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Genetic Variation for Weed Competition and Allelopathy in Rapeseed (*Brassica napus L.*)

Harsh Raman, Nawar Shamaya and James Pratley

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Abstract

Rapeseed (canola, *Brassica napus* L.) is the second major oilseed crop of the world and provides a source of healthy oil for human consumption, meal for stock markets and several other by-products. Several weed species afflict the sustainable production and quality of canola. Various agronomic practices such as crop rotation, stubble management (e.g. burning), minimum tillage, application of herbicides and cultivation of herbicide resistant varieties have been deployed to minimise yield losses. There is no doubt that herbicide-tolerant cultivars enable management of weeds which are difficult to control otherwise. However, widespread usage increases the risk of herbicide resistance. This is becoming a major impediment in sustaining high crop productivity. Allelopathic and weed competitive varieties are potential tools to reduce the dependence on herbicides and could be grown to suppress weed growth in commercial canola. Genetic variation and 'proxy' traits involved in both crop competition as well as allelopathy have been reported. Further research is required to link genetic variation in weed competition and allelopathy, and genetic/genomic marker technologies to unravel effective alleles to expand breeding activity for weed interference in canola.

Keywords: canola, allelopathy, weed competition, genetic variation, QTL mapping, genome wide association analysis

1. Introduction

Rapeseed (canola, *Brassica napus* L, 2n = 4X = 38) belongs to the family *Brassicaceae,* which is widely distributed across subtropical to temperate regions. It is thought to be originated as a result of natural hybridisation event between *Brassica rapa* (2n = 2X = 20, genome AA) and

Brassica oleracea (2n = 2X =18, genome CC) [1]. Rapeseed is a close relative of *Arabidopsis thaliana*, a weed species widely distributed in the Northern hemisphere that diverged from *Brassica* ~20 million year ago [2]. Although rapeseed was domesticated approximately 400 years ago, it has become, in recent decades, the leading oilseed crop worldwide [3], providing about 13% of the world's edible oil supply [4]. In Australia, canola was commercially grown for the first time in 1969 [5]. During the last four decades, the rapeseed industry has expanded exponentially with the development and cultivation of canola quality varieties having less than 2% erucic acid and less than 40 micromoles/g meal glucosinolates as well as resistance to blackleg disease, caused by the fungus, *Leptosphaeria maculans*. Higher grain prices and deployment of high yielding and herbicide tolerant hybrid varieties have further played major roles in its expansion. Currently, canola is the third largest broad-acre crop in Australia and is grown on more than 2.3 million ha [6] in a range of environments (*i.e.* <200 mm to >800 mm rainfall) [5]. Canola is usually sown in rotation with cereal crops such as wheat and barley to manage weeds and diseases of both crop types. Research has shown that canola can increase yields of wheat by up to15% [7].

Several weed species such as wild radish (*Raphanus raphanistrum*), shepherd's purse (*Capsella bursa-pastoris*), capeweed (*Arctotheca calendula*), Indian hedge mustard (*Sisymbrium orientale*), annual ryegrass (*Lolium rigidum*) and Paterson's curse (*Echium plantagineum*) afflict the production of canola. Weeds compete with the canola crop for water and nutrient uptake, and for solar radiation. This results in a reduction in the grain yield as well as in grain quality. Up to 90% reduction in grain yield of canola has been reported under high infestation of wild radish [8]. Improved agronomic practices such as stubble burning, minimal tillage, crop rotation, and application of herbicides provide valuable tools in managing weed populations. The option of manual weeding is not cost-effective for broad-acre crops such as canola. Various herbicide groups (A, B, C, D, I, K, M, and N) are currently used to control weeds in canola [9] . In addition, crop rotations provide the opportunity to rotate herbicide groups and delay the evolution of herbicide-resistant weed populations.

