

South Dakota State University

Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange

Agronomy, Horticulture and Plant Science
Faculty Publications

Department of Agronomy, Horticulture, and
Plant Science

2023

Weed-induced Crop Yield Loss: A New Paradigm and New Challenges

David Horvath

USDA-ARS, Fargo, North Dakota, david.horvath@ars.usda.gov

Sharon A. Clay

South Dakota State University, sharon.clay@sdstate.edu

Clarence J. Swanton

University of Guelph

James V. Anderson

USDA-ARS, Fargo, North Dakota

Wun S. Chao

USDA-ARS, Fargo, North Dakota

Follow this and additional works at: https://openprairie.sdstate.edu/plant_faculty_pubs



Part of the [Agronomy and Crop Sciences Commons](#), and the [Weed Science Commons](#)

Recommended Citation

Horvath, David; Clay, Sharon A.; Swanton, Clarence J.; Anderson, James V.; and Chao, Wun S., "Weed-induced Crop Yield Loss: A New Paradigm and New Challenges" (2023). *Agronomy, Horticulture and Plant Science Faculty Publications*. 398.

https://openprairie.sdstate.edu/plant_faculty_pubs/398

This Article is brought to you for free and open access by the Department of Agronomy, Horticulture, and Plant Science at Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. It has been accepted for inclusion in Agronomy, Horticulture and Plant Science Faculty Publications by an authorized administrator of Open PRAIRIE: Open Public Research Access Institutional Repository and Information Exchange. For more information, please contact michael.biondo@sdstate.edu.

Special issue: Food security

Review

Weed-induced crop yield loss: a new paradigm and new challenges

David P. Horvath ^{1,*} Sharon A. Clay,² Clarence J. Swanton,³ James V. Anderson,¹ and Wun S. Chao¹

Direct competition for resources is generally considered the primary mechanism for weed-induced yield loss. A re-evaluation of physiological evidence suggests weeds initially impact crop growth and development through resource-independent interference. We suggest weed perception by crops induce a shift in crop development, before resources become limited, which ultimately reduce crop yield, even if weeds are subsequently removed. We present the mechanisms by which crops perceive and respond to weeds and discuss the technologies used to identify these mechanisms. These data lead to a fundamental paradigm shift in our understanding of how weeds reduce crop yield and suggest new research directions and opportunities to manipulate or engineer crops and cropping systems to reduce weed-induced yield losses.

Competition for resources is not required for weed-induced yield losses in crops

It has generally been accepted that crop yield loss occurs as a direct result of weeds competing for resources such as light, soil nutrients, space, carbon dioxide, and water [1]. Here, we define resource competition as the ‘capture of essential resources from a common, finite pool by neighboring individuals,’ [2,3]. Indeed, this mantra is so ingrained in the dogma of weed science and ecology that the statement is often made without references or a clear definition. A poll of about 200 weed scientists indicated that about 66% accepted this as settled fact (https://youtu.be/biMco_5XO-A?t=8). Additionally, a Google Scholar search of the phrase ‘weeds compete with crops for’ yielded nearly 1000 hits, yet almost none cite any specific study to corroborate that statement, and none of the cited literature definitively proved that limitations of any of these resources were the primary mechanisms of weed-induced yield loss. That said, there is no doubt that weeds take up available resources [4], and if these resources were limited and unable to meet the demand of crop growth, then yield loss would occur due to competition for resources [5]. There is also no doubt that adding nutrients and supplementing soil water can increase the growth and yield of crops. Thus, it appears logical to conclude that the resources used by weeds would reduce crop yield, and thus, the accepted paradigm has long been that weeds reduce yield through direct competition for resources. However, several observations suggest that resource competition is not the primary mechanism underlying weed-induced yield loss in crops in well-managed agroecosystems. Indeed, in the few studies where it was tested, weeds were able to reduce crop yield even when weeds were prevented from competing for resources (e.g., see [6]).

If weeds primarily reduced crop yields by limiting resources, then increasing resource inputs should negate yield losses as the resources approach levels that could fully support both crop and weeds. This, however, is rarely observed. In studies where this was attempted, weeds reduced crop yield, often at nearly the same percentage as they did without additional fertilization (Figure 1) [4,7–12]. Even under greenhouse settings where crops were watered daily and fertilized weekly, and the crops were taller than their competitor, weeds still reduced crop yield [13]. Even

Highlights

A commonly held misconception is that weeds reduce crop yield primarily because of resource competition.

Weed presence reduces crop yield regardless of resource availability based on the timing of the critical period for weed control, and resource supplementation, and weed density studies.

Weeds alter developmental trajectories of crops early in the growing season that often result in reduced yields.

Signals produced by weeds that alter crop growth include light quality alterations, soil-borne chemicals, and/or volatile chemicals.

Weed signals elicit a stress response in crops that may suppress growth through repression of the TARGET OF RAPAMYCIN (TOR) signaling system.

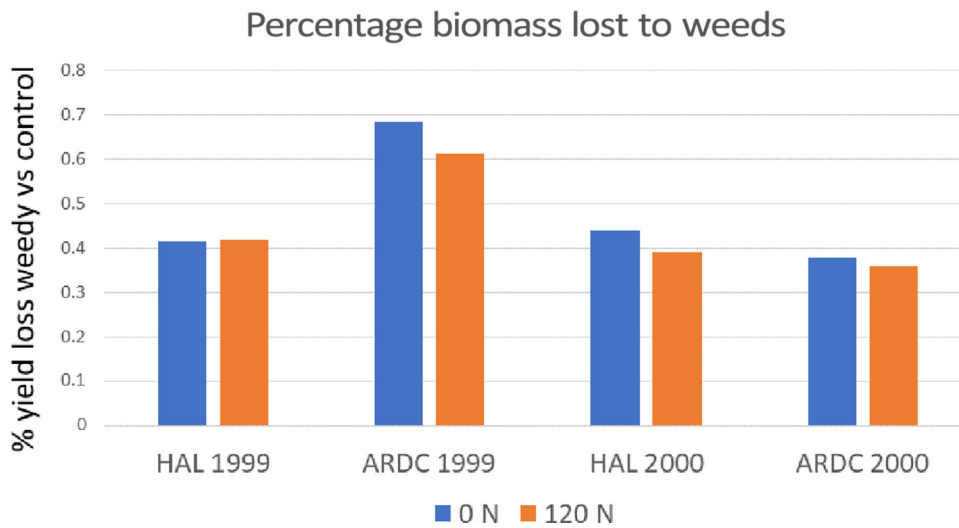
Identification of weed-inducible genes and promoters will provide tools to investigate mechanisms controlling crop-weed interactions and develop weed-tolerant crops.

¹USDA-ARS Edward T. Schafer Agricultural Research Center, Fargo, ND, USA

²South Dakota State University, Brookings, SD, USA

³University of Guelph, Ontario, Canada

*Correspondence: david.horvath@usda.gov (D.P. Horvath).



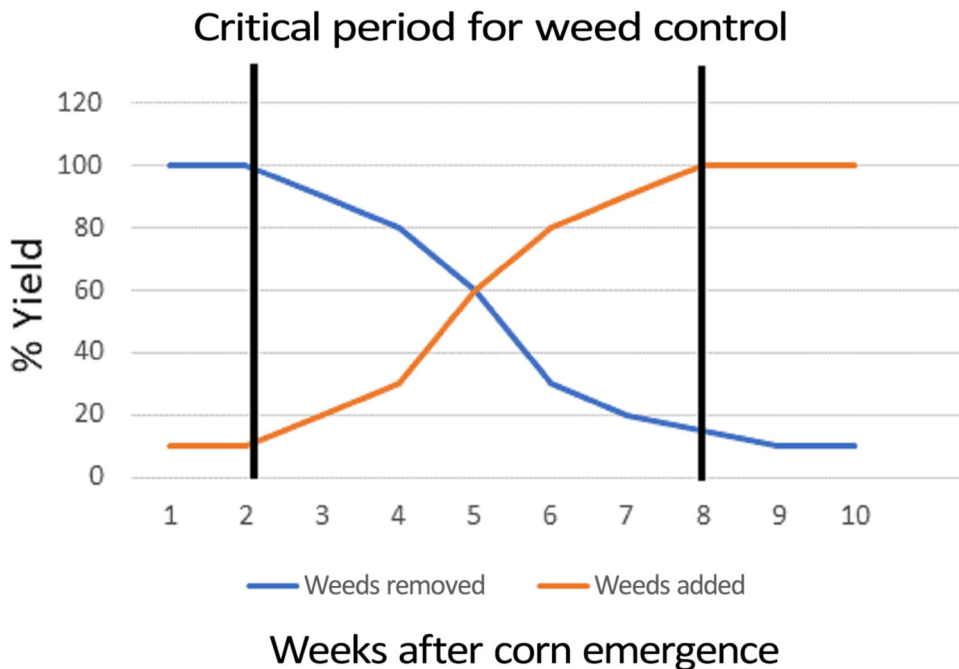
Trends in Plant Science

Figure 1. Typical data on yield or biomass loss caused by weeds with or without additional resources. These data were obtained from [4] and are now depicted as percent biomass lost to weeds under conditions where either nitrogen was not added (0N) or nitrogen was added at a rate of 120 kg per hectare (120N) over a 2-year period (1999 and 2000) at two locations [HAL (Haskell Agricultural Laboratory) and ARDC (University of Nebraska Agricultural Research and Development Center)] in a field study.

