Weed-plant interactions

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1 Introduction

Crop or desired plant species co-occur with undesired species and thereby the co-occurring species become weeds. This human-imposed quality is based on the perception that there is an interaction that results in some negative effect of the weed on the crop or desired species. At odds with this perception is an evolutionary perspective that would expect co-occurring species to select traits to minimize the interaction in a shared and limited resource pool as well as selection for traits to outcompete co-occurring plants. So which traits are more likely to be selected remains a question: Those that minimize interaction or those that intensify the interaction through competition (Grime 2006). It is quite possible that some co-occurring species may not be interacting in competition for resources, or competition may be minimal or indirect so that control of the undesired species is not required. Clearly, it becomes important to gain an understanding of the potential interaction among desired and undesired species and use that knowledge to instruct a management decision. All too often the decision to manage is reduced to selecting the best tool (usually herbicide) to get rid of the weed driven by the precautionary principle. The precautionary principle applied here is that when in doubt about the interaction between the weed and the crop one should control the weed. Unfortunately, controlling weeds can be expensive and can have environmental side effects. So there are trade-offs in the decision to control weeds and thus knowledge about the interaction between desired and undesired species should be gained to make the best decision about weed management (Swanton et al. 2015; Maxwell and Luschei 2004).

2 Crop-weed interactions: an evolutionary perspective

If plants are under selection to minimize interaction through a resource pool, one would expect that species that had co-occurred for many generations would have differentiated their respective *niche* requirements (Zuppinger-Dingley et al. 2014). Narrowly defined a species *niche* is a multidimensional space from which a plant gathers resources for growth and reproduction to sustain a population. Plants contribute the most pollen and seed thereby contribute the most traits to the population following natural selection. Since reproductive output is proportional to resources available to a plant, the plants with the most resources make the greatest contribution of traits. So resource capture by individual plants is not just driven by selection for niche differentiation but also intraspecific competition between individuals of the same species which tends to select for traits that allow plants to optimize resource consumption and use efficiency (Kraft et al. 2015). Interspecific competition between plants (between crops and weeds) may select for more niche differentiation traits.

The complexity of understanding and ultimately predicting the outcome of competitive interactions among individual plants, much less among species, becomes difficult given the different selective constraints or histories (Keddy 1989; Lavorel and Garnier 2002). In addition, one does not need to spend much time observing a multispecies plant community to see that natural selection must vary significantly across space and time so the interplay among the selective processes for niche differentiation, resource consumption, resource use efficiency and other competition-related traits is inconsistent (Rees et al. 2001; Dudley 1996; Kraft et al. 2015). What gives advantage to one set of traits in one place, or at one time, may not pay off for an individual at another point in space or time (e.g. Ellner 1985; Zuppinger-Dingley et al. 2014). Perennial plant species that must endure many conditions over time are challenged differently than annual species (Kunstler et al. 2016). Selection in one generation on one individual could be driven by one set of factors and another individual of the same species even in the same population could be driven by a different set of factors so if they interbreed what traits could we expect to emerge in a population? In fact, there is some consistency of selective forces and thus part of understanding the interaction among plants of different or even the same species is understanding the consistency of the environment that they have been selected upon (Kraft et al. 2015). Rotating crop species is a well-known strategy for weed management because it narrows the spectrum of species that can tolerate the temporal changes in the environment shared with the crop.

The agroecosystem environment is made up of abiotic and biotic components and these are heavily influenced by disturbance and human land management (inputs, etc.). In most crop systems soil and plant management has the goal to make the environment consistent for the crop which makes selection on the co-occurring weed species in any given generation relatively consistent. However, in crop rotations where the crop species with different life cycles, morphologies, physiologies and phenologies can change, selection is heterogeneous and thus successful traits to allow coexistence with the crops would be expected to decrease with increased crop or community diversity (Milbau and Nijs 2004). Alternatively, diverse mixtures of grasses can be selected for greater resource use efficiency traits than the same species grown in monocultures over eight generations (Zuppinger-Dingley et al. 2014). These results suggest that selection in species mixtures may therefore increase species coexistence and allow increased mixture yields in

agriculture. These results suggest that crops should be selected under mixture conditions including weeds, cover crops and companion crops.

