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Influence of Crop Competition and Harvest Weed Seed Control on Rigid Ryegrass (*Lolium rigidum*) Seed Retention Height in Wheat Crop Canopies

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Abstract

Harvest weed seed control (HWSC) is an Australian innovation, developed to target high proportions of weed seed retained at crop maturity by many major weed species. There is the potential, however, that a reduction in the average height of retained seed is an adaptation to the long-term use of HWSC practices. With the aim of examining the distribution of rigid ryegrass (*Lolium rigidum* Gaudin) seed through crop canopies, a survey of Australian wheat (*Triticum aestivum* L.) fields was conducted at crop maturity. Nine sites with medium to long-term HWSC use were specifically included to examine the influence of HWSC use on seed retention height. During the 2013 wheat harvest, *L. rigidum* and wheat plant samples were collected at five heights downward through the crop canopy (40, 30, 20, 10, and 0 cm above ground level) in 71 wheat fields. Increased crop competition resulted in higher proportions of *L. rigidum* seed in the upper crop canopy (>40 cm). The increase in plant height is likely a shade-intolerance response of *L. rigidum* plants attempting to capture more light. This plant attribute creates the opportunity to use crop competition to improve HWSC efficacy by increasing the average height of seed retention. Crop competition can, therefore, have a double impact by reducing overall *L. rigidum* seed production and increasing seed retention height. Examining the distribution of wheat biomass and *L. rigidum* seed through the crop canopy, we determined that reducing harvest height for HWSC considerably increased the collection of *L. rigidum* seed (25%) but to a lesser extent wheat crop biomass (14%). Comparison of + and − HWSC use at nine locations found no evidence of adaptation to this form of weed control following 5 to 10 yr of use. Although the potential for resistance to HWSC remains, these results indicate that this will not readily occur in the field.

Introduction

Weed seed retention at plant maturity has been identified as a weed control opportunity for the problematic annual weed species of Australian crop production systems. The major weeds, rigid ryegrass (*Lolium rigidum* Gaudin), wild radish (*Raphanus raphanistrum* L.), brome grass (*Bromus* spp.), and wild oats (*Avena* sp.) retain significant proportions of total seed production, at a height that allows collection during harvest (Walsh and Powles 2014). Once collected, these weed seeds are processed and then exit the harvester, primarily in the chaff fraction (Broster et al. 2016). The residue management systems on harvesters redistribute the straw and weed seed–bearing chaff material evenly across the field, effectively reseeding the collected weed seeds. Intercepting this process has now become a focus, with grain harvest recognized as a weed control opportunity. Subsequently, harvest weed seed control (HWSC) systems have been developed specifically to target weed seeds during commercial wheat (*Triticum aestivum* L.) crop harvest to prevent inputs to the seedbank (Walsh et al. 2013).

HWSC systems use a range of approaches to target the weed seed–bearing chaff fraction: chaff collection followed by burning/removal (chaff cart), concentration in narrow rows (chaff lining/tramlining) or in a narrow windrow with straw residues for subsequent burning (narrow windrow burning), collection in bales along with straw residues (bale direct system), and mechanical destruction during harvest (Harrington Seed Destructor [HSD], integrated HSD [iHSD], and Seed Terminator). When implemented effectively, these systems have been shown to be similarly effective in delivering high levels of weed seed destruction (>85%) and