in cases where the nitrogen level in corn was reduced due to weed pressure – for example [4], the addition of nitrogen had little impact on the percentage of nitrogen lost due to weed presence, suggesting that weeds were impacting nitrogen assimilation in the crop, regardless of the level of available nitrogen. This response cannot be attributed to competition *per se*, but rather to other physiological responses occurring within the crop. Thus, maintaining resource availability was not sufficient to prevent weed-induced yield loss or a reduction in nitrogen uptake and assimilation by crops.

Weed-induced yield losses in crops have been studied extensively and reviewed [1,14–18]. One interesting aspect of weed/crop competition is that the timing of weed seedling emergence relative to the crop is critical in determining the outcome of competition. Weeds that emerge early relative to the crop have the greatest impact on yield, whereas weeds that emerge during the later stages of crop vegetative growth have minimal impact on crop yield, even if they overtop the crop. This critical period for competition, as initially defined by Nieto *et al.*, has continued as an experimental design to influence further studies focused on the development of an integrated weed management strategy [15,19–23] (Figure 2). The critical period for weed control is also influenced by the weed and crop species, their density, and both soil and environmental conditions during the growing season [24].

In well-managed agroecosystems, resources are not generally limited early in the growing season, and water uptake and nitrogen assimilation are highest during the later stages of crop development, peaking during or just prior to grain filling (Figure 3). Yet, surprisingly, weed emergence during these later periods, when resources are most in demand, has minimal impact on yield. It could be argued that late emerging weeds are smaller and less vigorous and thus would not impact yield as greatly as weeds that emerged earlier in the season. However, although rare in the literature, there are studies where weeds that had emerged earlier in the season were transplanted into crops after the critical period for weed control [25]. This study included multiple weed species and two crop



Trends in Plant Science

Figure 2. Representation of the general impact of weed presence on the percentage of yield (y-axis) that defines the critical period for weed control for many crops. If weeds are removed very early in the growing season (blue trend line), yield loss is negligible, but yield loss increases as the duration of weed interference increases. Likewise, yield loss is substantial if weeds emerge early in the growing season (orange trend line) but have a negligible impact on yield if they emerge or are introduced later in the growing season.

species. Yet, even when adult weeds were introduced after the critical period for weed control, there was still minimal impact on crop yield. In many studies, weeds were tolerated before weeds switched from the juvenile to adult phase and after the crop switched from vegetative to reproductive growth, for example, between the six- to seven-leaf stage (about V4-5) in corn [26] or a period of about 4–6 weeks in most species [20,21]. Thus, weed presence during this developmental window results in irreversible yield losses. The fact that weeds impact crops early in the season, when nutrients generally are not limiting due to spring applications of fertilizer and soil moisture is generally abundant, suggests a mechanism other than direct resource competition as the primary mechanism for weed-induced yield losses – at least in well-managed agroecosystems.

Finally, the impact of weeds on crop yield loss is best described by a hyperbolic regression model [27,28] rather than a linear response [17,29]. There is a strong correlation between biomass accumulation and nutrient uptake [30]. If weeds were reducing yield by direct competition for resources, then one would expect a more linear impact on yield as weed biomass increased. Instead, although yield losses increase with increasing density or biomass, the rate of yield loss per unit weed is higher with low weed levels and decreases as weed density or biomass increases. Additionally, weed threshold studies have shown clearly that yield loss as a function of weed density was most pronounced for weeds that emerge at or very near the time of crop emergence (Figure 4). Pigweed seedling density of two plants m^{-1} within 12.5 cm of the soybean rows emerging at VE (emerged cotyledons) of soybean growth caused a 12.3% yield loss compared with 1.9% for weed emergence at VC (unifoliate leaf stage) and 0% for weed emergence at V2 (second trifoliate stage) [31]. Similar responses have been reported for pigweed and barnyard grass effect on corn yield [32,33]. Crop yield loss was determined primarily by timing of weed

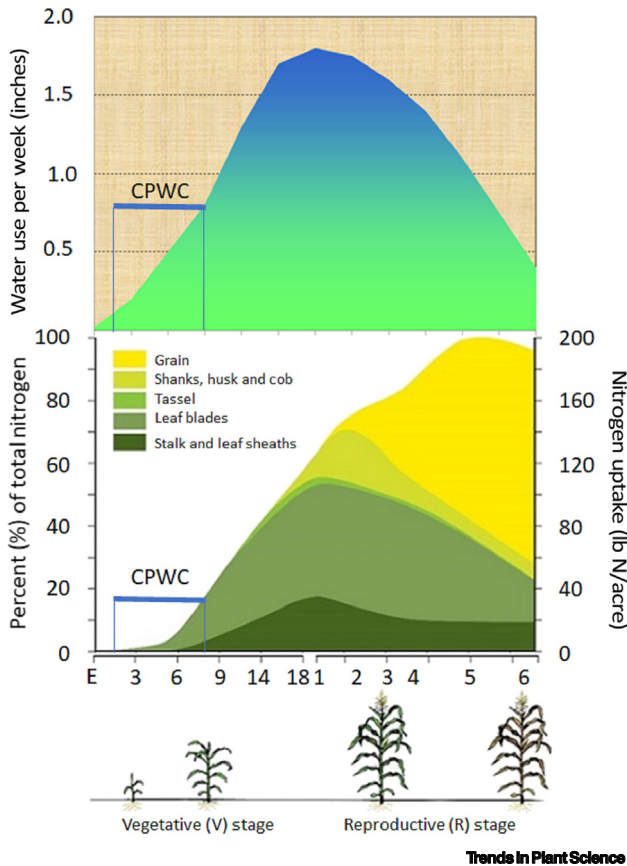


Figure 3. Graphic showing nitrogen and water use during corn development. Figures modified with permission from Mississippi State University Extension and Outreach (water use) and Iowa State University Extension and Outreach (nitrogen use). Note that at the end of the critical period for weed control (CPWC), less than 4 inches of the available soil water, and soil moisture levels are generally still high and less than 20% of the available nitrogen has been utilized.

emergence relative to the crop growth stage not weed density. These observations are not consistent with yield loss caused by resource limitation. Indeed, the observation that weeds have their greatest per-unit impact on yield at lower densities suggests that the primary mechanism for yield loss is due to the crop's response to an initial perception of weed presence.

Thus, there appears to be little evidence to support a paradigm where resource limitation is the primary cause of weed-induced yield loss in crops, at least in well-managed agroecosystems. Rather, the critical period for weed control has a pattern similar to other 'developmental windows' observed in both plants and animals where the response to a signal requires specific competencies and, when activated (or fail to activate), results in developmental trajectories that are irreversible [34]. Thus, the observation that weeds are only perceived in such a way as to impact crop yield in a narrow developmental window provides the basis for a new paradigm for weed-induced yield loss in crops.

In this review, we first discuss why weeds might reduce crop yield via mechanisms other than resource competition, the implications of these alternative hypotheses on the paradigm for crop–weed interactions, and the physiological and developmental changes induced by weed perception alone. Evidence that plants perceive and respond to neighboring plants is well documented and we will place these observations in the specific biological context of crop–weed interactions. Finally, we examine the mechanisms by which weeds might reduce crop growth and present potential directions for investigating and mitigating weed-induced yield losses in crops growing in well-managed agricultural settings.

