



Review

# Simulation Models on the Ecology and Management of Arable Weeds: Structure, Quantitative Insights, and Applications

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**Abstract:** In weed science and management, models are important and can be used to better understand what has occurred in management scenarios, to predict what will happen and to evaluate the outcomes of control methods. To-date, perspectives on and the understanding of weed models have been disjointed, especially in terms of how they have been applied to advance weed science and management. This paper presents a general overview of the nature and application of a full range of simulation models on the ecology, biology, and management of arable weeds, and how they have been used to provide insights and directions for decision making when long-term weed population trajectories are impractical to be determined using field experimentation. While research on weed biology and ecology has gained momentum over the past four decades, especially for species with high risk for herbicide resistance evolution, knowledge gaps still exist for several life cycle parameters for many agriculturally important weed species. More research efforts should be invested in filling these knowledge gaps, which will lead to better models and ultimately better inform weed management decision making.

**Keywords:** weed seedling emergence; crop-weed competition; weed population dynamics; gene flow; herbicide resistance; decision-support tools; predictive models

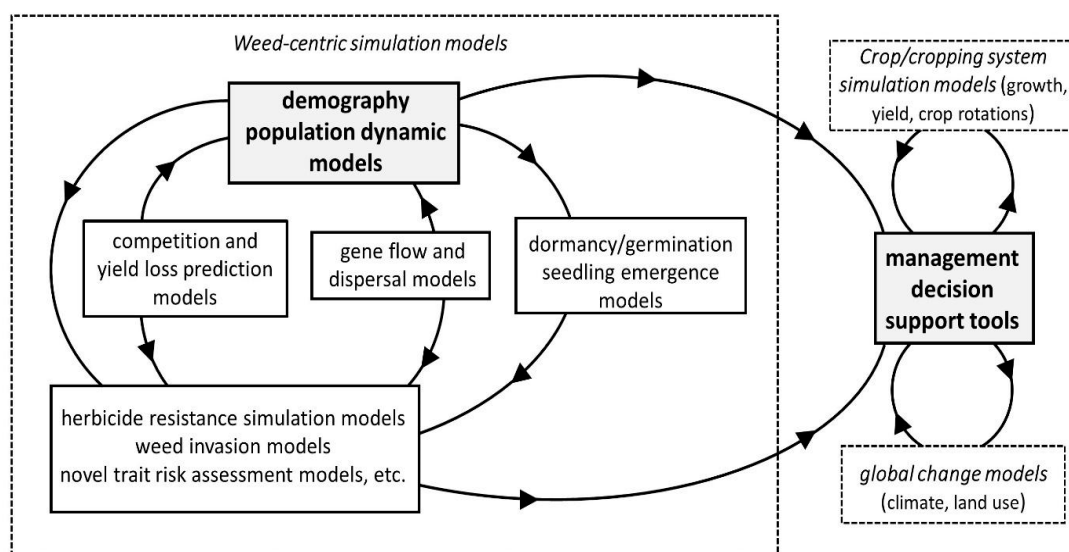
## 1. Introduction

Weeds present a major challenge to agricultural production worldwide [1]. They interfere with crops both through resource competition [2] and via non-competitive interactions [3,4] potentially causing severe crop yield losses. Research into the ecological factors affecting weed species dominance, such as their competitive interactions with crops and response to different management practices, among others, is vital for developing suitable strategies for tackling the threats posed by weeds effectively and economically [5,6]. Several experimental methods and approaches have been developed by researchers to facilitate a better understanding of weed ecological processes and inform management decisions [7,8].

Empirical studies, typically conducted using targeted field and controlled-environment experiments, allow for direct measurements of response variables and provide valuable information on the interaction of weeds with their environment and management practices. However, these measurements, per se, are insufficient for providing a deeper quantitative insight into the nature and dynamics of the interactions occurring within the field [9]. Moreover, measurement of long-term responses of new treatment combinations often requires expensive and time-consuming experiments. In this respect, simulation models are beneficial to researchers and practitioners [10,11]. Models can be used to accomplish three key purposes: understanding what has occurred, predicting what may happen, and evaluating outcomes of control methods [12]. Models facilitate *in silico* analysis of various scenarios without the necessity for conducting large-scale, long-term studies [13], and can also be used to provide best management practice recommendations, improve communication, and offer management support [14–16]. Models do not provide exact predictions of the future, but they offer valuable insights and facilitate decision making when nothing else can.

Weed models have evolved over many years, from simple descriptive models to more mechanistic models of weed–crop interactions and from models that simulate weed population dynamics to system-level models that encompass several important aspects of the broader system. In weed science, a plethora of models have been developed and tested to provide a quantitative understanding of weed ecology and management. These models interplay with each other in simulating weed demographic processes and management outcomes (Figure 1). Thorough reviews of the fundamentals of model development, analysis, and applications in weed–crop interactions and management are available [17–21]. However, knowledge is disjointed on how simulation models have been applied in different areas within the weed science domain to advance the science and management, and, to our knowledge, no comprehensive overview is available in this regard.

The objective of this review is to provide, using selected examples, the general structure of models, a synthesis of how models have been utilized in some of the key areas within weed science, what quantitative insights have been gained from such models, and what are the pragmatic outcomes for management. Our goal, however, is not to offer an extensive analysis of all published models in weed science. The scope of this review is limited to arable weeds occurring in agricultural production systems and the discussions may not necessarily apply to weeds in natural ecosystems. This review focuses on the current state-of-the-art of weed modeling, which is grouped here into five thematic areas. First, we present models on seed dormancy, germination, and seedling emergence, which inform the timing of weed seedling emergence and predict weed densities. Next, we provide an overview of models related to weed–crop interference and yield loss predictions. We then show approaches that model weed demographics and long-term population dynamics. We further offer insights into the models that simulate herbicide resistance (HR) evolution and gene flow. Finally, we summarize modeling initiatives that support management decision-making in cropping systems.



**Figure 1.** A schematic of the interplay between different models used to simulate key weed ecological processes and management outcomes. Models have been used to predict individual processes, such as seed dormancy changes, seed germination, seedling emergence, gene flow, dispersal, among others. Intra- and inter-specific competition governs the extent of damage caused by a given species and propagule production. In cropping situations, models predicting crop-weed competition and yield loss are used to understand the impact of uncontrolled weed escapes. Collectively, these models serve as sub-models in simulating weed demography and population dynamics. The weed population dynamic models, with the potential to simulate long-term population dynamics serve as a core component in the development of specialized models such as herbicide resistance simulation models, weed invasion models, etc. These specialized models are typically used by researchers to help answer fundamental research questions and inform best management strategies for specific field issues. Management decision support tools are used for assisting with management decision making by various stakeholders. These tools may differ in scope, but are designed to serve as user-friendly tools for simulating long-term biological and/or economic implications in response to different management scenarios. Additionally, other broader models such as crop growth/cropping system simulation models and global change models interact with weed population dynamic models in facilitating weed management decision making.

## 2. Modeling Weed Seed Dormancy, Germination, and Seedling Emergence

Dormancy is one of the most important attributes of weed seedbank dynamics, as it complicates the accurate prediction of both timing and quantity of seedling emergence. Environmental factors interact with each other, affecting the level of seedbank dormancy and therefore germination [22,23]. Temperature is considered the most important environmental variable regulating both changes in the level of weed seed dormancy and germination rate [24], while soil water potential is acknowledged as a temperature-modulating factor [25].

In annual weeds, the seasonal nature of field emergence results from the combined effect of soil temperature variability and the permissive thermal range for germination [26]. In turn, the amplitude of the germination permissive range is defined by the seedbank dormancy level, which is regulated by seasonal temperature changes and modulated by soil moisture conditions. Thus, field emergence is constrained to the time-window in which both soil temperature and water potential overlap (i.e., the hydro-thermal range) [27].

As seedbank dormancy is not a discrete attribute, different seed-fractions of a population have different requirements to overcome dormancy and thus become quiescent. Therefore, as indicated by Battla and Benech-Arnold [25], the quantification of the seedbank dormancy level should reflect both the average response, as well as the distribution of these requirements within the population. For this

purpose, threshold-based models are a useful tool for quantifying changes in the mean sensitivity of the population and the distribution of sensitivity thresholds among seed fractions [28].

There are numerous examples of the application of weed population models to describe changes in the level of seed dormancy [29–33]. Most of these models have been developed to evaluate the effect of temperature, and in some cases, its interaction with soil water potential. For example, Bouwmeester and Karssen [29,34] applied the concept of thermal-time using regression models aiming at describing seasonal changes in the level of dormancy and predict field emergence of *Polygonum persicaria* L. and *Sisymbrium officinale* (L.) Scop. Bauer et al. [30] developed a thermal-time model to quantify dormancy changes in *Bromus tectorum* L. during field after-ripening. In the latter model, the mean base water potential ( $\Psi_{b(50)}$ ) was used as a population dormancy index and the rate of change of  $\Psi_{b(50)}$  was linearly described as a function of after-ripening thermal-time accumulation.

Batlla and Benech-Arnold [31,35] developed a thermal-time model to quantify changes in the level of *Polygonum aviculare* L. dormancy using a stratification thermal-time index. Gianinetti and Cohn [32] using a hydro-time approach described primary dormancy release and the potential for secondary dormancy induction in *Oryza sativa* L. seeds. Alternatively, Gardarin et al. [33] proposed modeling the dynamics of emergence from a multispecies seedbank based on weed species seed traits (e.g., seed coat thickness, mass and shape). These represent a few examples of mechanistic-based models developed to gain insight into complex seedbank dormancy and germination dynamics. Mechanistic models make predictions from experimental information, however, site-specific data are often unavailable or cumbersome to gather [36]. Therefore, empirical models using known relationships are more commonly used for modeling weed seedling emergence under field conditions [37].

Empirical models incorporating the relationship between seedling emergence and growing degree days (GDD; °C day) can be categorized as thermal-time (TT), hydrothermal-time (HTT), and photo-hydrothermal-time (PhHTT) models. In thermal-time models, daily mean soil temperature (directly associated with air temperature) is accumulated above a specific threshold during the cropping season until weed emergence is completed [38]. Hydrothermal-time models include a combination of soil temperature and water potential in predicting weed seedling emergence [39,40]. In photo-hydrothermal-time models, photoperiod is used to modify TT based on day length [41]. Light quality and quantity may also influence seed germination, but these requirements are highly variable among weed species [42], and very few studies have utilized these parameters in models predicting seed germination for arable weeds.

The nonlinear regression (NLR) model that typically best describes weed seedling emergence, takes the following form (Equation (1)):

$$Y = f(X, \theta) + \varepsilon \quad (1)$$

where  $Y$  is cumulative emergence,  $\varepsilon \approx N(0, \sigma^2)$ ,  $X$  is cumulative GDD (TT, HTT or PhHTT), and  $\theta$  is a parameter vector. The regression function,  $f(X, \theta)$ , is typically an S-shaped nonlinear function that needs to be defined. Different regression functions have been fitted to weed seedling emergence data and, among these, Logistic, Weibull, and Gompertz are the most popular [43].

The use of NLR models has been questioned, mainly due to a lack of statistical robustness [44]. For instance, field data sampling is performed sequentially over the same experimental units. Consequently, observed cumulative emergence values obtained from consecutive monitoring are not statistically independent, resulting in positive autocorrelation of the residuals, which leads to erroneous predictions. Although emerged seedlings are counted in each date, the ‘new emergence’ events could have occurred any time during the interval between the two consequent counts. These ‘blind’ periods are known as ‘censored data’, which can lead to biased results. However, new approaches have been proposed which overcame these statistical issues and provided more reliable outputs [45,46]. Approaches based on survival analysis [47], genetic algorithms [48,49], artificial neural networks (ANNs) [50,51], and nonparametric estimation [43,52,53] have been developed for weed seedling emergence modeling.

In the past decade, global concern surrounding the social and environmental impacts of pesticides has led to an increased emphasis on reducing herbicide use. As a result, there is a new emphasis on optimizing herbicide dose and application timing. The use of modeling to predict both timing and magnitude of weed emergence is clearly imperative, yet not a fully deployed strategy for improving practical decision-making in weed management.

