Dynamics and management of crop-weed interference

Authors: Eric R. Page* and Chris J. Willenborg
First author: Research Scientist, Agriculture and Agri-food Canada, Greenhouse and Crops Processing Centre, 2585 County Rd. 20, Harrow, Ont., Canada, N0R 1G0; Second author: Assistant Professor, Department of Plant Sciences, University of Saskatchewan, Saskatoon, Saskatchewan S7N 5A8.
* Corresponding author E-mail: eric.page@agr.gc.ca

Summary
Weed management is one of the most critical factors influencing crop yield. By providing a window of weed-free growth early in the growing season, the size advantage that crop seedlings have over weeds can be utilized to reduce the intensity of direct competition for resources at the stages of crop development when yield is being determined. The goal of this review is to provide an overview of the process of crop-weed interference and explore avenues for improving weed control through the use of integrated weed management (IWM) strategies.

Introduction
Weed interference represents one of the most important factors limiting crop productivity in North America[21, 26]. Weed populations reduce crop yields by influencing the pattern of crop growth and development throughout the growing season and by directly competing with the crop for limiting resources, such as light, water or nutrients. Some of the factors that influence the magnitude of crop yield losses from weed interference include the timing of weed emergence relative to the crop, weed density, and the pattern of weed growth and development[10, 11, 27]. Although herbicides are widely used to manage weed populations, some weeds inevitably escape control and survive to produce seeds. These seeds are often retained in a soil seedbank that can survive over years or even decades[8]. It is this persistence that ensures efficacious weed management will remain a pressing issue for farmers for many years to come.

The goal of this review is to provide an overview of the process of crop-weed interference and explore avenues for improving weed control through the use of Integrated Weed Management (IWM) strategies. Specifically, in the following sections we will: 1) review some of the mechanisms underlying crop-weed interference; 2) explore why weed management during the early stages of crop growth is so important; and 3) examine how crop-weed interactions may influence crop tolerance to subsequent stressors. Finally, within this framework of crop-weed interactions, we will assess how cropping systems could be modified to take advantage of some of the differences between crop and weeds to better manage weed populations on an annual and multi-year basis.

On the importance of the timing of crop and weed emergence
The relative time of crop and weed emergence is perhaps the most important factor influencing the outcome of crop-weed competition. Although different densities and weed species can influence the magnitude of crop yield losses, weeds emerging at or near the time of crop emergence will have a much greater potential to cause yield losses than those emerging at later stages of crop development [11, 2]. For example, when barnyard grass (*Echinochloa crus-galli* L.) emerged shortly after corn (*Zea mays* L.), yield losses from weed interference increased with weed density (Figure 1). In contrast, when the same densities of barnyardgrass emerged at the 4th leaf tip stage of corn development (i.e., ~21 days after planting), they had little impact on crop yields at maturity. Similar results have also been observed for wild oat (*Avena fatua* L.) competition with wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.)[11]. In these crops, yield losses increased by approximately 3% for every day that wild oat emerged before the crop.