2. Development of herbicide resistant varieties

Several herbicide-tolerant canola varieties marketed as Clearfield™ (CL), Roundup Ready™ (RR), and Triazine Tolerant™ (TT) are currently cultivated to widen the herbicide spectrum for control of weeds in canola and other crops. This strategy has played a major role in transforming the canola industry in Australia. The first TT variety of canola, 'Siren', was developed in 1993. Since then, there has been a continuous supply of open-pollinated as well as hybrid TT varieties for commercial cultivation. Although TT varieties had a 10–15% yield penalty [10] and lower oil content, these varieties have been popular among growers particularly where wild radish has been a problem, accounting for 70% of the cropped area in some states of Australia. These varieties have enabled an effective and cost effective management of common weeds, particularly wild radish, and those which are resistant to Group A and B herbicides. The other herbicide tolerant varieties, RR and CL, do not impose yield penalties.

Canola seems to be particularly vulnerable to competition from broad-leaf weeds as there are limited commercial herbicide options available. The canola industry is thus becoming more and more reliant on the herbicide tolerant varieties to provide control options for these major weeds. Analysis of weed resistance status indicates that key canola weeds in Australia are well known for their multiple herbicide sites of action resistances (**Figure 1**) and so existing herbicide options are either compromised or are likely to be. In recent decades, the heavy reliance on herbicides has led to herbicide resistance in numerous weed species such as annual ryegrass and wild radish with major concern being the increased incidence in particular, to Group M herbicide, glyphosate (Roundup®). Many farmers use glyphosate as a pre-planting herbicide to provide a weed-free seedbed. The advent of Roundup Ready (RR) crop varieties has transformed the use of glyphosate into an in-crop broad spectrum, selective herbicide. As a result, it has become the last herbicide used in the season and so any escapes from that use help to build glyphosate-resistant weed populations in subsequent seasons [11].

Evaluation of the herbicides with the highest number of species for which herbicide resistance has been recorded (**Figure 2**) shows that of the 15 herbicides listed, eight are likely to be utilised in canola production, including Imazamox and Imazethapyr for CL canola, glyphosate for RR canola and atrazine and simazine for TT lines. With the development and commercial cultivation of genetically modified (GM) canola, there is now more flexibility to control a broad-spectrum of weeds through stacking of herbicide tolerant traits. For example, farmers now have access to hybrid varieties which have tolerance to glyphosate and triazines, providing pre-emergence as well as in-crop selective herbicide capability. Unfortunately, this gene stacking strategy for herbicide tolerance has further increased herbicide dependency [13] and is likely to lead to quicker herbicide resistance which in turn unfortunately will reduce weed control options.
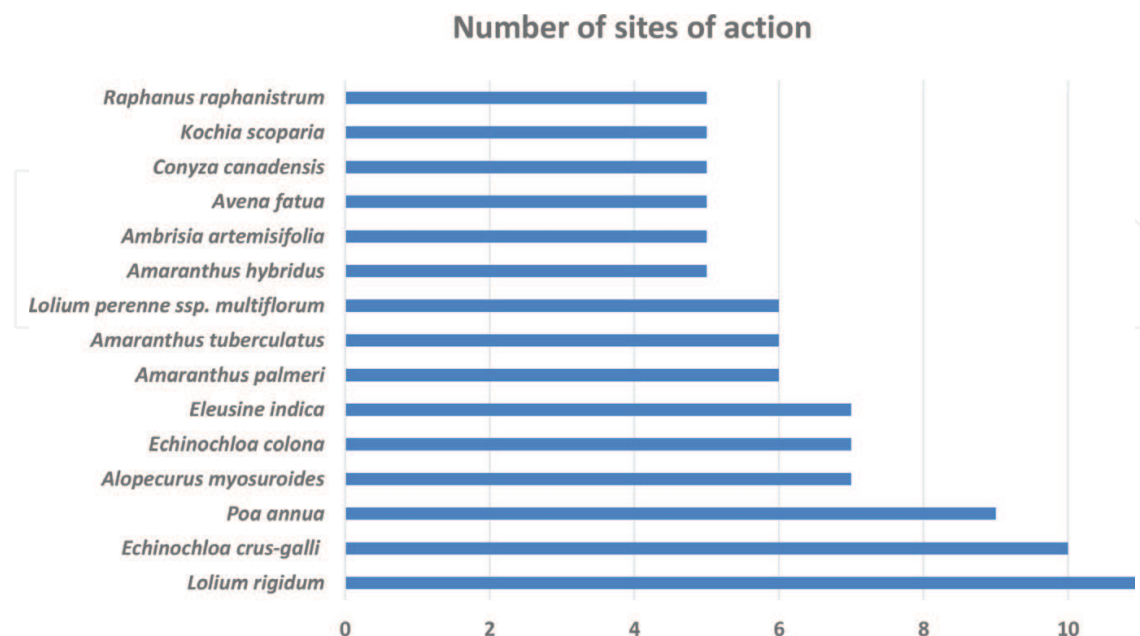

