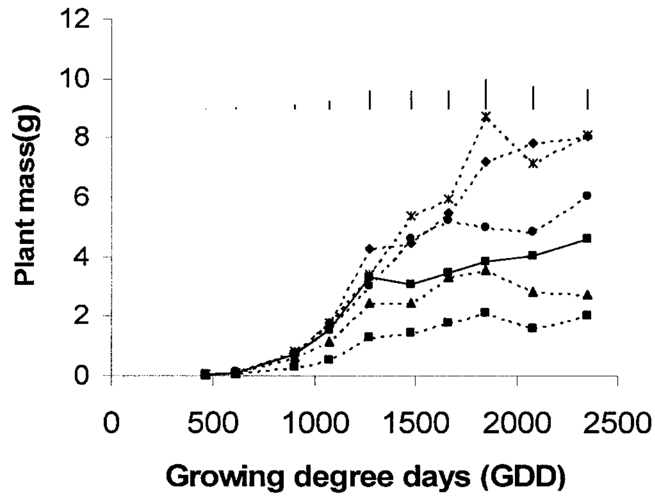

Fig. 4. Growth curves for wheat cultivar Tatiara grown in 1999 in monoculture (solid line) or in mixture (dashed lines) with oat (*Avena sativa* cv. Vasse) sown on the same day (■), 9 d (▲), 17 d (●), 28 d (◆), or 35 d (*) later than wheat. Vertical lines show standard errors for each sample date.

both oat and wheat had fewer heads and much lower final biomass than in 1998 (Tables 1 and 2). Successively later plantings of oat reduced the amount by which wheat was suppressed (Fig. 4). Linear interpolation between final yields from different times of sowing suggests that the growth of wheat in mixture and monoculture would have been equal (i.e., the two species would be equally competitive) had oat been sown 13 d after wheat. Oat would also have ceased to affect wheat had oat been sown 25 d after wheat. It is also noteworthy that the relative mass of both species was less than 1 for the two treatments in which the species were sown closest together. This indicates that they were unable to take full advantage of the available resources when in these mixtures.

Oat sown on the first date also appeared to grow slightly less well in mixture than in monoculture although this was only significant at maturity (Fig. 6). For later sowing dates, the suppression in mixture by wheat

