

PUBLISHED VERSION

Lemerle, D.; Cousens, R. D.; Gill, Gurjeet Singh; Peltzer, S. J.; Moerkerk, M.; Murphy, C. E.; Collins, Deborah Jane; Cullis, B.

[Reliability of higher seeding rates of wheat for increased competitiveness with weeds in low rainfall environments](#), *Journal of Agricultural Science*, 2004; 142:395-409.

Copyright © 2004 Cambridge University Press

PERMISSIONS

<http://journals.cambridge.org/action/stream?pageld=4088&level=2#4408>

The right to post the definitive version of the contribution as published at Cambridge Journals Online (in PDF or HTML form) in the Institutional Repository of the institution in which they worked at the time the paper was first submitted, or (for appropriate journals) in PubMed Central or UK PubMed Central, no sooner than one year after first publication of the paper in the journal, subject to file availability and provided the posting includes a prominent statement of the full bibliographical details, a copyright notice in the name of the copyright holder (Cambridge University Press or the sponsoring Society, as appropriate), and a link to the online edition of the journal at Cambridge Journals Online. Inclusion of this definitive version after one year in Institutional Repositories outside of the institution in which the contributor worked at the time the paper was first submitted will be subject to the additional permission of Cambridge University Press (not to be unreasonably withheld).

10th December 2010

<http://hdl.handle.net/2440/142>

Reliability of higher seeding rates of wheat for increased competitiveness with weeds in low rainfall environments

D. LEMERLE^{1,2*}, R. D. COUSENS^{1,3}, G. S. GILL^{1,4}, S. J. PELTZER^{1,5}, M. MOERKERK⁶,
C. E. MURPHY^{1†}, D. COLLINS⁷ AND B. R. CULLIS²

¹Co-operative Research Centre for Weed Management Systems

²Wagga Wagga Agricultural Institute, NSW Agriculture, PMB, Wagga Wagga, NSW 2650, Australia

³School of Resource Management, Institute of Land and Food Resources, The University of Melbourne, Victoria 3010, Australia

⁴School of Agriculture and Wine, The University of Adelaide, Roseworthy, SA 5371, Australia

⁵Agriculture Western Australia, 444 Albany Highway, Albany 6330, Australia

⁶Department of Primary Industries, Victorian Institute of Dryland Agriculture, Private Bag 260, Horsham, Victoria 3401, Australia

⁷Elizabeth Macarthur Agricultural Institute, Woodbridge Road, Menangle NSW 2568, PMB 8 Camden 2570, Australia

(Revised MS received 1 September 2004)

SUMMARY

Increasing crop competitiveness using higher seeding rates is a possible technique for weed management in low input and organic farming systems or when herbicide resistance develops in weeds. A range of wheat seeding rates were sown and resulted in crop densities between 50–400 plants/m² (current recommendations are 100–150 plants/m²) in the presence and absence of annual ryegrass (*Lolium rigidum* Gaud.) in three wheat cultivars at nine experiments in southern Australia. Wheat densities of at least 200 plants/m² were required to suppress *L. rigidum* and to a lesser extent increase crop yield across a wide range of environments (seasonal rainfall between 200–420 mm) and weed densities (50–450 *L. rigidum* plants/m²). Doubling crop density of all cultivars from 100 to 200 plants/m² halved *L. rigidum* dry weight (averaged over all experiments) from 100 g/m² to about 50 g/m². Higher crop densities gave diminishing marginal reductions in weed biomass, while cultivar differences in weed suppression were small. Grain yields ranged from 0.5 t/ha to over 5 t/ha depending on site and season. Maximum yields in the weed-free plots (averaged over environments and cultivars) were at 200 crop plants/m², and yield declined only slightly by 4–5% at densities up to 425 plants/m². In the weedy plots grain yield continued to increase up to the highest density but at a slower rate. The percentage yield loss from weed competition was of a smaller magnitude than the suppression of *L. rigidum* by wheat. For example, 100 wheat plants/m² led to an average 23% yield loss compared with 17% at 200 plants/m², and the probability of reduced crop grain size and increased proportion of small seeds was negligible at these densities. Cultivar differences in yield loss from weed competition were small compared with differences due to crop density. Adoption of higher wheat seed rates as part of integrated weed management is now strongly promoted to farmers.

INTRODUCTION

Weed management systems that rely heavily on herbicides are now accepted as unsustainable. The

widespread herbicide resistance in annual ryegrass (*Lolium rigidum* Gaud.) in Australia, for example, has forced a reconsideration of a range of non-chemical and cultural ways to reduce weed impacts. Such techniques are also required for low-input and organic farming systems. These methods may reduce weed impacts in the current year or, through reduction in weed survival, fecundity or seed rain, reduce populations in

* To whom all correspondence should be addressed.
Email: deirdre.lemerle@agric.nsw.gov.au

† Present address: Office of Gene Technology Regulator, PO Box 100 Woden ACT 2606, Australia.

future crops. Several such approaches to weed and crop management involve increasing the ability of the crop canopy to compete with the weed (reviews by Jordon 1993; Lemerle *et al.* 2001*a*; Mohler 2001). Crop competitiveness can be measured in two ways: as weed suppression; or as the ability of the crop to tolerate weed presence and maintain grain yield (see also Goldberg 1990). These two attributes are often (Lemerle *et al.* 1996), but not necessarily correlated (Lemerle *et al.* 2001*b*). Considerable attention has been given to the use of wheat cultivars with good competitiveness around the world, including Australia (Reeves & Brooke 1977; Lemerle *et al.* 1995; Cousens & Mokhtari 1998; Lemerle *et al.* 2001*b*), and modern semi-dwarf cultivars are less competitive than the older types (Lemerle *et al.* 1996). The potential of breeding for traits associated with competitiveness has also been examined (Lemerle *et al.* 1996; Rebetzke & Richards 1999; Mokhtari *et al.* 2002). Current cultivars may differ considerably in their competitive ability. For example, at a wheat density of 150 plants/m², Lemerle *et al.* (1995) recorded yield losses of 20–40% in strongly and weakly competitive cultivars, respectively. Although some cultivars may be consistently good competitors, there can be considerable variation between sites and years (Cousens & Mokhtari 1998; Lemerle *et al.* 2001*b*), making reliable recommendations about Australian cultivar competitiveness difficult.

Competition is the result of uptake of limited resources. By increasing crop seeding rate, and consequently crop plant density, the crop population as a whole will access an increasing amount of the available resources (Weiner *et al.* 2001), even though it may mean that individual plants are smaller. This conclusion is supported by many field studies that show increased wheat competitiveness with weeds at higher crop densities, for example in the UK (Moss 1985; Korres & Froud-Williams 1997), Denmark (Doll *et al.* 1995) and USA (Barton *et al.* 1992; Hashem *et al.* 1998).

Benefits of increased seed rate for weed competition have also been identified in Australia in a limited number of environments. In the southern winter-dominant, low-rainfall zone (where yields are generally dependent on growing season rainfall) recommended seeding rates are 50–75 kg/ha, equivalent to 100–150 plants/m² (McRae *et al.* 2003). Medd *et al.* (1985) found that increasing seeding rate from 75–200 plants/m² reduced biomass of the weed *L. rigidum* and increased wheat grain yield. When the crop seeding rate of ten wheat genotypes was doubled from 55 to 110 kg/ha (130 to 200 plants/m²), *L. rigidum* biomass was reduced by 43%, while crop yield loss was only slightly reduced (Lemerle *et al.* 1996). In the northern grain region, wheat densities up to 150 plants/m² were required to reduce seed production of *Avena* spp. and *Phalaris paradoxa* (Radford *et al.* 1980; Martin *et al.*

1987; Walker *et al.* 2002). Economic benefits of increased wheat density have also been demonstrated. Murphy *et al.* (2002) showed that increasing wheat density from 50 to 200 plants/m² in the presence of 200 *Avena* spp. plants/m² improved the annual crop gross margin from A\$220/ha to A\$402/ha.

As with the choice of crop cultivar to increase competitiveness, an increase in crop seeding rate needs to achieve a reliable, sizeable positive outcome for the farmer. Although theoretical studies and field studies may indicate that increases in seeding rate will consistently give positive advantages, many growers remain sceptical. Possible risks include lodging, increased incidence of disease, and reduced grain quality. Increased seeding rate increases the costs of sowing, through the cost of seed and the number of times required to fill up the seed drill. The perception that high crop seeding rates result in yield decline and poor grain quality has prevented widespread adoption in Australia and other countries. However, Anderson & Barclay (1991) found that, in the southern Australian environment under weed-free conditions, increases in wheat density from 50–200 plants/m² gave substantial gains in grain yield without any evidence of yield decline at the highest densities. Turner *et al.* (1994) also showed that a wheat crop grown at 200 plants/m² reached anthesis up to 20 days earlier than a crop grown at 25 plants/m², resulting in reduced moisture stress during grain filling and higher grain yield and lower screenings. Evidence from the northern zone indicates a reduction in grain yield with increasing plant density in treatments with inadequate stored moisture at planting (Fawcett 1964). In the presence of weeds, Medd *et al.* (1985) found a 10–15% reduction in average grain size as wheat density increased from 75 to 200 plants/m², and Walker *et al.* (2002) in Queensland found an even smaller percentage reduction in grain size as wheat density increased from 50 to 150 plants/m².