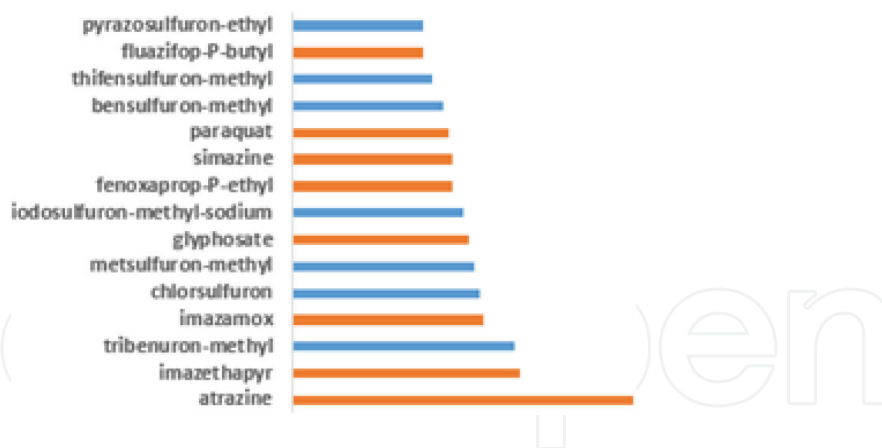**Figure 1.** Weed species resistance to multiple sites of actions [12].

Figure 2. Number of most common resistant species to individual active herbicides (adapted from Heap [12]). Herbicides for use on canola are indicated in orange.

Application of herbicides has its own limitations; the practice is expensive, there is a risk of spray drift to neighbouring crops, and weed resistance threatens the on-going efficacy of the herbicide armoury. An alternative approach is to breed new varieties with improved genetics for weed interference. This interference, which is environmentally friendly, can be of two types: high competitiveness and/or allelopathy. In either case the crop does most of the weed management and herbicides are used in a supplementary way, if at all.

3. Alternative approaches used for weed management: Interference

Crop interference as a tactic has been explored in some crops [14, 15]. It can be defined as the crop plants interfering with weed growth through competition for environmental resources [16] or the crop modifying the growth environment chemically to the disadvantage of the weed [16, 17]. These mechanisms are distinct but seem to act collectively to control weed populations under field conditions [18]. Although allelopathy includes growth promoting, and inhibiting effects, it is usually used to describe growth inhibiting effects [19]. Management practices also can and should assist these processes: for example, growers can manipulate crop sowing times and sowing rates to disadvantage the weeds relative to the crop as well as impose practices that minimise weed seed additions to the seed bank.

3.1. Genetic variation for weed competition

Crop competition is the ability of crops to adapt to weed infestation by accessing limited resources also sought by neighbouring weeds. Traits associated with weed competition are generally related to morphology and phenology of both weed and crop species [20]. Several traits related to competitive ability include plant height, tiller number, leaf angle, canopy structure, early vigour and time to maturity [20]. A good understanding of component attributes underlying those traits would provide an opportunity to improve weed competition of crops using genetic and genomic tools.

Morphological traits related to the interception of radiation by leaves which determine competitiveness for light, including leaf size, number and leaf area index, stem elongation, upward leaf movement [21–24] and leaf layer density [25], have not been studied in canola. These traits are associated with shade avoidance, enabling plants to photosynthesise and grow to improve their competitiveness [21, 22]. Height at maturity has also been reported to contribute to competitive ability [26, 27] although a negative relationship between plant height and weed infestation has been reported for canola [28] and wheat [27]. No such relationship has been found in rice [18]. This trait however tends to have a negative effect on grain yield due to a reduced harvest index.