As atmospheric CO_2 concentrations and subsequent climate changes have occurred, yet another temporal variation is introduced and the successful subset of available weed species to any given site may be even more narrowed and the interaction with the crop fundamentally changed (Blumenthal et al. 2014). Rees et al. (2001) evaluated multiple plant traits and their trade-offs in structuring annual plant communities based on empirical evidence from long-term studies. They identified that seed size, rapid exploitation and differential influence of seed herbivory often determine the importance of competition or colonization as the driving selective forces determining the relative success of different species in annual plant communities. Their observations lead to the *competition-colonization trade-off* hypothesis where small-seeded species are predicted to be good colonists, but poor competitors and large seeded species are good competitors for resources but poor colonists. Although there are exceptions to this hypothesis, consideration of the potential for predicting competitive outcomes between weeds and crops must start with initial plant (seed) size as a critical trait. For example, for two plants with identical abilities to compete for resources that germinate and emerge at the same time, the one that started from a larger seed will get larger than the smaller seeded one. Kraft et al. (2015) quantified average fitness and stabilizing niche differences between 102 plant species pairs and related the differences to 11 functional traits. Competitive fitness traits were correlated with exclusion of one of the species in a pair, but coexistence of the species pairs was not necessarily correlated with traits that they identified as niche differentiating. Coexistence of species pairs could only be associated with combinations of traits, representing differentiation in multiple dimensions. Thus, even in the relatively simple selective arena of agricultural systems there is yet to be a clear emergence of prevalence of competitive or niche differentiating traits in weeds. It is clear, however, that site-specific history could determine trait prevalence but may be not intensity of competition for resources.

3 The nature of shared resource pools

Plants begin growth as an individual genet by drawing on resources from the seed, producing a radicle followed by mainly haustorial cotyledons. True leaves are formed dedicated to photosynthesis and the plant begins drawing on resources from the surrounding environment. Resources shared among plants in the soil include water and nutrients and, above ground, light, physical space and CO_2. If we turn our focus to competition for nutrients and water in the soil profile the multidimensional niche from which an individual plant draws resources is tangible and sharing the same soil volume of root systems from different plants, or among ramets of the same plant, suggests the potential for competition for resources. It turns out that plants may physically overlap, but they may be phenologically offset in time so there is minimal simultaneous growth and draw on the resource pool. For example, some weed species mostly grow after crop harvest and/or crop senescence (e.g. *Kochia scoparia* and *Salsola kali* in dry land small grain systems) which minimizes their competition with the crop (niche differentiation). It is also possible for plants to have mutualistic relationships between species that by close association in space may improve their ability to germinate, grow and ultimately

Table 1 Types of interactions between plants of two different species where the sign + or – indicates positive and negative interactions or 0 means no interaction (adapted from Burkholder 1952)

Types of interaction between species A and B	Species A	Species B
No interaction	0	0
Competition	–	–
Mutualism	+	+
Commensalism	+	0
Amensalism	0	–
Parasitism	+	–

reproduce. There is terminology for the different relationships that can occur between two species sharing the same niche (Table 1).

