SYSTEMATIC STUDENT REVIEW

Canola Interference for Weed Control

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Abstract The increased incidence of herbicide-resistant weed species, and the related biological repercussions, poses a major threat to sustainable crop production. Integrated weed management, which involves greater reliance on non-chemical weed management tactics such as crop interference, needs to be included in canola production systems. Crop interference comprises both competition and allelopathy which favour the growth of the crop. This review examines canola plant traits associated with competitiveness and allelopathy. Competitive ability is evaluated by the ability of plant morphological traits to improve access to scarce light, nutrients and water in a limited space. Allelopathy refers to the harmful or beneficial effect of crop biochemicals on neighbouring weed species. Allelochemicals are a subset of secondary metabolites produced from intact living roots and crop residues that differ between cultivars and have specific defensive functions in the rhizosphere. Elite allelopathic cultivars can be identified by screening canola germplasm. The identification of the allelochemicals involved and their effects in the field also need to be explored. The impact of genetic variation, the mechanisms of allelopathic action, the source and fate of allelochemicals and associated biota in the rhizosphere all need to be considered in new cultivar development. The breeding of weed-suppressive allelopathic canola cultivars needs to be in the context of good agronomic performance. Although allelopathic canola cultivars are unlikely to eliminate all weed pressures in the field, the extent to which they contribute in weed management is worthy of exploration. It remains to be known whether combined competitive and allelopathic cultivars can be developed to maximise overall interference. The integration of agronomic practises with canola interference also needs to be developed.

Keywords Competition · Allelopathy · Root exudates · Rhizosphere · Metabolites

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Introduction

Canola (*Brassica napus* L.) is a member of *Brassicaceae* family with low glucosinolates and erucic acid content relative to traditional rapeseed (*B. napus* L.). It is a major oilseed crop, ranked as the second most important global source of vegetable oil [131]. Canola is also a potential source of specific protein and industrial raw materials including biopolymers, surfactants, adhesives and, more recently, biodiesel [170]. The annual worldwide increase in canola production has been substantial and it is predicted to exceed 15 million tonnes by 2015 [28, 29]. Australia is the world's second largest exporter of canola seed after Canada

and canola is Australia's third largest broad-acre crop after wheat and barley. The Australian Oilseed Federation [5] predicts that prospects for the Australian canola industry are excellent due to good commodity prices, market demand and its value in the farming system. Canola is, therefore, an attractive alternative crop for grain growers. The rapidly growing demand for canola worldwide implies both greater yield and greater area of production, utilising better management practises and improved cultivars.

Weeds commonly occur in canola crops [95] and their infestation is a major yield-reducing factor [139]. Weeds interfere with crop plants, causing serious impacts as a result of competition for either above or below-ground resources [113]. Canola is exposed to severe competition from weeds which are often considered as the most yield limiting factor in Canada [155]. In India, Gill et al. [63] reported that the magnitude of loss from weeds ranged from 30 to 50 %, depending on the growth and persistence of the weed population in the standing crop. Grass weeds, such as annual ryegrass (*Lolium rigidum*), vulpia (*Vulpia myuros*) and wild oat (*Avena fatua*) were most abundant in canola crop of south-eastern Australia [95]. Interference may be through severe soil nutrient depletion [173], water and shading.

Weed competition also reduces grain yield and quality and market value of the canola seed. In Canada, Rose and Bell [136] showed that presence of seeds of wild mustard (*Sinapis arvensis*) and stinkweed (*Thlaspi arvensis*) in canola seeds mixtures reduced the seed quality of canola by increasing the level of erucic acid in the extracted oil and the glucosinolate content of the remaining meal. In Australia, heavy infestations of wild radish (*Raphanus raphanistrum*) have reduced canola yields by up to 90 % [22] and such infestations greatly reduced the quality of canola meal both through crop stress and direct seed contamination of harvested product [33, 101].