### 3. Weed–Crop Interference and Yield Loss Prediction Models

The interactions between weeds and crops represent one of the most challenging problems to describe and understand in order to predict yields because they are at the same trophic level. Therefore, clear visual symptoms or signs of interference are difficult to identify until it is too late. Furthermore, without having a weed-free treatment for comparison, it is impossible to directly quantify the reduction in crop growth caused by weed interference.

In general, pest managers have used the quantification of pest density and activity and its relation to crop damage as the basis to develop models that predict yield loss and thresholds to determine the method and timing of weed control actions [54,55].

Several approaches have been implemented to relate weed density to crop yield loss. In general, the rectangular hyperbola has proven to describe the relationship between weed density and crop yield loss adequately [56] (Equation (2)).

$$YL = \frac{Id}{1 + \frac{I}{A}d} \quad (2)$$

where  $YL$  represents yield loss as a percentage of the expected crop yield under a weed-free scenario,  $d$  is weed density at a given time during the growing season,  $I$  is the percentage yield loss as  $d \rightarrow 0$ , and  $A$  is percentage yield loss when  $d \rightarrow \infty$ .

Although yield loss tends to increase as weed density increases, this is not always the case [57] because weed size in relation to the crop plays a major role in determining the level of interference [55]. Thus, a few large weeds might reduce yield more than many small weeds that are more likely to be outcompeted by the crop. Additionally, as the interval between crop and weed emergence increases, the intensity of weed interference decreases. Therefore,  $A$  and  $I$  in Equation (2) are likely to vary depending on weed emergence timing [56].

Weed biomass can be a robust predictor of crop yield loss [18,58]. Thus, the higher the weed biomass (regardless of density), the higher the reduction in crop yield. However, determining weed biomass is time-consuming and difficult to monitor in the field. Another problem with considering weed biomass alone for crop yield loss prediction is that it does not provide a clear indication of how much of that biomass was interfering with crop growth. Kropff and Spitters [59] developed a modeling approach to predict weed interference and crop yield loss for sugar beet–lambquarters and corn–barnyardgrass competition, based on the ratio between the leaf area of the weeds and the crop, which integrates three key components of weed–crop interference (Equation (3)). First, total leaf area is the result of weed density as well as leaf area per plant; second, leaf area is an important driver of photosynthetic activity and growth potential; third, weed leaf area also influences shading potential on crop plants, which in turn reduces crop photosynthesis and growth.

$$YL = \frac{qL_W}{1 + (q - 1)L_W} \quad (3)$$

where  $L_W$  is the weed proportion of the leaf area indices of both the crop and the weeds (Equation (4)), and  $q$  is a damage coefficient:

$$L_W = \frac{LAI_W}{LAI_C + LAI_W} \quad (4)$$

$LAI_W$  and  $LAI_C$  are the leaf area indices of the weed and the crop, respectively. An advantage of utilizing LAIs or relative leaf areas in crop yield loss prediction models is that this allows for modeling interference from multiple weed species [60].

The period during the growing season when weeds interfere with the crop is another important consideration when predicting yield loss [56,59]. The critical period of weed control is defined as the period of time when weeds must be controlled before yield losses are greater than a target threshold (usually 5% yield loss; [61,62]). In these models, chronological or thermal time was used to describe how weed interference duration, starting at crop emergence, will progressively reduce yield [59,63]. It is important to highlight that the focus of these models is quantifying an acceptable interference duration, for weeds that emerge with the crop or soon after crop emergence (i.e., early-emerging cohorts). The early-emerging cohorts are more likely to cause the greatest crop yield reductions because they will have a greater probability of shading and interfering with the crop by achieving greater LAIs and growth rates than that of later-emerging weeds [64]. From a management perspective, early emerging weeds are also more likely to survive post-emergence weed control actions due to their larger size at the time of application. Accuracy in the estimation of weed emergence dates, especially early during the growing season, is critical for yield loss prediction [65]. The use of additive and replacement (or substitutive) designs and models for investigating crop–weed competition in binary mixtures is also noteworthy [66,67].

Yield loss predictive models can also incorporate management and economic components, such as herbicide efficacy and cost to develop decision-aid systems and help growers optimize their weed control programs [54,68]. In general, those models predict yield loss based on weed pressure or interference potential and simulate scenarios of weed control programs with different efficacies and costs [69,70]. Prevention of yield loss is usually stated as a positive outcome of increased weed control efficacy [58,62]. Thus, growers can identify and choose the management program that increases the probability of reaching the target yield while minimizing weed control costs [69,70].

Advanced real-time sensing technologies can improve the accuracy of weed–crop interference models, as well as allow the incorporation of other important factors such as spatial heterogeneity into weed–crop interference models [18,68,71,72]. The challenges for quantifying leaf area in real-time in the 1980s and 1990s, that limited the application of models such as the one developed by Kropff and Spitters [59] are no longer an issue. The rapid advances in unmanned aerial vehicles with sensors and machine learning algorithms have the potential to quickly and effectively quantify the ratio of weed and crop leaf areas throughout the growing season and across large production fields [73]. This can also help reduce the challenges of accurately quantifying  $q$  (Equation (3)) for different weed species individually or as part of a community, as well as changes in  $q$  throughout the growing season within a species [74]. A major obstacle to accurately predicting yield losses is weed patchiness, and although many weed patches are stable from year to year, such aggregate distribution makes yield loss estimation very challenging [75,76]. In this regard, yield monitors in combine harvesters may offer a solution; yield monitors generate geospatial data of crop yield variation across a field, which can be overlaid with weed distribution information. Thus, combining the weed–crop interference maps with spatial yield maps will allow for the development of more robust yield loss prediction models. A similar approach can be developed for smart sprayers that use real-time weed detection with geo-referencing to make site-specific herbicide applications [75,76]. These applications can be tailored based on maps of weed distribution, ground cover, and leaf area.

An underlying assumption of most models is that conditions for growth are optimal for the crop and also for the worst weed; under those circumstances, the most important type of interference is shading [59]. Interference in the root zone has been addressed in just a few models to describe how weeds and crops compete for water and nutrients. Although more complex than light interference, models that include root zone dynamics are based on the proportion of the soil to which the weed and crop roots have access, as well as the level of overlap between the root systems of both species [65,77]. Water and nutrient availability and uptake are related to growth or yield potential

by parameterizing their effects on crop and weed photosynthesis. In this way, reductions in crop growth caused by light interception by weeds can be integrated with reductions in underground resource availability/uptake, because both converge in photosynthetic activity. This type of root zone dynamics (i.e., root growth–water availability relations) might become progressively more important with greater environmental variability, for example, irregular rainfall patterns or inadequate irrigation. Evaluation of existing predictive models under a wider range of conditions is the first step to addressing those issues.

Recently, noncompetitive interactions have been identified as important mechanisms determining crop yield potential under field conditions [78]. Low red: far red ratios in the light reaching crop seedlings as a result of weed shading can trigger the production of reactive oxygen species, damaging crop plant cells and reducing the season-long crop growth. These noncompetitive interactions have not been, so far, considered in yield loss predictive models. However, as more information is generated about this eco-physiological phenomenon, it might be important to explore the need to incorporate this component into predictive models. Noncompetitive interference may be particularly important for decision-aid systems that require accurate projections of absolute yield, though most models are based on relative yield loss.

Finally, it is worth noting that recent studies have indicated that weed–crop interactions can change due to weed evolutionary adaptations. For example, Ziska [79] described how *Avena fatua* L. in a 50-year period (i.e., very short time in evolutionary terms), has evolved to take advantage of modern higher atmospheric CO<sub>2</sub> levels, while the cultivated oats (*Avena sativa* L.) has not. Thus, the former has now a greater potential to outcompete the latter. Similar results have been reported for red rice (*Oryza sativa*) in comparison with cultivated varieties [80]. *Amaranthus palmeri* S. Wats. populations were reported to have evolved a taller phenotype when growing in cropping systems with tall crops when compared to short-statured crops [81]. *Amaranthus palmeri* has also evolved high nutrient-use efficiency when grown in cropping systems typically receiving high rates of nitrogen-based synthetic fertilizers [82].

Thus, evolutionary adaptive changes in weeds may need to be considered in weed–crop interference models. If weeds evolve to be more competitive over time, while the competitive ability of crops stays the same [78,79], predictive models will also progressively underestimate yield loss due to weed interference. Recurrent parameterization and recalibration of the models are needed to make weed–crop interference models relevant for decision-making and effective for yield loss prevention.

#### 4. Gene Flow Models

In the past, gene flow was not generally investigated within agricultural ecosystems. With the introduction of transgenic herbicide-resistant crops in the mid-1990s, there was renewed interest in quantifying and modeling intra- or interspecific pollen-mediated gene flow (PMGF). In the past 15 years, there has been a growing recognition among weed scientists and practitioners that the magnitude and extent of gene flow for weeds with high seed or pollen dispersal capability need to be better understood [83,84]. This section includes modeling seed-mediated gene flow (SMGF) and PMGF, but excludes modeling vegetative propagule (e.g., roots, rhizomes, stolons, tubers, bulbs) mediated gene flow.

##### 4.1. Seed-Mediated Gene Flow

In general, SMGF is inherently variable or stochastic and therefore difficult to model with high precision or accuracy. Consequently, comparatively few studies have evaluated or modeled SMGF; both of these types of assessments depend on seed size or morphology, type of dispersal vector, and environment. Only models of seed dispersal by wind have been described, as they are relatively easier to model and are much more advanced than for any other vector [85]. Although empirical models are often used to simulate SMGF, little knowledge is gained of the underlying mechanisms governing seed dispersal, such as horizontal or vertical wind speed and settlement velocity. Various mechanistic

models, comprising mathematical algorithms, have been developed to simulate seed dispersal by wind and the relative importance of physical and biological factors influencing SMGF. Seed dispersal by wind of horseweed (*Conyza canadensis* L. Cronq.) has perhaps been most extensively modeled, both empirically and mechanistically [86]. The simplest model uses a ballistic equation first developed in the late 1800s. For example, the distance traveled by seeds of the Asteraceae family is a product of the seed release height and the mean horizontal wind speed, divided by the terminal velocity (constant falling velocity of a seed in still air) [87]. More complex models incorporate vertically variable mean horizontal wind speed and air turbulence, with some models even accounting for discrepancies between airflow and seed motion. A power-law dispersal kernel is often used to simulate seed movement by wind [88,89]. For example, the equation for the inverse-Gaussian or Wald dispersal kernel,  $p(x)$ , is the following (Equation (5)):

$$p(x) = \frac{\lambda}{2\pi x^3} e^{-\frac{\lambda(x-\mu)^2}{2\mu^2 x}} \quad (5)$$

where  $x$  is the distance travelled, and  $\mu$  and  $\lambda$  are dispersal kernel parameters that depend on horizontal and vertical wind velocity statistics, seed terminal velocity and seed release height.

Dispersal kernels can provide the probability of seed immigration either per unit distance (one dimension) or per unit area (two dimensions). The statistical features of a dispersal kernel are influenced by the interaction of air turbulence processes and seed attributes. While turbulence processes are responsible for uplift and long-distance dispersal, seed attributes control its motion [89].

#### 4.2. Pollen-Mediated Gene Flow

We define PMGF as outcrossing frequency as a function of distance between pollen donor and receptor plants, not merely pollen grain dispersal dynamics (i.e., actual vs. potential PMGF, respectively). Similar to SMGF, accurately modeling PMGF is challenging, as it is influenced by numerous biological, environmental, and crop management factors and their interactions. The ultimate function should dictate the choice of model. One-dimensional empirical models using negative exponential, exponential power, or inverse power-law functions, have been mainly employed to describe PMGF in weeds [90]. The use of multiple datasets from a wide range of environments improves inference potential. Simple empirical models are best suited for field-scale trials or simple field arrangements, but are not robust for predicting PMGF across an agricultural landscape with multiple, spatially heterogeneous fields consisting of multiple pollen donors and receptors [84]. For the latter situation, individual dispersal functions or dispersal kernels can be integrated across a range of shapes, sizes, and arrangement of donor and receptor populations [91]. The data required to integrate dispersal kernels over a landscape are much more demanding than for simple regressions. A geometric fat-tailed inverse power-law function ( $Yg$ ) has been recommended as being appropriate for predicting PMGF at the landscape scale (Equation (6)) [92]:

$$g(a, b, r) = \frac{(b-2)(b-1)}{2\pi a^2} + \frac{(1+r)^{-b}}{a} \quad (6)$$

where  $a$  is the scale parameter,  $b$  is the shape parameter, and  $r$  is the distance between the pollen source and the sampling site.