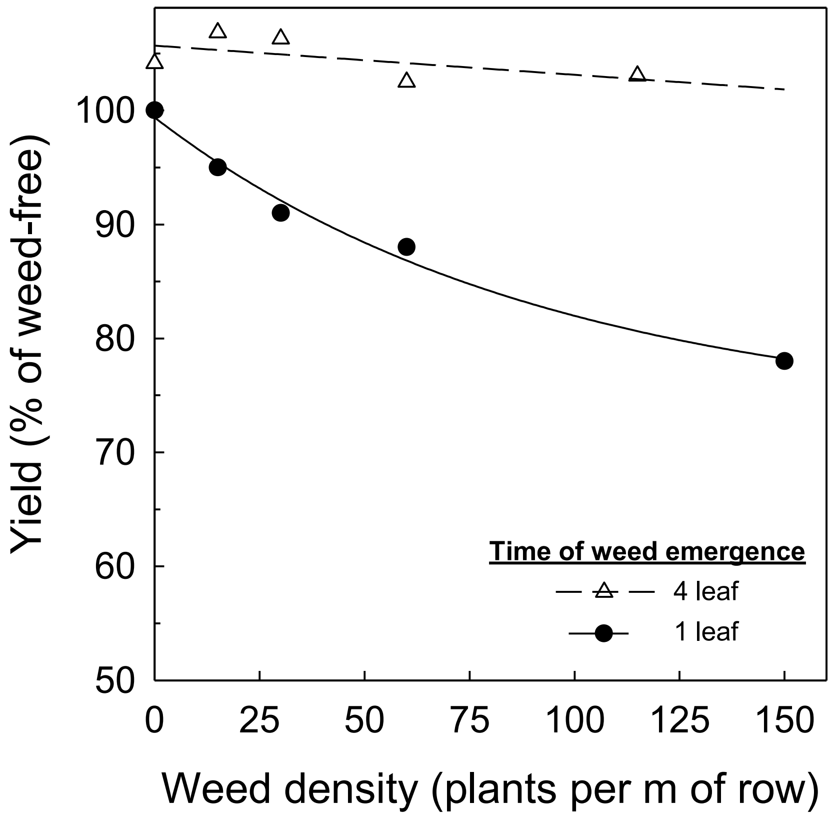

Figure 1. The impact of weed emergence timing and weed density on the yield of corn (*Zea mays* L.). Corn was planted in 76 cm rows and barnyard grass (*Echinochloa crus-galli* L.) emerged at either the one or four leaf stage of corn development. Adapted from Bosnic and Swanton (1997).

So why is the time of weed emergence relative to the crop so important in determining yield losses? One of the most likely reasons has to do with the initial size differences between crop and weed seedlings. The seeds and seedlings of crop species tend to be larger than those of most weeds and it is this initial size difference that helps the crop to gain a competitive advantage over the weeds and pre-empt resources needed for growth and development [5]. In fact, even a small advantage in size early in the growing season can translate into a significant advantage later on. As time progresses, a plant that is only slightly larger than its neighbour can suppress the growth of that neighbour because of its ability to simultaneously access photosynthetic light for itself and restrict its neighbour through shading. In contrast to soil borne resources like water or nutrients, light is a directional resource and it can be pre-empted by which ever plant grows the tallest and puts out the most leaf area. This competition is asymmetric because the plant that is being shaded (typically the weed) has little or no ability to impact the taller plant's access to light [24, 30]. Furthermore, this asymmetry is progressively increased as the crop canopy closes and light becomes the most important factor limiting plant growth and development.

The interaction between crop and weeds has most often been described by the concept of a critical period for weed control (CPWC). The CPWC represents the period of a crop's life cycle when weeds must be controlled in order to avoid unacceptable yield losses. For example, in soybean (*Glycine max* (L.) Merr.), the CPWC stretches from the V2 to the V4 stage of development [29]. This means that weeds emerging with the crop must be controlled before the 2 trifolioate stage in order to avoid yield losses greater than 5%. Similarly, weeds emerging after the 4th trifolioate stage do not need to be controlled as they too will not cause yield losses greater than 5% (Figure 2). When taken together, these two points in the development of a crop create a '*window for weed management*' that defines when weed interference is most detrimental to crop yield. The CPWC also fits well with our understanding of the importance of an initial size advantage for the crop shortly after emergence. If crop emergence is immediately followed by a period of weed-free growth, then the progressively denser crop canopy will suppress later flushes of weeds and prevent yield losses.