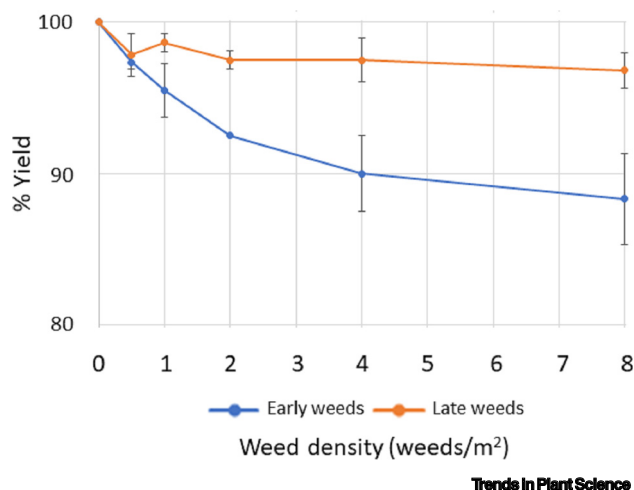


Figure 4. Graph of percent yield as a function of weed density demonstrating the classic parabolic curve usually obtained from similar experiments where weeds emerge early in the critical period for weed control, and the minimal impact of weeds that emerge near the end of the critical period for weed control. Data are the average of three plots over 2 years and two locations [32]. Error bars represent the standard error ($n = 3$).

Evolution of weed-induced yield loss

Resources are not usually limiting in well-managed agroecosystems, but all crops are derived from wild ancestors that evolved in conditions where resources were often limited. Plants are known to detect resource levels in their environment and respond by altering their growth and development to ensure seed production even when resources are limited. Because competitors often cause temporal changes in the levels of needed resources, it seems reasonable to assume that plants unable to detect neighboring plants and alter their developmental trajectory early in the season may not have the resources available to complete their lifecycle when resources are limited later. Plants that could detect potential competitors and adjust their development accordingly would have an evolutionary advantage. Indeed, the earlier a plant could respond to potential competitors, the better chance it would have to make the necessary adjustments in developmental programs required for flowering and seed production under conditions that were 'likely' to become resource limited.

Plants have evolved several alternative strategies to offset the impact of resource limitations on growth, development, and yield. For example, the production of allelochemicals to reduce the fitness of their competitors [35–37], alterations in developmental processes such as shifting growth and reproduction to occur before resources are limited [38–40], alterations in resource foraging strategies [41,42], increasing shoot length to gain a height advantage [43,44], and/or alterations in the microbiome that can positively or negatively impact plant growth and development [45,46]. There are also epigenetic changes that result from plant–plant interactions [47–49], including those that can alter a seedling's response to competitors in the next generation [50].

The need for preemptive initiation of defense and developmental responses designed to maximize the probability of reproductive success over growth should be minimal in well-managed cropland. Indeed, these responses, primordial in origin, may be deleterious to yield in modern cropping systems. For example, production of allelochemicals in response to competitors can be energetically expensive [51,52]. Reducing growth to ensure nutrient/water availability for flowering and seed production, early initiation of flowering, and similar responses might ensure some seeds make it to the next generation when resources are limited, but such alterations would be deleterious to yield if resources are not actually limited. Additionally, induction of stress responses that are now quantifiable during weed–crop interactions could limit growth through alterations in the physiological mechanisms that generally balance defense and growth

responses in plants [see section on the TARGET OF RAPAMYCIN (TOR) complex]. If the new paradigm is proven correct, even in part, then it should be possible to block or bypass the signals and pathways which crops evolved for early detection of potential competitors. This new paradigm would open new avenues of exploration for breeding and engineering crops to limit deleterious responses to weeds and manipulation of production practices to limit adverse interactions.

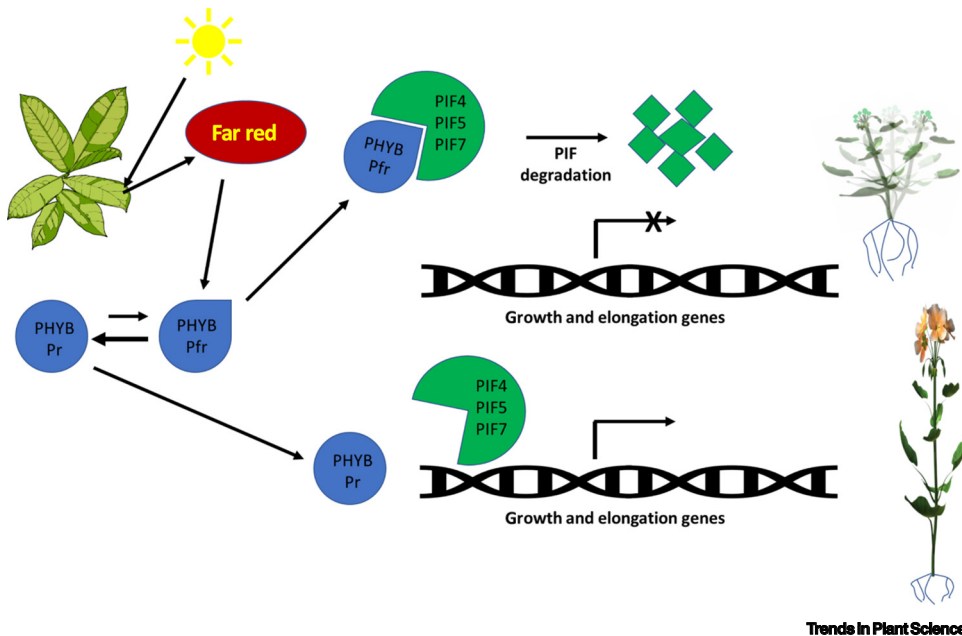
How crops perceive potential competitors

Plants have been shown to perceive neighboring plants through changes in light quality, below-ground soil-mobile signals, and volatile signals [53]. A recent and very comprehensive series of reviews related to these signaling processes has been published [105]. Thus, here, we will only provide a brief overview and focus on gaps and newer literature with the exception of requisite background information.

Light quality signals impact crop growth in the presence of weeds

Light quality signals in plant–plant communication have been studied at the molecular level since the early 1980s [44]. Most of this research focused on phytochrome responses in *Arabidopsis*, which is responsive to changes in the ratio of red to far-red light [54]. Chlorophyll absorbs red light and reflects far-red light. Phytochrome in crops can detect increases in far-red light reflected from neighboring plants [6,55–57]. The conformational change in phytochrome caused by far-red light alone mimics many of the changes in morphology associated with intense plant–plant competition, including stem elongation, changes in leaf angle, early flowering, and a redirecting of resources from root growth to shoot growth – even in the absence of competitors [44]. These developmental changes are often referred to as the ‘shade avoidance syndrome’ or ‘shade avoidance response’. Many of the pathways impacting various aspects of the shade avoidance response are well detailed [44]. Multiple genes are involved in these phytochrome-regulated controls of plant growth and development and signaling pathways involve numerous proteins – most notable being the PHYTOCHROME INTERACTING FACTORS (PIF) [44]. These downstream signaling components directly control expression of developmental genes and activate plant hormone responses that further alter developmental and physiological processes (Figure 5).

The shade avoidance responses can be advantageous in early competition for light and anticipated nutrient depletion. These phenological traits, however, tend to only show up primarily under high weed densities with very low red (R):far-red (FR) light ratios. Under most agricultural settings, direct shading is not usually a problem early in the season when pre-emergence herbicides and tillage have been used. Although taller plants with longer and thinner internodes are a common feature of heavy weed interference, less dense weed presence generally results in smaller crops with delayed development, and significant differences in root-to-shoot ratios generally associated with a classic shade avoidance response early in the season but not later in the season [56,57]. These observations suggest that the core mechanisms of plant competition under field conditions may be fundamentally different from the classical phenological traits associated with the shade avoidance response, although it is possible that the early impact of weeds on shoot-to-root ratios could result in the delays in crop development later in the season. In the few molecular-based studies of weed impact on crops under field conditions, gene expression changes associated with far-red light responses were observed [58,59]. The expression was observed even after weeds were removed and the crop plants had a chance to grow unimpeded and recover (4–6 weeks) from weed-generated signals [58]. Thus, even though classic shade avoidance phenologies may be absent, weed-detection processes may act through some of the signaling pathways normally associated with light quality perception.