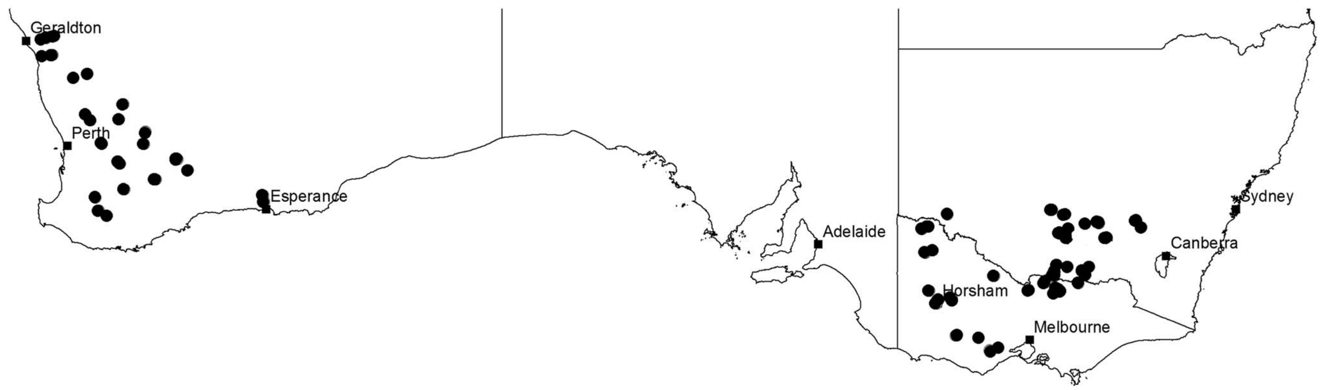

Figure 1. Locations of sampling sites across the western and southern grain production regions of Australia.

equivalent reductions in subsequent weed emergence (Walsh et al. 2017). Thus, growers can choose the HWSC option that best fits their production system.

Crop competition, as well as suppressing weed seed production, is also likely to increase the efficacy of HWSC by increasing the height of weed seed retention at crop maturity. The role of crop competition in reducing weed seed production has been established for the major weeds of Australian cropping: *L. rigidum* (Lemerle et al. 2004), *R. raphanistrum* (Walsh and Minkey 2006), *Avena* sp. (Radford et al. 1980), and *Bromus* spp. (Gill et al. 1987). Additionally, weeds of annual cropping systems are not normally shade tolerant (Gommers et al. 2013), and their growth and development is restricted under low light conditions (Zerner et al. 2008). A typical response to crop canopy shading by shade-intolerant species is a more erect growth habit (Morgan et al. 2002; Vandenbussche et al. 2005). The likely result of this response is that weed seed heads and pods will be produced higher in the crop canopy and, therefore, will be more prone to collection during grain harvest. As the efficacy of HWSC is directly related to weed seed collection, crop competition may increase the weed seeds available for control by increasing the collectable proportion.

There is little doubt that the dominant weed populations of cropping systems, if given the opportunity, will evolve resistance to all forms of weed control. In Australian cropping systems, as well as the countless cases of herbicide resistance evolution (Boutsalis et al. 2012; Broster et al. 2013; Owen et al. 2014), there are many instances of adaptation in dormancy patterns to avoid cultivation (Fleet and Gill 2012; Kleemann and Gill 2006; Owen et al. 2011). Globally, there are examples of resistance evolution to grazing, mowing, and even hand weeding (Barrett 1983; Gould 1991; McKinney and Fowler 1991). Resistance or adaptation to specific weed control strategies, regardless of mechanism or type, seems almost inevitable, particularly when large genetically diverse populations are persistently exposed to selection (Diggle and Neve 2001; Neve and Powles 2005). Resistance evolution in *L. rigidum* populations has been particularly dramatic, and there seems little doubt that this highly adaptable species has the potential to evolve resistance to all forms of weed control. With the increasingly frequent and widespread use of HWSC systems in Australian cropping, there is concern that *L. rigidum* will evolve resistance to this new form of weed control. The aims then of this study were to: (1) examine the distribution of retained *L. rigidum* seed through the canopies of mature wheat crops across Australian cropping regions, (2) determine the influence of wheat crop competition on the distribution of *L. rigidum* seed retention in wheat crop canopies, and (3) investigate the effects of HWSC use on seed retention of *L. rigidum* in wheat crops.