The main reason to identify the alternatives to competition as a process among weeds and crops or other desired species is that we may identify positive relationships and thus management would not require weed removal. In addition, the process of natural selection acting on weeds that are inherently disadvantaged in most crop systems would be to select traits that allow avoidance of competition with the crop as much as those traits selected to be more competitive with the crop. Thus, there may be specific environmental conditions where the weed does not affect the crop or the threshold for significant economic effect is higher than that for the biological effect (Cousens 1987). The environment influencing the weed-crop interaction is likely to vary on small spatial scales (m^2) and from growing season to growing season (Maxwell and Luschei 2004). Weed densities recorded across
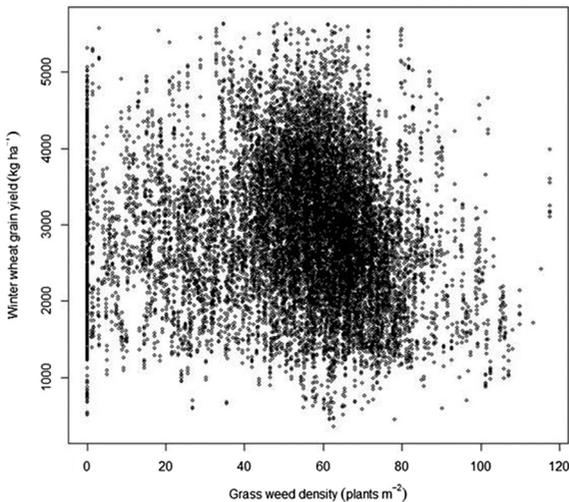

Figure 1 The relationship between dryland winter wheat grain yield and monocot weed density demonstrating variation indicative of variables other than weed abundance determining crop yield.

a wheat production field with site-specific yield information demonstrates the variation in weed impact across the field (Fig. 1). Clearly, factors other than weed density were playing a role in determining crop yield.

4 Direct competition for resources

Direct effects of interactions between plants through the resource pool are based on the study of resource uptake and allocation. Benjamin and Parks (2007) described an ecophysiological model for predicting monoculture and mixed species interactions to predict the effect of weeds on crops. Their 'Conductance' model provided a simple yet mechanistic method of simulating growth and competition for light based on space occupied by crown zones of plants in a range of competitive environments. Berger et al. (2013) similarly presented a spatially explicit, individual-based plant growth model (COMPETE) utilizing components of tested and validated mechanistic biophysical models (Maestra, PNM, LeachN and Gecros). The COMPETE model captures the major dynamics of the growth of a population of competing plants (i.e. formation of canopy hierarchies) and also simulates changes in plant transpiration as a function of plant size and competitive environment. Biophysical process models are gaining popularity particularly to predict plant species interaction changes that may occur with climate change in CO_2-enriched atmosphere. The current utility of these models at management decision spatial scales or special scales that would capture crop–weed interactions is challenged by a large number of parameters requiring measurement on expensive instruments (Deen et al. 2003).

Alternatively, competition for resources among plants may be captured if one assumes that the rate of resource uptake by individual plants is proportional to plant size, resources are finite but renewable by some rate, and plant size is asymptotic (Tilman 1988). For example, the following equations can be used to simulate growth of individual plants in a population over time when they are competing for resource in a shared pool.

$$RS_t = \frac{\delta RS}{\delta t} \tag{1}$$

$$RUN_t = \sum_{i=1}^{N} \left[v_s Si + \left(1 - \frac{q_s d_i}{1 + q_s d_i} \right) \right] \tag{2}$$

$$RAG_t = RAG_{t-1} + RS_t - RUN_t \tag{3}$$

$$GRi_t = \frac{GR_{max} RAG_t}{RAG_t + k_s} \tag{4}$$

$$Si_t = Si_{t-1} + GRi_t \tag{5}$$

where *RS* is the resource supply rate to an individual target plant's niche (neighbourhood); *RUN* is the sum of resources used by neighbouring plants over a specified time period (e.g. 1 week) and is a function of the sizes of *N* neighbour plants (S_i) at the previous time (starting with seed size) and their distances (d_i) from the target plant as well as