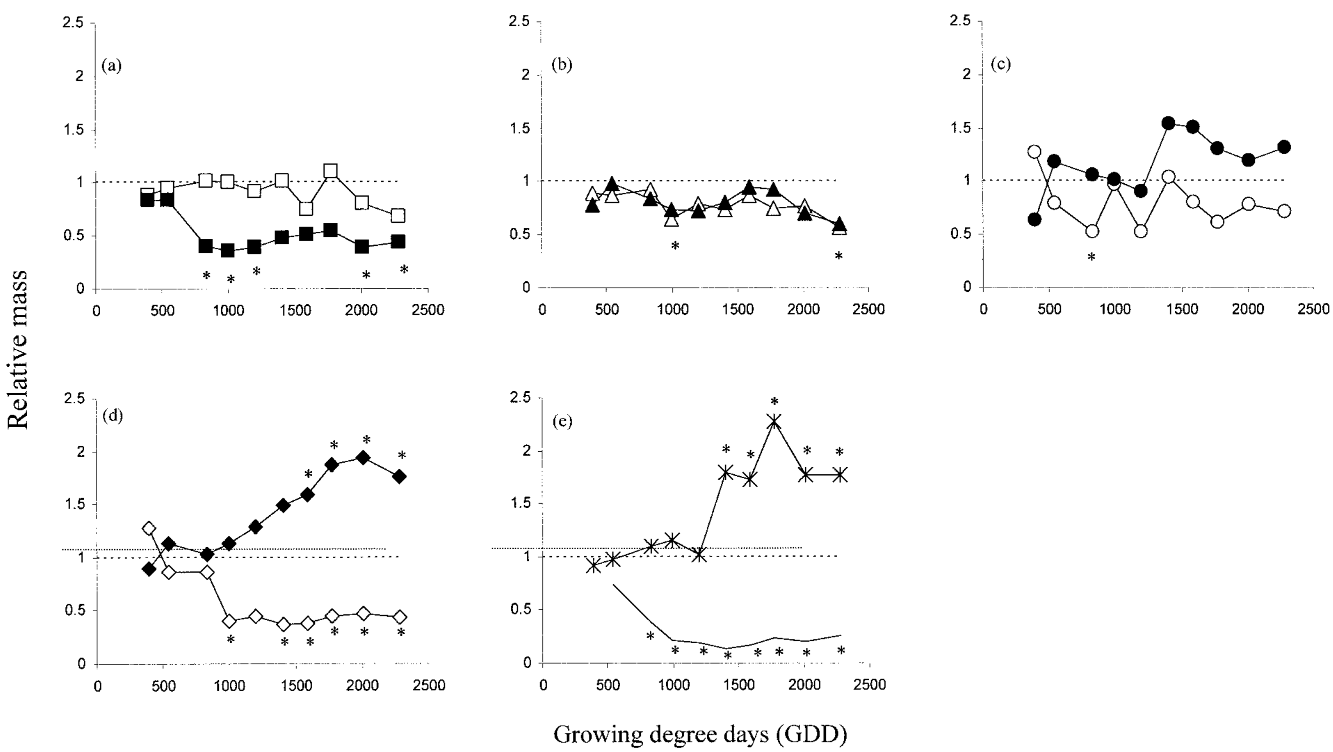

Fig. 5. Time courses of relative mass for wheat cultivar Tatiara and oat (*Avena sativa* cv. Vasse) (a) sown together or with oat sown (b) 9, (c) 17, (d) 28, or (e) 35 d after wheat in 1999. Wheat is shown as solid symbols and oat as open symbols [in (e), oat is shown without symbols]. An asterisk by a symbol indicates that the plant mass in mixture was significantly different ($P < 0.05$) than in monoculture (i.e., relative mass differed from 1).

Table 3. Durations of developmental stages for wheat and oat in the two timing-of-emergence experiments.

	1998		1999	
	Days	GDD†	Days	GDD
Sowing—50% emergence				
Wheat	15	133	17	162
Oat (sown with wheat)	18	159	16	144
Oat (sown 9 d after wheat)	–‡	–	17	162
Oat (sown 17 d after wheat)	–	–	14	133
Oat (sown 28 d after wheat)	–	–	17	185
Oat (sown 33 d after wheat)	17	123	–	–
Oat (sown 35 d after wheat)	–	–	16	169
Sowing—50% anthesis§				
Wheat monoculture	139	1370	121	1273

† Growing degree days (GDD) are calculated from sowing and are above a base of 0°C.
‡ Treatments marked by a dash were not included in that year.
§ Anthesis was not recorded for oat.

became increasingly pronounced. Reversal of competitive hierarchy did not occur part of the way through the season for any of the sowing dates (Fig. 5). As in 1998, wheat was taller than oat throughout growth for all sowing dates. When wheat and oat were sown on the same date, the height of wheat was suppressed in mixture from anthesis onwards; oat height was significantly suppressed in mixture when sown 28 and 35 d after wheat, in both cases from the five- to six-leaf stage of the wheat onwards.

Effects of Different *Avena* Taxa

There were significant differences among *Avena* taxa in monoculture, both for height and biomass. *Avena sativa* cv. Vasse plants were the heaviest throughout development (Fig. 7). *Avena strigosa* began as one of the lightest and shortest taxa but gained in the later stages to finish tallest (Fig. 8). *Avena fatua* and *A. sterilis* were similar in their patterns of growth. There was no effect of competition on plant height; all taxa except *A. sativa* were taller than wheat after about 1300 GDD. The only significant effect of wheat competition on *Avena* spp. plant weight was for *A. strigosa*, which grew better in monoculture than in mixture during the later stages of development (Fig. 9). There were no significant differences in the growth of wheat in mixture among the different oat taxa although when pooled across the last three harvests, the level of significance was 0.08. Throughout growth, the mean dry weight of wheat in mixtures was largest when growing with *A. strigosa*, whereas it was least in mixtures with *A. fatua* and *A. sterilis*.