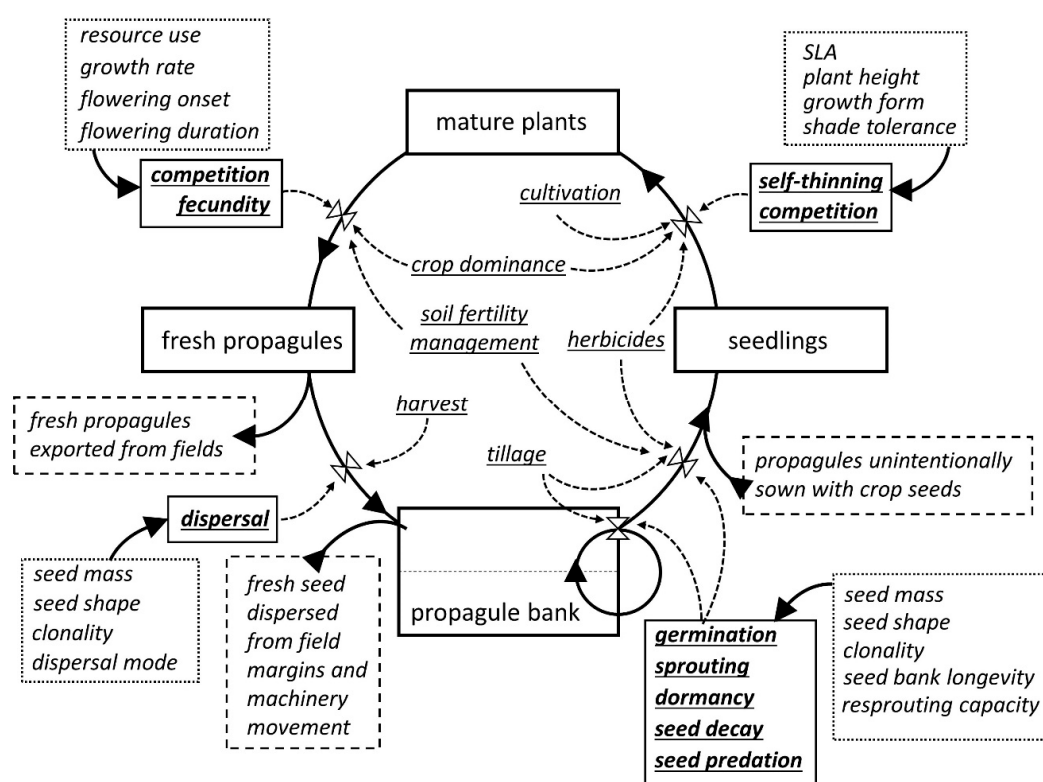
While dispersal kernels do not specifically address PMGF mediated by insects, Shaw et al. [93] suggest that the scale and form of functions describing insect-mediated pollen dispersal will be similar to those derived for wind dispersal.

Mechanistic models (deterministic or stochastic) offer potentially greater predictive ability and inference, especially for landscape-scale modeling of PMGF. However, few mechanistic models have been developed for PMGF in crops or weeds, reflecting the challenges in accurately simulating PMGF mediated by wind or insects. For example, although outcrossing rates tend to be high in areas



downwind from the pollen donor, the effect of gusts and nonprevailing winds on outcrossing is less predictable and amenable to modeling. Modeling of PMGF facilitated by insects has only been attempted at the local scale [94]. In general, mechanistic models are best suited to describing potential PMGF, i.e., three-dimensional pollen grain movement [95].

Weed population dynamic models encompass the key processes regulating the life cycle of the weed species under consideration, including, but not limited to, seedbank dynamics (viability, dormancy, germination), seedling emergence and establishment, inter and intraspecific competition, breeding system/gene flow, fecundity, and propagule dispersal (Figure 2). These processes act as filters and modulate the size and persistence of populations across growing seasons. These individual processes are typically included as sub-models, and multiple sub-models interact in simulating long-term population dynamics of a weed species. Sub-models for some of these important processes were discussed in the sections above. To be meaningful, weed population dynamic models require the most accurate estimates possible for key ecological processes. Such information is typically mined from published literature, where available, for the species under consideration or from comparable systems. For instance, researchers have extensively studied weed seed viability and longevity in the seedbank [96,97], and the seedling emergence window of several weed species [37,39,98,99]. Additionally, the efficacy of different management practices must be known, and preferably sourced from the literature. In situations where parameter estimates for important ecological processes and management efficacies are not available, experiments are conducted to obtain such values if resources permit; expert opinions have also been commonly utilized where appropriate.



**Figure 2.** General scheme of the life cycle of a hypothetical weed population in a crop field utilized in developing generic demographic models combined with specific functional traits. The diagram is structured around four main demographic stages (propagule bank, seedlings, mature plants, and fresh seeds). Agronomic management factors regulating demographic rates are shown. Ecological and physiological processes and the associated functional traits are presented. Fields are conceived as open systems that interchange weed propagules beyond their boundaries. Thus, some instances of immigration and emigration of propagules are indicated (dashed line boxes).

## 5. Weed Demography and Population Dynamic Models

Weed population dynamic models simulate the overall life cycle and demography of weeds and provide a means to understand long-term population trajectories without the need for long-term and oftentimes, impractical field studies [16]. These models offer valuable insights in areas where genetic, biological, and ecological knowledge is lacking and indicate where future empirical research efforts should be focused. When combined with long-term population response to management tactics, these models assist regulatory agencies with policy making, industry with developing stewardship programs, scientists with answering fundamental weed research questions, and crop advisors and weed managers alike with making appropriate recommendations and field management decisions.

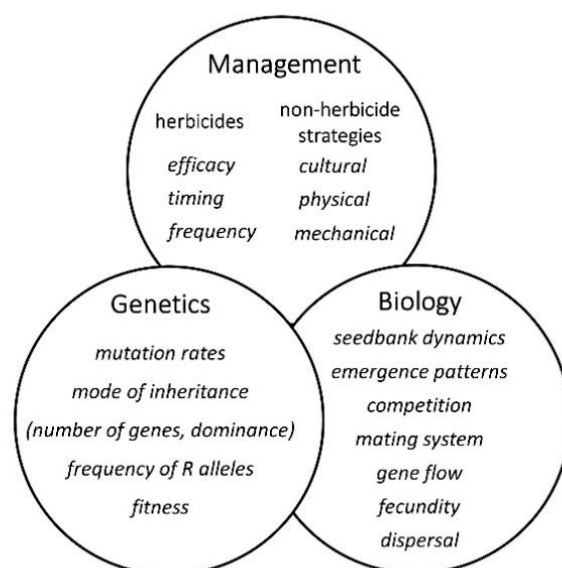
There are several practical examples of the utilization of weed population dynamic models as a component of much broader models aimed at providing valuable insights and assisting decision-making in different situations. These models are particularly helpful for understanding long-term changes to weed population sizes, which is of great value given that weed management efforts must consider the long-term consequences of current weed control efficacy and weed propagule production [100,101]. Models are used to explore realistic scenarios involving multiple criteria and objectives, including different crop types, rotations, and management strategies. Generic models combine demographic parameters characterizing population dynamics with functional traits. These models contribute to understanding weed shifts in response to farming practices, such as weed seedbank dynamics, weed suppression by crop dominance, and weed response to fertilization, soil disturbance, and herbicides. Weed population dynamic models have for instance been utilized to evaluate the value of diversified crop rotations in organic and conventional systems including both annual and perennial cash and cover crops on long-term management of troublesome weed species [102,103]. Below, we present select cases to illustrate how weed population dynamic models were used for understanding species shifts in relation to management in real agricultural scenarios.

Different modeling approaches were applied to simulate changes to long-term population sizes, particularly focusing on weed seedbanks. For instance, simple demographic models of seedbanks were used to simulate the responses of *Abutilon theophrasti* Medik. and *Setaria viridis* (L.) Beauv. in continuous maize cropping and two alternative crop rotations [104]. While *Abutilon theophrasti* seedbanks were almost unaffected, *Setaria viridis* seeds were nearly eliminated by crop rotations, revealing harsh winters as a strong demographic filter reducing *Setaria viridis* seed survival in the soil [104]. More recently, seedbank dynamics have been modeled with several approaches ranging from simple statistical models to complex generic models, which integrate equations based on physiological and ecological processes describing seed fate in the soil. The simplest approach used statistical modeling to simulate the effects of crop sequences on weed abundance in seedbanks of total weeds, monocotyledons, and dicotyledons [105], suggesting practical management implications. Hence, crop sequences may be simplified to crop management classes describing the sowing season, crop type, and target weed groups for herbicide application, such as grass and broadleaved weeds. Although this statistical methodology was applied to simple weed groups, it is also feasible to predict seedbank variations of individual species or functional groups [105].

Complex, multispecies models of annual weed floras were also developed to simulate weed dynamics of multiple species and cohorts at a daily path over several years or decades [18,33,106]. Multispecific models simulate weed seedbank dynamics on a daily path based on demographic parameters (mortality, dormancy, germination, and seedling emergence) for multiple weed species, which interact with cropping systems and environmental conditions. Another multispecies model based on functional traits successfully simulated the response of weeds to the increasing use of herbicides and fertilizers due to agricultural intensification [107]. Besides demographic parameters, the model included empirical functions that correlate to specific traits (seed weight and maximum plant height), predicting that most common species had stable or increasing population sizes under higher input levels, while nearly two-thirds of the species declined [107]. Colbach et al. [108] developed a multispecies model (FlorSys) to simulate crop yield loss due to competition for light between crops

and weeds, which was able to identify a few key parameters in crops and annual weeds that determine crop yield loss in a wide range of cropping systems, soils, and climates.

Population dynamic models have been used as an integral component of models simulating HR evolution in response to various herbicide use patterns and alternative management practices (Figure 3), and have provided valuable insights for understanding the risks, and alternatives for managing or slowing resistance evolution [109–115]. Herbicide resistance simulation models are discussed in more detail in the following section.



**Figure 3.** An illustration of the key components of herbicide resistance simulation models.

Weed population dynamic models have also been used as a core component of models assessing population-level response to the transfer of novel genetic alleles through gene flow, with implications for environmental risk assessment of novel crop technologies and developing suitable stewardship practices for risk mitigation. For example, the model by Werle et al. [116] used the population dynamic models of shattercane [*Sorghum bicolor* (L.) Moench ssp. *drummondii* (Nees ex Steud.) de Wet ex Davidse] and johnsongrass [*Sorghum halepense* (L.) Pers.] for assessing management options for mitigating risk associated with Inzen™ grain sorghum (resistant to acetolactate synthase-inhibiting herbicides) in grain sorghum production in the United States. The model development and specifics are provided as a case study in the supplementary material (supplementary material I).

## 6. Herbicide Resistance Simulation Models

Herbicides have become a mainstay of agricultural weed management since the first discovery and commercialization of synthetic herbicides in the 1940s. However, in almost all global agroecosystems where they have been used extensively, HR has evolved. By 2020, evolved HR has been documented in 262 weed species, with 23 of 26 known herbicide modes of action (MOA) affected [117]. Simulation models have been an important tool to understand the ecological, agricultural, and evolutionary drivers of resistance evolution, and the interactions between them [109,110,118–120]. Models are also useful to design and validate optimal, situation-specific resistance management strategies [112,114,121].

Most models used in weed ecology and management are based on weed demography and population dynamics (Figure 1) and models of HR are not different. However, simulating HR in weeds is a more complex process than simply predicting changes in weed density and abundance. Herbicide resistance simulation models typically consist of three integral components: the biology of the species, genetic drivers of resistance and management factors that dictate population dynamics and selection pressure (Figure 3).