The use of herbicides and herbicide tolerant canola cultivars has increased rapidly in Australia and worldwide. However, the over reliance on herbicides can reduce their effectiveness and lead to the evolution of herbicide-resistant weeds [12]. High population densities of some weed species necessitate the input of more herbicides but the high use of herbicides exacerbates the development of the resistance problem [77, 126]. The widespread use of triazine-tolerant (TT) canola cultivars has increased the use of triazine herbicides and has led to increased triazine-resistant populations of wild radish in Australia [72]. The escalating problem of herbicide-resistant weeds is a challenge to farmers as is the need to manage agrochemicals to minimise soil herbicide residues that can negatively impact on succeeding crops.

Integrated weed management systems have the potential to reduce herbicide use and their associated costs where there is greater reliance on non-chemical control tactics including enhancing crop interferences. It has been shown that the reliability of herbicide performance can be improved when combined with crop species or varieties of superior competitiveness [37, 91].

Interference is the term used to describe an induced effect by an individual plant on a neighbour through changes in the immediate environment [70]. It comprises competition and allelopathy. Zimdahl [173] reported that it is the total adverse effect that both plants exert on each other when growing in a common ecosystem. Competition is the negative interaction between two or more plant species for existence and superiority within a limited space [47]. Competition is greatest when available resources for both crop and weed are below the combined demand [47]. The phenomenon occurs between individuals of the same species (intra-species) and between individuals of different species (inter-species). Allelopathy is distinct from other negative plant interference in that the detrimental effect is through release of chemicals by a donor plant [133]. Molisch [109] indicated that this chemical interference can be both harmful and beneficial. At high concentrations allelopathic chemicals can act as inhibitors while at low concentrations they can sometimes stimulate neighbouring plant growth [110]. Weed responses to crop allelopathy have become well documented in recent decades [129, 135]. However, the impact varies depending on the plant species, cultivar, growth stage and various stress factors. In this review, we examine both forms of canola interference, competition and allelopathy, and discuss possible ways to maximise this beneficial attribute for improved weed control.

Competition

Crops and weeds compete for various resources. The competitive ability of a particular plant is a major factor in suppressing the competitor. An increase in the biomass and/or population density of one species is the most likely route to increase competition for resources and thus influence the growth and survival of the affected species [154]. Competition for resources between species occurs through both above and below-ground interaction. The competitive ability of a plant is an integrated response over time, with contributions from a range of traits.

Above-Ground Competition for Light and Related Canola Traits

Light is an essential determinant of the energy balance of the soil and plant, and it drives water and nutrient transport [10]. Competition for light occurs in most cropping situations soon after seedling emergence [48, 131]. Plants

intercept light using different light attributing characters and a successful plant is not necessarily the plant with more foliage but the plant with foliage in an advantageous position for light interception relative to that of its competitors [47]. Leaves are the principal source of assimilate production during the vegetative phase. In rapeseed (*B. napus*), the lower leaves have been shown to export assimilates basipetally, while the upper leaves exported assimilates almost exclusively acropetally [102]. They translocated and re-translocated the mobile nutrients in the plant system before they senesced [144]. Leaves of rapeseed exerted and developed source-sink capacity during the early growth stage, the expansion rate of leaves being positively correlated with seed yield [38, 153]. Thus, during early development, light interception by the rapeseed plant influences growth rate that determines competitiveness with neighbours. Plant height, leaf size, number and leaf area index are directly related to the interception of radiation by leaves. In Canada, Beckie et al. [13] indentified from field observations that canola height was as an important criterion of plant competitiveness for resources. Daugovish et al. [41] confirmed that the greater competitive ability of wild oat or yellow mustard over canola was attributed to greater plant growth rate and plant height.

Other plant morphological traits such as stem elongation, upward leaf movement [21, 61, 110, 124] and leaf layer density [46] all contribute to competitiveness for light. These plant components usually relate to shade avoidance, allowing plants to photosynthesise and grow to become more competitive [11, 21, 124]. Further, the variation in morphological sensitivity of plants to light signals is known to vary among cultivars [86]. Thus, choice of a suitable shade-avoidance cultivar, combined with agronomic tactics (e.g. crop density and row arrangement), also helps to manipulate crop plant photomorphogenesis. In Australia, vigorous hybrid canolas have generally been shown to compete more successfully with, for example, annual ryegrass than did TT canola varieties [93]. The plant biomass measures of both cultivar types were negatively correlated with weed plant biomass [93]. The study was consistent with Canadian results that suitable vigorous hybrid genotypes provide more competition against weeds [68, 69, 171]. Vigorous hybrids produce tall plants with much foliage, thereby reducing light penetration to the weed canopy. Choice of vigorous cultivars can be an effective crop interference tactic for weed management especially in the early establishment phase of a canola crop.