Materials and Methods

Plant Sample Collection and Processing

To establish the distribution of retained *L. rigidum* seed through wheat crop canopies at maturity, samples were collected from wheat crops at 71 locations across the western and southern wheat belt regions of Australia (Figure 1). Sampled wheat crops were randomly selected, apart from the fields specifically selected for comparison of long-term effects of HWSC on *L. rigidum* seed retention. To evaluate the effect of mid- to long-term HWSC use, *L. rigidum* seed retention was compared in specifically targeted fields with recorded + and − HWSC use. At nine locations, two fields were selected—one where HWSC had been used at least five times and the other with no HWSC use. Within each field, areas with low to moderate (1 to 20 plants m^{-2}) *L. rigidum* plant density were typically targeted for sampling. In some instances, higher-density areas were sampled (Table 1). Sampling of *L. rigidum* and wheat plants was conducted over the initial 2 to 3 wk of the 2013 harvest (November to December, depending on the region). At each location, *L. rigidum* and wheat plants were counted and plant material samples were collected from within four 1.0-m^2 quadrats. In each quadrat, *L. rigidum* and wheat plants were sampled at five heights commencing at 40 cm above the soil surface and then at 10-cm intervals to the soil surface. The soil surface within the quadrat was swept with a brush to collect any seed, seed heads, and plant material that had fallen from wheat and *L. rigidum* plants. Collected plant samples were oven-dried at 70 C for 48 h and then weighed to determine wheat and *L. rigidum* biomass production values for each sampling height. Wheat and ryegrass seed heads were threshed and weighed to determine seed yields at each sampling height.

HWSC systems have been used more frequently in Western Australia than elsewhere; therefore, wheat fields from this region were specifically sampled to examine the effects of HWSC use on *L. rigidum* seed retention height. At nine locations, *L. rigidum* plants were sampled from wheat fields where HWSC had been used (5 to 10 treatments) and from nearby wheat fields where HWSC had never been used.

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Table 1. Site average wheat biomass and grain yield and corresponding rigid ryegrass plant density and seed production values at each of the 71 sites sampled to examine rigid ryegrass seed retention through wheat crop canopies.

	Wheat		Rigid ryegrass		
	Biomass	Yield	No of plants	No. of seed	Seed retention above 10-cm
Site	kg ha^{-1}		plants m^{-2}	seed m^{-2}	%
1	7,570	4,800	4.3	1882	83
2	10,070	2,700	1.8	1905	94
3	11,230	2,770	6.0	4001	76
4	7,680	2,400	9.0	4125	87
5	7,150	1,920	1.8	99	91
6	8,510	2,180	18.5	7192	93
7	8,230	3,180	1.3	87	84
8	6,030	2,230	35.3	6857	89
9	2,210	590	5.5	1539	95
10	9,680	3,020	5.8	4872	92
11	14,350	4,840	2.3	438	82
12	9,210	3,130	7.0	3064	92
13	14,200	3,680	4.3	1416	90
14	13,770	960	5.0	1150	86
15	13,830	5,870	8.8	549	51
16	9,040	3,860	3.8	1179	79
17	11,550	4,260	3.8	1232	69
18	10,910	4,590	2.3	1292	92
19	11,010	3,270	1.8	171	95
20	9,590	3,160	4.3	3101	89
21	7,440	2,720	4.0	967	83
22	15,860	6,670	2.5	1472	85
23	6,350	2,690	7.3	1511	76
24	3,290	500	1.5	474	94
25	2,420	670	31.8	810	82
26	2,990	1,050	12.3	1011	73
27	3,230	1,110	22.5	1277	54
28	15,010	5,230	9.0	1060	69
29	15,200	2,700	13.3	3185	83
30	10,070	2,900	3.0	559	67
31	9,390	3,450	1.7	501	71
32	9,050	2,750	12.8	4180	88
33	10,090	3,160	1.8	428	75
34	14,700	5,270	1.7	553	83
35	11,950	3,700	19.5	682	68
36	11,710	3,820	1.8	222	58
37	14,690	4,010	1.3	1553	99
38	10,230	3,670	9.0	1315	51
39	13,070	5,580	10.3	844	48
40	14,290	6,740	18.0	3680	77
41	16,990	8,630	3.3	1156	83
42	10,000	3,580	50.8	6075	74
43	14,880	6,540	4.0	1512	69
44	15,580	7,970	1.0	89	100
45	18,890	7,860	10.0	5490	80
46	15,140	6,690	3.8	161	96
47	6,210	2,730	5.7	1260	16
48	2,340	840	3.3	1184	60
49	9,630	3,660	7.3	2595	51
50	6,610	3,990	16.3	3799	70
51	10,490	4,470	6.0	577	87
52	6,810	3,560	23.0	5486	34
53	6,090	2,860	14.0	4163	75
54	7,170	3,140	4.3	346	40
55	8,180	3,220	34.5	4330	73
56	4,370	1,910	3.5	917	51
57	10,000	4,260	9.8	2273	57
58	8,030	3,130	7.0	497	85
59	4,570	2,280	4.0	1136	71
60	2,090	920	15.5	2057	48
61	7,740	3,540	19.6	3758	82
62	8,340	3,290	3.8	1872	89
63	4,030	2,270	2.8	850	63
64	2,190	870	2.5	430	36
65	6,520	2,850	34.7	6177	73
66	6,820	2,620	5.3	487	56
67	8,350	3,810	4.3	2206	64
68	7,730	3,540	4.0	960	66
69	11,180	4,460	4.0	1030	69
70	9,800	4,550	5.5	1346	57
71	11,330	4,740	2.5	926	90
Average	9,370	3,560	8.9	1938	74
SE	470	200	1.1	210	2