A number of issues therefore need to be clarified if reliable recommendations are to be made about increasing crop seeding rates for better competition with weeds. How much further do densities need to be increased in order to obtain a cost-effective increase in crop yield while at the same time minimizing the risk of reduction in grain quality? How much weed suppression will such densities achieve? How reliable is this, in terms of variability across sites and over time? To address such questions, experiments were conducted in a wide variety of low-rainfall cropping systems across southern Australia over 2 years.

MATERIALS AND METHODS

Experimental design

A series of nine linked multi-environment experiments were conducted in 1997 and 1998 over the four

Table 1. Site details, experimental design and ryegrass (*Lolium rigidum*) emergence in all experiments

Site codes	Location and State	Coordinates	Soil type	Year	Cultivars	Experimental design	Growing season rainfall (mm) April–November	Sowing date	<i>Lolium rigidum</i> density (plants/m ² (s.e.))
(a) NSW97	Wagga Wagga, New South Wales	35°07'S 147°18'E	Red-brown earth	1997	Janz, Pulsar, Trident	Split-plot	282	6 June	336 (38)
(b) NSW98				1998	Janz, Pulsar, Trident, Dollarbird	Split-plot	421	19 May	325 (14)
(c) VIC(A)97	Walpeup, Victoria	35°08'S 142°01'E	Deep sandy loam	1997	Janz, Pulsar, Trident	Strip-plot	199	19 June	78 (13)
(d) VIC(B)97	Dooen, Victoria	36°41'S 142°21'E	Self-mulching grey clay	1997	Janz, Pulsar, Trident	Strip-plot	242	10 June	47 (12)
(e) VIC(B)98				1998	Janz, Pulsar, Trident, Dollarbird	Strip-plot	314	17 June	461 (61)
(f) SA97	Roseworthy, South Australia	34°33'S 138°42'E	Solonchized brown soils	1997	Janz, Pulsar, Trident	Modified strip-plot	290	17 May	300 (10)
(g) SA98				1998	Janz, Pulsar, Trident, Dollarbird	Strip-plot	251	27 May	251 (12)
(h) WA(A)97	Wongan Hills, Western Australia	30°51'S 116°44'E	Deep sand	1997	Janz, Pulsar, Trident, Amery, Westonia	Strip-plot	257	18 June	230 (42)
(i) WA(B)98	Newdegate, Western Australia	33°07'S 118°50'E	Duplex, sand over ironstone	1998	Janz, Pulsar, Trident, Dollarbird, Westonia	Strip-plot	219	16 June	450 (87)

states of New South Wales (NSW), South Australia (SA) and Western Australia (WA) and Victoria, VIC (two sites in 1997). Experimental identifiers and characteristics are presented in Table 1. The field layout was either a split-plot or strip-plot randomized complete block design for ease of sowing. In a split-plot, sub-unit treatments are randomized independently within each unit, whereas in a strip-plot treatments are arranged in strips across each replication (Cochran & Cox 1957). In this case, the wheat crop was sown at right angles to the weed treatments, with factorial combinations of wheat cultivar × wheat seeding rate treatment randomly assigned to the rows of each block and weed presence/absence assigned to the columns of each block.

Three factors defined factorial treatment structure: wheat seeding rate, wheat cultivar, and weed presence/absence. Seeding rates of 25, 50, 100, 150 and 200 kg/ha were used in each experiment. Six cultivars with similar maturities were used in various combinations across the experiments, with Janz, Pulsar, and Trident being common to all. These cultivars were included because Trident is broadly adapted to a range of environments, Janz is poorly competitive and Pulsar is strongly competitive (Lemerle *et al.* 2001 *b*). The other cultivars were Dollarbird, Amery and Westonia and were only included in a limited number of experiments. For all experiments, the cultivars were derived from a single common seed supply.

Seeds of *L. rigidum* were scattered by hand after crop sowing and then raked in. All experiments had three replicates, except SA97 which had four. At several experiments extra weed treatments were included (*Raphanus raphanistrum* in WA97 and *Brassica napus* in NSW97 and NSW98), but because these were only in restricted environments the results were not of interest in this study.

The crop was sown using the machinery available at the site and with a standard fixed row spacing of approximately 18 cm (standard farmer practice) for all seeding rates. Sowing dates were 'mid-season' according to each site. All other farming operations, such as cultivations and fertilizers, were according to local site practice. Plot size averaged 2 × 8 m but varied slightly between experiments. The *L. rigidum* used at each site was a biotype adapted to the particular area; thus genotype × environment interactions could not be determined because site and biotype were confounded. This decision was made because of the considerable geographic differences in *L. rigidum* life history. A plant density of around 300 seedlings/m² was achieved by sowing *L. rigidum* at 10 kg/ha. The actual densities varied considerably between experiments and ranged from quite low densities (around 50 plants/m²) to over 450 plants/m² (Table 1). Rainfall was generally higher in 1998 in NSW and VIC, while in WA and SA more rain occurred in 1997 (Table 1).

Severe crop lodging during grain-filling and grain shedding at maturity occurred in Dollarbird and Pulsar in NSW in 1998.

Measurements

The *L. rigidum* plant density was measured at each experiment within 4–6 weeks of sowing by counting seedlings in five (0.01 m²) random quadrats per plot. The number and the size of each quadrat taken to determine wheat plant density varied across experiments from three to six quadrats and from 0.08 to 0.18 m², and at most experiments only the weed-free plots were sampled. The dry weight of *L. rigidum* was assessed destructively in quadrats (generally 2 × 0.185 m² per plot) at crop anthesis at six experiments. Crops were harvested by small-plot machinery at all experiments. Screenings (proportion of small grain) were assessed at six experiments by passing grain over a 2 mm slotted sieve. The 1000-grain weight, an estimate of mean grain size, was determined at four experiments for the retained grains.

Statistical analyses

All analyses were performed using ASREML, a mixed model analysis program (Gilmour *et al.* 2002).

Wheat plant density

In deriving a regression relation between crop grain yield (or *L. rigidum* dry weight) and crop plant density, it should be noted that crop density is measured with error; if not corrected, a (negative) bias in the regression will result (Fuller 1987). A *regression calibration* approximation technique (Carroll 1998) was used, where the regressor variable (in this case, crop density) is ‘corrected’ before proceeding to the regression analysis. For linear and log-linear regression models, this technique is often exact, except for a change in intercept (Carroll 1998, p. 20). For each experiment, the regression calibration technique was employed by fitting a mixed linear model to the quadrat crop densities:

$$\text{density} \sim \text{seedrate} * \text{cultivar} * \text{weed} + \{ \textit{design stratum} \} + \textit{plot} + \textit{error}$$

where the italicized terms are random effects, and residual error in this case is the measurement error. ‘Seedrate’, ‘cultivar’, ‘weed’ and ‘plot’ are factors representing the effects of seeding rate, cultivar, weed treatment and plots respectively, and the asterisk represents all main effects and interactions. The symbol text in the above formula ‘{*design stratum*}’ comprises the factors necessary to create the strata implied by the design at each experiment. The corrected crop density is the predicted crop density from this model.

The use of regression calibration should provide more robust estimates of crop density per plot than simply averaging the quadrat measurements. For instance, variation in these simple averages may be, in large part, attributable to spurious measurement error. Combining similar plots to form the broader average crop densities (e.g. plots with the same seeding rate and cultivar) could ‘average out’ measurement error, but in the process may discard too much information and be inefficient. The corrected crop densities will lie between the quadrat average and a broader ‘average’ crop density across similar plots. If plot variation is small in relation to measurement error, most of the variation between plots is probably measurement error, and so the corrected crop densities will be closer to the broader averages. Conversely, if the plot variation is relatively large, corrected crop densities will be closer to the individual quadrat averages.

For SA98, individual quadrat data were not available, so the estimates of plot and measurement error variance from the SA97 analyses were used.