Graphs of RP show few differences between the taxa (Fig. 9). Only the *A. strigosa* mixtures show development of competitive hierarchy, with wheat becoming more competitive than oat. Despite its late burst of growth in height and biomass, *A. strigosa* was unable to narrow the gap in competitiveness between it and wheat when growing in mixture.

Effects of Timing of Anthesis

The three Gamenya wheat lines had a very narrow range of times of flowering under field conditions, spanning only 6 d. Patterns of height development were, as a result, not significantly different among the lines. In 1999, wheat was considerably taller than *A. strigosa* during most of growth but was overtopped at the final

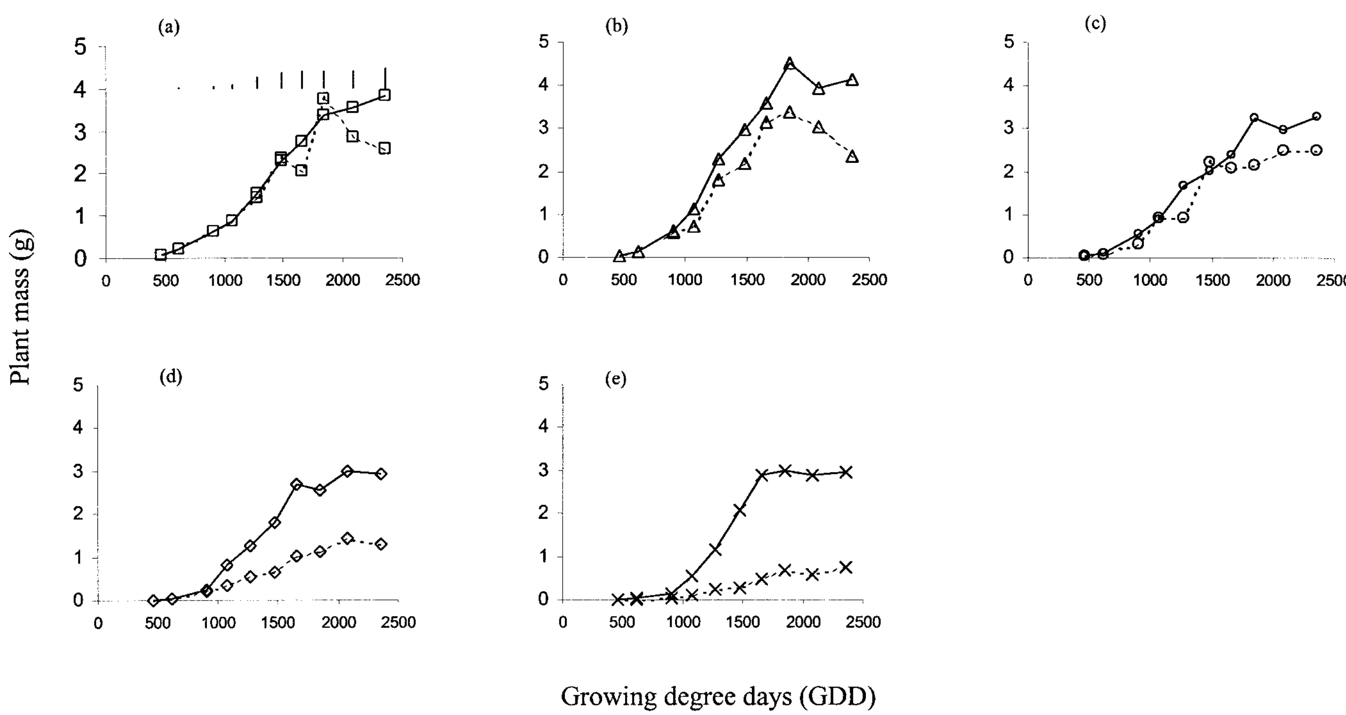

Fig. 6. Growth curves for oat (*Avena sativa* cv. Vasse) grown in 1999 in monoculture (solid line) or in mixture (dashed lines) with wheat cultivar Tatiara where oat was sown (a) on the same day or (b) 9, (c) 17, (d) 28, or (e) 35 d later than wheat. Vertical lines show standard errors for each sample date.