Trends in Plant Science

Figure 5. Far-red light is reflected from neighboring plants and causes PHYTOCHROME B to shift from the Pr to the Pfr conformation. PHYTOCHROME B-Pfr cannot bind and target the transcription factors PHYTOCHROME INTERACTING FACTORS (PIF) 4, 5, and 7 for degradation. Undegraded PIFs bind to and activate genes involved in growth and elongation including genes regulating gibberellic acid, and auxin production and signaling. Expression of these genes leads to elongated plant growth with fewer branches and earlier flowering.

Another suggested mechanism for weed-induced crop yield loss due to light signals rather than resource availability is through the generation of stress-inducing reactive oxygen species. Specifically, an increase in singlet oxygen is associated with the low R:FR light ratios in arabidopsis, soybean, and corn [60–62]. The increase in singlet oxygen under low R:FR light conditions has been associated with increased oxidative stress and increased susceptibility to damage by other factors that might enhance the oxidative stress of plants, such as exposure to 5-aminolevulinic acid (5-ALA) [63]. Also, it has been demonstrated that reducing oxidative stress by pretreating seeds with thiamethoxam, which is known to act as a scavenger of reactive oxygen species, can reduce the damaging effects in low R:FR environments [64]. Additionally, long-term impacts of FR light exposure on photosynthetic processes have been observed [65] which would be consistent with some of the yield-limiting impacts weeds have even if they are removed after the critical period for weed control. These observations point to potential physiological processes that could be targeted to reduce yield loss caused by a low R:FR growth environment during heavy weed infestations, though inhibiting this process will not likely protect plants from the primary mechanism of weed-induced yield losses that are observed at low weed densities.

One gap in the literature is how quickly these light quality signals dissipate. Although crops can perceive weeds through changes in light quality from a distance and can perceive these signals when the weed is below the crop canopy, surprisingly, there have been few studies that quantified these signals. We have found only two examples in the literature. In one study with soybean growing with *Amaranthus palmeri*, distance between the crop and weed made no difference to the soybean yield but did impact the yield of the amaranth [66]. Likewise, in another study, R:FR light signals as far as 30 cm from neighboring plants generated signals that resulted in altered growth of the target plant [67]. There are reasonably good molecular markers, such as PIF gene

expression or induction of downstream gibberellic acid biosynthesis of signaling genes, for investigating the induction of these light quality signals. Thus, it should be possible to measure crop responses to weeds grown in separate containers under controlled conditions to determine the spatial limits of light detection. However, some controls might be needed to isolate the light quality signals from any potential volatile signals in such a system.

The length of time a plant must be subjected to these light signals before a significant long-term deleterious impact on yield is observed is also unknown. We know that the critical period for weed control is 4–6 weeks long, and the impact accumulates through that developmental window. We also know that changes in gene expression following exposure to high levels of far-red light can be very fast (in a matter of seconds) [68], and that plants can sense and respond to light signals even before they emerge from the soil. Soybean seedlings, for example, show altered shoot-to-root growth ratios prior to emergence if they are grown in the presence of a competitor [69]. Also, although we know changes occurring in response to the light quality signals are advantageous during high levels of competition, they can be deleterious to the overall yield. However, we do not know the quantitative impact of these light signals that are needed to cause the irreversible yield losses observed under field and greenhouse conditions.

Another gap in the current state of knowledge is the seeming disconnection between the phenology of classic shade avoidance responses and the observed impact of weeds on crop plants in the field. More research is needed to understand why weeds usually cause crops to show delayed development and generally less above- and belowground biomass under moderate weed pressure rather than classic shade avoidance phenotypes expected from increased far-red light exposure. It may be that previous studies with arabidopsis, particularly those where weed interference was simulated by enhancing the level of far-red light, may not accurately represent weed–crop interactions under field conditions. It might also be that far-red light detection in conjunction with other weed-generated signals results in different developmental trajectories. Far-red light might also alter nitrogen assimilation and oxidative stress which amplify weed impacts, as has been implicated in at least one study (W. Kramer, MSc dissertation, University of Guelph, 2021). Understanding why weeds at lower densities cause different responses than expected could help identify the signaling processes that need to be blocked or mitigated to reduce crop yields.

Belowground signals and impact on crop growth in the presence of weeds

Plants are also able to recognize the presence of neighboring plants using belowground (soil) signals. Plants can detect and distinguish between other species and even closely related relatives by sensing root exudates alone and altering their root morphology accordingly [35,70–72]. In ecology, the observed loss of yield when plants were grown in close proximity is often referred to as ‘the tragedy of the commons’. It has long been observed that plants will show minimal reduction in growth if grown in the same pot, provided the roots of each plant are separated by an impermeable barrier. However, once the root-to-root contact is established, the plants show reduced growth – even in cases where resources were augmented to reduce competition for those resources [73]. These studies have been criticized because soil volume was altered, which complicates interpretation of the results [74]. Several studies have been done to control for soil volume effects by preventing direct root-to-root contact with a permeable barrier that still allows the sharing of signals between the two plants without the subsequent change in available soil volume [75]. Such studies still showed reduced yield when plant-to-plant contact was allowed. Interestingly, in at least one study, loss of growth was observed to be species specific, suggesting that some, but not all, plants respond to neighbors in the same way [73].

Other studies suggest that signals between plants may actually be a response to perceived sensing of available soil volume through the concentration of specific root exudates. In such a scenario, each plant in a pot contributes to total exudates, and thus, two plants would generate twice as much as one plant in a pot. One intriguing study examined the ability of plants to respond to just changes in soil volume [76]. In that study, a set of designs based on mesh pots in soil or hydroponic solutions allowed diffusion of soluble signals while simultaneously controlling for nutrient levels and limiting the volume in which roots could expand. That study also found that early responses to substrate volume were not dependent on root density or the effects of physical contact with the root barriers. However, after roots started to become crowded, there was a response limiting root growth. From these findings, it was concluded there is an early and highly soluble signal that specifically senses substrate volume and limits shoot growth, and a later signal that is less soluble and senses root density to adjust the growth of the roots to match the available volume [76]. The published results were obtained with spring wheat. However, the authors claimed to have observed similar results in wheat, barley, and oilseed rape. Although the nature of the signals is not well understood, these data clearly indicate belowground signals generated from neighboring plants can be detected and can alter plant growth and development. It is possible, if not probable, that differences in species-specific responses to nearby weeds noted previously [74] could be due to recognition of, or failure to recognize, substrate volume signals from the other species.

Other belowground weed-generated signals that could reduce crop yield are the production of allelopathic chemicals by weeds. Only a limited number of studies have successfully identified allelopathic chemicals produced by certain species [35]. That said, developing systems to enhance production of allelopathic chemicals by crops could reduce weed interference and thus should be explored. For example, increasing the production of ticin (5,7,4'-trihydroxy-3',5'-dimethoxyflavone), a known allelopathic chemical produced by rice [77], may help reduce weed-induced yield loss, and ultimately the weed seed bank. Similarly, enhancing production of chemicals such as DIMBOA-glc [2-(2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one)- β -D-glucopyranose] by wheat [78] or sorgoleone (2-hydroxy-5-methoxy-3-[(80Z,110Z)-80,110,140-pentadecatriene]-p-benzoquinone) by sorghum [79] could result in greater yield by reducing growth of nearby weeds. Toward that goal, considerable efforts have gone into understanding the biochemical processes required for production of specific allelopathic chemicals and the genes controlling the enzymatic processes required for their production [80,81]. Additionally, efforts have been taken to identify cultivars with higher allelopathic chemical production [82,83].

The response to weeds is a rather general phenomenon while allelopathic chemical production and response is often species specific. Thus, the production of allelopathic chemicals – though clearly important for some specific weed-induced crop yield losses – is not likely to be a general factor impacting most crop–weed interactions. Consequently, there is a need to identify these general neighbor-detection (and/or soil-volume-detection) signals and develop methods and technologies for quantifying and characterizing these more generalized signals. Hydroponic systems as described previously [76] could offer an excellent opportunity to both investigate these soil volume-sensing signals and to investigate signals involved in interspecific plant–plant interactions. For example, in the study of substrate volume- and root density-sensing signal, only a single plant was examined in the described hydroponic system [76]. These studies could easily be extended to study the response of a plant to both inter- and intraspecific interference. It will also be important to identify the receptors of these signals and the mechanisms regulating the transduction of these signals into changes in crop phenology in response to weeds.