Below-Ground Competition for Nutrients and Water and Associated Canola Traits

Competition for below-ground resources constitutes an important aspect of crop-weed interaction. This below-ground interference has been reported to reduce plant performance more than do above-ground relations [165]. Below-ground competition usually occurs for space, soil nutrients and water. Plants take up soil nutrients mainly by diffusion and mass flow mechanisms from the depletion zone (the concentration gradient surrounding the roots) [118]. The competitive ability of a crop plant is likely determined by its capacity to make use of nutrients from this zone [47] and plants usually invest relatively more resources into roots compared with shoots for below-ground competition [125]. Efficient nutrient acquisition by roots becomes an important key for plant competitive ability. Characteristics related to nutrient and water uptake include plant root size and depth, relative growth rate, biomass, root density and total surface area [1, 2, 31, 55]. The canola plant has an extensive root system [161] with abundant root hairs [66] to give it high root surface area and large potential to extract nutrients from the soil [66]. Strong and Soper [152] reported that roots of *Brassica* plants proliferate in areas of high nutrient concentration, although differences exist among genotypes in their ability for nutrient acquisition. Nitrogen uptake by canola, for example, has been linked to total root biomass rather than higher uptake per unit of length [81]. However, Laine et al. [89] demonstrated that if one half of the canola root system was starved of nitrogen, the other half was still able to supply the shoot with sufficient nitrogen through increased uptake per unit of root length. The optimisation of canola root traits for nutrient acquisition may link with its competitive ability against different weed species.

The conversion of soil resources to plant biomass (referred to as nutrient use efficiency) differs between species and cultivars [31]. A typical canola plant usually has a higher demand for phosphorus and potassium than does a wheat plant [29, 137, 152]. These demands may influence success in gaining a greater share of the other nutrients to establish dominance over a less successful weed species. Duan et al. [50] reported that the rate of root biomass accumulation in canola was positively correlated with increased lateral root length [50] while, in another study, canola biomass was negatively correlated with weed biomass [92]. The biomass of canola was regulated by the reduced pH in the rhizosphere resulting from the release of organic acids by its roots [50]. In soil, insoluble phosphorus usually becomes more readily available to canola roots through the acidification of soil near the rhizosphere [2, 73, 138]. Understanding the process involved in the acquisition of soil resources, and the associated mechanisms by which canola competes, may help improve the below-ground competitive ability of canola for nutrient acquisition in the presence of weeds.

Plants provide a pathway for water movement between the soil and the atmosphere. This path begins in the soil

with water uptake and is influenced by numerous biotic and abiotic factors [31]. Plants experience competition for water when the moisture supply in the soil environment is reduced (e.g. uptake by neighbour) or is exceeded by the evaporative demand [130]. Donald [47] asserted that the success of any cereal plant for water competition depends on the rate and completeness with which it can make use of the soil water supply. This capacity for water uptake by crops is determined by several attributes within the environment such as transpiration rate and stomatal resistance capacity [31, 78] and the efficiency of water use by plant roots and leaves [75]. Poor stomatal control, for example, results in relatively high plant water use and this may increase competitiveness if the plant neighbours are water conservers [130]. In canola, it is assumed that hybrid cultivars with early vigour use available soil water more quickly, thereby making it relatively unavailable for use by neighbouring weeds. The competitive ability of a cultivar may increase in a specific location due to the environmental influence on evapotranspiration. Although the mechanisms were not clear, it has been suggested that in cool environments hybrid canola induces non-favorable conditions for weed growth by reducing soil resources [68]. Essential nutrients, once inside the canola plant, can be relocated to support growth and, advantageously, they are, therefore, not available to neighbouring weed species.