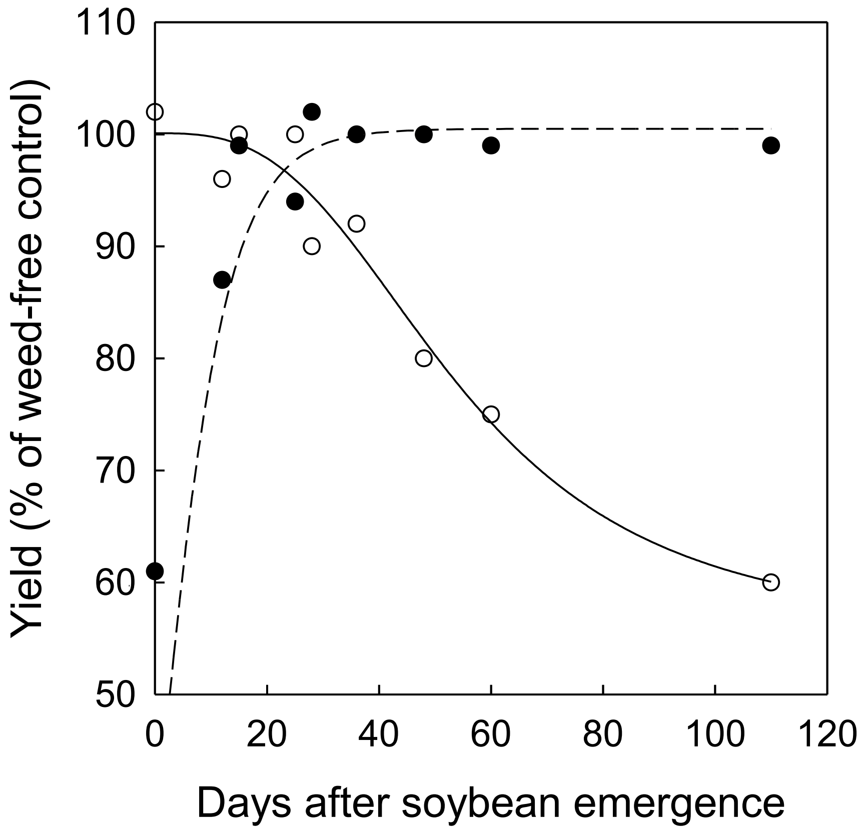

Figure 2. The critical period for weed control in soybean (*Glycine max* (L.) Merr.). The open circles and complete line describe the critical time for weed removal when weeds are present from the time of crop emergence. The closed circles and dashed line describe the critical weed free period, which represent the time from emergence that a crop must be kept weed free in order to prevent unacceptable yield losses. Together, these two lines define the critical period for weed control, which is represented by the hatched box. Adapted from Van Acker et al. (1993).

Mechanisms underlying crop-weed interactions

When describing how weeds influence the growth and development of the crop, it is important to distinguish between the terms competition and interference. Competition is traditionally viewed as a process involving a limiting resource, such as light, water or nutrients; whereas interference is a more general term that encompasses competition for resources but also includes indirect effects that a weed can have on the crop simply by being present in a field. The term interference is very broad and can even describe how chemicals excreted into the environment by one species of plant can impact the growth and development of another species; a phenomenon called allelopathy. Crop-weed interference also encompasses the early physiological responses of the crop that are triggered by the presence of nearby weeds. It is well established that plants can perceive the presence of a neighbouring competitor and adjust their growth in anticipation of competition for a resource that will become limiting later on in the growing season (e.g., light). To accomplish this, plants rely on a complex system of sensors to detect the presence of neighbours or competitors based on the spectrum of light reflected from the leaves of other plants [25]. Green plants absorb red (R) light and reflect far-red (FR) light because R light is used in photosynthesis, whereas FR is not. This selective absorption/reflection reduces the ratio of R to FR light reflected from the surface of a leaf. Shifts in the R/FR ratio are perceived by plant photoreceptors called phytochromes, which translate the information received into a biological reaction called the shade avoidance response [4].