Statistical Analyses and Data Presentation

To examine the influence of crop competition on *L. rigidum* seed production, seed number at each sampling height was converted to percent cumulative seed production and contrasted against wheat biomass production. There was a linear relationship between crop biomass and seed retention above a 40-cm canopy height. Microsoft Excel was used to plot the linear relationship of seed retention above 40 cm against wheat crop biomass. No relationship between seed retention and wheat crop biomass was observed at any other canopy height (unpublished data). To further examine the influence of crop biomass on *L. rigidum* seed retention, we compared the influence of high (≥12,000 kg ha^{-1}) and low (≤7,000 kg ha^{-1}) biomass–yielding wheat crops for their effects on the distribution of retained *L. rigidum* seed through the crop canopy.

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Table 2. Average wheat biomass and yield, *L. rigidum* seed production and seed retention for high wheat biomass, low wheat biomass and all sites of southern and western wheat belt regions in 2013.

Biomass groupings (sampling site no.)	Wheat[a]		*L. rigidum*	
	Biomass	Yield	No. of seeds	Seed retention above 10 cm
	———kg ha^{-1}———		seeds m^{-2}	%
High biomass (>12 t ha^{-1}) (average 17 sites)	14,850 (340)	5,470 (450)	1,470 (314)	79 (3)
Low biomass (<7 t ha^{-1}) (average 19 sites)	4,480 (440)	1,920 (250)	2,180 (483)	67 (5)
Average (71 sites)	9,230 (490)	3,480 (210)	1,938 (210)	74 (2)

[a]Numbers in parentheses are the standard errors of the mean of respective numbers of sampling sites.

ANOVAs, using a linear mixed model (GenStat 2015), compared the cumulative *L. rigidum* seed retention values in the canopy above 10-cm height for each of the nine + and nine − HWSC site comparisons. One-way ANOVA using a general linear model compared total annual *L. rigidum* seed production for each site comparison. Where differences occurred, means were separated using Fisher's protected LSD at $\alpha = 0.05$.

Results and Discussion

Lolium rigidum plants retained greater proportions of total seed production in the upper canopy when grown in competition with higher biomass–yielding wheat crops. A survey of 71 wheat fields across several agroecological zones (Figure 1) resulted in the collection of seed retention data from wheat fields with a wide range of biomass production values (2,085 to 18,885 kg ha^{-1}) (Table 1). Sampling at 10-cm increments down through the crop canopy at each of the sampling sites identified a large variation in proportion of total seed production (16% to 100%) retained above 10 cm (Table 1). Despite this variation, there was a trend for higher *L. rigidum* seed retention in high biomass–yielding crops. Segregating sites into high (≥12,000 kg ha^{-1}) and low (≤7,000 kg ha^{-1}) biomass–yielding groups provided a clearer indication of the biomass effects on seed retention. For instance, average seed retention above 10-cm canopy height was 67% in low-biomass crops and increased to 79% in high-biomass crops (Table 2).