In wheat, Coleman et al. [29] and Mokhtari et al. [30] showed the normal distribution for phenotypic variation for competitive ability traits in populations derived from crosses between competitive and non-competitive parents. This suggests that the competitive ability trait is controlled by quantitative genes which have minor and moderate effects. Competitive ability associated traits seem to have moderate to highly heritability. In bread wheat, [29] estimated narrow-sense heritabilities for different agronomic and morphological traits associated with weed competition to be: high for flowering date (0.99) and height stem elongation (0.91); low for tiller number (0.34), leaf area index during stem extension (0.18–0.31) and crop dry matter (0.18). Mokhtari et al. [30] estimated the narrow-sense heritability of percentage yield loss due to the weed competition in $F_2:F_3$ populations of wheat: 0.25 for the population derived from crossing two late flowering time parents and 0.57 for the population derived from crossing between two early flowering time parents.

In rice, broad-sense heritability of weed biomass and crop grain yield under weedy conditions was reported [31] to be high (0.64 to 0.79) for 40 upland rice cultivars grown under weed and weed-free conditions. Another study by Zhao et al. [32] also found that broad-sense heritability was high, being 0.88 for early vigour and 0.81 for crop height 4 weeks after seeding. Although heritability is an indication of phenotypic variation due to genetic effects, the estimation of broad and narrow-sense heritabilities for traits are influenced by population structure and environmental factors.

The genetic bases and extent of variation associated with competitive ability in *Brassica* crops have received attention. In canola, plant height, leaf size, leaf number and leaf area index, stem elongation, upward leaf movement and leaf density are considered as the most important attributes for above ground competition for light; and plant root size and depth, relative growth rate, biomass, root density and total root surface area are the most important traits for below ground competition for space, soil nutrients and water [33]. However, only limited component traits have been studied so far to determine the extent of genetic variation in *Brassica* species. For example, Beckie et al. [34] compared the competitive ability of canola with yellow mustard (*B. juncea*) against wild oats. Yellow mustard was superior in competitiveness to canola due to its rapid growth and plant height resulting in early-season crop biomass accumulation. It has also been shown that canola hybrid varieties are more competitive than open pollinated varieties due to their faster growth and biomass accumulation [35]. Harker et al. [36] confirmed the stronger competitive ability of hybrid canola varieties especially under cool and low growing degree day conditions. In an Australian study, Asaduzzaman et al., (unpublished) compared the weed

competiveness of 16 *Brassica napus* genotypes representing open pollinated, F_1 hybrid and TT lines against annual ryegrass and associated weeds and showed that open pollinated and hybrid genotypes reduced weed shoot biomass by 50% compared with less vigorous TT genotypes. In a recent study, Shamaya et al. [37] evaluated the competitive ability of 26 canola genotypes against annual ryegrass (*Lolium rigidum*) under field and glasshouse conditions to study the phenotypic traits associated with weed competition. Under both conditions, the canola biomass, mostly leaf biomass measured in the glasshouse only, was positively associated with competitive ability.

3.2. Detection of QTL for weed competitiveness

Several studies have employed the Quantitative Trait Locus (QTL) mapping approach for detecting, localising and determining the magnitude of loci affecting phenotypic variation for weed competition in plants (**Table 1**). The QTL mapping approach is based on the statistical association between phenotypic and molecular marker polymorphism data. Several molecular markers such as Restriction Fragment Length Polymorphism (RFLP), Single Feature Polymorphism (SFP), Diversity Arrays Technology (DArTs), Random Amplified Polymorphic DNAs (RAPDS), Simple Sequence Repeats/Microsatellites (SSRs), Amplified Fragment Length Polymorphisms (AFLPs), Cleaved Amplified Polymorphic Sequence (CAPs) and Sequence-Related Amplified Polymorphism (SRAP) have been used extensively to genotype populations for genetic analyses [38–44]. More recently, whole genome sequencing methods enabled to develop new marker systems such as genotyping by sequencing based on the complexity reduction methods including DArTseq, Single Nucleotide Polymorphisms (SNPs), restriction-site associated DNA (RAD), RNA-Seq and sequence captures that are more suitable for high-throughput analyses [45–50].

