Dual direction allelopathy: the case of canola, wheat and annual ryegrass

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Abstract
The exploitation of allelopathy for enhanced weed suppression is in its infancy despite major advancements in our knowledge of weed suppressive cultivars. Crop species, including wheat and canola have been identified as potentially being weed suppressive against annual ryegrass. However, the contribution of crop allelopathy to interference is complex to elucidate within a field context. Traditionally, experiments involving allelopathy only investigate one species as the donor and the other as the target, irrespective of the putative duality of allelopathic responses between some species. In this paper we investigate dual direction allelopathic responses between canola and annual ryegrass at the seedling stage utilising laboratory growth assays, specifically the equal compartment agar method (ECAM). By manipulating experimental conditions, such as sowing density, time of sowing and plant proximity, we compare the efficiency of each species to exert an allelopathic effect on the other. Both species exert an inhibitive effect on the other dependant on the starting experimental conditions which they are subjected. We found that increasing the time that each species grows in the agar before introduction of the other species significantly inhibits the growth of the later sown species, up to 83.6% inhibition of canola root length by annual ryegrass. Density also played an important role in determining the level of root inhibition found for both species. Canola and wheat varietal differences were observed in respect to the level of annual ryegrass inhibition found. This paper discusses the implications of these results in the larger context of varietal selection for weed suppression.

Key words
Interference, plant competition, crop weeds, roots

Introduction
"*Interactions between neighbouring plants are so complex, tight and apparently impossible to disentangle that it may be wise to cease to look for simple effects*" (Harper, 1977). Australian farming systems, and increasingly global agriculture, have moved to conservation mode through reduction in tillage. For this to be successful, there has necessarily been a high dependence on herbicides for weed management. Herbicides have been highly efficacious in their abilities to control weeds but the continued evolution of weed resistance to many herbicides has threatened to undermine the conservation agriculture revolution. The need is apparent for there to be new options developed for weed control including a more intensive consideration of the plant's own capabilities to manage their own environments. The study of plant interference is gaining momentum although the current systems of plant breeding largely ignore the abilities of a variety to exercise control over its weed challengers.

The difficulty in studying interactions between plants is due to the complex nature of plant interference, defined as the combined effect of competition for resources, and allelopathy. Allelopathy is distinct from other forms of interference as it relies on the production of chemicals that may inhibit or enhance the growth of plants in close proximity. The ability of an individual plant to induce a negative effect on a neighbouring plant through chemically mediated changes in the immediate environment should be of great interest for breeding weed suppressive crop cultivars. The challenge however experimentally is that demonstrating the effect of allelopathy in the absence of other interference components may lead to erroneous conclusions when relating results back to a field context. Moreover, the difficulty in conceptualising chemical interactions between two or more species impedes our understanding further. Nevertheless, great advancements have been made in disentangling some of these interacting effects and applying allelopathy to weed control.

Wheat (*Triticum aestivum* L.) and canola (*Brassica napus* L.) are Australia's first and third largest broad-acre crops respectively. In particular, the future prospects for the Australian canola industry are excellent. Good commodity prices, market demand, and canola's usefulness in the farming system as a break crop make canola an attractive alternative crop for grain growers. However, losses due to weed pressure is a major yield limiting factor of canola (Lemerle *et al*., 2012). Weed such as annual ryegrass (*Lolium rigidum Gaud*.) limit attainable yields of many broad-acre crops. The rapid evolution of herbicide resistance in annual ryegrass limits control options and call for integrated control methods such as allelopathic crop varieties.

The development of crops with the capability to exert allelopathic effects on crop weeds through root exudates is an attractive prospect (Olofsdotter *et al*. 2002). Research has shown this potential in wheat (Wu *et al*. 2000), barley (Bertholdsson 2004, 2005; Lovett, 1994), rice (Dilday *et al*. 1994; Seal et al. 2004; Gealy *et al*., 2005), and canola (Asaduzzaman *et al*., 2014). In these studies, the genetic variation of crop cultivars tested yielded a range of allelopathic responses and the identification of highly expressing genotypes.