species-specific resource use efficiency (v_s) and competition intensity (q_s) parameters. *RAG* is the resources available for growth in the neighbourhood for the next time increment based on what resources remain after use in the previous time (RAG_{t-1}) step, the resource supply rate (*RS*) and the *RUN*. *GRi* is the growth rate of the target plant and is a function of the maximum growth rate (GR_{max}), *RAG* and a species-specific growth efficiency parameter (k_s). Then the size of each plant at the end of each time step is Si_t calculated using Equations 1–5 in sequence. Assigning an *x* and *y* coordinate to each plant in a community allows calculation of each individual plant size over time and a mechanistic, yet empirically based, way to determine individual plant performance in a community where resources are shared (Milbau et al. 2007; Weiner 1982). The performance of plants in a multispecies community can also be explicitly considered with species-specific parameter values. In addition, by varying *RS* over time and space one can examine the range of environmental effects on competitive outcomes. This individual-based model can be parameterized by tracking plant sizes through a growing season and then estimating the resource dynamics without actually measuring the resource pool. More importantly it allows an understanding
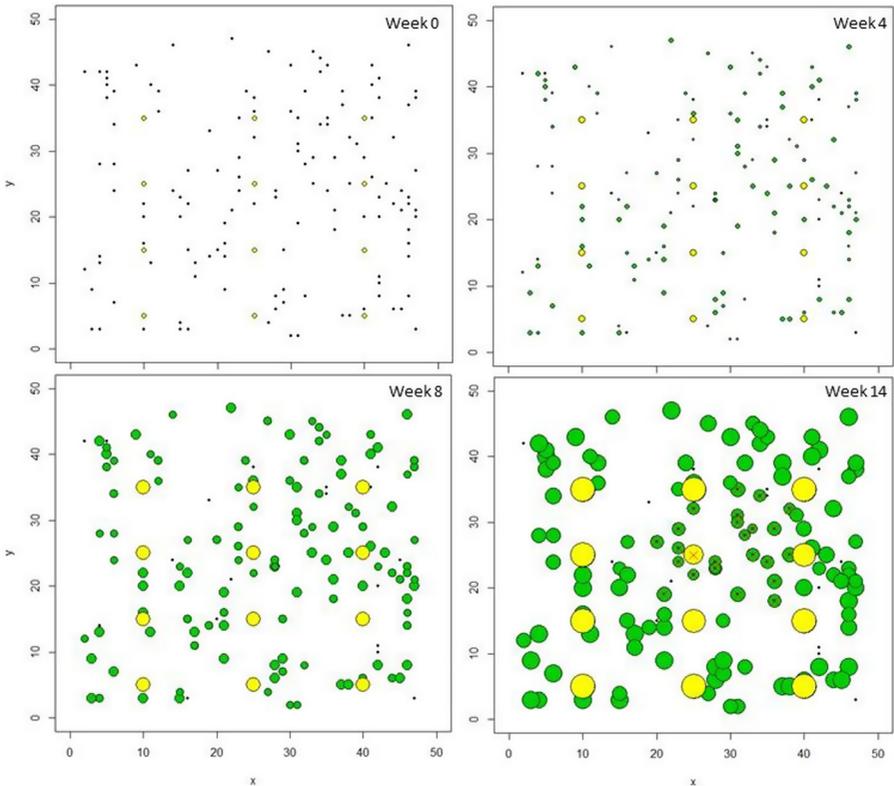

Figure 2 Plant maps showing time steps over growing season when at week 0 plants are seed (black dots) and crop (yellow dots). As plants grow circles enlarge depending on resources available. Weeds are green and crop plants are yellow. Red x indicates plants that died because they did not grow for three consecutive weeks due to lack of resources.

of the complicated dynamics among individual plants drawing on a shared resource pool and thus a theoretical basis for the quantification of impacts of weeds on crops (McGlade 1999). This model provides a visualization of the competition process (Fig. 2). What it does not account for is indirect competition where the same 3-dimensional space is shared by two species but they do not necessarily interact through the same resource pool.