The influence of crop biomass on *L. rigidum* seed retention appears to be stronger in the upper canopy. There is a relatively weak linear relationship between wheat biomass and *L. rigidum* seed retention above the 40-cm canopy height (Figure 2). The indication is that *L. rigidum* responded to increased wheat crop competition by increasing the proportion of seed retained in the upper canopy. The influence of crop competition on *L. rigidum* seed retention is more evident when average seed retention values for the high (≥12,000 kg ha^{-1}) and low (≤7,000 kg ha^{-1}) wheat biomass sites are plotted along with the average values of all sites (Figure 3). These groupings clearly identified the increased proportion of seed retained higher in the crop canopy in response to competition from high biomass–producing wheat crops.

With increasing biomass production, it is expected that there will be increased crop competition with *L. rigidum* plants for light as well as for nutrients and soil moisture (Zimdahl 2007). The increase in average seed retention height is likely due to shade avoidance by annual *L. rigidum* plants growing within wheat crops. *Lolium* spp., like many annual weeds, are shade intolerant (Ehret et al. 2015; Morgan and Smith 1979), and a common morphological response to shading is stem elongation (Holt 1995; Smith 1982). As a shade-avoidance strategy, stem elongation in grasses leads to an increase in plant height as plants attempt to intercept more light. Thus, the increased proportion of seed retained higher in the canopies of higher biomass–yielding wheat crops occurs because of the shade-avoidance strategy of *L. rigidum* plants. This biological attribute of shade-intolerant weed species

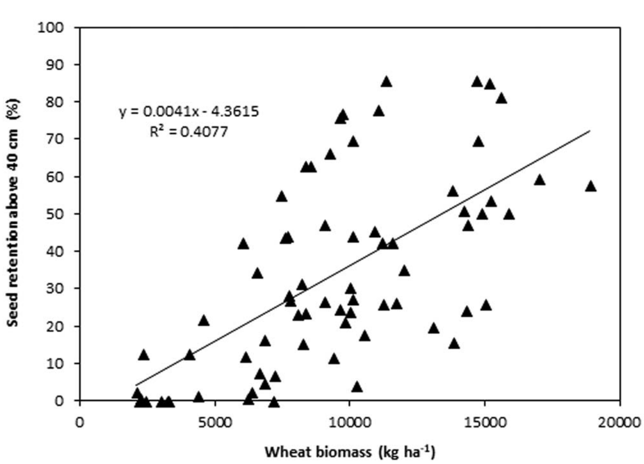

Figure 2. Relationship between cumulative proportion of *Lolium rigidum* seed retention above 40 cm and wheat biomass.

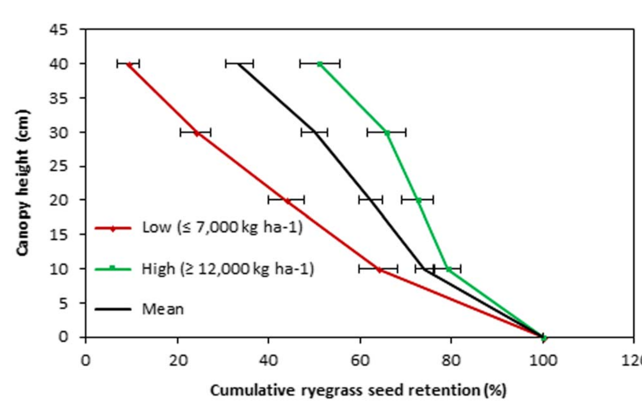

Figure 3. Cumulative rigid ryegrass seed retention for high (≥12,000 kg ha^{-1}) and low (≤ 7,000 kg ha^{-1}) wheat biomass sites and average of all sites. Bars represent the standard errors of the mean values from high, low and all sampling sites.

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Table 3. *Lolium rigidum* cumulative seed retention (%) above 10-cm canopy height for sites with and without medium to long-term use of HWSC.