Allelopathy is a multi-directional process

It is now possible to use a relatively simple method to evaluate the impact of one species on another through chemical exudates. The Equal Compartment Agar Method (ECAM) developed by Wu et al. (2000b) is now widely used and there is strong correlation evidence that the laboratory outcomes link closely with performance in the field (Asaduzzaman et al., 2014; Seal *et al*., 2004). In most cases for production agriculture this effect has been a study of crop on weed. What is usually ignored is the reverse reaction where the weed also exudes chemicals that potentially compromise the impact from the crop (Moore *et al*., 2010). This is shown in Figure 1 for wheat and Figure 2 for canola.

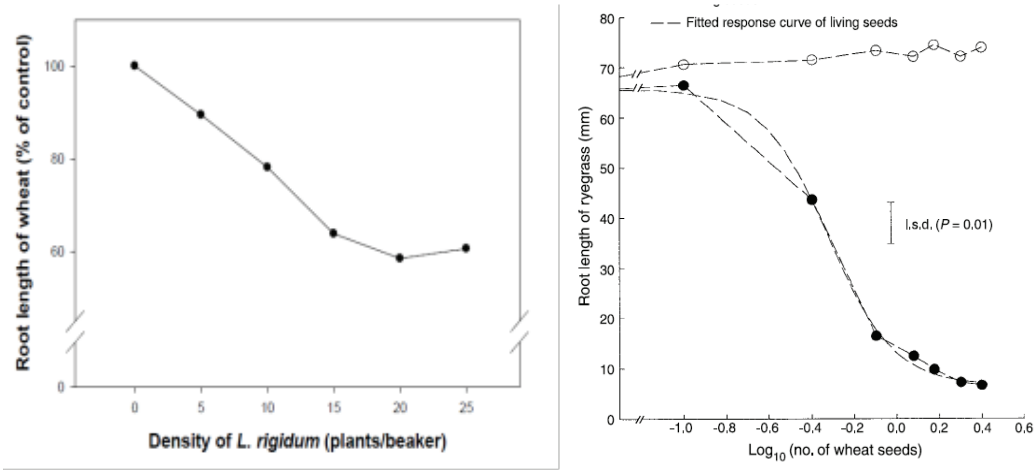

Figure 1. Effect of annual ryegrass density on root length of wheat (LHS – Moore *et al*., 2010) and effect of wheat density on annual ryegrass root length (RHS Wu *et al*., 2000)

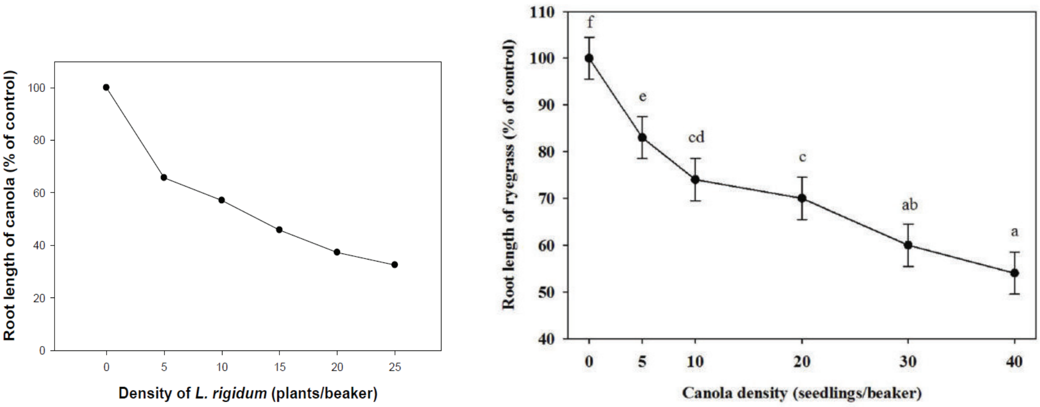

Figure 2. Effect of annual ryegrass density on root length of canola (LHS – Moore *et al*., 2010) and effect of canola density on annual ryegrass root length (RHS – Asadazzuman *et al*., 2014)

Consideration of the interaction in only one direction therefore may lead to outcomes in the field that do not support the notion that the crop may be able to provide itself a degree of weed control.