Grain yield or L. rigidum dry weight-crop density relationship

For these two responses, a multi-site mixed model cubic smoothing spline analysis was used (Verbyla *et al.* 1999). The use of non-parametric regression, via cubic smoothing splines, enables the fitting of non-linear relations without necessitating assumptions on the shape of the relation. This method incorporates the splines into a mixed model framework, enabling their use in combination with other design and treatment factors in complex experiments. After preliminary inspection of the data, knot points for the density spline were chosen to be 27, 50, 100, 200, 300, 400, 500, 600 and 679 plants/m². For weedy or weed-free plots, the symbolic representation of the yield model was:

$$\begin{aligned} \text{yield} &\sim \text{cultivar} * \text{weed} * \text{lin}(\text{density}) \\ &+ \text{expt} * \text{lin}(\text{density}) \\ &+ \text{cultivar} * \text{weed} * \text{spl}(\text{density}) \\ &+ \text{expt} * \text{cultivar} * \text{weed} * (\text{lin}(\text{density}) \\ &+ \text{spl}(\text{density})) \\ &+ \{ \textit{design stratum} \} + \textit{error} \end{aligned}$$

where the asterisks indicate all main effects and interactions. Random components are shown in italics. The linear and non-linear (spline) effects of crop density are denoted ‘lin(density)’ and ‘spl(density)’ respectively. ‘Weed’ is a factor representing weed presence/absence. ‘Expt’ and ‘cultivar’ are factors representing the effects of experiment and cultivar respectively. The *design stratum* component comprises factors that are necessary to create the strata inferred by design at each experiment.

For *L. rigidum* dry weight, a square root transformation was necessary to correct a mean-variance relation. The symbolic representation of the model fitted to the weedy plots was, using the same notation as the yield model above:

$$\begin{aligned} \text{sqrt}(\text{rdrw}) \sim & \text{cultivar} * \text{lin}(\text{density}) \\ & + \text{expt} * \text{lin}(\text{density}) \\ & + \text{cultivar} * \text{spl}(\text{density}) \\ & + \text{expt} * \text{cultivar} * (\text{lin}(\text{density})) \\ & + \text{spl}(\text{density}) + \{\text{design stratum}\} + \text{error}. \end{aligned}$$

In each model, the residual error at each experiment was modelled as a separable autoregressive process of order 1 (Gilmour *et al.* 1997). Crop density was rescaled to have a mean value of zero to improve interpretability of terms not involving crop density and the stability of the estimation process of the parameters. A correlation was also fitted between the corresponding random coefficient terms (e.g. between *cult.expt* and *cult.expt.lin(density)* and between *weed.expt* and *weed.expt.lin(density)* of Table 2). Although the yield-density relation was not of interest for the additional weed treatments (*R. raphanistrum* and *B. napus*), these data were retained to preserve the spatial integrity of each experiment. Similarly, the data for the weed-free plots were also retained in the *L. rigidum* dry weight model. For these plots a saturated model, which did not involve modelling the density response, was used, comprising all interactions of experiment, cultivar, weed and seeding rate.

A parsimonious random effects model for each variate was developed by successive applications of the residual likelihood ratio test, where terms were removed in hierarchical fashion. Following Stram & Lee (1994), the approximate *P* value for the test was calculated as $0.5 * P(\chi^2_a > d)$, where *d* is the observed residual likelihood ratio statistic. In some cases, removal of a term necessitated the removal of another term (*viz.* the covariance with an associated random coefficient terms); in these cases, the test was calculated as $0.5 * P(\chi^2_a > d) + 0.5 * P(\chi^2_b > d)$. The degrees of freedom are noted as either (0,1) or (1,2) for these respective cases in Table 2. Approximate *F* statistics for fixed components were calculated, respecting marginality (*i.e.* main effects were adjusted for other main effects, second order interactions for main effects and other second order interactions etc.). The denominator degrees of freedom was set as the residual degrees of freedom, which is anti-conservative, therefore for inference the size α was set to 0.01. In Tables 3 and 4 and in the Figs, estimates of means involve random effects, and so what are referred to as 'S.E.S' or 'S.E.D.S' are in fact square roots of the average prediction error variance. Nevertheless, for simplicity, they may be interpreted as approximate S.E.S or S.E.D.S.

Table 2. The *F*-statistics for fixed components from the cubic smoothing splines modelling and the residual likelihood ratio tests for random components in the parsimonious model on *Lolium rigidum* dry weight and crop yield. The terms are cultivar (C), weed (W), density (D) and experiment (E)

Term	<i>L. rigidum</i> dry weight		Wheat grain yield	
	D.F.	F/LRT	D.F.	F/LRT
Fixed effects				
E	4	20.4	8	51.1
C	5	2.43	5	7.47
W	–	–	1	1.62
lin(D)	1	19.2	1	2.41
W.C	–	–	5	1.70
E.lin(D)	4	7.78	8	2.86
C.lin(D)	5	0.89	5	3.34
W.lin(D)	–	–	1	9.02
W.C.lin(D)	–	–	5	1.57
Random effects				
E.W	–	–	(1,2)	11.5
E.W.lin(D)	–	–	(1,2)	8.59
E.C	(0,1)	14.2	(1,2)	18.8
E.C.lin(D)	NS	–	(1,2)	9.54
E.W.C	–	–	(0,1)	7.05
E.W.C.lin(D)	–	–	NS	–
spl(D)	(0,1)	39.8	(0,1)	21.4
W.spl(D)	–	–	NS	–
E.spl(D)	NS	–	NS	–
C.spl(D)	NS	–	NS	–
E.W.spl(D)	–	–	(0,1)	3.45
W.C.spl(D)	–	–	NS	–
E.C.spl(D)	NS	–	NS	–
E.W.C.spl(D)	–	–	NS	–

NS, random effects not included in the final parsimonious model.

– indicates terms not relevant for *L. rigidum* dry weight model.

Significant values (at $P=0.01$, 0.05 for fixed and random components respectively) are in italics.

Degrees of freedom for random effects are specified as '(a,b)' to indicate that the *P* value is calculated as $0.5 * P(\chi^2_a > d) + 0.5 * P(\chi^2_b > d)$. Refer to methods section or Stram & Lee (1994) for more information.

Screenings and grain weight

For the remaining response variables, the saturated model involving the design factors was fitted to the weedy and weed-free plots: *expt***cultivar***weed***seedrate* + {*design stratum*}, where 'seedrate' is a factor representing the effects of seeding rate. Screenings were analysed on a log scale to remove a mean-variance relation: differences on a log scale reflect multiplicative differences on the original scale (e.g. a doubling of 1–2% is more significant than an increase from 20–30%). As for grain yield and *L. rigidum* dry

Table 3. Influence of experiment and cultivar on *Lolium rigidum* dry weight means (back-transformed means (g/m²) in parentheses), at an average crop density of 225 plants/m² measured at five experiments. The average S.E.D. is on the transformed scale

Cultivar	Experiment				
	NSW97	SA97	SA98	WA(A)97	WA(B)98
Janz	8.7 (76.4)	5.5 (30.2)	7.4 (55.2)	5.3 (28.3)	9.7 (93.6)
Pulsar	7.9 (61.9)	5.7 (32.3)	6.0 (35.7)	4.8 (22.7)	9.2 (84.4)
Trident	8.3 (68.1)	6.0 (36.1)	7.0 (48.4)	5.2 (26.8)	9.5 (90.3)
S.E.D. (D.F. 377)	0.38	0.39	0.37	0.39	0.54

Table 4. Influence of experiment and cultivar on average crop yield losses from *Lolium rigidum* competition (t/ha), at an average crop density of 235 plants/m² measured at nine experiments. An average S.E.D. is shown for each experiment

Cultivar	Experiment								
	NSW97	NSW98	VIC(A)97	VIC(B)97	VIC(B)98	SA97	SA98	WA(A)97	WA(B)98
Janz	0.27	0.28	0.14	0.03	0.29	0.89	1.11	0.25	0.49
Pulsar	0.24	0.22	0.08	0.02	0.18	0.65	0.95	0.22	0.34
Trident	0.25	0.19	0.05	0.02	0.28	0.82	0.99	0.13	0.54
Dollarbird		0.12			0.13		0.86		0.50
S.E.D. (D.F. 1023)	0.092	0.117	0.040	0.048	0.093	0.090	0.063	0.085	0.076

weight, the residual error at each experiment was modelled as a separable autoregressive process of order 1, and so the data for *R. raphanistrum* and *B. napus* plots were retained to preserve spatial integrity. As for the yield and *L. rigidum* dry weight analyses, *F* statistics were calculated respecting marginality.

RESULTS

Wheat seeding rate and crop density relationship

Crop densities ranged from less than 100 to over 500 plants/m² (Fig. 1). Densities were more variable between the sites in 1997 than in 1998 (Figs 1a and b). Seasonal and site differences influenced the relationships to increasing crop seeding rate. The largest responses to increasing seeding rate were at NSW97 and VIC(A)97, whilst VIC(B)98 and SA showed the lowest responses. At the lowest seeding rate of 25 kg/ha, VIC(B)97 recorded the highest average crop density of 180 plants/m², whilst the other experiments ranged from 60 to 115 plants/m². At the highest seeding rate of 200 kg/ha, average crop densities ranged from about 300 plants/m² for SA97 and SA98 to 530 plants/m² for NSW97. The response to increasing crop density was lowest for VIC(B)97. On average, a seeding rate of 50 kg/ha produced about

130 plants/m², 100 kg/ha resulted in 230 plants/m², while 200 kg/ha resulted in about 400 plants/m² (Fig. 1c).