Comparison area	Site no.		Seed retention above 10 cm[a]		Seed production	
	− HWSC	+ HWSC[b]	− HWSC	+ HWSC	− HWSC	+ HWSC
			———%———		———seeds m^{-2}———	
1	56	48 (5)	57 a	52 a	798 a	1,091 a
2	64	68 (8)	35 b	78 a	429 a	879 a
3	59	58 (5)	75 b	85 a	1,136 a	494 a
4	54	66 (7)	46 a	59 a	346 a	487 a
5	53	47 (7)	71 a	36 a	3,940 a	982 b
6	65	70 (5)	72 a	48 a	6,176 a	1,188 b
7	71	55 (8)	89 a	69 a	926 b	4,144 a
8	51	49 (8)	52 a	50 a	1,091 a	2,366 a
9	50	63 (10)	80 a	56 a	3,287 a	817 b
Average			64	59	2,015 a	1,383b
SE			5	5	631	369

[a]Seed retention and seed production means with the same letter within the same row are not significantly different (P > 0.05)
[b]Numbers in parentheses are the numbers of HWSC operations in each field.

creates the opportunity to use shading through crop competition to increase weed seed retention height and, therefore, the efficacy of HWSC.

As expected, the seed production of *L. rigidum* plants was reduced when they grew in competition with higher biomass–yielding wheat crops. *Lolium rigidum* plants maturing in high-biomass wheat crops produced less seed (P < 0.05) than plants maturing in low-biomass crops (Table 2). However, despite wheat biomass increases (P < 0.05) of more than 70%, *L. rigidum* seed production (P < 0.05) was reduced by just 33%. This result indicates that increases in crop biomass alone are not sufficient to substantially reduce reproductive capacity of competing *L. rigidum* plants.

There was no clear evidence that a history of selection with HWSC has affected the height or amount of *L. rigidum* seed retention at crop maturity. It is speculated that HWSC, like all other forms of weed control, will impose a selection pressure that, if strong enough, will lead to resistance evolution. In the case of *L. rigidum*, the repeated use of HWSC is expected to result in plants that have a more prostrate growth habit and/or early seed shedding, both of which would result in a reduced proportion of seed retained above the low harvest height of 10 cm at crop maturity. Australian growers are now well aware of the potential for adaptation in *L. rigidum* populations and are reporting concerns of adaptation to HWSC. Across the nine + / − HWSC comparison locations, *L. rigidum* seed retention was not consistently reduced (P > 0.05) in fields where HWSC had been used between 5 to 10 times compared with nearby fields with no history of HWSC use (Table 3; Figure 4). Although seed retention was lower for six of the nine + / − HWSC comparison sites, there were only two instances (Site 64 vs. Site 68 and Site 59 vs. Site 58) where these differences were significant (P < 0.05) (Table 3). In all other comparisons there were no differences (P > 0.05) in seed retention above the 10-cm canopy height.

Lolium rigidum seed production was on average lower in fields with a history of HWSC use; however, this reduction was not consistent across all + / − HWSC comparisons. In fields with a 5- to 10-yr history of HWSC use, average *L. rigidum* seed production (1,383 seeds m^{-2}) was lower (P < 0.05) than in fields where there was no history of HWSC use (2,014 seeds m^{-2}). This lower average seed production for + HWSC fields was mostly due to large reductions (>2,000 seeds m^{-2}) in *L. rigidum* seed production for three of the comparisons (Table 3). For the majority of the + / − HWSC comparisons, there were no differences (P > 0.05) in seed production; however, lower (P < 0.05) seed numbers were recorded in the − HWSC field in one comparison (Site 71 vs. Site 55). As sampling sites were specifically located in areas where *L. rigidum* was present, there were no differences (P >0.05) in plant densities between + and − HWSC sites (unpublished data), which was what had been expected.

Lolium rigidum seed was retained uniformly through wheat crop canopies; therefore, the lowest practical harvest height would result in the highest seed collection and HWSC efficacy. On average across the 71 sampling locations, 34% of total *L. rigidum* seed production was retained at and above 40-cm canopy height (Figure 5). Cumulative seed retention values at decreasing canopy heights of 30, 20, and 10 cm were 50%, 62%, and 74%, respectively. Thus, reducing harvest height by 30 cm (from 40 to 10 cm)