Although nutrient levels seem to have limited impact on the signals resulting in weed-induced yield losses in crops under field or greenhouse conditions, there is some evidence that mechanisms

involved in nutrient sensing and nutrient acquisition also are impacted by belowground signals [12,84]. Particularly, based on transcriptomics studies, nitrogen and phosphorous acquisition and transport are impacted [85]. Although these nutrients are not generally lacking early in the season when crop plants are actively sensing their environments, they may be important later in the season when nutrients might become limiting in low-input agricultural settings. Information about the role and impact of these nutrient acquisition processes and the genes regulating these responses could be used to manipulate the growth and development of crops. However, as some of these changes may make the crop less competitive, such as those that limit nutrient uptake when the crop recognizes related individuals when in intraspecific competition [12], a comprehensive comparison between the responses designed to augment sharing over competition will be needed.

Above- and belowground volatile signaling in neighbor recognition and response

The generation of volatile signals in plant–plant communication was first recognized in plant defense responses to insect predation [86]. Additionally, volatile signals have been associated with a crop's ability to recognize and respond to potential plant competitors [87]. Also, the ability to perceive ethylene is required for tobacco to respond to other nearby tobacco plants [54]. Likewise, wheat has been shown to be responsive to volatile hormones such as jasmonic acid and (–)-loliolide, which are constitutively emitted from many plant species [36] and thus are potential general signals for detecting neighboring plants.

Because of their very nature, it is often difficult to control for or isolate volatile signals when investigating crop–weed interactions, and more studies that take these signals into account are warranted. Thus, in addition to identifying the biological and ecological relevance of these volatile signals, another challenge will be developing tools and methodologies to isolate biologically active volatile compounds. Although plants can clearly produce, perceive, and respond to both above- and belowground volatile compounds, information on the precise signaling processes and genes that control the perception and response to these compounds is lacking. There is a significant knowledge gap that could be filled using the same set of genetic and transcriptomic analyses noted previously for characterizing belowground signals. Volatile, light-quality, and soil-soluble signals in any combination likely control specific signaling processes to regulate gene expression. Thus, identifying candidate genes through associated genetic and transcriptomic analyses is warranted for all the signaling processes listed previously.

If not resource competition, how do weeds reduce crop growth?

Regulation of plant growth has long been a focus of study, and the roles plant hormones play in this process are well documented [88]. Hormones such as auxins, cytokinins, brassinosteroids, and gibberellic acid primarily enhance growth and others such as abscisic acid, salicylic acid, and jasmonic acid generally suppress growth. Biotic defense responses that included jasmonic and salicylic acid signaling were also implicated in intra- and interspecific competition in *Arabidopsis* [70,89]. The levels of abscisic acid, salicylic acid, jasmonic acid, and cytokinin were observed to increase in tobacco in response to the presence of neighboring plants [90].

How these stress-related hormones reduce growth is less well documented, as are the precise mechanisms by which environmental and developmental signals acting through changes in hormone levels and perception reduce cell division and cell size. Yet, some intermediate signaling molecules and their targets are known. For example, increases in abscisic acid levels are known to increase expression of a cell cycle inhibitor known as *KIP-RELATED PROTEIN 1 (KRP1)* [91]. Jasmonic acid downregulates *PLETHORA 1 (PLT1)* and *PLETHORA 2 (PLT2)* which positively regulate expression of *CDKB* (a gene required for cell division) through *HIGH PLOIDY 2 (HPY2)*

and *PLT1/2* genes [92]. Salicylic acid appears to regulate the cell cycle through the same mechanism as jasmonic acid [93].

Weed interference impacts the photosynthetic abilities of crop plants, even when weeds are not directly shading the crops [85,89]. Indeed, weed interference was shown to reduce photosynthates in most studies and as such is directly correlated with reduced growth [62].

The primary mechanism for regulating growth in eucaryotic organisms is the TOR signaling system [94]. The TOR complex is integral to an ancient and highly conserved signaling process present in eucaryotes that coordinates growth with nutrient availability and stress [95]. The TOR complex in plants is formed from three separate proteins TOR, REGULATORY-ASSOCIATED PROTEIN OF MTOR (RAPTOR), and LETHAL WITH SEC13 PROTEIN 8 (LST8). This complex regulates growth by initiating or modifying kinase signaling processes and is itself regulated through altered expression or transcript stability of/from the genes making up the TOR complex, and by post-translational interactions and molecules that can interfere with the stability of this complex [96]. The TOR complex integrates information on nutrient and sugar status, hormones, and circadian rhythm and then induces or represses the genes needed for cell division and expansion, nutrient acquisition and homeostasis, and hormone production and stability. Not all the specific genes and signaling molecules in many of these interactions are known; however, some have been elucidated [96]. Evidence for a role of the TOR kinase complex in crop–weed interactions comes primarily from transcriptome analyses which identified the TOR-regulating gene SUCROSE NONFERMENTING-RELATED PROTEIN KINASE 1 (SnRK1) as differentially expressed in response to weed interference in corn, soybean, and arabidopsis [13,59,89]. Additionally, some of the other responses to weed interference in these studies, such as induction of nutrient transporters [96], are known to be regulated by TOR kinase (Figure 6, Key figure).

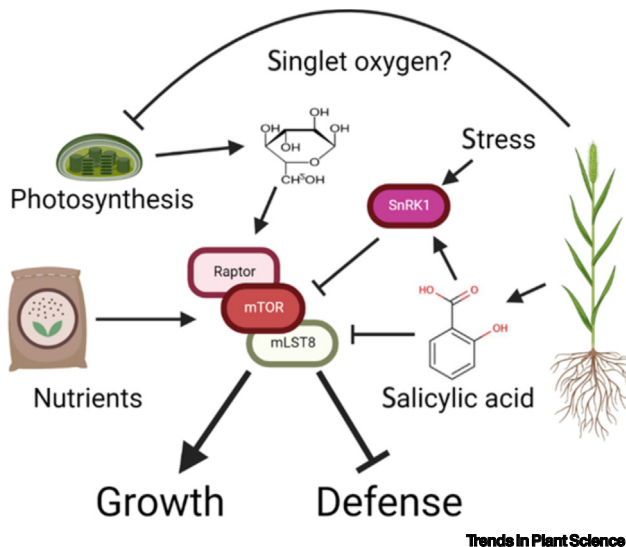
Considering the importance of the TOR signaling complex, there is a need to investigate the role of TOR signaling in crop–weed interactions. Given the possibility that weed-induced yield loss is directly the result of weed perception acting to inhibit TOR kinase signaling, preventing yield loss under well-managed agricultural settings might be as easy as preventing weed-generated signals from downregulating TOR signaling. Mutations that result in constitutive expression of TOR and other components of the TOR kinase complex exist in model systems such as arabidopsis and could be used to test this hypothesis. Thus, it should be possible to determine if preventing downregulation of the TOR kinase complex is sufficient to ameliorate weed-induced stresses. The TOR kinase complex is also required for maintaining the balance between defense and growth, and constitutively active TOR kinase has been shown to make plants more vulnerable to disease [97,98]. Thus, if TOR overexpression can reduce yield loss caused by weed interference, any system designed to overexpress TOR would have to limit that overexpression only when weeds are present. That will require identifying or creating strong weed-inducible promoters.