The individual plant approach to characterizing population response avoids the assumptions of population-based theory (Watkinson 1996; Cousens and Mortimer 1995), averaging individual plant responses and thereby ignoring individual variation that could be critical to weed management decisions. For example, the standard for characterizing weed-crop competition outcomes was the use of average plant biomass in a population as the response variable to intra- and interspecific densities (Shinozaki and Kira 1956; Spitters 1983; Firbank and Watkinson 1985; Radosevich 1987; Roush et al. 1989). Cousens (1991) suggested the more direct quantification of competition between crops and weeds with the hyperbolic equation where weed density (N) became a direct predictor of crop yield (Y):

$$Y = Y_{wf}\left(1 - \frac{iN}{1 + iN/a}\right)$$

where Y_{wf} is the weed-free crop yield (assumed to be the maximum possible yield) and i and a are shape parameters. This equation was modified to include emergence time of the crop relative to the weed (Cousens et al. 1987) and incorporated into simulation models to demonstrate a range of alternative weed management practices (Maxwell and O'Donovan 2007). The above models have been useful for understanding first principles of weed–crop interactions, but often require significant effort to estimate the parameters with small plot experiments and the parameter variation is high over crop growing regions and from year to year limiting the application of these responses (Jasieniuk et al. 1999).

The aforementioned approaches facilitated easy quantification of the effect of the weed on the crop and more importantly the effect of the crop on the weed to determine the future ramifications of leaving weeds if not managed. However, these approaches gloss over some aspects of the interaction between crop and weeds that the more individual-based models could pick up. Further, these glossed-over aspects could reveal opportunities for more integrated weed management. For example, the role of seed size of crop or weeds, emergence time of the crop relative to the weeds or crop plant spatial arrangement could all be manipulated in the model to explore ways to reduce the impact of weeds on a crop.

A number of studies have elucidated potentially important interactions among weeds, crops and cover crops that could represent effective ecologically based weed management. However, these empirical studies without a theoretical base often conclude with the requirement for more knowledge about what drives the crop-weed interaction in order to recommend general outcomes. A mounting number of studies have been conducted to evaluate how cover crops can influence weed population dynamics by maximizing competition with weeds (Mirsky et al. 2013; Den Hollander et al. 2007) and, when intercropped, minimize competition with the cash crop while maximizing competition with the weed (Benaragama et al. 2016; Hartwig and Amon 2002). In addition, some cover crops with legume species change the soil nitrogen dynamics favouring the crop or some of the weed species with little knowledge to base generalized weed management recommendations. An interesting study was conducted to evaluate how the relative proportions of cereal rye (*Secale cereale* L.) and hairy vetch (*Vicia villosa* Roth) sown in mixtures as a cover crop influenced winter annual weed suppression and vetch

nitrogen fixation (Hayden et al. 2014). Increasing the vetch in the cover mix increased nitrogen accumulation and improved weed suppression, but the mechanism for the successful result was not clear. Amini et al. (2014) provided a generalizable result drawing on competitive indices like crop leaf area index (LAI) (Zhao et al. 2006; Hansen et al. 2008) and growth rate to rank different crop varieties competitive potential with a single weed species (Steinmaus and Norris 2002; Kropff and Lotz 1992). If multiple weeds occur in the system the interactions become experimentally intractable. Thus, the understanding of the more complex weed community dynamics and effects on crops may require simulation models based on empirical parameterization of first principle relationships to build an understanding of the breadth of interactions and subsequent outcomes.