L. rigidum dry weight/crop density relationship

Table 2 shows that there were both highly significant linear and non-linear (spline) effects of crop density on *L. rigidum* dry weight. These linear effects also varied significantly by experiment (E.lin(D)). There were also significant interactions between experiments and cultivars (E.C), but no significant interactions involving both cultivar and crop density.

Increasing crop density reduced *L. rigidum* dry weight across the entire range of crop densities, but higher crop densities gave diminishing reductions, and the rate of reduction was lower at NSW97 and WA(A)97 than at the other experiments (Fig. 2a). Doubling crop density of all cultivars from 100 to 200 plants/m² halved *L. rigidum* dry weight (averaged over all experiments) from 100 g/m² to about 50 g/m² (Fig. 2b).

Cultivar differences in weed suppression were small (Table 3). In all experiments except SA97, average *L. rigidum* dry weight was lower for Pulsar than Trident or Janz (significantly in NSW97 and SA98), with Trident slightly lower than Janz at most experiments.

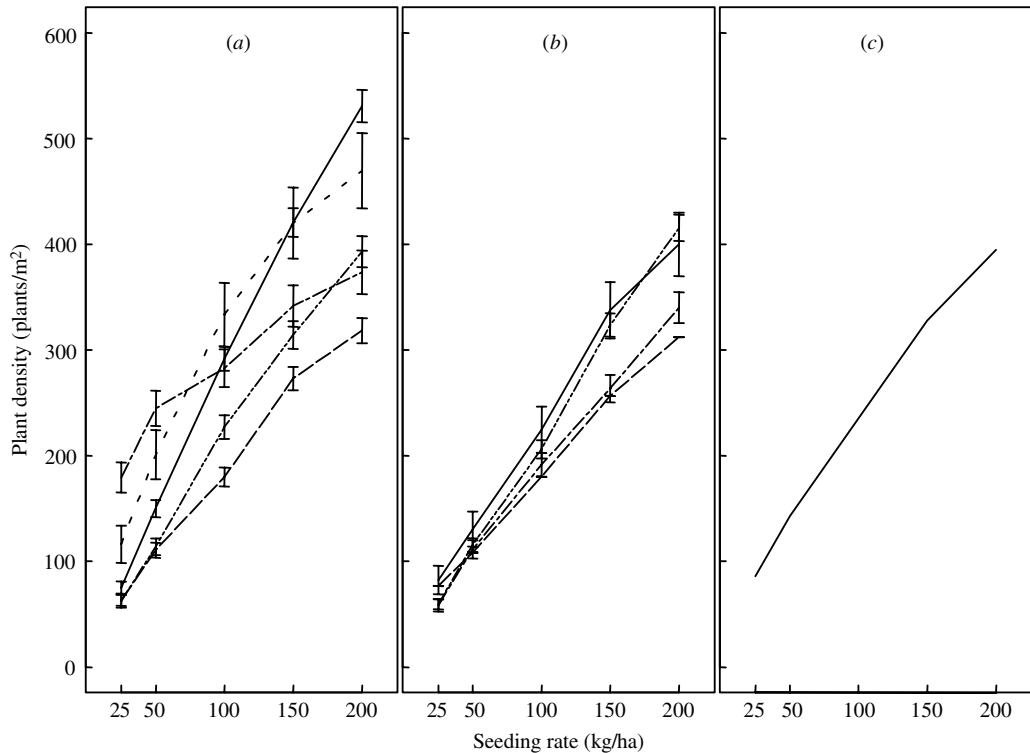


Fig. 1. Predicted crop density responses to crop seeding rate (a) at five sites in 1997 as indicated, NSW (—), VIC(A) (- - -), VIC(B) (---), SA (—), WA(A) (---); (b) at four sites in 1998, NSW (—), VIC(B) (- - -), SA (—), WA(B) (---); and (c) averaged over all sites and seasons. The error bars represent ± 1 s.e.

Crop grain yield/crop density relationship

Grain yields varied considerably between experiments, from less than 0.5 t/ha in VIC97 to over 5 t/ha in NSW98 (Fig. 3). As Table 2 shows, there were significant linear and non-linear (spline) effects of crop density on grain yield. The linear effects of crop density varied significantly between experiments and weed treatments (E.W.lin(D)), and between cultivars and experiments (E.C.lin(D)). Non-linear (spline) effects of crop density were highly significant (spl(D)), and also varied by weed treatment and experiment (E.W.spl(D)). There were also significant interactions between cultivar, weed treatment and experiment but not involving crop density (E.W.C).

Experiment and weed effects

Figure 3 shows the interactions between experiment, weed treatment and crop density on grain yield. Linear responses to increasing crop density varied markedly between experiments, with the most positive responses in NSW97, SA98 and VIC(B)97, and the most negative response in NSW98 due to

lodging and grain shedding. There was also significant non-linearity in this response, with the yield response to increasing density declining at higher crop densities. At low crop densities, there were clear differences in yield loss due to *L. rigidum* between experiments, ranging from the largest losses in SA97 and SA98 to minimal losses in VIC(B)97. The response to increasing crop density was greater for the weedy treatment in all experiments except VIC(B)97. In other words, yield losses due to *L. rigidum* reduced with increasing crop density. This was most pronounced at SA97 and SA98 in the lower range of plant densities (<225 plants/m²). The latter reflected the significant interaction between experiment, weed treatment and both linear and non-linear effects of crop density.

Cultivar effects

Figure 4 presents the predicted grain yield-density curves for each cultivar and experiment (viz. E.C.lin(D), Table 2). Janz had a stronger response to increasing density than Pulsar in NSW97, NSW98, SA97 and VIC(B)98, but there were similar responses in other experiments. The response of Trident to crop

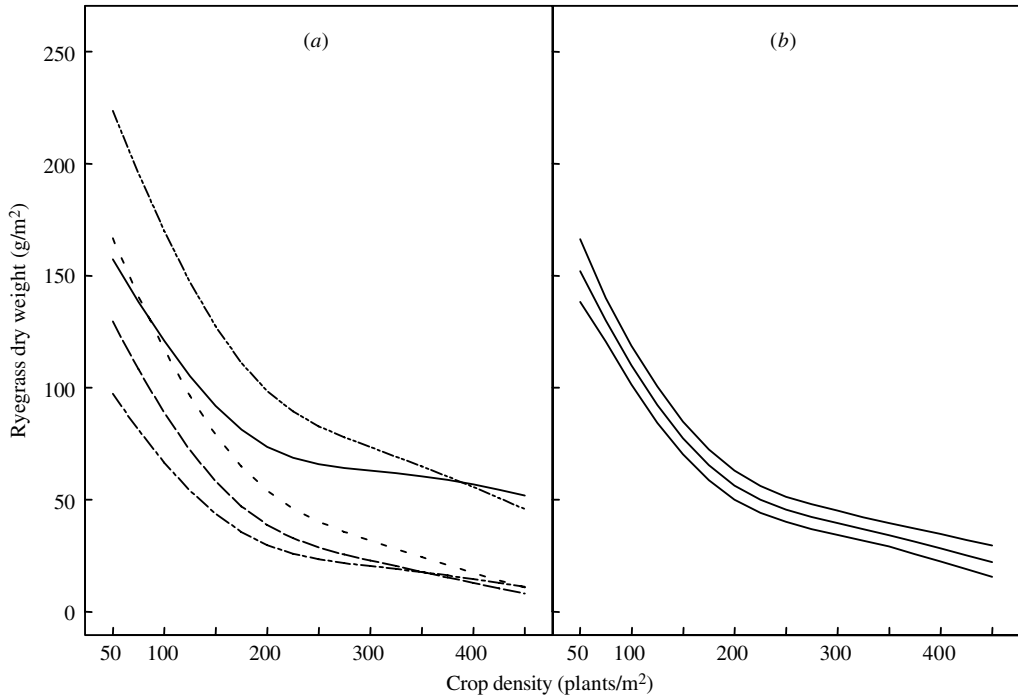


Fig. 2. Predicted ryegrass (*L. rigidum*) dry weight responses to crop density (a) at each of five experiments as indicated, NSW97 (—), SA97 (---), SA98 (· · ·), WA(A)97 (- · - ·), WA(B)98 (- - -), and (b) averaged over experiments. The outer lines represent ± 2 S.E.D. for the weedy versus weed-free comparison at each crop density.

density approximated the average response for Pulsar and Janz in most experiments, except for SA98 (lower response), and WA(B)98 (stronger response). Due to lodging Dollarbird showed a consistently lower response to crop density at all four experiments where it was sown.