Genetic and genomic analyses of crop–weed interactions

Two approaches (RNAseq and genome-wide association studies) have been used recently to identify the genes involved in the signaling processes through which crops perceive weeds. RNAseq analyses have identified genes differentially expressed in corn, soybean, teosinte, clover, and arabidopsis responding to weed interference [13,59,85,99–101]. These genes could serve as tools to dissect the signaling processes that result in the altered gene regulation in response to weed presence. For example, the *NUCLEOREDOXIN 1* gene was identified as a weed-inducible gene in corn [13] and teosinte [101]. The sequence conservation between the corn and teosinte promoters suggests that there may be *cis*-acting elements responsive to weed-detection systems. Identifying such *cis*-acting signals could provide the tools and information

Key figure

When weeds are perceived by the crop, they upregulate the SUCROSE NON-FERMENTING-1 (SNF1)-RELATED KINASE 1 signaling process directly or indirectly through increasing the salicylic acid signaling processes



Trends in Plant Science

Figure 6. Weeds may also reduce photosynthesis due to an increase in singlet oxygen and thus reduce glucose levels. These, in turn, result in repressed TARGET OF RAPAMYCIN (mTOR) kinase activity and thus a reduction in growth and an increase in defense processes. Abbreviations: mLST8, LETHAL WITH SEC13 PROTIEN 8; RAPTOR, REGULATORY-ASSOCIATED PROTEIN OF MTOR.

needed to identify the transcription factors that interact with them and begin the process of working backwards toward the receptors of the weed-generated signals (Figure 7). These *cis*-acting signals may also be useful for engineering strong and specific weed-inducible promoters for driving genes needed to prevent or circumvent the responses of crops to weeds.

Likewise, genetic approaches such as genome-wide association studies have been used to identify genes that alter growth and development in response to neighboring plants [102–104]. These genomic association studies can locate additional genes that may play a role in the signal transduction processes regulating crop phenological changes caused by weeds. Combined, these studies have potential to identify the genes and signaling pathways regulating the general reduction in crop yield in response to weeds. Additional studies are needed in diverse agroecosystems (particularly in cropping systems) to determine the generalities of these signaling processes.

Observations that hormone-responsive and hormone metabolism genes are differentially expressed by weed interference make for an intriguing correlation. Although increases in salicylic acid have been hypothesized to be responsible for yield loss in corn [13], to date there is no direct evidence that this hormone causes weed-induced yield loss in crops. More research is needed both to confirm the role of specific hormones implicated in weed interference and to identify the genes involved in the signaling processes. Systems, such as arabidopsis, where there are many lines available with mutations in specific hormone-signaling processes offer an excellent

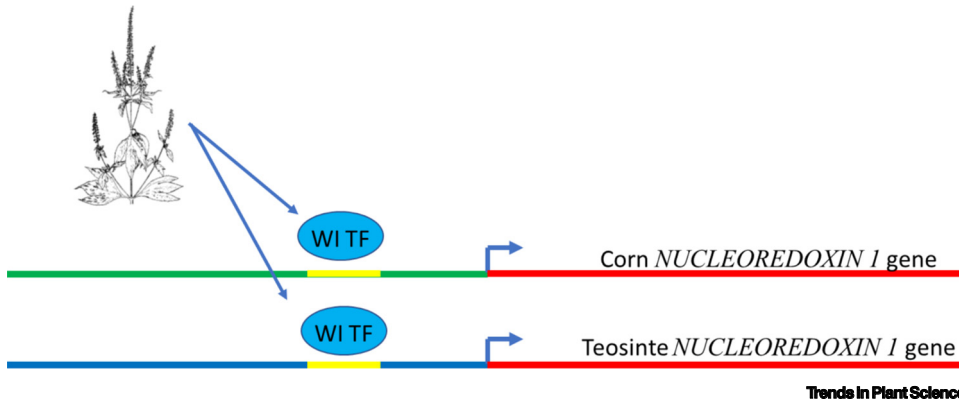


Figure 7. Diagram showing the conservation in the promoter regions of the weed-inducible *NUCLEOREDOXIN 1* genes from corn and teosinte may indicate regions of the promoter that are conserved and important for the weed-inducible regulation of these genes, possibly by containing the binding sites for weed-inducible transcription factors (WI TFs).

opportunity to test these hypotheses. Additionally, it should be possible to engineer corn plants that have salicylic acid degrading genes under the control of weed-inducible promoters to determine levels of weed perception.

Concluding remarks

The evidence presented here supports a shift from the direct resource competition paradigm that is often used to explain why weeds reduce crop yield. Based on this evidence, we propose a new paradigm where weeds initiate signaling processes early in the life cycle of crops that alter growth and development, well before resource limitations are perceived. These signaling processes could be separate or combined with signals generated by light quality. This opens the possibility that, by blocking deleterious physiological and developmental responses to weed-generated signals, crop yield losses may be greatly reduced in well-managed agroecosystems where water and nutrient levels are not limited. Blocking these signals could potentially mitigate yield losses even when resource limitations occur, since it targets a different mechanism for weed-induced yield loss. However, before this tactic can be realized, considerable research is needed to identify the genes and molecules required for perception and transduction of the weed-generated signals. Since some of these processes are required to protect the plant from predation, diseases, and other stresses, additional research will be needed to identify methods to specifically block these signaling processes only when weeds are present. Because crops respond differently to kin versus weeds, it is also necessary to ensure that responses to neighboring kin are not inhibited. It should be possible to find *cis*- and *trans*-regulatory elements to specifically block signals from non-kin. More transcriptomics studies are needed to provide sources of promoters and other *cis*-acting regulatory elements for engineering weed tolerance into crops. Likewise, given the genetic diversity in response to weeds that has been uncovered, more research on genome-wide association studies and genetic analyses is required to identify the gene targets for manipulating crop–weed interactions. The data mentioned previously also point to the need for developing better systems to study crop–weed interactions. Additionally, experimental systems that take advantage of hydroponic growing environments with permeable barriers must be developed to help differentiate between weed-specific and soil volume signals that impact growth. Likewise, experimental systems for capturing and identifying volatile plant signals will be helpful for advancing our understanding of the signaling mechanisms involved in weed–crop interactions. The ability to manipulate any of the systems discussed could be avenues for developing cropping systems where crops are partially or completely blind to weeds,

Outstanding questions

What weed-generated signals are primarily responsible for weed-induced yield losses in crops, and how can they be blocked?

How do mechanisms of weed–crop interactions compare among varying crop–weed combinations?

What is the nature of the receptors and transducers of the weed-generated signals that ultimately result in altered crop growth and development and subsequent yield loss?

What are the threshold levels and timing of weed-generated signals that are required before crop growth and yield are affected?

Do the threshold levels vary with crop age?

What are the implications for resource-independent plant–plant interference in ecology and evolution outside of the agroecosystem?

Can weed-regulated promoters be used to delay or stop early season weed-induced stress or enhance detection of early weed infestations?

Are there any potential unintended consequences of blocking weed perception in crops? For example, if weed signals are blocked, will crops die before reaching maturity, show reduced vigor, or show excessive dominance in the ecosystem and become invasive weeds themselves?

especially early in their growth cycle. Additionally, crops that are less responsive to competitors may also have reduced yield losses when grown with cover crops or in intercropped systems. Thus, development of weed-tolerant crops might also help reduce the impact that climate change is predicted to have on increasing weed pressure in cropping systems (see [Outstanding questions](#)).

Declaration of interests

No interests are declared.