The biology component simulates the overall life history and population dynamics of the species. For an annual species, it starts from dormant seeds in the soil seedbank to seed production and seedbank replenishment, encompassing seedbank dynamics, seedling emergence pattern, density dependence and competitive interactions, breeding system and gene flow, fecundity, seed dispersal, and post-dispersal seed loss (Figure 2). These models must also simulate the genetics of HR to account for changes in the frequency of different weed genotypes over time as resistance evolves. At the fundamental level, temporal models require some representation of the genetic basis and inheritance of resistance traits. Extensive research into the mechanisms and genetics of HR in global weeds has identified two major modes of resistance inheritance; single gene traits inherited in Mendelian fashion and polygenic (or oligogenic) traits inherited in a quantitative fashion [122]. When modeling genetic traits, both the random mutation rate and the initial frequency of resistance in the population at the beginning of the simulation can be included depending on the genetic basis being considered.

Various iterations of HR genetics and inheritance have been implemented in HR models. The simplest approach used by Pannell et al. [123] in the ryegrass integrated management (RIM) bioeconomic model of integrated weed management (IWM) has been to assume that resistance will evolve after a fixed number of herbicide applications. This approach avoids the requirement to explicitly simulate resistance genetics. Other models have explicitly simulated the evolution of Mendelian inheritance of single gene traits [110,121] to one or more herbicide MOA. Models examining simultaneous evolution of monogenic resistance to two herbicide MOA in a single weed population can be used to study interactions between management choices and population dynamics [115,124]. The most complex HR models have simulated the evolution of complex, multigenic resistance traits either through explicit modeling of the inheritance of a fixed number of genes that interact to determine the resistance phenotype [112] or by using estimates of trait heritability to model the evolution of resistance trait values under recurrent selection [125]. Gardner et al. [126] modeled the simultaneous evolution of major gene and quantitative resistance traits in a weed population.

Several species-specific and life history characteristics of weeds interact with genetics and selection (determined by management) to influence the rate of HR resistance evolution, and these characteristics have been variously incorporated into models. Management-related factors, such as crop choice, soil preparation, and the efficacy, timing, as well as frequency of use of herbicides, interact with biological factors to influence the speed of resistance evolution. The timing of weed germination influences the proportion of the population that is exposed to selection by a specific herbicide [113,119] and plant mating systems (inbreeding versus outcrossing) will also affect the rate of resistance evolution and the potential for dispersal of resistance alleles via seed and/or pollen [16].

Related to this, spatiotemporal dynamics [127] and environmental heterogeneity and dispersal [128] are important determinants of resistance spread. Between-species differences for these key determinants of resistance evolution mean that recommendations on managing HR developed with a species-specific HR model cannot be broadly applied to all species, even in the same environment. Further, the relative fitness of the HR weed (in the absence of the herbicide) has been an important biological component in HR models, as reviewed by Vila-Aiub et al. [129]. Additional factors relevant to HR modeling, such as temporal and spatial implicitness, deterministic versus stochastic models, and individual versus population-based models are discussed in [130].

The ultimate aim of HR models has been to inform the design of resistance management strategies and to understand how major agronomic and herbicide application variables may mitigate rates of HR evolution. Major areas of consideration have been the effects of herbicide mixtures and rotations on the evolution of resistance, the relative impacts of low and high doses on selection for resistance, and the potential for diverse weed management practices and IWM to mitigate or slow the evolution of resistance. Regardless of the way in which the genetics of resistance have been realized in models, the use of herbicide mixtures and diversity in the form of sequences have been shown to reduce the rate of resistance evolution. Herbicide mixtures were found to be effective because of the exponentially reduced possibility of weed populations simultaneously evolving resistance to

more than one MOA [121]. Herbicide sequences have the advantage of reducing selection pressure by ensuring that different weed cohorts are exposed to different herbicide MOA [113]. However, interactions between herbicides can be antagonistic or complementary [131].

The “dose debate” has been actively discussed for some time in the HR literature, with various views and perspectives on the potential for high versus low doses to select for resistance most rapidly. In their oligogenic model, Renton et al. [112] were able to show that reduced herbicide rates did accelerate selection for quantitative herbicide resistance in an outcrossing weed species. Gardner et al. [121] advocated the use of revolving high and low pesticide doses to slow the evolution of co-occurring major gene and quantitative resistance traits.

Simulations of HR in weeds can be used to explore the likely causes of previous occurrences of herbicide resistance. Long-term data records can be compared to partnered simulation outputs, thereby allowing investigations to isolate the causes of current HR problems. HR simulations can also be useful to predict the longevity of currently functioning herbicide-based weed control management systems. However, better predictions are provided using comparative analysis, due to the difficulty of determining the specific influences of the many factors which influence HR evolution. Resistance is a numbers game and HR models have also been used to demonstrate that driving weed populations to small sizes with alternative weed control approaches and crop rotations can significantly slow the evolution of resistance [119,128].

At their greatest extent, HR simulations will predict changes in density, allele frequency, and the spread and distribution of HR both within and between fields. Farmers need greater insights into the likelihood, causes, and projected trajectories of HR weed numbers. Simulations are a very useful tool to allow both farmers [123] and researchers [119] to explore or emphasize the advantages of locally implemented IWM, in their fight to protect herbicides from loss due to HR evolution.

## 7. Management Decision-Support Tools

Farmers and farm advisors developing weed management programs potentially encounter an impossible burden of information. This is because solutions to weed problems require knowledge of species-specific, temporally variable relationships among weeds, crops, and possible control interventions, as well as an understanding of short-term and long-term effects of weed management tactics [132,133]. Without interpretable information on the complexities and consequences of weed management interventions, farmers and farm advisors may develop weed management programs that are inefficient, ineffective, or injurious to nontarget organisms [134–137].

To assist farmers and farm advisors with complex weed management decisions, researchers develop decision-support tools (DSTs) that combine models of weed population dynamics with efficacy economics [138–140] and environmental impacts [139,140] of control tactics. These DSTs enable farmers and farm advisors to both simulate novel management options under local circumstances and learn concepts of sustainable management in the context of resident weed problems [141–143]. In addition to being useful for practitioners to better understand and manage local weeds, DSTs are instruments for researchers to conduct virtual studies that would be prohibitively expensive or impractical in the field [132]. By clarifying outcomes that are difficult to discover in the field and promoting adoption of novel tactics, DSTs accelerate development and adoption of optimal weed management strategies. Further, by promoting discourse between researchers and practitioners [143–146], DSTs contribute to the communication that fosters both research addressing practical problems and science-based revisions to implemented practice.

A systematic search for publications identified more than 100 peer-reviewed scientific papers pertaining to DSTs for weed management (Supplemental Material II, Table S1). This large number of publications is a consequence of the quantity of information required for DST development, as well the many DSTs that address weed problems within specific cropping systems and regions. Although each DST is unique, a DST can be categorized by the management time frame(s) that it addresses. A DST can either inform methods for the immediate control of weeds competing with a crop (i.e., DST for curative

tactics), or provide insights for reducing weed population growth and reducing weed infestations in the future (i.e., DST for preventive management) (Table 1). In addition, a single DST can provide guidance for both curative tactics and preventive management [133,138]. Curative and preventative DSTs often include economic considerations to simulate financial implications of weed management decisions.

**Table 1.** Characteristics and requirements for the two general types of decision support tools (DSTs) for weed management. Weed management DSTs utilize bioeconomic models that either inform methods for the immediate control of weeds (i.e., DST for curative tactics), or provide insights for reducing weed population growth (i.e., DST for preventive management).

Model Characteristic	DST for Curative Tactics	DST for Preventive Management
Projected output	Short-term control outcomes and current season profit responses for possible tactics for controlling weeds	Weed infestation and revenue responses to different combinations of tactics occurring over multiple years
Time frame	Single growing season	Multiple growing seasons
Information needed for development	<ul style="list-style-type: none"> <li>○ Economic costs for potential tactics</li> <li>○ Tactic efficacies against targeted weeds</li> <li>○ Environmental effects on control outcomes</li> <li>○ Impacts of escaped weeds on crop yield and quality</li> <li>○ Expected price received for harvested product</li> </ul>	<ul style="list-style-type: none"> <li>○ Demographic rates that determine weed population dynamics at annual time steps</li> <li>○ Genetic basis and inheritance of adaptive traits in weed populations</li> <li>○ Seedbank processes</li> <li>○ Weed suppressive effects of different combinations of management tactics</li> <li>○ Economic costs for potential management tactics</li> <li>○ Management tactic consequences on availability and performance of control strategies in subsequent growing seasons</li> </ul>
Primary service to farmers and farm advisors	Prescriptive recommendations for specific weed problems	Means for investigating novel, multiyear strategies for managing weed communities or problematic weed biotypes

Decision-support tools for curative tactics enable farmers and farm advisors to compare likely short-term outcomes for possible control interventions. Although some DSTs model short-term outcomes for mechanical control tactics [132,147–149]; most curative tactic DSTs inform decisions on chemical weed control [69,137,145,150–153]. These DSTs provide guidance for choices involving the necessity of an herbicide application, the types of herbicides to include in an application, herbicide rates, and application timings [69,132,140,154–157]. Further, many DSTs for curative tactics provide forecasts on financial consequences for possible weed control procedures, for example [69,132,154–157]. Curative tactic DST development requires information on intervention costs and expected benefits, which are conditioned by both intervention efficacies against targeted weeds and impacts of escaped weeds on crop yield and quality. As intervention efficacies are influenced by sizes of targeted plants [150,158] and densities of targeted infestations [151,152], DSTs for curative tactics can require users to input data on weed density, target plant size, and weather variables that drive both weed phenology and weed responses to herbicides [66,134]. Curative tactic DSTs may also require users to provide real-time information on crop and field conditions [153]. This is because impacts of escaped

weeds are influenced by crop developmental stage at the time of the intervention [159], and the suitability of specific tactics can be affected by crop rotation, crop stage, and environmental parameters.

Decision-support tools for preventive management perform two general tasks: first, they project weed infestation and revenue responses to different combinations of interventions occurring over multiple years, and second they present weed and profit projections in manners relevant to the intended audience [142,143,146–149,160,161]. By executing these tasks, DSTs for preventive management allow farmers and farm advisors to gain insights into systems and practices that avert weed problems and reduce weed densities over time. Decision-support tools for preventive management are built with life history models that simulate weed population dynamics at annual time steps [11]. Many DSTs for preventive management focus on weed species with annual life histories. These DSTs frequently include weed population dynamic models with sub-models for seedbank processes such as change in seedbank density or fluctuation in seedbank depth structure [133,142,149,160,161]. Additional information required for preventive management DST development includes data on tactic costs [162,163], as well as tactic consequences on weed population growth, and the performance of available control tactics in subsequent growing seasons [133,142,164].

Similar to DSTs for curative tactics, DSTs for preventive management feature user-friendly interfaces that allow farmers and farm advisors to customize and compare possible sequences of management interventions that would be impractical to evaluate in the field. However, unlike curative tactic DSTs, preventive management DSTs do not provide explicit instructions for cost-effective control of specific weed problems [138]. Such recommendations would likely be inaccurate because exact conditions and prices are difficult to predict years ahead. Rather than sources for prescriptive recommendations, DSTs for preventive management are instruments for teaching foundational concepts in weed management [141–143]. Educational programs on IWM [141,142], HR management [142,161,165], and seedbank management [152,166] have each used DSTs to demonstrate general concepts in local circumstances. As adoption of a novel tactic is more likely if the tactic is presented under local circumstances [167], and because DSTs foster experimentation intrinsic to learning [168], DSTs for preventive management can be central to educational efforts that promote new approaches to weed management.

## 8. Conclusions

This review, using selected examples, provides an overview of the general structure of weed models, a synthesis of how models have been utilized in key areas within weed science and management, what quantitative insights have been gained from such models, and what pragmatic outcomes for management are possible using models. Within the five thematic areas, there were key learnings and applications. However, users must be mindful of the inherent limitations of simulation models in terms of what they can and cannot offer, the challenges with parameter estimates, and the robustness of model predictions. Thus, the user must evaluate, interpret, and apply the model predictions accordingly.