Two strategies based on Quantitative Trait Locus (QTL) mapping and genome-wide association mapping (genome-wide association study, GWAS) approaches have been used to understand the genetic basis of natural variation for weed interference in various crop plants such as rice, corn, wheat, cowpea, barrel clover, peas, sorghum, sunflower and *A. thaliana* [51–57]. In *B. napus*, QTL for various traits of agronomic importance including seed germination/plant emergence, fractional ground cover (early vigour), plant biomass, flowering time, plant height, plant maturity, grain yield, resistance to various biotic and abiotic stresses and seed shattering have been mapped using traditional and GWAS [49, 58–74]. However, no QTL associated with weed competition and/or allelopathy has been identified to date.

QTL for weed competition traits have been mapped in cereals and other crops. For example, in wheat Coleman et al. [29] utilised the genetic linkage map based on RFLP, AFLP, SSR, known genes and protein markers of doubled haploid (DH) populations derived from Cranbrook/Halberd to investigate the genetic control of various traits involved in grain yield loss and suppression of ryegrass growth. These traits included the width of the second leaf, canopy height, light interception at early stem elongation, tiller number, days to anthesis and plant height. Several consistent QTL for flag leaf area, flag leaf length, flag leaf width, height at stem elongation, and tiller number were identified in the vicinity of photo-period genes (*Ppd-B1* and

Competitive ability

Species	Population type	Population size	Trait	Season	Chromosome	R^2	Reference
Wheat (*Triticum aestivum* L.)	Doubled haploid lines derived from Cranbrook/ Halberd	161	Yield	1999	3A	12.2	Coleman et al. [29]
					3B	9.8	
			1000 – grain weight	1998	5A	11.0	
					2D	8.4	
				1999	5A	12.0	
					2B	9.9	
Wheat (*Triticum aestivum* L.)	Recombinant inbred lines derived Opata 85/ and synthetic W7984	108	Early Season Vigour	2005	5A	16	Reid [75]
				2006	5A	22	
			Days to Heading	2005	5A	21	
				2006	5A	21	
			Day to Anthesis	2005	5A	20	
				2006	5A	17	
			Days to Maturity	2005	5A	13	
				2006	5A	19	
			Weed Suppression	2005	5A	14	
				2006	5A	15	

Allelopathy

Species	Population type	Population size	Trait	Season	Chromosome	R^2	Reference
Wheat (*Triticum aestivum* L.)	Doubled haploid lines derived from Tasman (strongly allelopathy) Sunco (weakly allelopathy)	271	Reduction in annual ryegrass using the Equal-Compartment-Agar-Method [89]		2B	29	Wu et al., [57]
Rice (*Oryza sativa* L.)	F$_2$ – F$_3$ population derived from *Indica* line PI312777 (strongly allelopathy) *Japonica* cv Rexmont (weakly allelopathy)	192	Reduction in lettuce root length using water-soluble extract method [116]		1, 3, 5, 6, 7, 11, 12	9.4– 16.1	Ebana et al., [112]
Rice (*Oryza sativa* L.)	Recombinant inbred lines derived from crossing cv IAC 165 (strongly allelopathy) and cv CO39 (weakly allelopathy)	142	Reduction in barnyard grass root length using relay seeding technique method [117]		3	12	Jensen et al., [113]
					3	7.2	
					8	8.5	
Rice (*Oryza sativa* L.)	Doubled haploid lines derived from *Japonica* Jingxi17 (strongly allelopathy) *Indica* Zhaiyeqing 8 (weakly allelopathy)	123	Reduction in lettuce root length using water-soluble extract		3	10.24	Dali et al., [118]
					9	8.24	
					10	8.27	
					12	9.79	
Rice (*Oryza sativa* L.)	Recombinant inbred lines derived from *Indica* cv AC1423 (strongly	150	Reduction in *Echinochloa crus-galli* root length using		4	11.1	Jensen et al., [114]