References

- Reddy, C. (2018) A study on crop weed competition in field crops. *J. Pharmacogn. Phytochem.* 7, 3235–3240
- Grime, J.P. (1979) Succession and competitive exclusion. In *Ecology and Design in Amenity Land Management*, pp. 57–70, Wye College
- Trinder, C.J. *et al.* (2012) A new hammer to crack an old nut: interspecific competitive resource capture by plants is regulated by nutrient supply, not climate. *PLoS One* 7, e29413
- Lindquist, J.L. *et al.* (2010) Effect of nitrogen addition and weed interference on soil nitrogen and corn nitrogen nutrition. *Weed Tech.* 24, 50–58
- Plenet, D. and Lemaire, G. (2000) Relationships between dynamics of nitrogen uptake and dry matter accumulation in maize crops. Determination of critical N concentration. *Plant Soil* 216, 65–82
- Rajcan, I. and Swanton, C.J. (2001) Understanding maize-weed competition: resource competition, light quality and the whole plant. *Field Crops Res.* 71, 139–150
- Bandein, J.D. and Buchholtz, K.P. (1967) Competitive effects of quackgrass upon corn as modified by fertilization. *Weeds* 15, 220–224
- Young, F.L. *et al.* (1984) Quackgrass (*Agropyron repens*) interference on corn (*Zea mays*). *Weed Sci.* 32, 226–234
- Kropff, M.J. (1993) Mechanisms of competition for nitrogen. In *Modelling Crop-Weed Interactions* (Kropff, M.J., ed.), pp. 77–82, CAB International
- Norsworthy, J.K. and Oliveira, M.J. (2004) Comparison of the critical period for weed control in wide- and narrow-row corn. *Weed Sci.* 52, 802–807
- Lindquist, J.L. *et al.* (2007) Comparative nitrogen uptake and distribution in corn and velvetleaf (*Abutilon theophrasti*). *Weed Sci.* 55, 102–110
- Benaragama, D. and Shirliffe, S.J. (2020) Weed competition in organic and no-till conventional soils under nonlimiting nutrient conditions. *Weed Sci.* 68, 654–663
- Horvath, D.P. *et al.* (2019) Varying weed densities alter the corn transcriptome, highlighting a core set of weed-induced genes and processes with potential for manipulating weed tolerance. *Plant Genome* 12, 190035
- Nieto, H.J. *et al.* (1968) Critical periods of the crop growth cycle for competition from weeds. *PANS* 14, 159–166
- Nichols, V. *et al.* (2015) Weed dynamics and conservation agriculture principles: a review. *Field Crop Res.* 183, 56–68
- Zimdahl, R.L. (2018) Herbicides and soil. In *Fundamentals of Weed Science* (5th edn) (Zimdahl, R.L., ed.), pp. 445–464, Academic Press
- Swanton, C.J. *et al.* (1999) Weed thresholds: theory and applicability. In *Expanding the Context of Weed Management* (Buhler, D.D., ed.), pp. 9–29, CRC Press
- Bilas, R.D. *et al.* (2021) Friends, neighbours and enemies: an overview of the communal and social biology of plants. *Plant Cell Environ.* 44, 997–1013
- Zimdahl, R.L. (1980) *Weed-crop competition—a review*, 195. International Plant Protection Center
- Van Acker, R. *et al.* (1993) The critical period of weed control in soybean [*Glycine max* (L.) Merr.]. *Weed Sci.* 41, 194–200
- Martin, S.G. *et al.* (2001) Critical period of weed control in spring canola. *Weed Sci.* 49, 326–333
- Azimah, A.K. *et al.* (2018) Critical period for weed control in *Stevia rebaudiana* (Bert.) Bertoni. *J. Trop. Agric. Food Sci.* 46, 91–98
- Charles, G.W. *et al.* (2019) Determining the critical period for weed control in high-yielding cotton using common sunflower as a mimic weed. *Weed Tech.* 33, 800–807
- Knezevic, S. *et al.* (2002) Critical period for weed control: the concept and data analysis. *Weed Sci.* 50, 773–786
- Clay, S.A. *et al.* (2005) Growth and fecundity of several weed species in corn and soybean. *Agron. J.* 97, 294–302
- McDaniel, C.N. *et al.* (1988) Cell-lineage patterns in the shoot apical meristem of the germinating maize embryo. *Planta* 175, 13–22
- Spitters, C.J. *et al.* (1989) Competition between maize and *Echinochloa crus-galli* analysed by a hyperbolic regression model. *Ann. Appl. Biol.* 115, 541–551
- Kropff, M.J. *et al.* (1991) A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Res.* 31, 97–105
- Cousens, R. (1985) A simple model relating yield loss to weed density. *Ann. Appl. Biol.* 107, 239–252
- Roland, G. *et al.* (2017) Sugar beet yield loss predicted by relative weed cover, weed biomass and weed density. *Plant Protect. Sci.* 53, 118–125
- Dieleman, A. *et al.* (1995) Empirical models of pigweed (*Amaranthus* spp.) interference in soybean (*Glycine max*). *Weed Sci.* 43, 612–618
- Knezevic, S.Z. *et al.* (1994) Interference of redroot pigweed (*Amaranthus retroflexus*) in corn (*Zea mays*). *Weed Sci.* 42, 568–573
- Bosnic, A.C. *et al.* (1997) Influence of barnyardgrass (*Echinochloa crus-galli*) time of emergence and density on corn (*Zea mays*). *Weed Sci.* 45, 276–282
- Fawcett, T.W. *et al.* (2015) Adaptive explanations for sensitive windows in development. *Front. Zool.* 12, S3
- Duke, S. *et al.* (2015) Proving allelopathy in crop–weed interactions. *Weed Sci.* 63, 121–132
- Kong, S.H. *et al.* (2018) Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. *Nat. Commun.* 9, 1–9
- Wang, N.Q. *et al.* (2021) Root exudate signals in plant–plant interactions. *Plant Cell Environ.* 44, 1044–1058
- Munguia-Rosas, M.A. *et al.* (2011) Meta-analysis of phenotypic selection on flowering phenology suggests that early flowering plants are favoured. *Ecol. Lett.* 14, 511–521
- Lankinen, A. *et al.* (2013) Allocation to pollen competitive ability versus seed production in *Viola tricolor* as an effect of plant size, soil nutrients and presence of a root competitor. *Oikos* 122, 779–789
- Thurber, C. *et al.* (2014) The evolution of flowering strategies in US weedy rice. *Am. J. Bot.* 101, 1737–1747
- Schofield, E.J. *et al.* (2019) Cultivar differences and impact of plant–plant competition on temporal patterns of nitrogen and biomass accumulation. *Front. Plant Sci.* 10, 215
- Ljubotina, M.K. *et al.* (2019) Effects of neighbour location and nutrient distributions on root foraging behaviour of the common sunflower. *Proc. R. Soc. B.* 286, 20190955
- Green-Tracewicz, E. *et al.* (2012) Light quality and the critical period for weed control in soybean. *Weed Sci.* 60, 86–91
- Huber, M. *et al.* (2021) Light signalling shapes plant–plant interactions in dense canopies. *Plant Cell Environ.* 44, 1014–1029
- Guo, Q. *et al.* (2019) Plant–plant interactions and N fertilization shape soil bacterial and fungal communities. *Soil Biol. Biochem.* 128, 127–138