Plant avoidance and tolerance mechanisms to soil water stress are related to its root morphology and distribution. Pavlychenko and Harrington [122] found that the considerable depth of the root systems of wheat provided good adaption for drought tolerance and weed competition. Likewise in canola, a deep root system is likely a key trait of the plant's ability to access sufficient water. Canola roots have been shown to extract water from a depth of 150 cm although up to 95 % of the total seasonal uptake was removed from the top 105 cm of the soil profile [114]. Thus, cultivars with a deep root system trait may become more competitive by being able to adjust their avoidance or tolerance of soil water stress. Roots of canola and other *Brassica* species, however, are poorly adapted to dry regions and so agronomic adjustment of these early-seeding or early-maturing cultivars may be needed to improve tolerance to competition through better water use efficiency during the seed filling stage. In Western Australia, the early sowing and early flowering cultivars of *B. napus* produced the greatest total dry weight and seed yield due to efficient water use compared with a late sowing [153]. Early flowering cultivars also showed better competitive ability in Canada because they proliferated their root systems as soon as they sensed a water source, enabling them to fully utilise those resources [32]. These data demonstrate key aspects of canola roots in competitive interference: tolerance of water

stress without changes in physiological adaption; and canola root architecture and cellular mechanisms.

Selecting a Competitive Canola Ideotype

The crop ideotype consists of morphological and physiological traits which contribute to enhanced yield relative to currently prevalent crop cultivars. Such a plant will make minimum demand on resources per unit of dry matter production [48]. The design of crop ideotypes, however, may likely involve modifications related to the environment. An evaluation of the competitive ability of different cereal crops, such as rice, wheat and barley, clearly showed that no one ideotype was appropriate for every environment [168]. Different combinations of plant traits could confer the best competitive advantage depending on growing season, climatic conditions and competitiveness with weed species as well as the timing of the competition [168]. Olofsdotter et al. [119] reported that the best competitive plants also have good biotic and abiotic stress resistance. Little consideration has been given to the inclusion of specific plant traits for strong competiveness with weeds to enhance yield stability. Understanding which traits are most strongly associated with competitive advantage of canola is important for developing new cultivars and should include allelopathy in the development of a canola ideotype.

Allelopathy

The term allelopathy originated from the Greek word "allelon" meaning each other and "pathos" meaning suffering and was first introduced by Austrian plant physiologist Molisch [109]. The word "pathos" also means "feeling" or "sensitive" and could, therefore, be used to describe both positive (sympathetic) and negative (pathetic) interactions [65]. The concept of allelopathy received further attention by Rice [132]. He defined allelopathy as an important mechanism of plant interference mediated by the addition of plant-produced secondary products into the rhizosphere [133]. The organic secondary products involved in inhibitory or stimulatory effects are referred to as allelochemicals and these can be released through volatilisation, leaching from plant leaves, residue decomposition and active root exudation [36, 133]. Chemicals with allelopathic potential are present in nearly all plants and their respective tissues [164]. Under the appropriate environmental conditions, these phytotoxic compounds may be released into the environment in sufficient quantities to affect the growth of neighbouring plants [163]. Allelopathy is a significant component of crop/weed interference and, therefore, a potential weed

management tool [15, 82, 117]. Allelopathy includes the use of phytotoxic chemicals released from crop residues as well as from intact roots of living plants [163, 164].