Competitive ability

Species	Population type	Population size	Trait	Season	Chromosome	R²	Reference
	allelopathy)/*cv.* Aus196 (weakly allelopathy)		relay seeding technique method [117]				
			Echinochloa crus-galli root length from greenhouse pot set-up		4	9.6	
			Echinochloa crus-galli root biomass from greenhouse pot set-up		3	5.0	
					6	6.9	
			Echinochloa crus-galli shoot length from greenhouse pot set-up		3	5.9	
					8	7.1	
			Echinochloa crus-galli shoot biomass from greenhouse pot set-up		8	5.1	
					12	5.8	
Rice (*Oryza sativa* L.)	Recombinant inbred lines derived from cv. Zhong-156 (strongly allelopathy)/cv. Gumei-2 (weakly allelopathy)	147	Allelopathy index determined by secondary metabolite		11	16.5	Zhou et al. [111]

Table 1. Genetic analysis of mapping populations for crop competitiveness and allelopathy.

Ppd-D1) on the group 2 chromosomes. Three QTL for plant height at anthesis were detected on chromosomes 3A, 4B and 5A. No QTL for crop yield loss in the presence of ryegrass or ryegrass dry matter suppression was identified in this population, likely due to the complex nature of this trait [29]. However this study reported that ryegrass dry matter was suppressed for DH lines of wheat with greater leaf area index, more tillers, taller plant height and later flowering. High genetic correlations between leaf area index and grain yield loss (r = −0.81) as well as suppression of ryegrass (r = −0.91) were observed indicating that traits contributing to early ground cover would be important for developing competitive wheat genotypes. Another wheat study conducted in the northern region of Canada determined a cluster of QTL associated with traits implicated in weed competition [75] using 108 recombinant inbred lines derived from a cross between Mexican wheat, Opata 85, and a synthetic wheat accession, W7984. Early vigour, day to heading, day to anthesis, day to maturity and weed suppression were mapped to the same region on chromosome 5A corresponding to the position of the

vernalisation gene *Vrn-A1,* suggesting that flowering time may be associated with weed suppression.

In rice (*Oryza sativa* L), a mapping population developed from a cross between a weed-suppressive 'indica' rice line and a non-weed suppressive 'japonica' cultivar was used to study the genetic bases of variation for seedling germination, shoot length and dry matter weight. Thirteen QTL were detected and each QTL explained 5–10% of the phenotypic variation of the traits [76].

GWAS has been employed to investigate the genetic architecture of weed competition in *A. thaliana*, and rice [51, 55]. For example, a set of 195 accession of *A. thaliana* grown with the presence and absence of bluegrass, *Poa annua*, were analysed for trait (29 phenotypes related to phenology, resource acquisition, hoot architecture, seed dispersal, fecundity, reproductive strategy and survival)-marker association [51]. Several significant SNP associations for yield (fruit number on basal branches) with and without weed competition were identified. This study further identified a candidate gene, *TSF* (*TWIN SISTER OF FT*) which was associated with flowering time, duration of flowering, climate variation, the number of primary branches and escape strategy to competition, suggesting adaptive strategy to escape competition. However, no such study has been conducted in canola to identify genes which control weed competition and/or allelopathy.

3.3. Genetic variation for allelopathy

Allelopathy is a mechanism whereby a plant ensures itself a competitive advantage by placing phytotoxins into the adjacent environment [17]. Numerous allelochemicals that affect weed species have been identified and characterised [77]. Their existence varies with species and variety, and will almost always operate as a 'cocktail' of chemicals from any one source. An et al. [78], for example, showed that the allelopathic capability of *Vulpia* spp. involved more than 20 separate compounds. The role of allelopathy in suppression of weed growth has been studied in a range of crops including wheat [57], rice [79–82], barley [83], cotton [84], and sorghum [85].

Different laboratory based assays used to measure the allelopathy activity have been reviewed by Wu et al. [90]. These include the 'plant-box method' [86], the 'relay-seeding technique' [87], the 'equal-compartment-agar-method' or ECAM [88–90], and hydroponic methods [91, 92]. Generally, these assays involve growing of seedlings of the donor plants (*e.g.* crop species) in the presence of, or followed by, weed species for a short period of time. The allelopathic crops such as *Brassica rapa, B. juncea, B. nigra, B. hirta* and *B. napus* exude phytotoxic compounds [93–97] which suppress the growth of the weed species depending on the tolerance of the receiver plants to the chemicals being exuded. In the field, it is necessary to recognise that there would be an exchange of allelopathic chemicals between crop and weed with the outcome determined by relative potency of the allelochemicals and the tolerances of the receiving plants to the chemicals received [98]. Allelopathic activity is measured as the reduction of weed root growth in the presence of allelochemicals relative to that in the absence of the donor plants.