Figure 5 shows the average response of each cultivar and weed treatment to increasing crop density. The interaction between weed treatment, cultivar and linear density (W.C.lin(D)) was not significant, although there were interactions of linear density with weed (W.lin(D)) and cultivar (C.lin(D)). The percentage yield loss in the weedy treatments was about 20% for all cultivars at 200 plants/m². The average responses for Janz, Pulsar and Trident were remarkably similar in spite of the differences between experiments. For the weed-free treatments, grain yield for these three cultivars increased with crop density to approximately 225 plants/m², after which it declined. Grain yield continued to increase in the weedy treatments beyond 225 plants/m², to a lesser extent for Pulsar. Pulsar, on average, had a smaller yield loss at low plant densities than Janz or Trident, but its average size of yield loss with increasing crop density was also smaller. In contrast, the grain yield of Dollarbird declined at densities above about 200

plants/m² in the weedy, and to a greater extent in the weed-free treatments.

Differences in the average yield loss due to *L. rigidum* between cultivars across experiments are shown in Table 4. Some experiments showed moderate (>0.5 t/ha) but significant differences between Janz, Trident and Pulsar (SA97, SA98, WA(B)98), but at other experiments the differences were smaller (e.g. NSW97, VIC(B)97). On average, Janz tended to greater yield loss whereas Pulsar was generally less affected.

Average effects

The average relationship between wheat density and grain yield is shown in Fig. 6a, and the percentage yield loss in Fig. 6b. In the absence of weeds, grain yield ranged from 2.2 to 2.3 t/ha when crop density increased from 100 to 200 plants/m². In the presence of weeds, 100 wheat plants/m² led to an average 23% yield loss compared with 17% at 200 plants/m². Although yield declined slightly (about 0.1 t/ha) above 200 plants/m² in the absence of weeds, in the presence of weeds yield continued to increase over the entire range of densities (Fig. 6a). Clearly the marginal return on an increase in crop density declined monotonically (Fig. 6b).

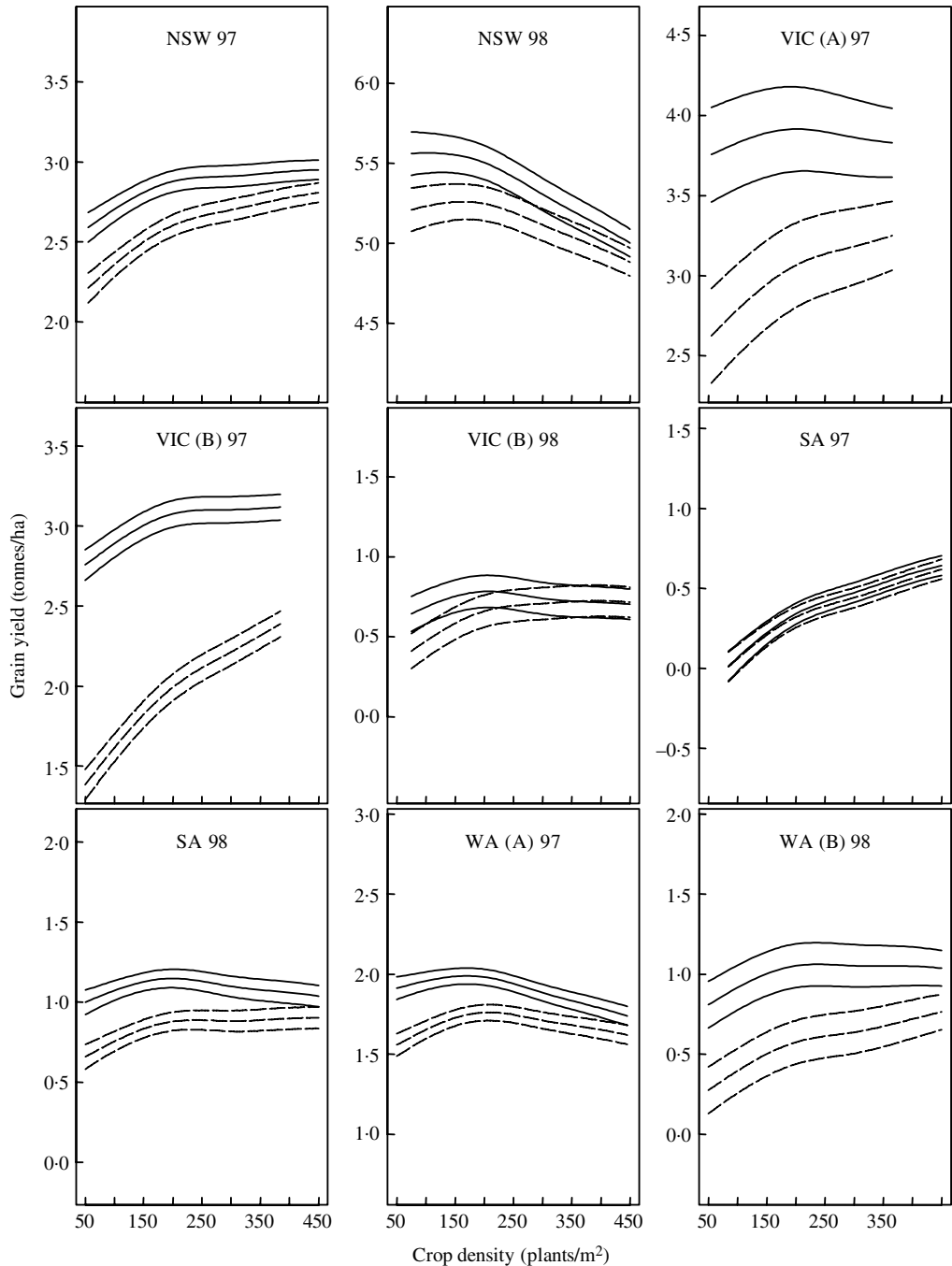


Fig. 3. Predicted grain yield responses to crop density at nine experiments, as indicated weedy (---) and weed-free (—). The outer lines represent ± 1 S.E.D. for the weedy versus weed-free comparison at each crop density.

Screenings and crop seeding rate

There were significant effects of experiment and seeding rate (E.SR), and experiment by cultivar (E.C)

on screenings (Table 5). Average percentage screenings varied considerably between experiments, and the effect of seeding rate also varied significantly between experiments (Fig. 7). At WA(A)97 and

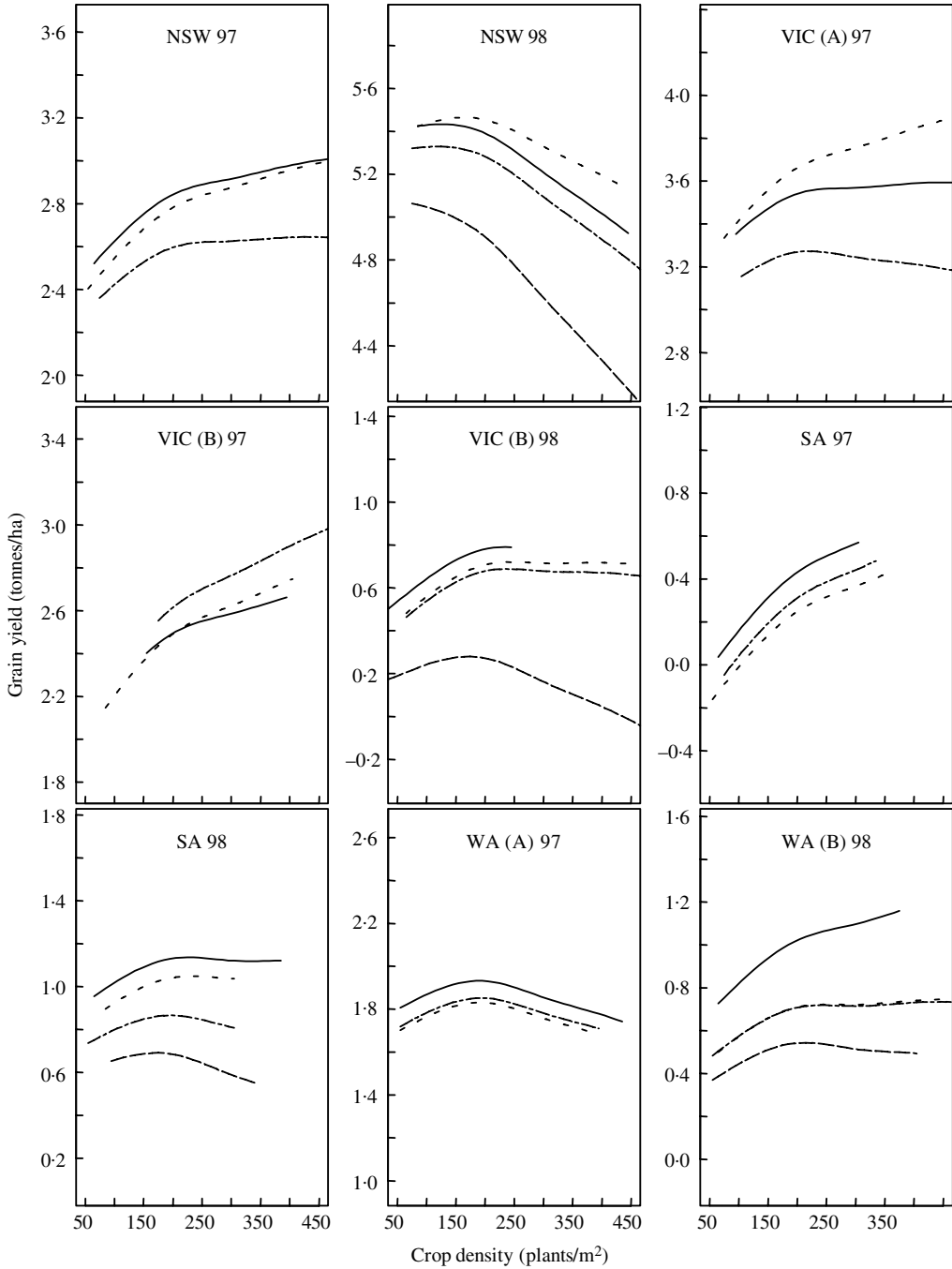


Fig. 4. Predicted grain yield responses to crop density for nine experiments, averaged over weed treatments. Four cultivars are shown Janz (---), Pulsar (....), Trident (—) and Dollarbird (— ·) over the range of crop densities at each experiment.