5 Indirect effects of competition

A good example of indirect competition for resources that looks like competition would be where three plants share nearly the same space but one has root morphology that places most of its roots deep in the soil profile while the co-occurring species have mid-profile or shallow root systems (Fig. 3). The shallow root system species captures small
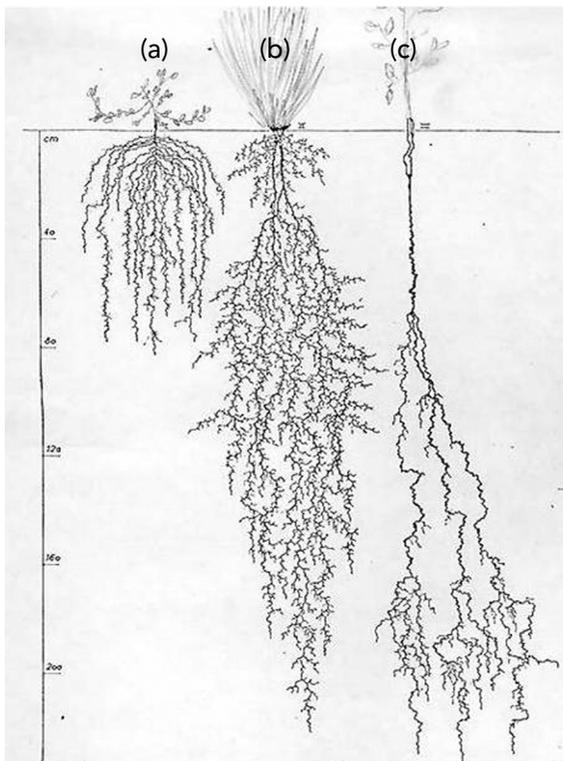

Figure 3 Three co-occurring species with different morphologies enabling them to occupy the same area but minimizing niche overlap.

volume rain event moisture and has adapted this strategy for climates where growing season precipitation comes in small pulses. The other species commits to deeply stored soil moisture that may get stored outside of the growing seasons. Under dry conditions with pulse rain events the shallow-rooted species usurp all of the moisture and are able to increase biomass whereas the deep-rooted species slows its growth as it depletes the deep soil moisture reserve. If our measurement of competition is based on relative growth of these two species one may conclude that the shallow-rooted species outcompetes the deep-rooted species for resources even though the two species are not drawing on the same resource pool (direct competition) and have adapted morphologies to effectively share the same 2-dimensional space. In a dry growing season following a wet winter, the deep-rooted species may gain more biomass and appear as the superior competitor for resources. The weed ecologist may observe these contrasting results in the field in different years and thus design the definitive experiment to determine which species is the superior competitor for resources. He/she plants the two species together in a shallow pot and determines that one species has a higher relative growth rate than the other and definitively concludes that the deep-rooted species is more efficient at drawing on the resource pool. This is direct competition because each species is competing directly with the other for resources in the same space. The results of the experiment, however, may be irrelevant to the field condition where these two species co-occur but never draw on the same resource pool because their root morphologies use different niche space.

Another example of an indirect interaction that could easily be interpreted as direct competition for resources in a shared pool is where one species like a cover crop draws down the resource pool for weed species which in turn releases the crop from competition. Wells et al. (2013) showed that rye (*Secale cereale*) used as a cover crop in soybeans could pull down the soil nitrogen to a level that redroot pigweed (*Amaranthus retroflexus*) could not tolerate but the soybeans could thrive making it look like the competition was directly between the soybeans and pigweed.

In some cases the opposite of competition (mutualism or commensalism) has been shown where co-occurring crops and weeds resulted in enhanced resource availability, creating a direct facilitation (Brooker et al. 2016). Phosphorous availability can be enhanced on acidic soils by the secretion of organic acids and phosphatases by one species (Hinsinger et al. 2011; Li, Zhang and Zhang 2013) or N transfer from nitrogen-fixing legumes to co-occurring crops or weeds (Laberge et al. 2011; Bedousac et al. 2015). Increased availability of water in the upper layers of the soil profile through hydraulic lift is shown to increase soil water for co-occurring plants (Prieto et al. 2012). Niche complementarity can result as facilitation from herbivore protection or pollinator attraction (Brooker et al. 2015). Indirect facilitation through the soil microbial community has also been documented (Van der Heijden et al. 1998; Bennett, Daniell and White 2013). A meta-analysis indicated that arbuscular mycorrhizal fungi can directly suppress weeds that are weak hosts for the fungi, but also can indirectly suppress some strong host weeds in the presence of strong host crops that ultimately obtain the advantage (Li et al. 2016). These facilitative processes can differentially provide advantage to the weeds or crop in any given system at any particular time, so their interpretation must be made with caution and careful understanding of the drivers in variation before applying what appears to be a definitive outcome or assumption about the outcome of the interaction (e.g. Fig. 1 where detection of the negative effect of weeds is hard to distinguish). Direct competition for resources between weeds and crops can be occurring, but may be masked by niche differentiation, facilitative or mutualistic processes.