46. Louarn, G. *et al.* (2020) Two decades of functional–structural plant modelling: now addressing fundamental questions in systems biology and predictive ecology. *Ann. Bot.* 14, 501–509
47. Venturilli, S. *et al.* (2015) Plants release precursors of histone deacetylase inhibitors to suppress growth of competitors. *Plant Cell* 27, 3175–3189
48. Puy, J. *et al.* (2018) Improved demethylation in ecological epigenetic experiments: testing a simple and harmless foliar demethylation application. *Methods Ecol. Evol.* 9, 744–753
49. Ramos-Cruz, D. *et al.* (2021) Epigenetics in plant organismic interactions. *Curr. Opin. Plant Biol.* 61, 102060
50. Clements, D.R. *et al.* (2021) Ten ways that weed evolution defies human management efforts amidst a changing climate. *Agronomy* 11, 284
51. Fernandez, C. *et al.* (2016) The impact of competition and allelopathy on the trade-off between plant defense and growth in two contrasting tree species. *Front. Plant Sci.* 7, 594
52. McCoy, R.M. *et al.* (2022) Allelopathy as an evolutionary game. *Plant Direct* 6, e382
53. Sharifi, R. *et al.* (2021) Social networking in crop plants: wired and wireless cross-plant communications. *Plant Cell Environ.* 44, 1095–1110
54. Pierik, R. *et al.* (2004) Density-induced plant size reduction and size inequalities in ethylene-sensing and ethylene-insensitive tobacco. *Plant Biol.* 6, 201–205
55. Liu, J.G. *et al.* (2009) The importance of light quality in crop–weed competition. *Weed Res.* 49, 217–224
56. Page, E.R. *et al.* (2009) Does the shade avoidance response contribute to the critical period for weed control in maize (*Zea mays*)? *Weed Res.* 49, 563–571
57. Page, E.R. *et al.* (2010) Shade avoidance: an integral component of crop–weed competition. *Weed Res.* 50, 281–288
58. Moriles, J. *et al.* (2012) Microarray and growth analyses identify differences and similarities of early maize response to weeds, shade, and nitrogen stress. *Weed Sci.* 60, 158–166
59. Horvath, D. *et al.* (2015) RNAseq reveals weed-induced PIF3-like as a candidate target to manipulate weed stress response in soybean. *New Phytol.* 207, 196–210
60. Bartoli, C.G. *et al.* (2009) Control of ascorbic acid synthesis and accumulation and glutathione by the incident light red/far-red ratio in *Phaseolus vulgaris* leaves. *FEBS Lett.* 583, 118–122
61. Page, M.T. *et al.* (2017) Singlet oxygen initiates a plastid signal controlling photosynthetic gene expression. *New Phytol.* 213, 1168–1180
62. McKenzie-Gopsill, A.G. *et al.* (2019) Early physiological and biochemical responses of soybean to neighbouring weeds under resource-independent competition. *Weed Res.* 59, 288–299
63. Afifi, M. *et al.* (2012) Early physiological mechanisms of weed competition. *Weed Sci.* 60, 542–551
64. Afifi, M. *et al.* (2015) Thiamethoxam as a seed treatment alters the physiological response of maize (*Zea mays*) seedlings to neighbouring weeds. *Pest Manag. Sci.* 71, 505–514
65. McKenzie-Gopsill, A.G. *et al.* (2020) Duration of weed presence influences the recovery of photosynthetic efficiency and yield in common bean (*Phaseolus vulgaris* L.). *Front. Agron.* 2, 593570
66. Korres, N. *et al.* (2019) Effects of palmer amaranth (*Amaranthus palmeri*) establishment time and distance from the crop row on biological and phenological characteristics of the weed, implications on soybean yield. *Weed Sci.* 67, 126–135
67. Cressman, S. *et al.* (2011) Weeds and the red to far-red ratio of reflected light, characterizing the influence of herbicide selection, dose, and weed species. *Weed Sci.* 59, 424–430
68. Smith, H. *et al.* (1990) Reflection signals and the perception by phytochrome of the proximity of neighbouring vegetation. *Plant Cell Environ.* 13, 73–78
69. McKenzie-Gopsill, A.G. *et al.* (2020) Rapid and early changes in morphology and gene expression in soya bean seedlings emerging in the presence of neighbouring weeds. *Weed Res.* 56, 267–273
70. Biedrzycki, M.L. *et al.* (2010) Kin recognition in plants: a mysterious behaviour unsolved. *J. Exp. Bot.* 61, 4123–4128
71. Semchenko, M. *et al.* (2014) Plant root exudates mediate neighbour recognition and trigger complex behavioural changes. *New Phytol.* 204, 631–637
72. Karban, R. (2021) Plant communication. *Annu. Rev. Ecol. Evol. Syst.* 52, 1–24
73. Hardin, G. (1968) The tragedy of the commons. *Science* 162, 1243–1248
74. Semchenko, M. *et al.* (2007) Challenging the tragedy of the commons in root competition, confounding effects of neighbour presence and substrate volume. *J. Ecol.* 95, 252–260
75. O'Brien, E.E. *et al.* (2008) Games roots play, effects of soil volume and nutrients. *J. Ecol.* 96, 438–446
76. Wheeldon, C.D. *et al.* (2020) Wheat plants sense substrate volume and root density to proactively modulate shoot growth. *Plant Cell Environ.* 44, 1202–1214
77. Kong, C.H. *et al.* (2007) Activity and allelopathy of soil flavone O-glycosides from rice. *J. Agric. Food Chem.* 55, 6007–6012
78. Quader, M. *et al.* (2001) Allelopathy, DIMBOA production and genetic variability in accessions of *Triticum speltaoides*. *J. Chem. Ecol.* 27, 747–760
79. Weston, L.A. *et al.* (2013) Sorghum allelopathy—from ecosystem to molecule. *J. Chem. Ecol.* 39, 142–153
80. Jiang, B. *et al.* (2020) A flavonoid monomer tricin in gramineous plants, metabolism, bio/chemosynthesis, biological properties, and toxicology. *Food Chem.* 320, 126617
81. Hussain, M.I. *et al.* (2021) Unraveling Sorghum allelopathy in agriculture: concepts and implications. *Plants* 10, 1795
82. Bertholdsson, N.O. (2004) Variation in allelopathic activity over 100 years of barley selection and breeding. *Weed Res.* 44, 78–86
83. Rahaman, F. *et al.* (2021) Allelopathic effect of selected rice (*Oryza sativa*) varieties against barnyard grass (*Echinochloa crus-galli*). *Plants* 10, 2017
84. Pélessier, R. *et al.* (2021) Plant immunity: good fences make good neighbors? *Curr. Opin. Plant Biol.* 62, 102045
85. Horvath, D.P. *et al.* (2018) Weed presence altered biotic stress and light signaling in maize even when weeds were removed early in the critical weed-free period. *Plant Direct* 2, e00057
86. Baldwin, I.T. *et al.* (1983) Rapid changes in tree leaf chemistry induced by damage. evidence for communication between plants. *Science* 221, 277–279
87. Ninkovic, V. *et al.* (2019) Who is my neighbor? Volatile cues in plant interactions. *Plant Signal. Behav.* 14, 1634993
88. Gaspar, T. *et al.* (2003) Changing concepts in plant hormone action. *In Vitro Cell. Dev. Biol. Plant.* 39, 85–105
89. Masclaux, F.G. *et al.* (2012) Transcriptome analysis of intraspecific competition in *Arabidopsis thaliana* reveals organ-specific signatures related to nutrient acquisition and general stress response pathways. *BMC Plant Biol.* 12, 227
90. Chen, B.J.W. *et al.* (2019) Presence of belowground neighbors activates defense pathways at the expense of growth in tobacco plants. *Front. Plant Sci.* 11, 751
91. Wang, H. *et al.* (1998) ICK1, a cyclin-dependent protein kinase inhibitor from *Arabidopsis thaliana* interacts with both Cdc2a and CycD3, and its expression is induced by abscisic acid. *Plant J.* 15, 501–510
92. Chen, Q. *et al.* (2011) The basic helix–loop–helix transcription factor MYC2 directly represses PLETHORA expression during jasmonate-mediated modulation of the root stem cell niche in *Arabidopsis*. *Plant Cell* 23, 335–3352
93. Wang, Z. *et al.* (2020) Salicylic acid promotes quiescent center cell division through ROS accumulation and down-regulation of PLT1, PLT2, and WOX5. *J. Integr. Plant Biol.* 63, 583–596
94. Dobrenel, T. *et al.* (2016) TOR signaling and nutrient sensing. *Ann. Rev. Plant Biol.* 67, 261–285
95. Saxton, R.A. *et al.* (2017) mTOR signaling in growth, metabolism, and disease. *Cell* 168, 960–976
96. Burkart, G.M. *et al.* (2020) A tour of TOR complex signaling in plants. *Trends Biochem. Sci.* 46, 417–428
97. Deprost, D. *et al.* (2007) The Arabidopsis TOR kinase links plant growth, yield, stress resistance and mRNA translation. *EMBO Rep.* 8, 864–870
98. De Vleeschauwer, D. *et al.* (2018) Target of rapamycin signaling orchestrates growth–defense trade-offs in plants. *New Phytol.* 217, 305–319

99. Schmid, C. *et al.* (2013) Belowground neighbor perception in *Arabidopsis thaliana* studied by transcriptome analysis, roots of *Hieracium pilosella* cause biotic stress. *Front. Plant Sci.* 4, 296
100. Bowsher, A.W. *et al.* (2017) Transcriptomic responses to conspecific and congeneric competition in co-occurring *Trifolium*. *J. Ecol.* 105, 602–615
101. Bruggeman, S.A. *et al.* (2020) Teosinte (*Zea mays* ssp *parviglumis*) growth and transcriptomic response to weed stress identifies similarities and differences between varieties and with modern maize varieties. *PLoS One* 15, e0237715
102. Baron, E. *et al.* (2015) The genetics of intra- and interspecific competitive response and effect in a local population of an annual plant species. *Funct. Ecol.* 29, 1361–1370
103. Libourel, B.E. *et al.* (2019) The genomic architecture of competitive response of *Arabidopsis thaliana* is highly flexible between monospecific and plurispecific neighborhoods. *bioRxiv* Published online January 31, 2019. <https://doi.org/10.1101/536953>
104. Menendez, Y.C. *et al.* (2021) Unraveling the impact on agronomic traits of the genetic architecture underlying plant-density responses in canola. *J. Exp. Bot.* 72, 5426–5441
105. *Plant Cell Environ.* 44, 995–1277 Special Issue: Plant–Plant Interactions