Shade avoidance can be thought of as a plants' way to delay or avoid the negative consequences of competing with a neighbour. It involves producing more leaves at the expense of roots, growing taller to shade out the competitor and changing the position of its leaves so that it intercepts more light [1, 22]. In essence, seedlings expressing shade avoidance are attempting to maintain their initial size advantage over their nearby competitors. Although this response is predicted to increase the reproductive capacity of individuals in natural ecosystems,[23] the benefits of expressing a shade avoidance response in a highly managed agricultural system are less clear. For example, it is well established that crop seedlings express shade avoidance in response to weedy competitors and that this occurs during the time leading up to the start of the CPWC [18, 7]. Crop seedlings expressing shade avoidance are positioning themselves to compete with weeds for light later in the growing season by putting more emphasis on stem and leave growth and less on roots. Unfortunately for the crop, these efforts may be in vain, as any subsequent weed management practices will remove the weeds before direct competition can occur. Thus, the shifts in crop growth and development accompanying shade avoidance may in fact come at a cost to the yield potential of the crop. For example, when soybean seedlings were stimulated to express a shade avoidance response, in the absence of any direct competition for resources, the mature plants had smaller roots, fewer branches and produced less yield when compared with seedlings that did not express a shade avoidance response [6, 7]. Research conducted in corn has produced similar results and the expression of shade avoidance in both crops also reduced stand uniformity [16, 17]. Ultimately, when crop seedlings are exposed to weeds shortly after emergence, the expression of a shade avoidance response pushes the seedlings off their normal course of growth and development. In particular, the shift in growth from roots to shoots may create situations where mature plants are more susceptible to subsequent stressors (i.e., drought, nutrient limitations, etc.) later on in the growing season when yield is being formed.

Weeds represent the first of many challenges that a crop may encounter from emergence to maturity. As with the shade avoidance response described above, each challenge or stressor that a crop overcomes changes the pattern of growth and development. When they occur on their own, these changes may or may not result in a significant yield loss. However, when they occur in sequence or in combination, the changes resulting from one stressor may predispose the crop to the effects of a second stressor, such that the result is an additive or multiplicative yield loss at maturity. For example, corn plants that expressed shade avoidance in response to weeds early in the growing season were more susceptible to a subsequent drought than plants that had not been exposed to weeds [20]. In this case, the expression of shade avoidance alone did not result in a statistically significant yield loss; however, when it was combined with drought stress, the yield loss was greater than when plants experienced drought stress alone (i.e, 27% vs. 19% yield loss, respectively). This interaction nicely illustrates the importance of early season weed control as a risk management strategy. By ensuring that the period following crop emergence is weed-free, it enables the crop seedlings to further cement their size advantage over later emerging weeds and prevents any unnecessary adjustments in growth and development that may magnify yield losses from subsequent stressors.

Sustainable crop production through Integrated Weed Management

In the previous sections, we have discussed some of the mechanisms underlying crop-weed interference, addressed why weed management during the CPWC is needed for preserving yield potential and highlighted the fact that yield at maturity represents the sum of all biotic and abiotic stressors that a crop encounters over the course of the growing season. Although the value of early season weed control as an annual risk management strategy cannot be overstated, it should always be viewed within the context of a larger IWM strategy that has the long-term goal of producing stable, sustainable crop yields over years and decades. IWM has been defined as '*the application of numerous alternative weed control measures, which include cultural, genetic, mechanical, biological, and chemical means of weed control*' [28]. The fundamental principal of IWM is that no one method of weed management is solely responsible for providing complete weed control. Rather, several weed control measures might be used throughout a growing season, with distinct or overlapping windows, such that both the short-term goal of optimizing annual yield and the long-term goal of sustainability are addressed.

An example of a long-term IWM goal might be managing the size and composition of the soil seedbank. This goal is focused on reducing weed seed production at the end of the each growing season so that over time, the seedbank becomes more easily managed. Numerous studies have demonstrated that weed growth and seed production decrease as crop density increases[11, 12, 13]. High density crops occupy more space early in the growing season and this helps to pre-empt resources that weeds need for seed production later in the season[31]. Weeds growing within a high density stand will accumulate less biomass and return fewer seeds to the soil seedbank. In barley, for instance, wild oat seed production was reduced by almost 70% when the plant density increased from 135 to 425 plants m^{-2} [3]. If weed seed production is decreased over several consecutive seasons, the impact on the size of the soil seedbank can be quite significant. In a recent study of IWM strategies for Western Canada, doubling barley seeding rates from 200 to 400 seeds m^{-2} over an eight year period reduced the wild oat seed bank at the end of the study by an average of 35%[13]. Furthermore, when higher seeding rates were combined with other IWM practices, including crop and herbicide rotation, the size of the wild oat seed bank at the end of the study was decreased by an average of 57%.