6 Spatial and temporal dynamics

Most crops have been selected under conditions of plentiful resources, whereas weeds were more likely required to survive and produce offspring in a wide range of growing conditions. Thus one might expect that under a typical crop production scenario the crop might be better physiologically equipped to rapidly use resources than the co-occurring weed species. It has been widely shown that crops can offer significant competition to weeds in many cases (Andrew et al. 2015; Rasmussen 2004). Planting strategies such as narrow row spacing and early planting that maximize competition often provide advantage to the crop over co-occurring weeds and those advantages can translate across generations (Evers and Bastiaans 2016; Fahad et al. 2015; Kolb and Gallandt 2013; Maxwell and O'Donovan 2007). Planting depth and/or planting time can also increase crop competition with weeds by maximizing the likelihood of the crops capturing soil resources ahead of the weeds.

Increasing crop density by decreasing the distance between rows and/or decreasing within-row plant spacing is an optimization problem that maximizes the effect of the crop on the weed without affecting the marketable crop product. Intraspecific competition can be just as effective on the crop as interspecific competition. Generally, rectangularity near 1.0, the ratio between inter-row and intra-row distance between plants (Willey and Heath 1969), has been identified as optimum. However, research that specifically addresses the light interception by the crop canopy resulting in weed shading is also important and may reveal different ideal crop plant arrangements to maximize competition for light (Maddonni et al. 2001).

Competition for light and the influence of light quality may be interpreted as competition. The mere presence of another species can influence the reflected light quality which can have negative effects on the growth of a neighbour plant (Gundel et al. 2014; Balare an Casal 2000). It has been shown that light quality can change plant morphologies to avoid (niche differentiate) competition for light. Liu et al. (2009) proposed that changes in the red to far red ratio of light acts as an early signal of pending competition by a physiologically triggered shade avoidance response that additionally had a physiological cost-limiting plant growth. Traits that provide advantages in a competitive environment can have trade-offs, and sorting among the different mechanisms that determine weed effects on crops is no easy task and experimentally requires special methods (Swanton et al. 2015).

7 Conclusion

There is great need for understanding the potential for weed impact on crops. Plant competition for resources in a shared environment is an important aspect of understanding effects. Thousands of dollars are often spent on a single production field to control weeds and sometimes with significant potential for non-target environmental impact. Unfortunately most weed management is conducted under the precautionary principle, because there is great uncertainty about the extent of weed effects on current or future crops if not managed. Even with weeds that have been extensively studied and their crop effects quantified, translation of study results to field scale has rarely been accomplished. Annual variability and site-to-site variability have challenged the ability to make prescriptive recommendations. It has become clear that fundamental processes

including competition for resources among plants and interpreting ecological processes for management recommendations requires an understanding of how to scale those processes appropriately. This remains a great challenge for Weed Scientists.

8 Where to look for further information

Future research into the interaction between weeds and desired plant species would best be focused at the individual spatial scale where each plant neighbourhood is characterized to specifically capture the potential resource interactions (Damgaard and Weiner 2017). Stratified random selection of target individual plants in a plant community followed by neighbour plant quantification by height, canopy cover, distance from target and angular dispersion in the neighbourhood are effective ways to discern the spectrum of plant interactions in a community (Bussler et al. 1995). Neighbourhood approaches to study competition for resources are often considered too detailed to be useful for management. However, a frequency distribution of properly selected neighbourhood conditions in a plant community can provide a mechanism to scale up inference space meaningful to management. Useful publications and papers cited within the chapter are listed at:

http://plen.ku.dk/english/employees/?pure=en%2Fpersons%2Fjacob-weiner(dd3c08ff-333b-4591-9968-3957845a6fa1)%2Fpublications.html.

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