two harvests (Fig. 10a). In 2000, wheat was only marginally taller than *A. sativa* during early growth and increased this height advantage later (Fig. 10b). Wheat grew significantly better in mixture with oat in 1999 than in monoculture, whereas oat was suppressed considerably. This was reflected in a rapid separation of the RP of the two species (Fig. 11a). In 2000, there were no significant differences in growth of either species in monoculture and mixture and hence similar patterns in RP (Fig. 11b). The difference in RP between the 2 yr (confounded with oat taxa) was greater than that found between taxa within a single year (Fig. 9).

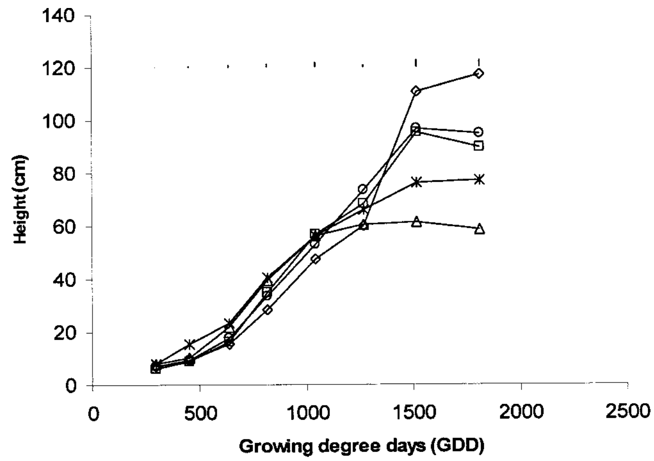

Fig. 8. Growth in height of wheat cultivar Tatiara (*) and *Avena* species in monoculture in 2000: *A. fatua* (□), *A. strigosa* cv. Saia (◇), *A. sterilis* (○), and *A. sativa* cv. Vasse (△). Vertical lines show standard errors for each sample date.

DISCUSSION

These experiments have given clear answers to at least some of the questions posed earlier in the paper while they lead to further testable hypotheses for others.

Are the Same Patterns Found in Temperate and Mediterranean Cropping Systems?

In a previous study of competition between *A. fatua* and both a winter wheat and a winter barley in the UK, reversals or cessation of competitive superiority were recorded at two sites differing in soil type and climate (Cousens et al., 1991). In the present Australian study, there was no clear evidence of such dynamics: Once set, a competitive hierarchy established during early growth was maintained. There are a number of reasons for differences between the two studies. Clearly the envi-