“All models are wrong, but some are useful”. This popular quote by the British statistician George E.P. Box clearly illustrates that models cannot accurately predict the future reality, but can provide quantitative estimations of what are the likely outcomes with a level of certainty. Researchers, managers, regulators, and policy makers alike resort to models when the future trends are not obvious and when they can benefit from a knowledge-based prediction of the future to facilitate informed decision making. While model predictions are not exact, they can be useful to project future trajectories. From a field management standpoint, models are invaluable for comparative evaluation of different management options and select the ones with the most negative impact on long-term weed population dynamics. Considering that model predictions are associated with some level of uncertainty, the outputs can be appropriately presented as a range of probable outcomes, rather than a point estimate.

There have been several examples of successful application of simulation models for arable weeds in understanding specific life history processes or long-term population dynamics for optimizing management interventions. A notable example is the ‘Soycal’ app (<https://cropwatch.unl.edu/soycal/>)

[app/index.html](#)) that provides weed seedling emergence advisories based on seedling emergence models. Likewise, there have been practical uses of DSTs for guidance on weed management decisions [16,142,145]. DSTs have also been used as an educational or instructional tool to disseminate research knowledge [146,167]. Models are not always meant to be directly used by farmers. In several cases, models were used by researchers to develop best management practice (BMP) recommendations, which were then disseminated to practitioners. A good example is the glyphosate resistance simulation model for Palmer amaranth developed by Neve et al. [169], which was used to compare various management programs and develop a BMP recommendation. DSTs are often used to transform and deliver complex models in a user-friendly format. Grower use of DSTs are also very limited, but they are predominantly used by crop consultants, industry representatives, and agrichemical distributors who typically provide management recommendations to farmers. This was evident from a recent user survey conducted for the PAM model [142] by Lindsay et al. (unpublished data).

It is, however, important to recognize that only a small proportion of the models (including DSTs) ever developed were widely applied to real-world problems in pest management [141,143,144]. Reasons for low rates of adoption include, but are not limited to: practitioners consider models not relevant to local conditions; practitioners not having time to learn model operational procedures; models are inadequately maintained to keep pace with temporal changes in weed community structure, crop production economics, and computer software standards [141,143,144,170,171]. For DSTs, considering the challenges associated with their development and maintenance, they may be more suited for education rather than prescription. DSTs have been invaluable in the instruction of difficult-to-demonstrate concepts and BMPs to practitioners, researchers, students, and policy makers who collectively influence weed management practices now and in the future.

A sound consideration to the important mechanisms influencing weed demographic processes, a proper representation of such mechanisms in the model framework, and robust model parameter estimation are vital for ensuring satisfactory model performance. While research on weed biology and ecology has gained momentum over the past four decades, especially on weeds with high risk for herbicide resistance evolution, knowledge gaps still exist for several life cycle parameters for many agriculturally important weed species. We still commonly rely on assumptions and opinions for key model parameters, which affects the robustness and reliability of model predictions. More research efforts should be invested in filling these knowledge gaps. In addition to the statistical noise, uncertainty in parameter values and field variability may influence model performance. Thus, models should incorporate stochasticity, especially for those parameters determined to be important based on sensitivity analysis. Moreover, evolutionary adaptation in weeds is expected to alter the magnitude of weed–crop interference, and thus recurrent parameterization and recalibration of these models may be required. Knowledge gaps also exist on the development of multi-species models of weed dynamics. Perennial weeds, including those species with both vegetative and seed perpetuation strategies, require more attention.

Spatially explicit models that consider the interactions of neighboring fields and farms at the landscape scale require special attention. In this respect, dispersal of propagules that are often associated with the movement of agricultural machinery between farms need adequate consideration in the models. Related to this, PMGF also plays an important role, but knowledge gaps exist on the rate, magnitude, and scope of PMGF in a number of problematic weed species such as Palmer amaranth and kochia. This has accelerated the urgency of developing and validating more comprehensive mechanistic gene flow models. Such models will allow weed researchers and practitioners to better identify the key factors driving short- and long-distance gene flow in different mobile weed species in different environments, thereby facilitating more proactive mitigation strategies and tactics. To realize this goal, various dispersal kernel models can form the basis for enhancing predictive capabilities of weed seed and pollen movement across heterogeneous landscapes.

Given the complexity of developing these models, establishing open code-sharing databases may tremendously benefit researchers and accelerate model development. Further, investing more efforts



on translating complex models into user-friendly website applications for practitioners may promote practical implementation.

**Supplementary Materials:** The following are available online at <http://www.mdpi.com/2073-4395/10/10/1611/s1>, Supplementary material I: Weedy Sorghum Case Study; Supplemental Material II Table S1: A list of research publications focused on weed management decision support tools.

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## References

- Oerke, E.C. Crop losses to pests. *J. Agric. Sci.* **2006**, *144*, 31–43. [[CrossRef](#)]
- Zimdahl, R.L. *Weed Crop Competition: A Review*; International Plant Protection Center: Corvallis, OR, USA, 1980.
- Ballare, C.L.; Casal, J.J. Light signals perceived by crop and weed plants. *Field Crops Res.* **2000**, *67*, 149–160. [[CrossRef](#)]
- Page, E.R.; Tollenaar, M.; Lee, E.A.; Lukens, L.; Swanton, C.J. Shade avoidance: An integral component of crop-weed competition. *Weed Res.* **2010**, *50*, 281–288. [[CrossRef](#)]
- Bhowmik, P.C. Weed biology: Importance to weed management. *Weed Sci.* **1997**, *45*, 349–356. [[CrossRef](#)]
- Van Acker, R.C. Weed biology serves practical weed management. *Weed Res.* **2009**, *49*, 1–5. [[CrossRef](#)]
- Cousens, R. A simple model relating yield loss to weed density. *Ann. Appl. Biol.* **1985**, *107*, 239–252. [[CrossRef](#)]
- Radosevich, S.R. Methods to study interactions among crops and weeds. *Weed Technol.* **1987**, *1*, 190–198. [[CrossRef](#)]
- Kropff, M.J.; Lotz, L.A.P. Systems approaches to quantify crop-weed interactions and their application in weed management. *Agric. Syst.* **1992**, *40*, 265–282. [[CrossRef](#)]
- Kropff, M.J. Modelling the effects of weeds on crop production. *Weed Res.* **1988**, *28*, 465–471. [[CrossRef](#)]
- Holst, N.; Rasmussen, I.A.; Bastiaans, L. Field weed population dynamics: A review of model approaches and applications. *Weed Res.* **2007**, *47*, 1–14. [[CrossRef](#)]
- Haefner, J.W. *Modeling Biological Systems: Principles and Applications*, 2nd ed.; Springer: Berlin/Heidelberg, Germany, 2005.
- Andrew, I.K.S.; Storkey, J. Using simulation models to investigate the cumulative effects of sowing rate, sowing date and cultivar choice on weed competition. *Crop Prot.* **2017**, *95*, 109–115. [[CrossRef](#)] [[PubMed](#)]
- Doyle, C.J. Mathematical models in weed management. *Crop Prot.* **1991**, *10*, 432–444. [[CrossRef](#)]
- Lacoste, M.; Powles, S. Upgrading the RIM model for improved support of integrated weed management extension efforts in cropping systems. *Weed Technol.* **2014**, *28*, 703–720. [[CrossRef](#)]
- Neve, P. Simulation modelling to understand the evolution and management of glyphosate resistance in weeds. *Pest Manag. Sci.* **2008**, *64*, 392–401. [[CrossRef](#)]
- Bastiaans, L.; Storkey, J. Descriptive and Mechanistic Models of Crop-Weed Competition. In *Weed Research: Expanding Horizons*; Hatcher, P.E., Froud-Williams, R.J., Eds.; John Wiley & Sons: West Sussex, UK, 2017; Chapter 2; pp. 33–60.
- Colbach, N.; Collard, A.; Guyot, S.H.M.; Meziere, D.; Munier-Jolain, N. Assessing innovative sowing patterns for integrated weed management with a 3D crop: Weed competition model. *Eur. J. Agron.* **2014**, *53*, 74–89. [[CrossRef](#)]
- Kropff, M.J.; van Laar, H.H. *Modelling Crop-weed Interactions*; CAD International: Wallingford, UK, 1993.

20. Park, E.S.; Laurence, R.B.; Andrew, R.W. The theory and application of plant competition models: An agronomic perspective. *Ann. Bot.* **2003**, *92*, 741–748. [[CrossRef](#)] [[PubMed](#)]
21. Renton, M.; Chauhan, B.S. Modelling crop-weed competition: Why, what, how and what lies ahead. *Crop Prot.* **2017**, *95*, 101–108. [[CrossRef](#)]
22. Vleeshouwers, L.M.; Bouwmeester, H.J.; Karssen, C.M. Redefining seed dormancy: An attempt to integrate physiology and ecology. *J. Ecol.* **1995**, *83*, 1031–1037. [[CrossRef](#)]
23. Benech-Arnold, R.L.; Sánchez, R.A.; Forcella, F.; Kruk, B.; Ghera, C.M. Environmental control of dormancy in weed soil seed banks. *Field Crops Res.* **2000**, *67*, 105–122. [[CrossRef](#)]
24. Vleeshouwers, L.M.; Kropff, M.J. Modelling field emergence patterns in arable weeds. *New Phytol.* **2000**, *148*, 445–457. [[CrossRef](#)]
25. Batlla, D.; Benech-Arnold, R.L. Predicting changes in dormancy level in weed seed soil banks: Implications for weed management. *Crop Prot.* **2007**, *26*, 189–197. [[CrossRef](#)]
26. Karssen, C.M. Seasonal patterns of dormancy in weed seeds. In *The Physiology and Biochemistry of Seed Development, Dormancy and Germination*; Khan, A.A., Ed.; Elsevier: Amsterdam, The Netherlands, 1982; pp. 243–270.
27. Batlla, D.; Benech-Arnold, R.L. Predicting changes in dormancy level in natural seed soil banks. *Plant Mol. Biol.* **2010**, *73*, 3–13. [[CrossRef](#)] [[PubMed](#)]
28. Bradford, K.J. Threshold models applied to seed germination ecology. *New Phytol.* **2005**, *165*, 338–341. [[CrossRef](#)] [[PubMed](#)]
29. Bouwmeester, H.J.; Karssen, C.M. The dual role of temperature in the regulation of the seasonal changes in dormancy and germination of seeds of *Polygonum persicaria* L. *Oecologia* **1992**, *90*, 88–94. [[CrossRef](#)] [[PubMed](#)]
30. Bauer, M.C.; Meyer, S.E.; Allen, P.S. A simulation model to predict seed dormancy loss in the field for *Bromus tectorum* L. *J. Exp. Bot.* **1998**, *49*, 1235–1244.
31. Batlla, D.; Benech-Arnold, R.L. A quantitative analysis of dormancy loss dynamics in *Polygonum aviculare* L. seeds: Development of a thermal time model based on changes in seed population thermal parameters. *Seed Sci. Res.* **2003**, *13*, 55–68. [[CrossRef](#)]
32. Gianinetti, A.; Cohn, M.A. Seed dormancy in red rice. XII: Population-based analysis of dry-after ripening with a hydrotime model. *Seed Sci. Res.* **2007**, *17*, 253–271. [[CrossRef](#)]
33. Gardarin, A.; Dürr, C.; Colbach, N. Modeling the dynamics and emergence of a multispecies weed seed bank with species traits. *Ecol. Model.* **2012**, *240*, 123–138. [[CrossRef](#)]
34. Bouwmeester, H.J.; Karssen, C.M. Annual changes in dormancy and germination in seeds of *Sisymbrium officinale* (L.) Scop. *New Phytol.* **1993**, *124*, 179–191. [[CrossRef](#)]
35. Batlla, D.; Benech-Arnold, R.L. Seed dormancy loss assessed by changes in *Polygonum aviculare* L. population hydrotime parameters: Development of a predictive model. *Seed Sci. Res.* **2004**, *14*, 277–286. [[CrossRef](#)]
36. Grundy, A.C. Predicting weed emergence: A review of approaches and future challenges. *Weed Res.* **2003**, *43*, 1–11. [[CrossRef](#)]
37. Forcella, F.; Benech-Arnold, R.L.; Sanchez, R.E.; Ghera, C.M. Modeling seedling emergence. *Field Crop Res.* **2000**, *67*, 123–139. [[CrossRef](#)]
38. Izquierdo, J.; Bastida, F.; Lezaún, J.M.; Sánchez del Arco, M.J.; Gonzalez-Andujar, J.L. Development and evaluation of a model for predicting *Lolium rigidum* emergence in winter cereal crops in the Mediterranean area. *Weed Res.* **2013**, *53*, 269–278. [[CrossRef](#)]
39. Werle, R.; Sandell, L.D.; Buhler, D.D.; Hartzler, R.G.; Lindquist, J.L. Predicting emergence of 23 summer annual weed species. *Weed Sci.* **2014**, *62*, 267–279. [[CrossRef](#)]
40. Zambrano-Navea, C.; Bastida, F.; Gonzalez-Andujar, J.L. A hydrothermal seedling emergence model for *Conyza bonariensis*. *Weed Res.* **2013**, *53*, 213–220. [[CrossRef](#)]
41. Royo-Esnal, A.; Gesch, R.W.; Forcella, F.; Torra, J.; Recasens, J.; Necajeva, J. The role of light in the emergence of weeds: Using *Camelina microcarpa* as an example. *PLoS ONE* **2015**, *10*, e0146079. [[CrossRef](#)]
42. Bewley, A.; BlackSeeds, M. *Physiology of Development and Germination*, 2nd ed.; Plenum Press: New York, NY, USA, 1994.
43. Gonzalez-Andujar, J.L.; Chantre, G.R.; Morvillo, C.; Blanco, A.M.; Forcella, F. Predicting field weed emergence with empirical models and soft computing techniques. *Weed Res.* **2016**, *56*, 415–423. [[CrossRef](#)]
44. Cao, R.; Francisco-Fernández, M.; Anand, A.; Bastida, F.; Gonzalez-Andujar, J.L. Computing statistical indices for hydrothermal times using weed emergence data. *J. Agric. Sci.* **2011**, *149*, 701–712. [[CrossRef](#)]