WA(B)98, screenings increased with crop seeding rate from 13.1 and 14.6%, respectively, at 100 kg/ha (equivalent to 200 plants/m²), to 15.6 and 18.4%

respectively, at 200 kg/ha. At VIC(A)97 and VIC(B)97, there were also significant but small increases, while at NSW97 screenings significantly

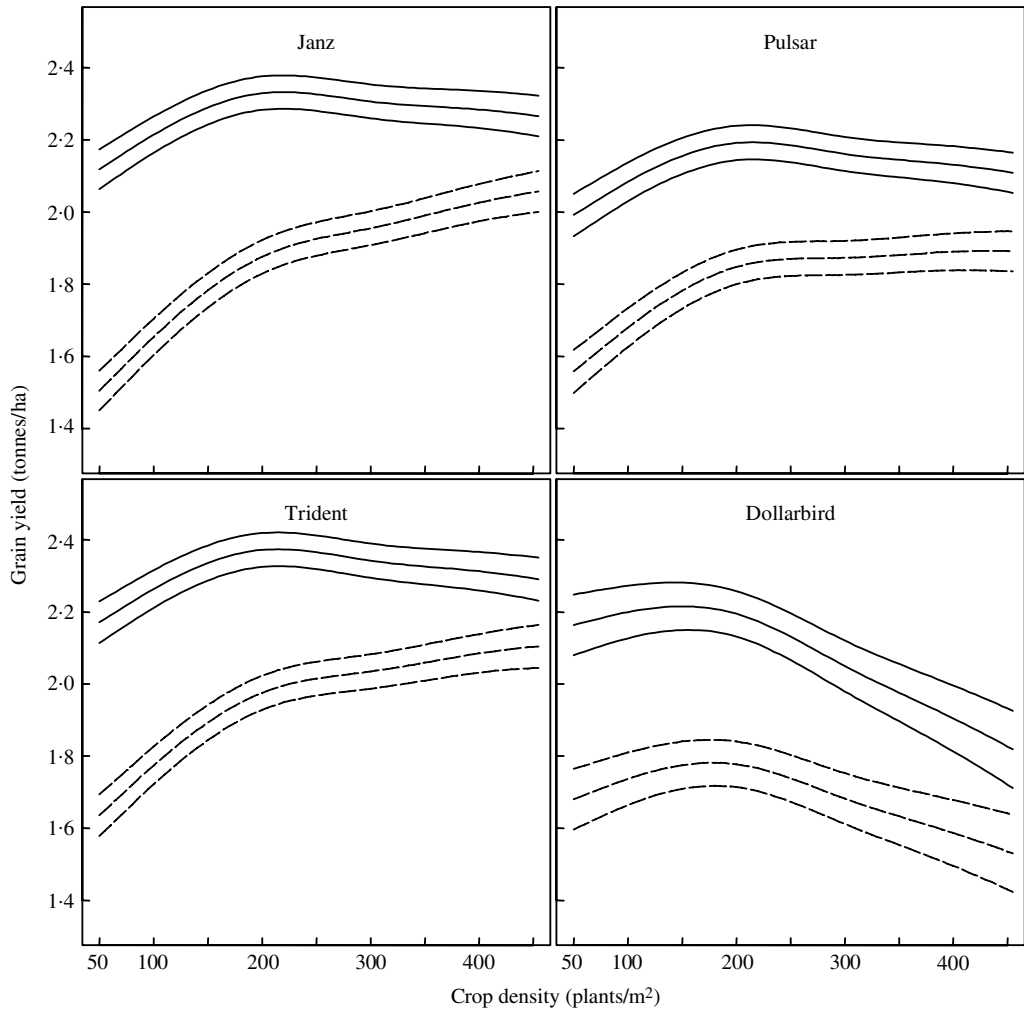


Fig. 5. Predicted grain yield responses to crop density for four cultivars Janz, Pulsar, Trident and Dollarbird. Treatments as indicated, weedy (- -) and weed-free (—). The outer lines represent ± 1 S.E.D. for the weedy versus weed-free comparison at each crop density.

declined with increasing seeding rate, and at SA97 there was no apparent change. Effects of cultivar varied across experiments: at SA97 and WA(B)98, Trident had lower screenings than Janz or Pulsar (2.0 and 3.4% lower), at NSW97 Trident had higher screenings (2.2% higher), whilst in VIC(A)97 and WA(A)97 Janz had higher screenings than Pulsar or Trident (0.3 and 5.0% higher), and in VIC(B)97 there was negligible difference. Screenings were not significantly affected by weed treatment.

Grain weight and crop seeding rate

There were significant effects of cultivar, seeding rate, and experiment on grain weight (Table 5), and

significant interactions between experiment and each of cultivar, weed treatment and seeding rate (E.C, E.W, E.SR). There were also significant interactions between cultivar, weed treatment and seeding rate (C.W.SR). Average grain weight (per 1000 grains) varied significantly between the four experiments (25.1 g in VIC(A)97, 30.4 g in VIC(B)97, 32.1 g in NSW97, and 33.8 g in WA(B)98). Grain weight was significantly reduced as seeding rate increased (Fig. 8). This negative response to seeding rate varied marginally between experiments, but the average response was a decrease of 0.5 g from 50 kg/ha (100 plants/m²) to 100 kg/ha. Cultivar effects varied across experiments, with higher average grain weights being recorded for Pulsar at VIC(A)97 than for the other two

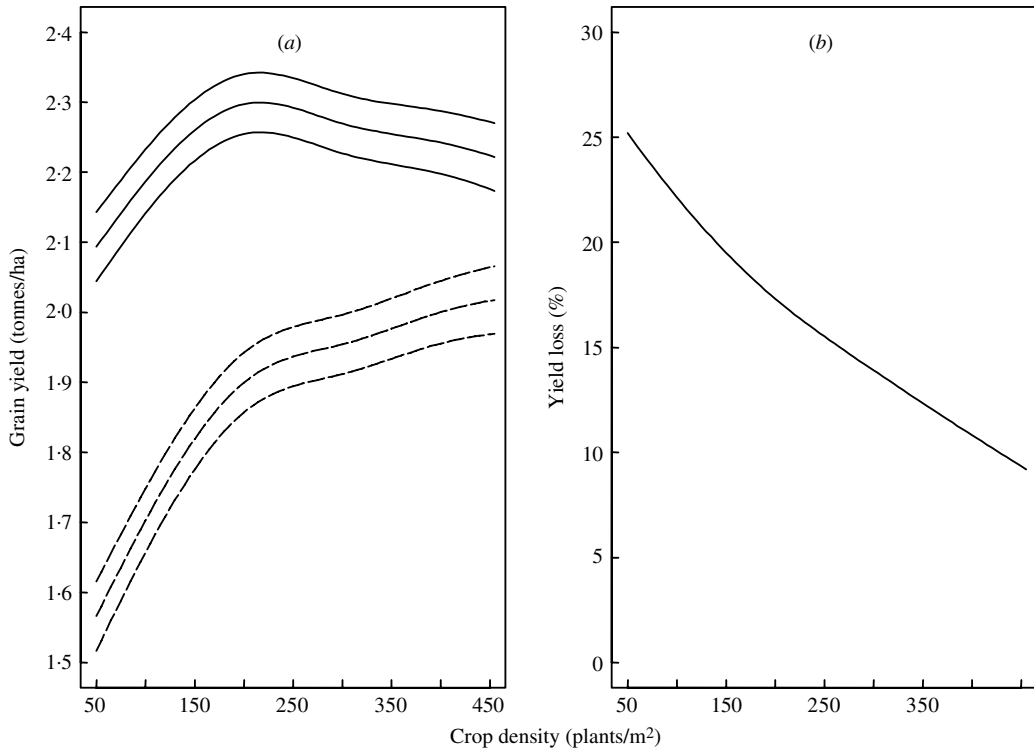


Fig. 6. Predicted grain yield responses to crop density, averaged across cultivars Janz, Trident and Pulsar and across all nine experiments. This is presented as (a) predicted grain yield, as indicated weedy (---) weed-free (—), and the outer lines represent ± 1 S.E.D. for the weedy versus weed-free comparison at each crop density, and (b) percentage yield loss due to weeds.

cultivars (1.7 g higher), and higher average grain weights for Trident at VIC(B)97 and NSW97 (3.0 and 1.4 g higher, respectively). The effect of weed treatment varied between experiments. The weedy plots had higher average grain weights for VIC(B)97 (1.2 g higher), but the other three experiments showed lower average grain weights. In the weedy plots grain weights were 0.6, 0.7 and 1.2 g lower in NSW9, VIC(B)97 and WA(B)98, respectively. The interaction between cultivar, weed treatment and seeding rate reflected only minor differences in the effects of weed treatment and seeding rate between cultivars Amery and Westonia. These are adapted to Western Australia and were grown only at these sites, however these data were retained in the analysis to keep the integrity of the field trials to facilitate spatial analysis, as were the extra weed treatments.