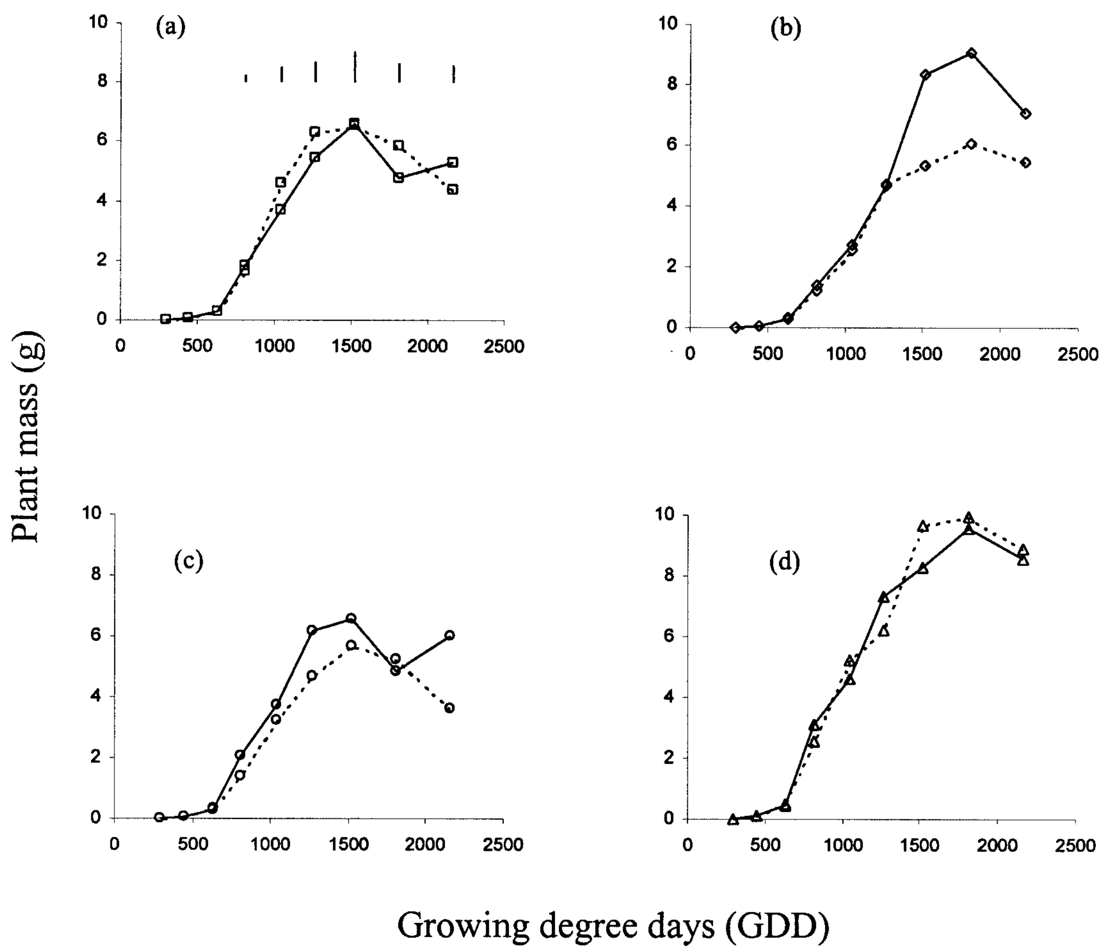

Fig. 7. Growth curves for *Avena* species grown in monoculture (solid lines) or in mixture (dashed lines) with wheat cultivar Tatiara in 2000: (a) *A. fatua*, (b) *A. strigosa* cv. Saia, (c) *A. sterilis*, and (d) *A. sativa* cv. Vasse. Vertical lines show standard errors for each sample date.