One question often raised is whether the laboratory method reflects performance under field conditions. Seal et al. [99] for rice and Asaduzzaman et al. [88] for canola both showed high correlations between the ECAM method in the laboratory and field performance. The other question is how field performance can be attributed to allelopathy. Unfortunately, there is no simple measure. In some cases inspection of the roots of affected plants show symptoms of inhibited development, such as root pruning, thickened roots and distortions not normally seen. In most cases, it has to be assumed that if field performance matches that in the laboratory then allelopathy is at least part of the explanation. Root exudates can be collected and analysed for bioactive compounds. Such compounds can be then applied to the receiver plants to ensure that the same outcome is achieved as described in [100]. Weidenhamer [101] has shown that it is possible to measure the presence of allelochemicals *in situ* in the rhizosphere using a sorptive coated stir bar inserted into the measurement zone for subsequent analysis by HPLC.

Phytotoxic allelochemicals have also been identified in *Brassica* plant residues and exudates that are known to suppress weed infestation [19, 95, 102]. *Brassica* species are also well known to synthesise glucosinolates which have shown allelopathic effects on pathogens due to the production of isothiocyanates. This process has been coined biofumigation [103, 104].

Genetic variation for allelopathy in canola and its related species, *Sinapis alba L.* has been studied [93, 105, 106]. Asaduzzaman et al. [107] investigated allelopathy among 70 diverse accessions of canola using annual ryegrass (*Lolium rigidum*) as the 'test' weed. The range of allelopathic impacts is shown in **Figure 3**. One *B. napus* cultivar of Australian origin, cv 'Av-Opal', was strongly allelopathic both in the laboratory and in the field whereas commercial cv. Barossa was at the other extreme in both laboratory and field. Field study showed that the allelopathic trait is independent of plant biomass and grain yield, and no consistent relationship between plant height and weed competitive ability was found among genotypes.

The greater weed suppression ability of cv. Av-Opal was confirmed in a two-year field study against annual ryegrass and other weeds (shepherd's purse, Indian hedge mustard and barley
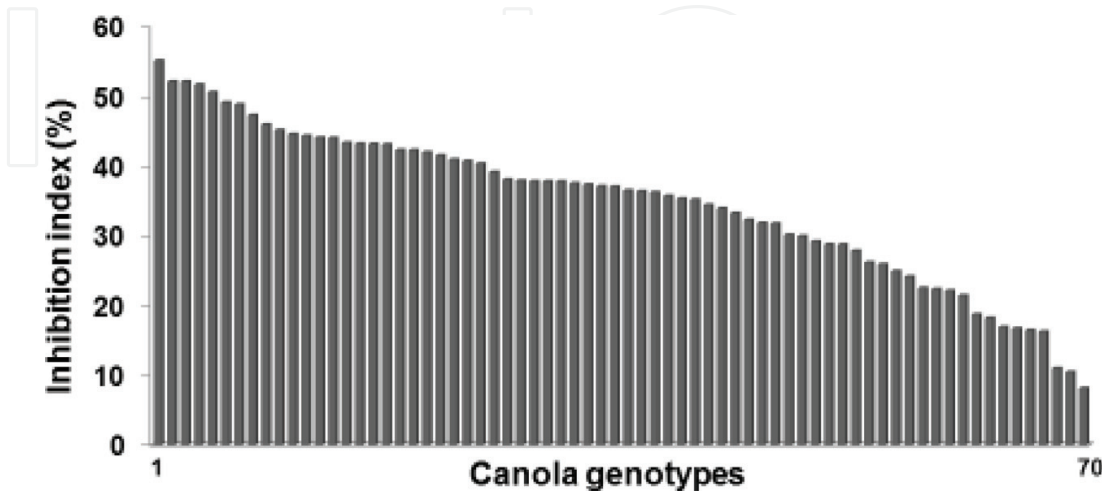