There is variation in potency across varietal germplasm

In order to make progress it is important to explore the range of potency present in the crop germplasm. This has been done in the Australian context for both wheat (Wu *et a*l., 2000b) and canola (Asaduzzaman *et al*., 2014). These investigations show that there is large degree of variation between varieties in their impacts on annual ryegrass. In the case of wheat Wu *et al*. (2000a) demonstrated that there was a strong link to genetic lines. It makes sense that the most potent of these varieties are further considered and evaluated under field conditions as demonstrated by Asaduzzaman *et al*., (2014b).

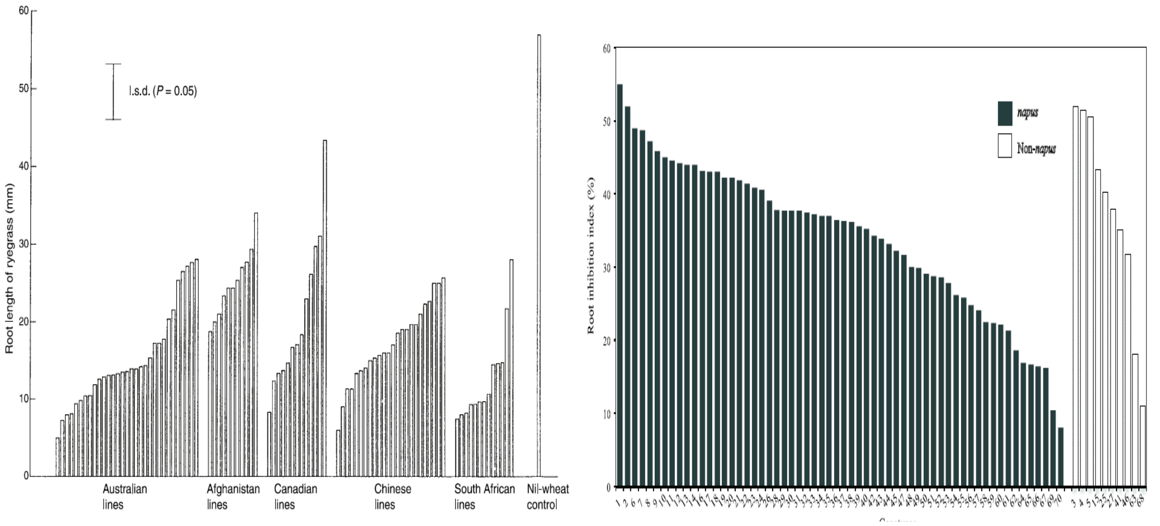

Figure 3. The effect of variety of wheat (LHS – Wu *et al.*, 2000) and canola (RHS – Asaduzzaman *et al.*, 2014) on root growth of annual ryegrass.

What then is missing from these studies is the evaluation of the strong allelopathic varieties to the exudates of the weed, in this case annual ryegrass. It is not known whether the strongly allelopathic varieties also have strong tolerance of the ryegrass allelochemicals. Logic suggests that the most useful varieties are likely to be those with strong allelopathy and with strong tolerance to the allelopathy of their competitors. Unfortunately we do not know the answers because of the long history of breeding cultivars under weed free conditions – thus a long line of crop varieties that are totally reliant on herbicides for control of their competitors. This is an unsustainable paradigm in a world where the prospect of new herbicide modes of action is rare.

Is resistance likely with allelopathic varieties?

One of the key factors driving the interest in allelopathic varieties is herbicide resistance. Allelopathy is also a chemical option, albeit a natural chemistry one. If misused then resistance might be expected to evolve as for synthetic chemicals. There will be differences however in that allelopathy is usually a chemical mix of many chemicals presumably with different modes of activity and that may reduce the rate at which the buildup occurs. The important aspects here are that there is no panacea and that allelopathy needs careful management as with other weed management options. Whether a range of cultivars with different allelochemistries can be developed rests with investment of R&D.

Conclusions

Alternative options to herbicides need to be found if conservation agriculture is to be sustained. Allelpathy is one such alternative. There is now strong evidence that it occurs and that potency exists in commercial cutivars of several crops. There is a strong genetic base that suggests that allelopathic capability can be bred for in new varieties. However it needs to be considered in a multi-directional framework where the tolerance of the variety to the weed's allelopathic challenge may be as important as the crop variety's allelopathic potency towards the weed. Continued breeding of varieties under weed free conditions will perpetuate the strong dependence on synthetic herbicides that are currently threatend by weed resistance.

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