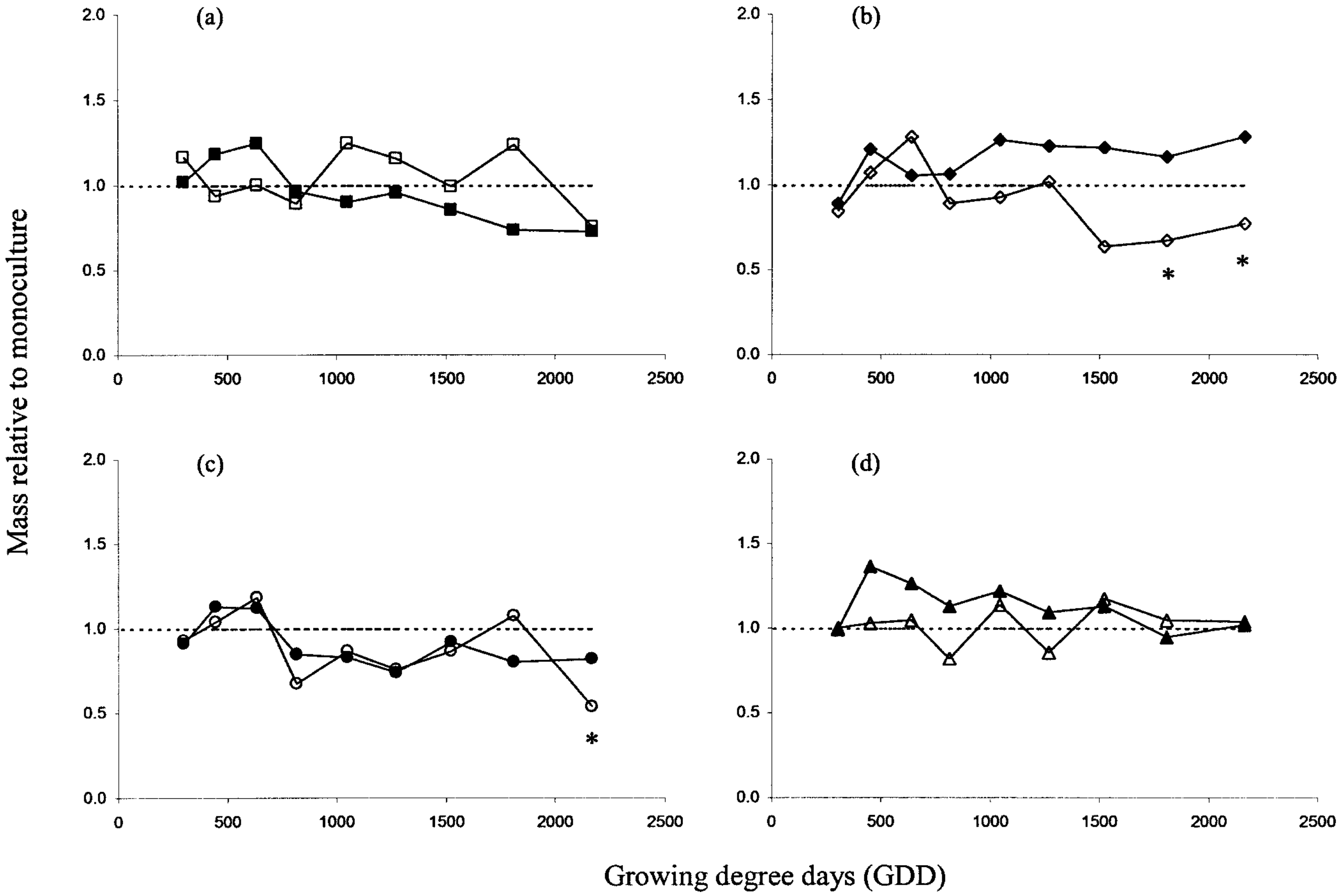

Fig. 9. Time courses of relative mass for wheat cultivar Tatiara and *Avena* species in 2000: (a) *A. fatua*, (b) *A. strigosa* cv. Saia, (c) *A. sterilis*, and (d) *A. sativa* cv. Vasse. Wheat is shown as solid symbols and *Avena* spp. as open symbols. An asterisk by a symbol indicates that the plant mass in mixture was significantly different ($P < 0.05$) than in monoculture (i.e., relative mass differed from 1).

ronments differ: Nutrient and water availability in the UK were almost certainly greater. This would have led to more intense competition for light. If an initially poor competitor, such as a species with small seeds and hence small plants, is to *overtake* a better competitor, it must have some positive advantage later during growth. In the water-limited environment of Australia, little water is left after anthesis, thus making it difficult for any species to take advantage from traits that convey greater superiority later on for any resource.

One of the hypothesized reasons for changeovers in competitive hierarchy was the relative patterns of height growth of the species: In the UK, the *A. fatua* canopy overtopped the wheat in the later stages of development. If competition for light is less important in the Australian study, then mechanisms associated with height will be of lesser importance. The oat cultivar (*A. sativa* cv. Vasse) was consistently shorter than wheat, making it less likely that a reversal of competitive hierarchy would occur and indirectly supporting the height development hypothesis to explain the results from the UK study. However, even where there was a late reversal in height advantage in the Australian study (*A. strigosa*, Fig. 8), there was no reversal of competitive hierarchy. The interaction between height development and resource availability will be examined further in experiments using genotypes of contrasting height in which resource supply is also varied (Cousens et al., 2003).

Are the Differences between Studies caused by the *Avena* Taxa Used?