Allelopathy of Canola Residues

Crop allelopathy evidence initially came from studies of the use of organic mulches and cover crops to suppress weed emergence. The presence of growth inhibiting substances in plant residues was reported by Collinson [39]. The decomposition products of residues can exert effects on weed germination and establishment [14, 107, 127, 128, 163] either taken up by the recipient singly, additively or synergistically [54], adsorbed onto soil colloids [40], modified or reduced or biochemically modified (including non-toxic chemicals into toxic chemicals) by soil organisms [58, 147]. These inhibitory allelopathic effects of residues of both native and cultivated *Brassica* spp and their relatives have been reported for weed suppression. Boydston and Hang [24] reported that residues of soil-incorporated foliage of canola suppressed plant populations of common lambsquarters (*Chenopodium album*), redroot pigweed (*Amaranthus retroflexus*), barnyard grass (*Echinochloa. crus-galli*), hairy nightshade (*Solanum sarrachoides*) and longspine sandbur (*Cenchrus longispinus* [Hack.] Fern.) [24]. In Australia, Jones et al. [80] reported that residues of barley, wheat and canola showed adverse effects on the survivability, growth and dry matter production of paradox grass (*Phalaris paradoxa*), wild oat (*A. fatua*) and turnip weed (*Rapistrum rugosum*). Several subsequent weed suppression studies showed that *Brassica* cover crops, such as rapeseed and mustard, have high potential to be used in an alternative weed management system. The researchers concluded that an allelopathic mechanism was involved [3, 24, 25, 85, 158]. Tissue damage and then hydrolysis of the *Brassica* plants released glucosinolate breakdown products, including isothiocyanates, oxazolidinethiones, ionic thiocyanate (SCN−) and organic cyanides [25, 67]. Most breakdown products of glucosinolates are volatile, whereas hydroxamic acids are water-soluble. In the soil, hydroxamic acids can be transformed into more toxic compounds by neighbouring weed species [59, 62]. Although the specific modes of action of these compounds on target weed species have not been thoroughly investigated, most compounds showed inhibitory effects on other species through reduced and delayed germination or inhibition of seedling emergence [115, 116]. The level and the time course of allelochemical release and of other residue-mediated alterations in the soil are largely dependent on the amount and decomposability of the residue, on soil biological, chemical and physical characteristics [34, 96] or on residue management practises [88]. It is unclear whether canola living roots release these compounds in exudation or whether release occurs only during decomposition, and it is worthy of further investigation.

Biofumigation

Biofumigation is defined as the use of biocidal compounds, primarily isothiocyanates, used as commercial fumigants, or released by *Brassicaceous* plants used as green manure or rotation crops, for suppression of soil-borne pests and pathogen [4, 83]. Such compounds have relatively high vapour pressure and are thoroughly dispersed throughout the surrounding soil where they may affect soil-borne fungi, pathogen, insects and nematodes [111]. This finding has led to an increased interest in the development of biofumigation strategies, where naturally formed isothiocyanates could be used as a control measures. Incorporation of *Brassicaceous* plants in order to control pathogens and nematodes has proven to be effective in several studies [108, 112]. The use of canola as a break crop to help control take-all fungus (*Gaeumannomyces graminis*) in cereal rotations in Australia is also an example of this biofumigation effect. However, the inconsistent results in biofumigation studies (reviewed by Matthiessen and Kirkegaard) [103] implied that other factors were involved. The profile of isothiocyanate production varies between *Brassica* species [84, 142, 143, 149, 159], between individuals of the same genotype [53, 84], and even within different plant tissues of a single individual [57, 104]. Furthermore, it needs to be considered that there are beneficial organisms including biocontrol agents, that are also affected by glucosinolate breakdown products and their presence may have consequences for pest control in an integrated pest management (IPM) agro-ecosystem. The existence of the biofumigation capability, however, is demonstrative of the potential of root exudation for crop management. Their role for weed control remains to be evaluated fully.

Canola Allelopathy by Intact Roots of Living Plants

Weed suppression via living plant exudation is considered a promising approach to exploit allelopathy in annual crops [7, 51, 52, 134]. Belz [15, 16] claimed that weed suppression by crop plant root exudation is a valuable mechanism if this trait can be exploited in much the same way as defence mechanisms against insects or pathogens. The approach has already been reviewed for major grain crops including rice [45, 145], wheat [17, 169] and barley [17, 18, 97]. Those reviews showed that the allelopathic ability of a crop plant to defend itself against weeds was possible and there was considerable genetic variability to exploit such mechanism among cultivars. The family *Brassicaceae*

is often reported as having allelopathic properties that can affect establishment and growth of other species by root exudation [14, 98, 156]. An intercropping study between wild mustard and broccoli demonstrated that broccoli yield was reduced by 50 % due to the phytotoxic effect of plant exudation from wild mustard [79]. In the USA, cultivated or naturally occurring mustards often formed relatively pure stands when well established and, in the wild, they can be successful invaders of native grasslands [14, 163]. In Turkey, Uremis et al. [156] found that root exudates of the rapeseed cultivar Westar influenced the root growth of redroot pigweed (*A. retroflexus* L.), black nightshade (*Solanum nigrum* L.), common purslane (*Portulaca oleracea* L.), cutleaf ground cherry *(Physalis angulata* L.) and jungle rice *(Echinochloa colonum)* more than shoot growth, whereas other cultivars Jumbuck, Tobin, Lisoune and Galant showed less allelopathic activity through their root-secreted chemicals. This suggests that canola plants are also likely to show allelopathy through root exudation and raises the prospects of creating elite allelopathic canola genotypes with improved weed-suppressive capability.