DISCUSSION

Increasing crop density suppresses weed growth and reduces losses in grain yield from competition consistently across the very different environments/wheat genotypes and years of southern Australia.

Moreover, the concerns of farmers about grain size reductions are not supported, except at seeding rates above those that would be cost-effective in practice. If 'typical' current seeding rates are doubled, average weed biomass in a given site or year is halved. As weed biomass is highly correlated with weed seed production (Watkinson & White 1985), this decrease will translate into reduced weed seedbank replenishment. In addition, crop yields in the presence of weeds usually increased with crop density, at least up to this doubled density. Crop yield loss from weed competition declined from 23% at a seeding rate of 50 kg/ha to 17% at the higher seeding rate of 100 kg/ha. If there were no weeds present, the risk of reduced yields at high densities was minor unless densities exceeded 200 plants/m², and this occurred mainly in the cultivar Dollarbird due to lodging. No incidence of disease was observed at even the highest crop densities. Therefore, the present results suggest that advice to farmers on higher seeding rates is more reliable than choice of cultivar for enhancing wheat competitiveness.

Other ways of increasing crop competitiveness have been proposed, for example, the placement of fertilizer within crop rows may be effective in favouring crop

Table 5. The F-statistics for wheat screenings and grain weight. Crop seeding rate (SR), cultivar (C), weed (W), density (D) and experiment (E). Significant values at $P=0.01$ are in italics

Term	Screenings (Error D.F. = 492)		Grain weight (Error D.F. = 247)	
	F_{inc}	D.F.	F_{inc}	D.F.
C	<i>17.0</i>	5	<i>18.2</i>	4
SR	<i>6.46</i>	4	<i>12.3</i>	4
W	0.243	1	0.149	1
E	<i>78.8</i>	5	<i>83.2</i>	3
C.SR	1.81	20	1.89	12
C.W	2.89	5	0.991	4
SR.W	0.837	4	1.86	4
E.C	<i>8.01</i>	11	<i>13.9</i>	4
E.SR	<i>3.34</i>	20	<i>2.59</i>	12
E.W	2.47	5	<i>7.05</i>	3
C.SR.W	0.801	20	<i>2.44</i>	12
E.C.SR	1.43	44	0.736	16
E.C.W	1.39	11	1.16	4
E.SR.W	1.01	20	2.04	12
E.C.SR.W	1.43	44	1.65	16

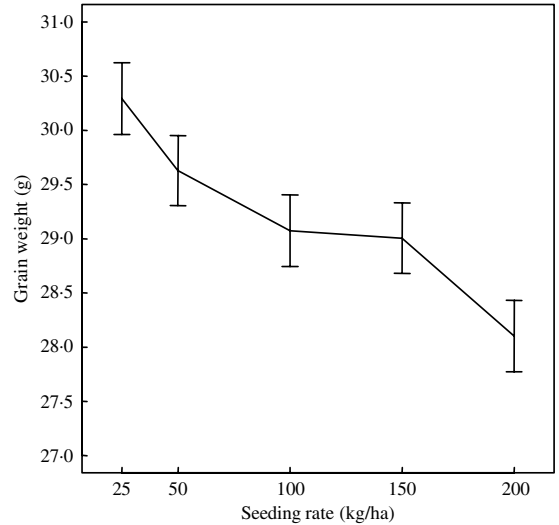


Fig. 8. Grain weight (1000-grain weight) with increasing crop seeding rate averaged over four experiments and all cultivars. The error bars represent ± 1 s.e.

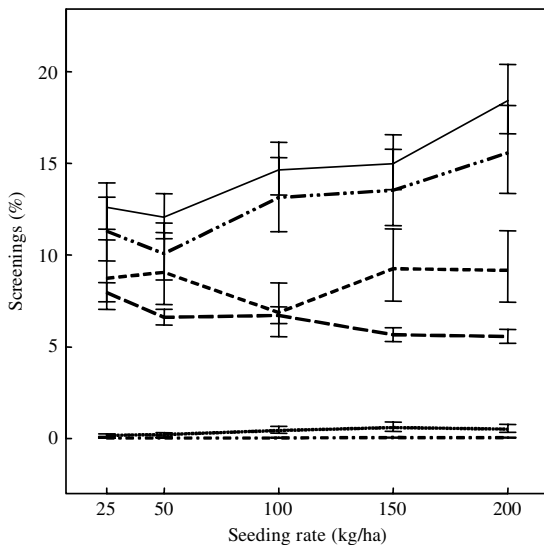


Fig. 7. Percentage screenings with increasing crop seeding rate at six experiments, as indicated: NSW97 (---), VIC(A)97 (.....), VIC(B)97 (-.-.-.-), SA97 (-.-.-), WA(A)97 (-.-.-.-), WA(B)98 (—). The error bars represent ± 1 s.e.

rather than weed growth (Di Tomaso 1995; Blackshaw 2004). Preliminary Australian evidence supports this (Koetz *et al.* 2002), but crop and weed responses were highly variable probably due to strong interactions between species and the environment.

Row spacings and planting patterns can also produce a more competitive crop stand and in some cases the advantage can be large (Weiner *et al.* 2001). In Australia, the trend to row spacings greater than 18 cm for stubble handling in conservation farming systems is likely to lead to reduced competitiveness and requires further study.

Management of herbicide-resistant *L. rigidum* is possible by using carefully planned combinations of a number of cultural control options (Gill & Holmes 1997). The effectiveness of such practices in controlling *L. rigidum* varies considerably with technique: 20–40% control with delayed seeding (sometimes in conjunction with an autumn cultivation), 40–60% with stubble burning, 80–90% with cutting a crop for hay or green manure, 60–80% with capture of weed seed at harvest (Gill & Holmes 1997). These compare with about 50% control with higher wheat seeding rate found in the present study.

The potential to breed wheat cultivars for competitiveness with weeds has been hypothesized (Lemerle *et al.* 1996). An economic analysis showed benefits of selection for increased competitiveness in a conventional wheat breeding programme but the rate of progress with other important characteristics such as yield are reduced, indicating that agronomic practices like increased seeding rates are a more appropriate option (Brennan *et al.* 2001). The heritabilities of morphological traits associated with competitive ability (e.g. height, early vigour, tillering capacity and leaf size) were reduced due to large genotype \times year interactions, making genetic gain through phenotypic selection difficult (Coleman *et al.* 2001). However, the

identification of quantitative trait loci associated with competitive ability repeatable over seasons shows potential for marker-assisted selection for weed competitiveness and requires further examination.

In conclusion, the adjustment of crop seeding rate can be a useful tool in suppression of weeds in the low rainfall environments of Australia and other parts of the world with similar climates. The benefits achieved may be less than for other management methods, but their effect is very consistent. If used in combination with other techniques (including herbicides) as part of an integrated management package (Walker *et al.* 2002), considerable reductions in weed seed production and crop yield loss can be achieved.

However, increases in seeding rate incur costs, not just in the quantity of grain needed, but also in the time lost in filling the seeder more often. An economic appraisal of the technique is now needed.

The Grains Research and Development Corporation and the Cooperative Research Centre for Weed Management Systems provided funds for the programme of several of the individual researchers. Russel Argall conducted the experiments at both sites in Victoria; Rob Davidson helped with the experiments in South Australia; and Shane Rudd, Peter Lockley and Bill Littlewood helped with experiments in NSW. Tracey Lee helped collate the data.