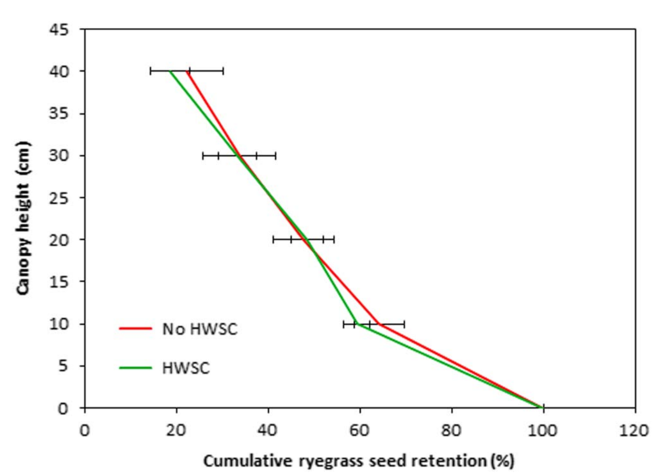

Figure 4. Cumulative rigid ryegrass seed retention as influenced by plus (9 sites) and minus (9 sites) HWSC use over 5–10 years. Bars represent the standard errors of the mean values for plus and minus HWSC sampling sites.

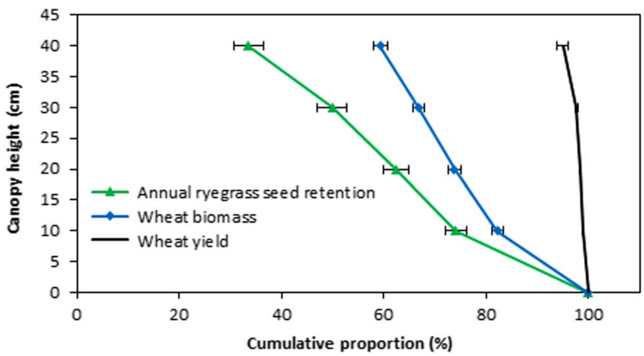

Figure 5. The cumulative proportions of *Lolium rigidum* seed retention, wheat biomass, and wheat yield at decreasing wheat crop heights. Bars represent the standard errors of the mean of 71 sampling sites.

would potentially double HWSC efficiency, from 34% to 70%. Within the crop canopy (10 to 40 cm), there was, on average, a 13% increase in *L. rigidum* seed retention with each 10-cm decrease in height. This uniform distribution of *L. rigidum* seed throughout the crop canopy means that even if a low 10-cm harvest height cannot be achieved, any height reduction will lead to a proportional increase in seed collection during harvest.

Reducing wheat crop harvest height to increase the efficacy of HWSC does not markedly increase the amount of crop biomass collected. To maximize weed seed collection, growers using HWSC systems typically use the lowest practical wheat crop harvest height (10 to 15 cm). The long-held belief is that HWSC systems considerably slow harvest operation, because lowering the harvest height to collect weed seeds markedly increases the amount of crop biomass that the harvester needs to process. Based on average grain heights of the sampled wheat crops, a harvest height of 30 cm would have ensured the collection of at least 98% of grain (Figure 5). At this height, 50% of total *L. rigidum* seed production would have been collected along with 67% of total crop biomass. In contrast, the minimum practical harvest height of 10 cm would have increased *L. rigidum* seed collection to 74% with 82% crop biomass collected. Therefore, reducing harvest height from 30 to 10 cm to increase *L. rigidum* seed collection by 24% would have resulted in the collection of just an additional 15% of wheat biomass. This survey of 71 wheat crops demonstrated that the major proportion of wheat crop biomass is located at or above the harvest height required for grain collection. Lowering the harvest height for more effective HWSC does not substantially increase the amount of crop biomass collected.

The overall efficacy of HWSC systems on weed populations is directly related to the proportion of total seed production that can be collected during the harvest operation. This survey of Australian wheat fields determined that *L. rigidum* seed retention at crop maturity is highly variable and, therefore, will result in variable results for HWSC. The impact of crop competition/shading on seed retention indicates the potential for using agronomic approaches to increase the proportion of seed retained at a height that can be collected during harvest. Using agronomy to increase crop competition will have the dual effect of increasing HWSC efficacy and reducing weed seed production. Although there is no evidence of field-evolved resistance to HWSC, increasing the proportion of total seed production collected will increase selection pressure. Countering this is the reduced genetic diversity that occurs when weed populations are dramatically reduced through HWSC use as part of a weed management program.

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