Figure 3. Allelopathic effect of 70 canola genotypes on root length of annual ryegrass seedlings (lsd = 10) [107].

grass) relative to cv. Barossa [28, 107]. Interestingly, Av-Opal was not exceptionally competitive as it is of short stature and poorly adapted to adverse environmental conditions [28]. In a subsequent study, Asaduzzaman et al. [108] investigated the biochemical basis of the allelopathy and detected numerous bioactive secondary metabolites including sinapyl alcohol, *p*-hydroxybenzoic acid and 3,5,6,7,8-pentahydroxy flavones in the root exudates. A comparison of the allelopathic capabilities between cv. Av-Opal and cv. Barossa is shown in **Figure 4**.

3.4. Detection of QTL for allelopathy

The genetic bases of allelopathy activity have been investigated in wheat [57, 110] and in rice [111–115]. For wheat, doubled haploid lines were developed from the strongly-allelopathic cultivar Tasman and the non-allelopathic cultivar Sunco. Significant differences were recorded for root growth of annual ryegrass between the doubled haploid lines [89]. Analysis of RFLP, AFLP and SSRs markers identified two major QTLs on chromosome 2B associated with wheat allelopathy.

In rice, several QTL have been detected across the rice genome and these QTL explain 5–36.6% of phenotypic variation in crop interference traits (**Table 1**). Jensen et al. [113] identified four major QTL on chromosomes 2, 3 and 8 which accounted for 35% of total variation of the allelopathic activity in the RIL population derived from japonica cv. IAC165 (allelopathic parent) and indica cv CO39. Ebana et al. [116] identified a major QTL on chromosome 6 accounting for 16.1% of the phenotypic variance in an F_2 population of 192 lines from indica line PI312777/japonica line Rexmont. Jensen et al. [114] identified QTL for RLSWRL and GHWRL on the same genomic marker interval, confirming that major genes for weed root length may be located in this region. The most important QTL were on chromosomes 3, 5, 8

Figure 4. A comparison of a strongly allelopathic cultivar (AV-opal, left) and a weakly allelopathic cultivar (Barossa, right) [109]. Barossa plot showing extensive growth of different weeds.

and 11 [111, 116]. This indicates that allelopathy activity in cereal is controlled by quantitative loci. The relatively low phenotypic variation for the individual QTL is explained by the difficulty in measuring the allelopathic traits at the individual genotype level.

4. Conclusions

Herbicide resistance is a major impediment in sustaining high crop productivity. The lack of new chemical modes of action becoming available emphasises the need for novel approaches to control weeds. Crop competitiveness and allelopathy are potential tools to reduce the dependence on synthetic chemical inputs and in so doing may extend the lives of key herbicides. A challenge for researchers is to be able to separate competitiveness from allelopathy in the field. For crop producers it does not really matter whether it is one or the other or both as long it works. A further challenge for researchers is attracting funds to undertake this work to commercial outcomes.

What are the prospects of herbicide resistance evolution occurring to allelochemicals? Of course the risks exist but they are likely to be much lower for at least two reasons: firstly allelopathy relies on a mix of chemicals at any one time from a single crop; and different crops have different mixes of chemicals so that in a rotation of crops, weeds will be exposed to chemicals of different modes of action only once or twice in a rotation cycle.

Phenotyping traits associated with allelopathic activity, such as reduction of weed growth in the laboratory and field, with high-throughput genotyping technology such as sequencing and mapping populations, allow researchers to detect QTL and genes associated with allelopathy and weed competition. It is an open question whether weed competition and allelopathy are distinct traits, but if this is the case, both traits could be pyramided in a single variety. In addition to genetic and phenotypic information, functional 'omic' data, such as identification of secondary metabolites, can be integrated in the QTL analysis leading to the detection of genes and pathways responsible for allelopathy activity. This would enable the development of novel alleles to expand breeding activity for weed interference in canola.

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Conflict of interest

Authors do not have conflict of interest to declare.

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