REFERENCES

- ANDERSON, W. K. & BARCLAY, J. (1991). Evidence for differences between three wheat cultivars in yield response to plant population. *Australian Journal of Agricultural Research* **42**, 701–713.
- BARTON, D. L., THILL, D. C. & SHAFII, B. (1992). Integrated wild oat (*Avena fatua*) management affects spring barley (*Hordeum vulgare*) yield and economics. *Weed Technology* **6**, 129–135.
- BLACKSHAW, R. E. (2004). Application method of nitrogen fertilizer affects weed growth and competition with winter wheat. *Weed Biology and Management* **4**, 103–113.
- BRENNAN, J. P., LEMERLE, D. & MARTIN, P. (2001). *Economics of increasing wheat competitiveness as a weed control weapon*. Contributed paper presented to the 45th Annual Conference of the Australian Agricultural and Resource Economics Society. CD-ROM. Adelaide, Australia: Australian Agricultural and Resource Economics Society.
- CARROLL, R. J. (1998). Measurement error in epidemiological studies. In *Encyclopedia of Biostatistics* (Eds P. Armitage & T. Colton), Vol. 4, pp. 2491–2519. New York, NY: John Wiley & Sons. This is available from CiteSeer (scientific literature digital library) at <http://citeseer.nj.nec.com/30037.html>.
- COCHRAN, W. G. & COX, G. M. (1957). *Experimental Designs*. New York: John Wiley & Sons.
- COLEMAN, R. K., GILL, G. S. & REBETZKE, G. J. (2001). Identification of quantitative trait loci for traits conferring competitiveness in wheat (*Triticum aestivum* L.). *Australian Journal of Agricultural Research* **52**, 1235–1246.
- COUSENS, R. D. & MOKHTARI, S. (1998). Seasonal and site variability in the tolerance of wheat cultivars to interference from *Lolium rigidum*. *Weed Research* **38**, 301–307.
- DI TOMASO, J. M. (1995). Approaches for improving crop competitiveness through the manipulation of fertilization strategies. *Weed Science* **43**, 491–497.
- DOLL, H., HOLM, U. & SOGAARD, B. (1995). Effect of crop density on competition by wheat and barley with *Argemone githago* and other weeds. *Weed Research* **35**, 391–396.
- FAWCETT, R. G. (1964). Effect of certain conditions on yield of crop plants. *Nature* **204**, 858–860.
- FULLER, W. A. (1987). *Measurement Error Models*. New York, NY: John Wiley & sons.
- GILL, G. S. & HOLMES, J. E. (1997). Efficacy of cultural control methods for combating herbicide-resistant *Lolium rigidum*. *Pesticide Science* **51**, 352–358.
- GILMOUR, A. R., CULLIS, B. R. & VERBYLA, A. P. (1997). Accounting for natural and extraneous variation in the analysis of field experiments. *Journal of Agricultural, Biological and Environmental Statistics* **2**, 269–293.
- GILMOUR, A. R., CULLIS, B. R., WELHAM, S. J. & THOMPSON, R. (2002). *ASReml Reference Manual 2nd edition, Release 1.0*. NSW Agriculture Biometrical Bulletin 3. Orange, NSW 2800, Australia: NSW Agriculture.
- GOLDBERG, D. E. (1990). Components of resource competition in plant communities. In *Perspectives on Plant Competition* (Eds J. B. Grace & D. Tilman), pp. 27–49. New York, NY: Academic Press.
- HASHEM, A., RADOSEVICH, S. R. & ROUSH, M. L. (1998). Effect of proximity factors on competition between winter wheat (*Triticum aestivum*) and Italian ryegrass (*Lolium multiflorum*). *Weed Science* **46**, 181–190.
- JORDON, N. (1993). Prospects for weed control through suppression. *Ecological Applications* **3**, 84–91.
- KOETZ, E., LEMERLE, D., GOOD, T. & SUTHERLAND, S. (2002). Strategic nitrogen application for weed suppression in wheat. In *Proceedings 13th Australian Weeds Conference* (Eds H. Spafford Jacob, J. Dodd & J. H. Moore), pp. 67–70. Perth, Australia: Plant Protection Society of WA.
- KORRES, N. E. & FROUD-WILLIAMS, R. J. (1997). The use of varietal selection and seed rates for enhanced weed suppression in winter wheat (*Triticum aestivum* L.). In *Proceedings of the 1997 Brighton Crop Protection Conference – Weeds*, Vol. 2, pp. 667–668. Farnham, UK: British Crop Protection Council.
- LEMERLE, D., VERBEEK, B. & COOMBES, N. E. (1995). Losses in grain yield of winter crops from *Lolium rigidum* competition depend on crop species, cultivar and season. *Weed Research* **35**, 503–509.
- LEMERLE, D., VERBEEK, B., COUSENS, R. D. & COOMBES, N. E. (1996). The potential for selecting spring wheat varieties strongly competitive against weeds. *Weed Research* **36**, 505–513.
- LEMERLE, D., GILL, G. S., MURPHY, C. E., WALKER, S. R., COUSENS, R. D., MOKHTARI, S., PELTZER, S. J., COLEMAN, R. & LUCKETT, D. J. (2001a). Genetic improvement and agronomy for enhanced wheat competitiveness with

- weeds. *Australian Journal of Agricultural Research* **52**, 527–548.
- LEMERLE, D., VERBEEK, B. & ORCHARD, B. (2001*b*). Ranking the ability of wheat varieties to compete with *Lolium rigidum*. *Weed Research* **41**, 197–209.
- McRAE, F. J., McCAFFERY, D. W. & CARPENTER, D. J. (2003). *Winter Crop Variety Sowing Guide 2003*. Agdex 110/10, Orange, NSW, Australia: NSW Agriculture.
- MARTIN, R. J., CULLIS, B. R. & McNAMARA, D. W. (1987). Prediction of wheat yield loss due to competition by wild oats (*Avena* spp.). *Australian Journal of Agricultural Research* **38**, 487–499.
- MEDD, R. W., AULD, B. A., KEMP, D. R. & MURISON, R. D. (1985). The influence of wheat density and spatial arrangement on annual ryegrass, *Lolium rigidum* Gaudin, competition. *Australian Journal of Agricultural Research* **36**, 361–371.
- MOHLER, C. L. (2001). Enhancing the competitive ability of crops. In *Ecological Management of Agricultural Weeds* (Eds M. Liebman, C. L. Mohler & C. P. Staver). Cambridge: Cambridge University Press.
- MOKHTARI, S., GALWEY, N. W., COUSENS, R. D. & THURLING, N. (2002). The genetic basis of variation among wheat F₃ lines in tolerance to competition by ryegrass (*Lolium rigidum*). *Euphytica* **124**, 355–364.
- MOSS, S. R. (1985). The influence of crop variety and seed rate on *Alopecurus myosuroides* competition in winter cereals. In *Proceedings of the 1985 Brighton Crop Protection Conference – Weeds*, pp. 701–708. Farnham, UK: British Crop Protection Council.
- MURPHY, C., LEMERLE, D., JONES, R. & HARDEN, S. (2002). Use of density to predict crop yield loss between variable seasons. *Weed Research* **42**, 377–384.
- RADFORD, B. J., WILSON, B. J., CARTLEDGE, O. & WATKINS, F. B. (1980). Effect of wheat seeding rate on wild oat competition. *Australian Journal of Experimental Agriculture and Animal Husbandry* **20**, 77–81.
- REBETZKE, G. J. & RICHARDS, R. A. (1999). Genetic improvement of early vigour in wheat. *Australian Journal of Agricultural Research* **50**, 291–301.
- REEVES, T. G. & BROOKE, H. D. (1977). The effect of genotype and phenotype on the competition between wheat and annual ryegrass (*Lolium rigidum* Gaud.). In *Proceedings of the 6th Asian-Pacific Weed Science Society Conference* (Eds M. Soerjani, D. E. Barnes & T. O. Robson), pp. 167–172. Jakarta, Indonesia: Asian-Pacific Weed Science Society.
- STRAM, D. O. & LEE, J. W. (1994). Variance components testing in the longitudinal mixed effects model. *Biometrics* **50**, 1171–1177; correction *Biometrics* **51**, 1196.
- TURNER, N. C., PRASERTSAK, P. & SETTER, T. L. (1994). Plant spacing, density, and yield of wheat subjected to post anthesis water deficits. *Crop Science* **34**, 741–748.
- VERBYLA, A. P., CULLIS, B. R., KENWARD, M. G. & WELHAM, S. J. (1999). The analysis of designed experiments and longitudinal data using smoothing splines (with discussion). *Applied Statistics* **48**, 269–312.
- WALKER, S. R., MEDD, R. W., ROBINSON, G. R. & CULLIS, B. R. (2002). Improved management of *Avena ludoviciana* and *Phalaris paradoxa* with more densely sown wheat and less herbicide. *Weed Research* **42**, 257–270.
- WATKINSON, A. R. & WHITE, J. (1985). Some life-history consequences of modular construction in plants. *Philosophical Transactions of the Royal Society, London B* **313**, 31–51.
- WEINER, J., GRIEPENTROG, H.-W. & KRISTENSEN, L. (2001). Suppression of weeds by spring wheat *Triticum aestivum* increases with crop density and spatial uniformity. *Journal of Applied Ecology* **38**, 784–790.