Recently, several studies have focused on evaluating of the potential of cereals, such as wheat and barley, to serve as high density weed-suppressing crops[32, 15, 16, 9]. The premise behind this research is to develop cropping systems that utilize the initial size advantage of the crop to suppress weeds and reduce or eliminate the need for chemical weed control measures. Not only could high density weed-suppressing crops help to reduce the incidence of herbicide-resistant weeds but they have the potential to be a cost neutral option if the increased expenditure for seed can be offset with the savings made in herbicides. Nevertheless, these types of cropping systems still require some agronomic improvement to maximize their profitability.

One of the major hurdles to using planting density as a tool for weed management is the fact that crop yields often reach a plateau and can even decline as density increases beyond an optimum[31]. Currently, the optimal or recommended plant density for a crop is based on maximizing crop yield in a weed-free environment. It is most commonly defined as the density at which further increases in seed costs exceed the expected return on any increases in yield. It is easy to imagine that, as plant density increases above the optimum, interference among crop seedlings will increase. This often results in a decline in yield per plant and a plateau in yield per hectare. Weed suppression, on the other hand, will increase as density increase above the optimum; however, it also levels off at high crop densities. Interestingly, these two plateaus (in terms of crop yield and weed suppressive ability) may be related to the spatial orientation that is used when planting a crop.

When a crop is planted in rows, seedlings are very crowded in one direction. As planting density is increased, the point at which crop seedlings begin to interfere with one another is accelerated. With respect to weed suppression, increasing crop density also helps to occupy the inter-row space; however, the crops' ability to do so is limited by its capacity to branch out laterally. In recent studies, it has been hypothesized that a shift from planting in traditional rows to a more uniform crop spacing may help to overcome the plateaus observed in yield and weed suppression when the planting density of the crop is increased[31, 32]. For example, Weiner et al. (2001) observed that weed biomass declined as wheat density was increased from 200 to 600 seeds m^{-2} (Figure 3). When the crop was sown in a uniform pattern at 600 seeds m^{-2}, weed biomass declined by 65% and yield increased by 60% relative to a crop sown in traditional rows at a conventional planting density (300-350 seed m^{-2}). The benefits associated with a uniform planting pattern can likely be attributed to the fact that interference among crop seedlings is delayed (relative to traditional row planting) and the rate of canopy closure is accelerated

(Figure 4). Although such changes would require fairly significant adjustment to farming equipment and implements, as well as the development of varieties adapted for growth at higher densities, high density weed suppressive crops have the potential to simultaneously reduce the reliance on chemical weed control practices and push yields past the plateaus of the current recommended planting density.