Canola Root Exudates and Phyto-Chemistry

Plant living root hairs and actively growing primary and secondary roots typically release large quantities of secondary metabolites (known as root exudates) [19]. This phenomenon has long been regarded as a passive process of secreted photosynthetically fixed carbon into the soil [9]. Root exudates or secondary metabolites represent one of the largest direct inputs of plant chemicals into the rhizosphere and almost certainly root exudates comprise the major sources of allelochemicals [19]. Stressed plants secrete particular secondary metabolites for their defensive activity [6, 162]. For example, *Arabidopsis thaliana* (*Brassicaceae*) secretes a large number of defence metabolites when grown alone [6]. However, once a plant neighbour is identified, the repertoire of metabolites is reduced but overall their secretion increases significantly [6]. In addition to the role in plant defence, some metabolites have physiological functions by serving as mobile and toxic nitrogen transport and storage compounds [166, 167]. However, these multiple functions do not compromise the main role of secondary metabolites as chemical defence and signalling compounds [166].

Exuded compounds are highly species-specific. They move safely into the environment through a variety of plant sequestration (e.g. sub-cellular vesicles) and transport mechanisms (e.g. protein embedded) [9, 19, 162]. Allelopathy in *Brassica* spp. appears to be associated with the presence of several groups of exudated metabolites such as phenylpropanoid, flavonoids, isothiocyanates and glucosinolates [26, 85, 90, 115, 116, 119, 121, 166]. These sulphur-containing compounds are indole derivatives at the C-3 position of the indole ring [44, 123]. Phenylpropanoids have a wide variety of functions including defence against microbial attack and other sources of injury [74]. Glucosinolates provide pathogenic organism defence [106] and can accumulate and modify to yield a variety of products including isothiocyanates, thiocyanates and nitriles but this depends on the nature of glucosinolates and the stress imposed [35, 105]. Choesin and Boerner [35] measured the direct release of isothiocyanate from growing the root of *B. napus* but they did not evaluate its effect on weed species.

Research is needed to clarify the type of chemicals released by intact canola roots and their role in weed inhibition. Such findings would facilitate investigation of the biochemistry and metabolomic pathways of these chemicals in plants in respect of canola allelopathy. It would also provide opportunities for new weed controlling cultivars.

Root Exudates and Rhizosphere Communication

The rhizosphere is the narrow region of soil directly influenced by root secretions and associated soil biota [19, 157]. In this zone, plant root-secreted chemicals can influence several processes such as resources (e.g. soil nutrients) and non-resource plant-mediated interaction [133], microbial communities and their populations [9] and neighbouring plant species [147]. These influences may play an important role in communication between other plants in the rhizosphere [160].

Root-Microbes Communication

Survival of a plant species in a particular rhizosphere depends on the mechanisms of adaption to interaction with biotic and abiotic components. The root rhizosphere is considered the place that provides habitat for plant roots and microorganisms and is inhabited by a wide range of microorganisms, including bacteria, fungi, algae, viruses and protozoa. These microbes may have a profound effect on allelopathic activity by altering and/or transforming the amount of allelochemicals [153]. On the other hand, allelochemicals may also influence the microbial community [71, 87] and these mechanisms can involve both stimulation (by providing nutrient sources) and inhibition (by interfering with nutrients) [124]. Various soil-borne organisms are highly sensitive to the *Brassica* plant-secreted 2-phenylethyl isothiocyanate, with bacteria being more tolerant than eukaryotic organisms [150]. In contrast,

growth of ectomycorrhizal fungi was found to be stimulated by root exudates of various *Brassica* spp. [172]. Rumberger and Marschner [140, 141] reported that canola roots released sufficient amounts of 2-phenylethyl isothiocyanate into the soil rhizosphere to have a selective effect on the bacterial community. Bacterial community composition was significantly correlated with phenylethyl isothiocyanate concentration and moreover changed with plant growth stage [140, 141]. However, despite high residence time of this chemical, Choesin and Boerner [35] found in their study that this root secretion did not have an inhibitory effect on *Medicago sativa* L. This suggests that specific signals might be exchanged between *Brassica* plants and microorganisms, although this is not yet clear. It would be also interesting to know whether the possible allelopathic chemicals described for canola roots act directly against the neighbouring plants or indirectly through modifications by soil microorganisms.