Of necessity, the Australian study used *A. sativa* for the staggered sowing experiments, whereas the UK study used *A. fatua*. However, there are often differences in growth and development between populations of *A. fatua* (Thurston, 1957; Whalley and Burfitt, 1972), and the generality of the previous study needed to be examined with different material. The importance of oat genotype was assessed in a single experiment by comparing four species of *Avena*, including three hexaploids and one tetraploid. *Avena strigosa* was clearly less competitive than wheat and the other *Avena* species, despite stronger late biomass growth than *A. fatua* and *A. sterilis* (Fig. 7) and a late burst of height extension (Fig. 8). *Avena fatua*, *A. sterilis*, and *A. sativa* resulted in similar dynamics in competition, again with no clear patterns of reversal of competitive hierarchy. Although not conclusive, the fact that similar dynamics were found in morphologically very different taxa in Australia suggests that the use of *A. fatua* in the UK may not be responsible for the reversals in competitive hierarchy found only in that study.

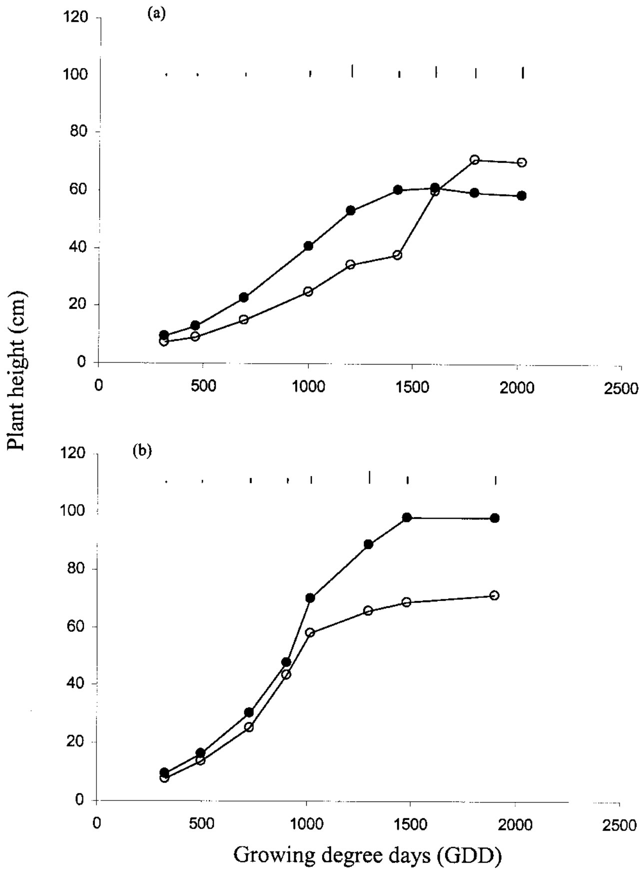

Fig. 10. Growth in height of wheat cultivar Gamenya (closed symbols) and oat (open symbols) in (a) 1999 and (b) 2000. Data are averaged over three wheat lines differing in flowering date and over both monoculture and mixture. Oat was *Avena strigosa* cv. Saia in 1999 and *A. sativa* cv. Vasse in 2000. Vertical lines show standard errors for each sample date.