45. Das, S.K.; Kumar, A.; Das, B.; Burnwal, A. On soft computing techniques in various areas. *Comp. Sci. Info. Tech.* **2013**, *3*, 59–68.
46. Onofri, A.; Piepho, H.P.; Kozak, M. Analyzing censored data in agricultural research: A review with examples and software tips. *Ann. Appl. Biol.* **2019**, *174*, 3–13. [[CrossRef](#)]
47. Onofri, A.; Gresta, F.; Tei, F. A new method for the analysis of germination and emergence data of weed species. *Weed Res.* **2010**, *50*, 187–198. [[CrossRef](#)]
48. Hadi, M.R.H.S.; Gonzalez-Andujar, J.L. Comparison of fitting weed seedling emergence models with nonlinear regression and genetic algorithm. *Comput. Elect. Agric.* **2009**, *65*, 19–25. [[CrossRef](#)]
49. Blanco, A.M.; Chantre, G.R.; Lodovichi, M.V.; Bandoni, J.A.; López, R.L.; Vigna, M.R.; Gigón, R.; Sabbatini, M.R. Modeling seed dormancy release and germination for predicting *Avena fatua* L. field emergence: A genetic algorithm approach. *Ecol. Model.* **2014**, *272*, 293–300. [[CrossRef](#)]
50. Chantre, G.R.; Blanco, A.M.; Forcella, F.; Van Acker, R.C.; Sabbatini, M.R.; Gonzalez-Andujar, J.L. A comparative study between nonlinear regression and artificial neural network approaches for modeling wild oat (*Avena fatua*) field emergence. *J. Agric. Sci.* **2014**, *52*, 254–262. [[CrossRef](#)]
51. Chantre, G.R.; Vigna, M.R.; Renzi, J.P.; Blanco, A.M. A flexible and practical approach for real-time weed emergence prediction based on Artificial Neural Networks. *Biosyst. Eng.* **2018**, *170*, 51–60. [[CrossRef](#)]
52. Cao, R.; Francisco-Fernández, M.; Anand, A.; Bastida, F.; Gonzalez-Andujar, J.L. Modeling *Bromus diandrus* seedling emergence using nonparametric estimation. *J. Agric. Biol. Environ. Stat.* **2013**, *18*, 64–86. [[CrossRef](#)]
53. Barrerios-Ures, D.; Francisco-Fernández, M.; Cao, R.; Fraguera, B.; Doallo, R.; Gonzalez-Andujar, J.L.; Reyes, M. Analysis of interval-grouped data in weed science: The binnednp Rcpp package. *Ecol. Evol.* **2019**, *9*, 10903–10915. [[CrossRef](#)]
54. Sattin, M.; Zanin, G.; Berti, A. Case history for weed competition/population ecology: Velvetleaf (*Abutilon theophrasti*) in corn (*Zea mays*). *Weed Technol.* **1992**, *6*, 213–219. [[CrossRef](#)]
55. Spitters, C.J.T.; Kropff, M.; de Groot, W. Competition between maize and *Echinochloa crus-galli* analysed by a hyperbolic regression model. *Ann. Appl. Biol.* **1989**, *115*, 541–551. [[CrossRef](#)]
56. Cousens, R. An empirical model relating crop yield to weed and crop density and a statistical comparison with other models. *J. Agric. Sci.* **1985**, *105*, 513–521. [[CrossRef](#)]
57. Swinton, S.M.; Buhler, D.D.; Forcella, F.; Gunsolus, J.L.; King, R.P. Estimation of crop yield loss due to interference by multiple weed species. *Weed Sci.* **1994**, *42*, 103–109. [[CrossRef](#)]
58. Christensen, S. Crop weed competition and herbicide performance in cereal species and varieties. *Weed Res.* **1994**, *34*, 29–36. [[CrossRef](#)]
59. Kropff, M.J.; Spitters, J.T. A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. *Weed Res.* **1991**, *31*, 97–105. [[CrossRef](#)]
60. Florez, J.A.; Fischer, A.J.; Ramirez, H.; Duque, M.C. Predicting rice yield losses caused by multispecies weed competition. *Agron. J.* **1999**, *91*, 87–92. [[CrossRef](#)]
61. Nieto, H.J.; Brondo, M.A.; Gonzales, M.A. Critical periods of the crop growth cycle for competition from weeds. *PANS (C)* **1968**, *14*, 159–166. [[CrossRef](#)]
62. Kim, D.S.; Brain, P.; Marshall, E.J.P.; Caseley, J.C. Modelling herbicide dose and weed density effects on crop: Weed competition. *Weed Res.* **2002**, *42*, 1–13. [[CrossRef](#)]
63. Weaver, S.E.; Kropff, M.J.; Groeneveld, R.M.W. Use of ecophysiological models for crop-weed interference: The critical period of weed interference. *Weed Sci.* **1992**, *40*, 302–307. [[CrossRef](#)]
64. Kropff, M.J.; Lotz, L.A.P.; Weaver, S.E.; Bos, H.J.; Wallinga, J.; Migo, T. A two-parameter model for prediction of crop loss by weed competition from early observations of relative leaf area of the weeds. *Ann. Appl. Biol.* **1995**, *126*, 329–346. [[CrossRef](#)]
65. Deen, W.; Cousens, R.; Warringa, J.; Bastiaans, L.; Carberry, P.; Rebel, K.; Riha, S.; Murphy, C.; Benjamin, L.R.; Cloughley, C.; et al. An evaluation of four crop: Weed competition models using a common data set. *Weed Res.* **2003**, *43*, 116–129. [[CrossRef](#)]
66. Snaydon, R.W. Replacement or additive designs for competition studies. *J. Appl. Ecol.* **1991**, *28*, 930–994. [[CrossRef](#)]
67. Rejmanek, M.; Robinson, G.R.; Rejmankova, E. Weed-crop competition: Experimental designs and models for data analysis. *Weed Sci.* **1989**, *37*, 276–284. [[CrossRef](#)]

68. Keller, M.; Gutjahr, C.; Mohring, J.; Weis, M.; Sokefeld, M.; Gerhards, R. Estimating economic thresholds for site-specific weed control using manual weed counts and sensor technology: An example based on three winter wheat trials. *Pest Manag. Sci.* **2014**, *70*, 200–211. [[CrossRef](#)]
69. Bennett, A.C.; Price, A.J.; Sturgill, M.C.; Buol, G.S.; Wilkerson, G.C. HADSS™, Pocket HERB™, and Web HADSS™: Decision aids for field crops. *Weed Technol.* **2003**, *17*, 412–420. [[CrossRef](#)]
70. Wilkerson, G.G.; Modena, S.A.; Coble, H.D. HERB: Decision model for postemergence weed control in soybean. *Agron. J.* **1991**, *83*, 413–417. [[CrossRef](#)]
71. Barroso, J.; Fernandez-Quintanilla, C.; Maxwell, B.D.; Rew, L.J. Simulating the effects of weed spatial pattern and resolution of mapping and spraying on economics of site-specific management. *Weed Res.* **2004**, *44*, 460–468. [[CrossRef](#)]
72. Onyango, C.; Marchant, J.; Grundy, A.; Phelps, K.; Rader, R. Image processing performance assessment using crop weed competition models. *Precis. Agric.* **2005**, *6*, 183–192. [[CrossRef](#)]
73. Apolo-Apolo, O.E.; Perez-Ruiz, M.; Martinez-Guanter, J.; Egea, G. A mixed data-based deep neural network to estimate leaf area index in wheat breeding trials. *Agronomy* **2020**, *10*, 175. [[CrossRef](#)]
74. Bastiaans, L.; Kropff, M.J.; van Laar, H.H. Design of weed management systems with a reduced reliance on herbicides poses new challenges and prerequisites for modeling crop-weed interactions. *Field Crops Res.* **2000**, *67*, 161–179. [[CrossRef](#)]
75. Gerhards, R.; Gutjahr, C.; Weis, M.; Keller, M.; Sökefeld, M.; Möhring, J.; Piepho, H.P. Using precision farming technology to quantify yield effects attributed to weed competition and herbicide application. *Weed Res.* **2012**, *52*, 6–15. [[CrossRef](#)]
76. Colbach, N.; Forcella, F.; Johnson, G.A. Spatial and temporal stability of weed populations over five years. *Weed Sci.* **2000**, *48*, 366–377. [[CrossRef](#)]
77. Graf, B.; Gutierrez, A.P.; Rakotobe, O.; Zahner, P.; Delucchi, V. A simulation model for the dynamics of rice growth and development: Part II-The competition with weeds for nitrogen and light. *Agric. Syst.* **1990**, *32*, 367–392. [[CrossRef](#)]
78. Afifi, M.; Swanton, C. Early physiological mechanisms of weed competition. *Weed Sci.* **2012**, *60*, 542–551. [[CrossRef](#)]
79. Ziska, L.H. Could recent increases in atmospheric CO<sub>2</sub> have acted as a selection factor in *Avena fatua* populations A case study of cultivated and wild oat competition. *Weed Res.* **2017**, *57*, 399–405. [[CrossRef](#)]
80. Ziska, L.H.; Tomecek, M.B.; Gealy, D.R. Competitive interactions between cultivated and red rice as a function of recent and projected increases in atmospheric carbon dioxide. *Agron. J.* **2010**, *102*, 118–123. [[CrossRef](#)]
81. Bravo, W.; Leon, R.G.; Ferrell, J.A.; Mulvaney, M.J.; Wood, C.W. Evolutionary adaptations of Palmer amaranth populations (*Amaranthus palmeri*) to nitrogen fertilization and crop rotation history affect morphology and nutrient-use efficiency. *Weed Sci.* **2018**, *66*, 180–189. [[CrossRef](#)]
82. Bravo, W.; Leon, R.G.; Ferrell, J.A.; Mulvaney, M.J.; Wood, C.W. Differentiation of life-history traits among Palmer amaranth populations (*Amaranthus palmeri*) and its relation to cropping systems and glyphosate sensitivity. *Weed Sci.* **2017**, *65*, 339–349. [[CrossRef](#)]
83. Beckie, H.J.; Busi, R.; Bagavathiannan, M.V.; Martin, S.L. Herbicide resistance gene flow in weeds: Under-estimated and under-appreciated. *Agric. Ecosyst. Environ.* **2019**, *283*, e106566. [[CrossRef](#)]
84. Beckie, H.J.; Hall, L.M. Simple to complex: Modelling crop pollen-mediated gene flow. *Plant Sci.* **2008**, *175*, 615–628. [[CrossRef](#)]
85. Cousens, R.; Dytham, C.; Law, R. *Dispersal in Plants: A Population Perspective*; Oxford University Press: Oxford, UK, 2008; 240p.
86. Dauer, J.T.; Mortensen, D.A.; Vangessel, M.J. Temporal and spatial dynamics of long-distance *Conyza canadensis* seed dispersal. *J. Appl. Ecol.* **2006**, *44*, 105–114. [[CrossRef](#)]
87. Andersen, M.C. An analysis of variability in seed settling velocities of several wind-dispersed Asteraceae. *Am. J. Bot.* **1992**, *79*, 1087–1091. [[CrossRef](#)]
88. Stephenson, C.M.; Kohn, D.D.; Park, K.J.; Atkinson, R.; Edwards, C.; Travis, J.M. Testing mechanistic models of seed dispersal for the invasive *Rhododendron ponticum* (L.). *Perspect. Plant Ecol. Evol. Syst.* **2007**, *9*, 15–28. [[CrossRef](#)]
89. Nathan, R.; Katul, G.G.; Bohrer, G.; Kuparinen, A.; Soons, M.B.; Thompson, S.E.; Trakhtenbrot, A.; Horn, H.S. Mechanistic models of seed dispersal by wind. *Theor. Ecol.* **2011**, *4*, 113–132. [[CrossRef](#)]