Root-Root Communication

Crop plant roots are continually interacting with roots of neighbouring plant species; and are capable of detecting and responding in multiple ways [20, 42, 56, 99, 148]. Roots may communicate with other roots with the help of various secondary metabolites, which are secreted into the rhizosphere in response to biotic and abiotic stresses.

Several research studies suggest that such a response of roots to their neighbours is not only explained by nutrients but also involves non-nutrient causes [8, 9]. Cahill and McNickle [27] divided these apparent non-nutrient root responses into three classes: (a) segregation (root growth away from neighbours), (b) neutral (no specific directionality of root growth) and (c) aggregation (root growth towards neighbouring roots). The actual sensing of the neighbour presence might be based on either physical touching of roots [100] or without physical touching via chemicals signals released by roots [6, 76]. For chemical signals, secondary metabolites have been largely credited with being involved in plant–plant interaction on the assumption that these compounds tend to be phytotoxic and persist in the soil [6]. Of course, such compounds could be hormonal or pseudo-hormonal in their influence on non-same neighbours. Pierik et al. [124] reported that the high specificity of root exudates has the potential to transport such specific signals into the rhizosphere. It has been reported that the proteins in the root exudates are secreted differently depending upon the presence and identity of the neighbouring root [6, 43]. Such canola-neighbour root interactions have not been elucidated. Establishing these interactive mechanisms by canola exudates will elucidate the true complexity of the competitive arena (Fig. 1).
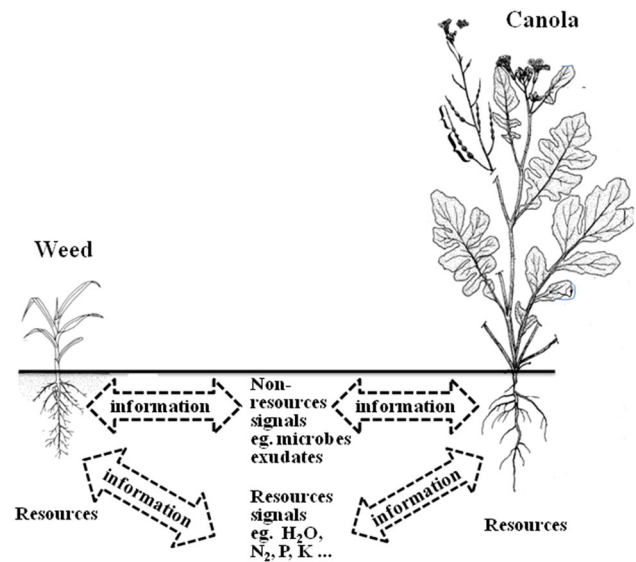

Fig. 1 Canola-weed below-ground interactions (resources and non-resources based) involve various signals, such as variations in nutrient concentrations, soluble root exudates and the activities of soil microbes

Conclusions

Herbicide-resistant weeds can increase the cost of canola production and reduce yields. Weeds may become a greater economic issue, if non-chemical weed management tactics are ignored. To maintain a sustainable production system and effectively manage the weed burden, an integrated weed management program incorporating crop interference needs to be included in the canola crop production system. The implementation of a high interference strategy for canola in the field requires a fuller understanding of canola competition and allelopathy on weeds. This includes a greater knowledge of the response of plants to their environment and to the stresses created by neighbouring weeds. Such elucidation will help to understand which traits matter under which conditions. Understanding the regulatory mechanisms that enable an individual canola plant to optimise these traits is a key to understanding canola-weed competition. The need for further experimentation to estimate accurately the relative ranking of current canola varieties for competitive ability at regional level is desirable. Evidence thus far suggests that some varieties are consistently more competitive than others, but considerable environmental variation exists, making reliable recommendations for farmers difficult. Growing vigorous crops by the many means possible is the challenge [94]. Changing farming practises, such as the move from conventional cultivation to reduced tillage and stubble retention systems, may influence weed growth and population dynamics [30]. More research is needed to determine the

impact of variety competitive ability on weed seed production for population dynamics modelling, particularly with respect to closely related weed species such as wild radish and wild mustard, to assist in predicting the long-term benefits of integrated weed management in a canola production system.