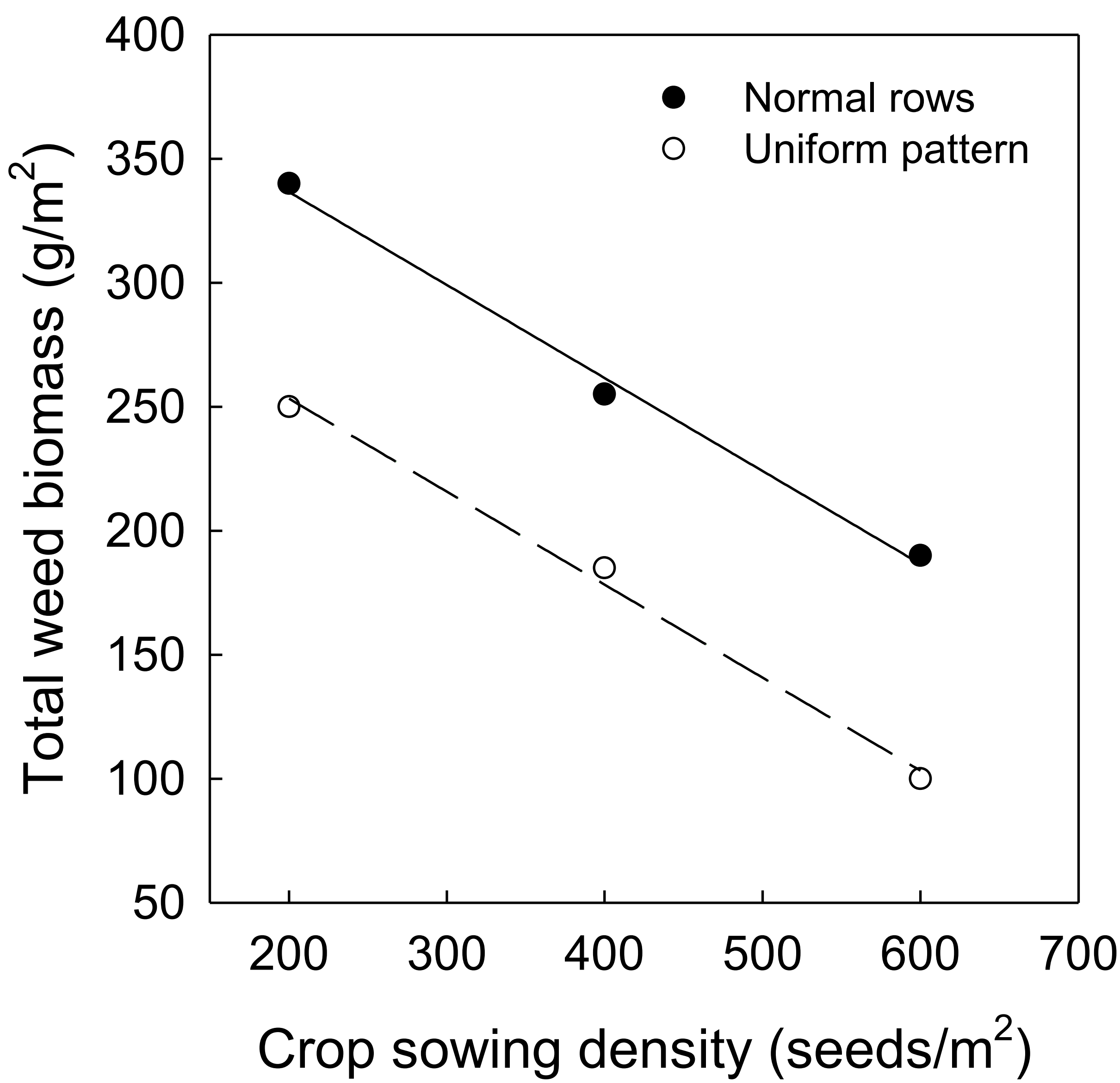

Figure 3. The influence of spring wheat (*Triticum aestivum* L.) sowing density and spatial arrangement on weed biomass accumulation. Adapted from Weiner et al. (2001; 2010)

Figure 4. The effect of planting density and spatial arrangement on weed interference. The trial was conducted in Denmark and rapeseed (*Bassica napus* L.) was used a surrogate weed, at a rate of 200 plants m^{-2}, in a spring wheat crop (*Triticum aestivum* L.). Row spacing was 12.8cm for the crop sown in traditional rows. Top photo: low crop density (200 seeds m^{-2}), sown in rows; Middle photo: high crop density (600 seeds m^{-2}), sown in rows; Bottom photo: high crop density (600 seeds m^{-2}), sown in a uniform pattern. Photo credit: J. Weiner.

Conclusions

Weed management is one of the most critical factors influencing crop yields at maturity. To continue to successfully manage weed populations, cropping systems need to be designed to utilize any innate competitive advantages possessed by the crop in order to enhance the potential for weed suppression and increase crop yields. By providing a window of weed-free growth early in the growing season, crop seedlings are able to follow their normal pattern of growth and development and maintain their maximum yield potential. During this period, crop seedlings will cement their size advantage over later emerging weeds and this will help to reduce the intensity of direct competition for resources when yield is being determined. A crops' ability to suppress weeds can be enhanced if it is able to pre-empt limiting resources by acquiring them earlier in the growing season or sequestering them in the form of more crop plants per unit area. Although increases in the planting density of the crop and a shift from the standard row planting pattern to a more uniform spacing represent significant departures from management practices currently in use, they have the potential to increase weed suppression, delay interference among crop seedlings and increase crop yields. Such changes would fit well within an IWM strategy that is focused both on short-term yield optimization and the long-term sustainability of our cropping systems.

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