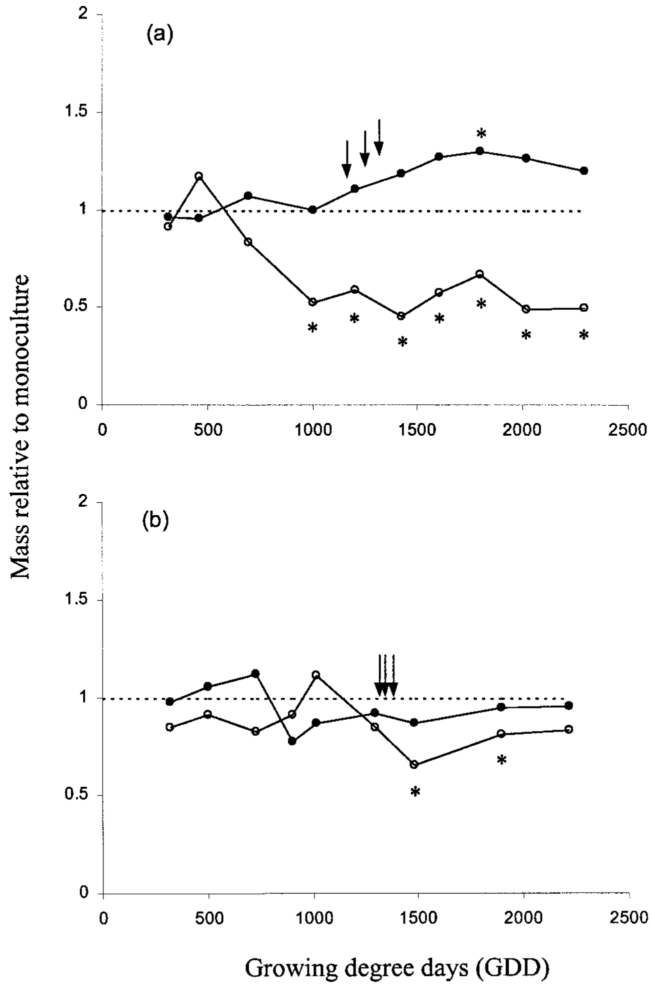

Fig. 11. Time courses of relative mass for lines of wheat cultivar Gamenya, averaged over three lines differing in flowering date (times of anthesis are shown by arrows), in comparison with (a) *Avena strigosa* cv. Saia in 1999 and (b) *A. sativa* cv. Vasse in 2000. Wheat is shown as solid symbols and *Avena* spp. as open symbols. An asterisk by a symbol indicates that the plant mass in mixture was significantly different ($P < 0.05$) than in monoculture (i.e., relative mass differed from 1).

Does the Timing of the Reversal of Competitive Hierarchy Change if the Phenological Development of the Species is Staggered?

At the conclusion of the UK study, it was suggested that changing the time of emergence of the species would move the time at which the crossover in competitive hierarchy occurred. As discussed above, no competitive hierarchy reversal was seen in the Australian study. Hence, delay in emergence of one competitor merely made it less competitive. The importance of relative time of emergence of competitors in the determination of crop yield loss has been shown on numerous occasions (e.g., Cousens et al., 1987; Lotz et al., 1996; Håkansson, 1997). An 8- or 9-d shift in time of emergence made a considerable difference as to which species dominated (Fig. 5).

In contrast, a 6-d difference in time of anthesis had no detectable effect on the dynamics of competition (Fig. 10). Delay of sowing immediately puts a plant at a disadvantage in competition because it will have less leaf area, root development, and height than neighboring plants. Delay in flowering has little or no effect on early growth and hence does not affect early capture of resources. However, it might have a greater effect in a system where there is considerable late competition. Although different wheat genotypes were used in the staggered sowing date and the time-of-anthesis experiments, the lack of influence of flowering date was maintained in two year–*Avena* species experiments. This is further evidence to reject the hypothesis that the UK results were due to relative timing of phenological events in favor of a mechanism involving relative patterns of height growth under conditions of strong competition for light.

Competition between plants in this study was clearly intense, as shown by the considerable suppression of late-emerging plants and the consequently greater growth of the early emerging species in mixtures. This competition begins quite early, as has been shown previously for wild oat and wheat (Chancellor and Peters, 1974). However, in most cases, the RP of plants (as measured by the ratio of mass in mixture to that in monoculture) remained constant throughout most of later growth, indicating that either later competition was not occurring or that it was not amplifying the early differences established in plant size. This appears to be in contrast to other studies in Western Australia in which late competition can be considerable (S. Mokhtari and C. Zaicou, personal communication, 1995). It must be appreciated, however, that our studies involved plants spaced out on a grid. Under conditions of low rainfall and high early competition, perhaps lateral root growth is limited, and this restricts later competition. This might not be the same in additive competition experiments or where competitors are placed at random because on average some weed plants will be in very close proximity to crop plants; hence, competition may extend later. The extent of late competition in replacement-series experiments could be examined by time-of-removal studies: To our knowledge, time-of-removal studies have almost exclusively been applied to additive experimental designs.

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