Communication between canola shoots and the roots is also important to ensure the shoot is adequately receiving below-ground resources for enhancing above-ground competition. Potential already seems to exist for breeding enhanced canola competitive ability through greater early vigour and below-ground root characteristics. Competitiveness of canola can be increased by breeding for suitable plant traits and by manipulation of the management system but the benefits and costs of crop competitive ability need to be evaluated. The competitive ability of a specific genotype in a particular environment may be much lower in another environment.

Increasingly, studies reveal that non-resources crop interference such as allelopathy plays an important role in some crop species. This opens the possibility to explore and utilise canola allelopathy. Below-ground plant–plant competition is more complex than above-ground and interdisciplinary research is needed to enable thorough understanding of canola allelopathy.

The role of chemical signals between canola and other organism in the rhizosphere needs further study. The same chemical signal may deter one organism while attracting another [7]. Plants rarely secrete just one substance and so there may be a blend of potential signals from molecules which are highly selective [49, 124]. In addition, ecological knowledge indicates that below-ground interactions could potentially be transformed to above-ground responses in plants. Integration of the different technology platforms are needed to understand the complex network of canola plant responses to various external factors including regulation via various signalling pathways.

In order to evaluate to what extent canola contributes in the crop-weed interference mechanism, the first task is to evaluate the existence of genetic variation of allelopathy in canola under laboratory conditions. Crop laboratory bioassays can demonstrate the potential chemical interference among crop cultivars within a limited time frame. Interestingly, much effort has been put into the development of sound screening protocols and most existing screening techniques are reliable, fast, cheap and space limited.

Laboratory bioassays are also suitable for understanding different aspects of allelopathy (e.g. release of chemicals from the donor plant, fate and persistence in soil, growth and uptake of allelochemicals) [23, 60] but it is also important to know the fate of these chemical compounds in the soil and their interaction with abiotic and biotic influences. The outcomes of this research should address the

sources of variation in allelopathy between cultivars. The bioactivity of the chemicals released by intact roots, however, may be compromised by an allelopathic species and could be rendered unavailable by the combined interactions of soil texture, organic matter, temperature and soil microbes [9, 64, 151]. The exudation of these compounds will determine the allelopathic effect. In the field, allelopathic effects are difficult to measure [120] and dependence on parallel in vitro experiments is required. Seal et al. [146] found that laboratory screened allelopathic rice cultivars performed well in the field and proved to be active against multiple weed species. More recently, field testing has been expanded from rice to wheat and barley.

Discovery of the allelochemicals involved in interference is essential by both traditional and advanced metabolomics methods (with HPLC, IR, GC/LC MS-QTOF and NMR etc.). Metabolomics is an important tool for an unbiased view of metabolites with combined principal components analysis. If canola cultivars produce and release sufficient amounts of herbicidal compounds, then the biochemistry of the exudation process needs to be understood.

Study of the genetic control of the allelopathic traits is important for the development of competitive canola varieties. In a study of allelopathic activity of population of 400 F_2 rice plants on duck salad (*Heteranthera limosa*), Dilday et al. [45] found that rice allelopathic activity was normally distributed, suggesting that the rice allelopathic trait was quantitatively inherited. The genetic study of allelopathy is still in its infancy but it does represent a promising new frontier for future research. Modern methodologies in molecular genetics and biochemistry have made this type of research more rapid and more direct than in the past. To develop high-yielding commercial canola cultivars with elevated allelopathic activity without sacrificing other agronomic traits, breeders' time and resources should be allocated after confirmation of significant crop allelopathic performance in the field. Allelopathy alone is unlikely to control all weeds but its enhancement will be a potential contributor for a sustainable integrated weed management system.

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