90. Ganie, Z.A.; Jhala, A.J. Modeling pollen-mediated gene flow from glyphosate-resistant to -susceptible giant ragweed (*Ambrosia trifida* L.) under field conditions. *Sci. Rep.* **2017**, *7*, e17067. [[CrossRef](#)] [[PubMed](#)]
91. Klein, E.K.; Lavigne, C.; Picault, H.; Renard, M.; Gouyon, P.H. Pollen dispersal of oilseed rape: Estimation of the dispersal function and effects of field dimension. *J. Appl. Ecol.* **2006**, *43*, 141–151. [[CrossRef](#)]
92. Devaux, C.; Lavigne, C.; Austerlitz, F.; Klein, E.K. Modelling and estimating pollen movement in oilseed rape (*Brassica napus*) at the landscape scale using genetic markers. *Mol. Ecol.* **2007**, *16*, 487–499. [[CrossRef](#)] [[PubMed](#)]
93. Shaw, M.W.; Harwood, T.D.; Wilkinson, M.J.; Elliott, L. Assembling spatially explicit landscape models of pollen and spore dispersal by wind for risk assessment. *Proc. Roy. Soc. B* **2006**, *273*, 1705–1713. [[CrossRef](#)]
94. Ramsay, G. Pollen dispersal vectored by wind or insects. In *Gene Flow from GM Plants*; Poppy, G.M., Wilkinson, M.J., Eds.; Blackwell Publishing Ltd.: Oxford, UK, 2005.
95. Jackson, S.T.; Lyford, M.E. Pollen dispersal models in quaternary plant ecology: Assumptions, parameters, and prescriptions. *Bot. Rev.* **1999**, *65*, 39–75. [[CrossRef](#)]
96. Baskin, C.C.; Baskin, J.M. Germination ecophysiology of herbaceous plant species in a temperature region. *Am. J. Bot.* **1988**, *75*, 286–305. [[CrossRef](#)]
97. Burnside, O.C.; Wilson, R.G.; Weisberg, S.; Hubbard, K.G. Seed longevity of 41 weed species buried 17 years in eastern and western Nebraska. *Weed Sci.* **1996**, *44*, 74–86. [[CrossRef](#)]
98. Buhler, D.D.; Hartzler, R.G. Emergence and persistence of seed of velvetleaf, common waterhemp, woolly cupgrass, and giant foxtail. *Weed Sci.* **2001**, *49*, 230–235. [[CrossRef](#)]
99. Forcella, F.; Wilson, R.G.; Dekker, J.; Kremer, R.; Cardina, J.; Anderson, R.L.; Alm, D.; Renner, K.A.; Harvey, R.G.; Clay, S.; et al. Weed seed bank emergence across the Corn Belt. *Weed Sci.* **1997**, *67*, 123–129. [[CrossRef](#)]
100. Bagavathiannan, M.V.; Norsworthy, J.K. Late-Season seed production in arable weed communities: Management implications. *Weed Sci.* **2012**, *60*, 325–334. [[CrossRef](#)]
101. Norsworthy, J.K.; Korres, N.E.; Bagavathiannan, M.V. Weed seedbank management: Revisiting how herbicides are evaluated. *Weed Sci.* **2018**, *66*, 415–417. [[CrossRef](#)]
102. Davis, A.S.; Dixon, P.M.; Liebman, M. Cropping system effects on giant foxtail demography: II. retrospective perturbation analysis. *Weed Sci.* **2003**, *51*, 930–939. [[CrossRef](#)]
103. Liebman, M.; Nichols, V.A. Cropping system redesign for improved weed management: A modeling approach illustrated with giant ragweed (*Ambrosia trifida*). *Agronomy* **2020**, *10*, 262. [[CrossRef](#)]
104. Jordan, N.; Mortensen, D.A.; Prenzlów, D.M.; Cox, K.C. Simulation analysis of crop rotation effects on weed seedbanks. *Am. J. Bot.* **1995**, *82*, 390–398. [[CrossRef](#)]
105. Bohan, D.A.; Powers, S.J.; Champion, G.; Houghton, A.J.; Hawes, C.; Squire, G.; Cussans, J.; Mertens, S.K. Modelling rotations: Can crop sequences explain arable weed seedbank abundance. *Weed Res.* **2011**, *51*, 422–432. [[CrossRef](#)]
106. Munier-Jolain, N.M.; Guyot, S.H.M.; Colbach, N. A 3D model for light interception in heterogeneous crop: Weed canopies. Model structure and evaluation. *Ecol. Model.* **2013**, *250*, 101–110. [[CrossRef](#)]
107. Storkey, J.; Moss, S.R.; Cussans, J.W. Using assembly theory to explain changes in a weed flora in response to agricultural intensification. *Weed Sci.* **2010**, *58*, 39–46. [[CrossRef](#)]
108. Colbach, N.; Gardarin, A.; Munier-Jolain, N.M. FLORSYS: A mechanistic model of cropping system effects on weed flora based on functional relationships with species traits. In Proceedings of the 15th International EWRS Symposium, Kaposvar, Hungary, 12–15 July 2010.
109. Gressel, J.; Segel, L.A. The paucity of plants evolving genetic resistance to herbicides: Possible reasons and implications. *J. Theoret. Biol.* **1978**, *75*, 349–371. [[CrossRef](#)]
110. Maxwell, B.D.; Roush, M.L.; Radosevich, S.R. Predicting the evolution and dynamics of herbicide resistance in weed populations. *Weed Technol.* **1990**, *4*, 2–13. [[CrossRef](#)]
111. Jasieniuk, M.; Maxwell, B.D. Population genetics and the evolution of herbicide resistance in weeds. *Phytoprotection* **1994**, *75*, 25–35. [[CrossRef](#)]
112. Renton, M.; Diggle, A.; Manalil, S.; Powles, S. Does cutting herbicide rates threaten the sustainability of weed management in cropping systems. *J. Theor. Biol.* **2011**, *283*, 14–27. [[CrossRef](#)]
113. Neve, J.K.; Norsworthy, K.L.; Smith, I.A. Modelling evolution and management of glyphosate resistance in *Amaranthus palmeri*. *Weed Res.* **2011**, *51*, 99–112. [[CrossRef](#)]

114. Bagavathiannan, M.V.; Norsworthy, J.K.; Smith, K.L.; Neve, P. Modeling the evolution of glyphosate resistance in barnyardgrass (*Echinochloa crus-galli*) in cotton-based production systems of the Mid southern United States. *Weed Technol.* **2013**, *27*, 475–487. [[CrossRef](#)]
115. Bagavathiannan, M.V.; Norsworthy, J.K.; Smith, K.L.; Neve, P. Modeling the simultaneous evolution of resistance to ALS- and ACCase-inhibiting herbicides in barnyardgrass (*Echinochloa crus-galli*) in Clearfield® rice. *Weed Technol.* **2014**, *28*, 89–103. [[CrossRef](#)]
116. Werle, R.; Brigitte, T.; Lindquist, J.L. Modeling shattercane dynamics in herbicide-tolerant grain sorghum cropping systems. *Ecol. Model.* **2017**, *343*, 131–141. [[CrossRef](#)]
117. Heap, I. International Survey of Herbicide Resistant Weeds. 2020. Available online: [www.herbicideresistance.org](http://www.herbicideresistance.org) (accessed on 28 September 2020).
118. Mortimer, A.M.; Ulf-Hansen, P.F.; Putwain, P.D. Modelling herbicide resistance—a study of ecological fitness. In *Achievements and Developments in Combating Pesticide Resistance*; Denholm, I., Devonshire, A.L., Hollomons, D.W., Eds.; Elsevier Science Publishers: Essex, UK, 1992; pp. 283–306.
119. Neve, P.; Diggle, A.J.; Smith, F.P.; Powles, S.B. Simulating evolution of glyphosate resistance in *Lolium rigidum* I: Population biology of a rare resistance trait. *Weed Res.* **2003**, *43*, 404–417. [[CrossRef](#)]
120. Renton, M.; Busi, R.; Neve, P.; Thornby, D.; Vila-Aiub, M. Herbicide resistance modelling: Past, present and future. *Pest Manag. Sci.* **2014**, *70*, 1394–1404. [[CrossRef](#)]
121. Diggle, A.J.; Neve, P.B.; Smith, F.P. Herbicides used in combination can reduce the probability of herbicide resistance in finite weed populations. *Weed Res.* **2003**, *43*, 371–382. [[CrossRef](#)]
122. Powles, S.; Yu, Q. Evolution in action: Plants resistant to herbicides. *Annl. Rev. Plant Biol.* **2010**, *61*, 317–347. [[CrossRef](#)]
123. Pannell, D.J.; Stewart, V.; Bennett, A.; Monjardino, M.; Schmidt, C.; Powles, S.B. RIM: A bioeconomic model for integrated weed management of *Lolium rigidum* in Western Australia. *Agric. Syst.* **2004**, *79*, 305–325. [[CrossRef](#)]
124. Somerville, G.J.; Powles, S.B.; Walsh, M.J.; Renton, M. Modeling the impact of harvest weed seed control on herbicide resistance evolution. *Weed Sci.* **2018**, *66*, 395–403. [[CrossRef](#)]
125. Liu, C.; Bridges, M.E.; Kaundun, S.S.; Glasgow, L.; Owen, M.D.K.; Neve, P. A generalized individual-based algorithm for modelling the evolution of quantitative herbicide resistance in arable weed populations. *Pest Manag. Sci.* **2017**, *73*, 462–474. [[CrossRef](#)]
126. Gardner, S.; Gressel, J.; Mangel, M. A revolving dose strategy to delay the evolution of both quantitative vs. major monogene resistances to pesticides and drugs. *Int. J. Pest. Manag.* **1998**, *44*, 161–180. [[CrossRef](#)]
127. Richter, O.; Zwerger, P.; Bottcher, U. Modelling spatio-temporal dynamics of herbicide resistance. *Weed Res.* **2002**, *42*, 52–64. [[CrossRef](#)]
128. Somerville, G.J.; Powles, S.B.; Walsh, M.J.; Renton, M. How do spatial heterogeneity and dispersal in weed population models affect predictions of herbicide resistance evolution? *Ecol. Model.* **2017**, *362*, 37–53. [[CrossRef](#)]
129. Vila-Aiub, M.; Neve, P.; Powles, S. Fitness costs associated with evolved herbicide resistance alleles in plants. *New Phytol.* **2009**, *184*, 751–767. [[CrossRef](#)] [[PubMed](#)]
130. Somerville, G.J.; Sønderkov, M.; Mathiassen, S.K.; Metcalfe, H. Spatial modelling of within-field weed populations: A review. *Agronomy* **2020**, *10*, 1044. [[CrossRef](#)]
131. Busi, R.; Gaines, T.A.; Powles, S. Phorate can reverse P450 metabolism-based herbicide resistance in *Lolium rigidum*. *Pest Manag. Sci.* **2017**, *73*, 410–417. [[CrossRef](#)]
132. Wiles, L.J.; King, R.P.; Sweizer, E.E.; Lybecker, D.W.; Swinton, S.M. GWM: General weed management model. *Agric. Syst.* **1996**, *50*, 355–376. [[CrossRef](#)]
133. Parsons, D.J.; Benjamin, L.R.; Clarke, J.; Ginsburg, D.; Mayes, A.; Milne, A.E.; Wilkinson, D.J. Weed Manager—A model-based decision support system for weed management in arable crops. *Comput. Electron. Agric.* **2009**, *65*, 155–167. [[CrossRef](#)]
134. Oriade, C.; Forcella, F. Maximizing efficacy and economics of mechanical weed control in row crops through forecasts of weed emergence. In *Expanding the Context of Weed Management*; Food Products Press: Binghamton, NY, USA, 1999; pp. 189–206.
135. Scursioni, J.A.; Forcella, F.; Gunsolus, J. Weed escapes and delayed weed emergence in glyphosate-resistant soybean. *Crop Prot.* **2007**, *26*, 212–218. [[CrossRef](#)]

136. Schutte, B.J.; Hager, A.C.; Davis, A.S. Respray requests on custom-applied, glyphosate-resistant soybeans in Illinois: How many and why. *Weed Technol.* **2010**, *24*, 590–598. [[CrossRef](#)]
137. Nowell, L.H.; Moran, P.W.; Schmidt, T.S.; Norman, J.E.; Nakagaki, N.; Shoda, M.E.; Mahler, B.J.; Van Metre, P.C.; Stone, W.W.; Sandstrom, M.W.; et al. Complex mixtures of dissolved pesticides show potential aquatic toxicity in a synoptic study of Midwestern U.S. streams. *Sci. Total Environ.* **2018**, *613–614*, 1469–1488. [[CrossRef](#)]
138. Pandey, S.; Medd, R.W. A stochastic dynamic programming framework for weed control decision making: An application to *Avena fatua* L. *Agric. Econ.* **1991**, *6*, 115–128. [[CrossRef](#)]
139. Lodovichi, M.V.; Blanco, A.M.; Chantre, G.R.; Bandoni, J.A.; Sabbatini, M.R.; Vigna, M.; López, R.; Gigón, R. Operational planning of herbicide-based weed management. *Agric. Syst.* **2013**, *121*, 117–129. [[CrossRef](#)]
140. Berti, A.; Bravin, F.; Zanin, G. Application of decision-support software for postemergence weed control. *Weed Sci.* **2003**, *51*, 618–627. [[CrossRef](#)]
141. Wilkerson, G.C.; Wiles, L.J.; Bennett, A.C. Weed management decision models: Pitfalls, perceptions, and possibilities of the economic threshold approach. *Weed Sci.* **2002**, *50*, 411–424. [[CrossRef](#)]
142. Lindsay, K.; Popp, M.; Norsworthy, J.; Bagavathiannan, M.; Powles, S.; Lacoste, M. PAM: Decision support for long-term Palmer amaranth (*Amaranthus palmeri*) control. *Weed Technol.* **2017**, *31*, 915–927. [[CrossRef](#)]
143. Lacoste, M.; Powles, S. Beyond modeling: Considering user-centered and post-development aspects to ensure the success of a decision support system. *Comput. Electron. Agric.* **2016**, *121*, 260–268. [[CrossRef](#)]
144. Kragt, M.E.; Llewellyn, R.S. Using a choice experiment to improve decision support tool design. *Appl. Econ. Perspect. Policy* **2014**, *36*, 351–371. [[CrossRef](#)]
145. Colas, F.; Cordeau, S.; Granger, S.; Jeuffroy, M.-H.; Pointurier, O.; Queyrel, W.; Rodriguez, A.; Villerd, J.; Colbach, N. Co-development of a decision support system for integrated weed management: Contribution from future users. *Eur. J. Agron.* **2020**, *114*, 126010. [[CrossRef](#)]
146. Bessette, D.; Wilson, R.; Beaudrie, C.; Schroeder, C. An online decision support tool to evaluate ecological weed management strategies. *Weed Sci.* **2019**, *67*, 463–473. [[CrossRef](#)]
147. Kristensen, K.; Rasmussen, I.A. The use of Bayesian network in the design of a decision support system for growing malting barley without use of pesticides. *Comput. Electron. Agric.* **2002**, *32*, 197–217. [[CrossRef](#)]
148. Neuhoff, D.; Schulz, D.; Köpke, U. Potential of decision support systems for organic crop production: WECOF-DSS, a tool for weed control in winter wheat. In Proceedings of the International Scientific Conference on Organic Agriculture, Adelaide, Australia, 21–23 September 2005.
149. Zambrano-Navea, C.; Bastida, F.; Gonzalez-Andujar, J.L. A cohort-based stochastic model of the population dynamic and long-term management of *Conyza bonariensis* in fruiting tree crops. *Crop Prot.* **2016**, *80*, 15–20. [[CrossRef](#)]
150. Sarangi, D.; Jhala, A.J. Biologically effective rates of a new premix (atrazine, bicyclopyrone, mesotrione, and S-metolachlor) for preemergence or postemergence control of common waterhemp [*Amaranthus tuberculatus* (Moq.) Sauer var. *rudis*] in corn. *Can. J. Plant Sci.* **2017**, *97*, 1075–1089.
151. Dieleman, J.A.; Mortensen, D.A.; Martin, A.R. Influence of velvetleaf (*Abutilon theophrasti*) and common sunflower (*Helianthus annuus*) density variation on weed management outcomes. *Weed Sci.* **1999**, *47*, 81–89. [[CrossRef](#)]
152. Schutte, B.J. Measuring interference from midseason tall morning glory (*Ipomoea purpurea*) to develop a model for teaching weed seedbank effects on chile pepper. *Weed Technol.* **2017**, *31*, 155–164. [[CrossRef](#)]
153. Renner, K.A.; Black, J.R. SOYHERB-A computer program for soybean herbicide decision making. *Agron. J.* **1991**, *83*, 921–925. [[CrossRef](#)]
154. Lyon, L.L.; Keeling, J.W.; Dotry, P.A. Evaluation and adaptation of the HADSS<sup>®</sup> computer program in Texas Southern High Plains cotton. *Weed Technol.* **2004**, *18*, 315–324. [[CrossRef](#)]
155. Ford, A.J.; Dotry, P.A.; Keeling, J.W.; Wilkerson, J.B.; Wilcut, J.W.; Gilbert, L.V. Site-specific weed management in cotton using WebHADSS<sup>™</sup>. *Weed Technol.* **2011**, *25*, 107–112. [[CrossRef](#)]
156. Gonzalez-Andujar, J.L.; Fernandez-Quintanilla, C.; Bastida, F.; Calvo, R.; Izquierdo, J.; Lezaun, J.A. Assessment of a decision support system for chemical control of annual ryegrass (*Lolium rigidum*) in winter cereals. *Weed Res.* **2011**, *51*, 304–309. [[CrossRef](#)]
157. Gonzalez-Andujar, J.L.; Fernandez-Quintanilla, C.; Bastida, F.; Calvo, R.; Gonzalez-Diaz, L.; Izquierdo, J.; Lezaun, J.A.; Perea, F.; Sanchez del Arco, M.J.; Urbano, J.M. Field evaluation of a decision support system for herbicidal control of *Avena sterilis* ssp. *ludoviciana* in winter wheat. *Weed Res.* **2010**, *50*, 83–88. [[CrossRef](#)]

158. Meyer, C.J.; Norsworthy, J.K. Influence of weed size on herbicide interactions for Enlist™ and Roundup Ready® Xtend® technologies. *Weed Technol.* **2019**, *33*, 569–577. [[CrossRef](#)]
159. Knezevic, S.Z.; Evans, S.P.; Blankenship, E.E.; Van Acker, R.C. Critical period for weed control: The concept and data analysis. *Weed Sci.* **2002**, *50*, 773–786. [[CrossRef](#)]
160. Benjamin, L.R.; Milne, A.E.; Parsons, D.J.; Cussans, J.; Lutman, P.J.W. Using stochastic dynamic programming to support weed management decisions over a rotation. *Weed Res.* **2009**, *49*, 207–216. [[CrossRef](#)]
161. Lacoste, M.; Powles, S. RIM: Anatomy of a weed management decision support system for adaptation and wider application. *Weed Sci.* **2015**, *63*, 676–689. [[CrossRef](#)]
162. Cousens, R.; Doyle, C.J.; Wilson, B.J.; Cussans, G.W. Modelling the economics of controlling *Avena fatua* in winter wheat. *Pestic. Sci.* **1986**, *17*, 1–12. [[CrossRef](#)]
163. Gonzalez-Diaz, L.; Bastida, F.; Gonzalez-Andujar, J.L. A bioeconomic model for the analysis of control strategies for *Lolium rigidum* and *Avena sterilis* ssp. *ludoviciana* in winter wheat. *Int. J. Plant Prod.* **2020**, *14*, 37–42. [[CrossRef](#)]
164. Stanton, R.A.; Pratley, J.E.; Hudson, D.; Dill, G.M. A risk calculator for glyphosate resistance in *Lolium rigidum* (Gaud.). *Pest Manag. Sci.* **2008**, *64*, 402–408. [[CrossRef](#)] [[PubMed](#)]
165. Beckie, H.J.; Harker, N.K.; Hall, L.M.; Holm, F.A.; Gulden, R.H. Risk assessment of glyphosate resistance in western Canada. *Weed Technol.* **2011**, *25*, 159–164. [[CrossRef](#)]
166. Borger, C.P.D.; Riethmuller, G.P.; Renton, M. Weed Seed Wizard: A tool that demonstrates the value of integrated weed management tactics such as harvest weed seed destruction. *Comput. Electron. Agric.* **2018**, *147*, 27–33. [[CrossRef](#)]
167. Llewellyn, R.S.; Pannell, D.J.; Lindner, R.K.; Powles, S.B. Targeting key perceptions when planning and evaluating extension. *Aust. J. Exp. Agric.* **2005**, *45*, 1627–1633. [[CrossRef](#)]
168. Attonaty, J.M.; Chatelin, M.H.; Garcia, F. Interactive simulation modeling in farm decision-making. *Comput. Electron. Agric.* **1999**, *22*, 157–170. [[CrossRef](#)]
169. Neve, P.; Norsworthy, J.K.; Smith, K.L.; Zelaya, I.A. Modeling glyphosate resistance management strategies for Palmer amaranth (*Amaranthus palmeri*) in cotton. *Weed Technol.* **2011**, *25*, 335–343. [[CrossRef](#)]
170. Jørgensen, L.N.; Noe, E.; Langvad, A.M.; Jensen, J.E.; Ørum, J.E.; Rydahl, P. Decision support systems: Barriers and farmers' need for support. *Bull. OEPP* **2007**, *37*, 374–377. [[CrossRef](#)]
171. Kanatas, P.; Travlos, I.S.; Gazoulis, I.; Tataridas, A.; Tsekoura, A.; Antonopoulos, N. Benefits and limitations of decision support systems (DSS) with a special emphasis on weeds. *Agronomy* **2020**, *10*, 548. [[CrossRef](#)]

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