Short communication. Integration of emergence and population dynamic models for long term weed management using wild oat (*Avena fatua* L.) as an example

L. González-Díaz¹, E. Leguizamón², F. Forcella³ and J. L. González-Andújar¹*

¹ Crop Protection Department. Instituto de Agricultura Sostenible (CSIC). Apdo. 4084. 14080 Córdoba, Spain
² Facultad de Ciencias Agrarias. Universidad Nacional de Rosario. Rosario. Argentina
³ USDA-ARS. North Central Soil Conservation Research Laboratory. Morris, MN 56267. USA

Abstract

Weed emergence models and weed population models have shown to be important tools for decision making. However, there have been no attempts to integrate a weed emergence model with a population dynamics model to build an improved model with increased predictive capacity. In this paper, a method of integrating both types of model is presented and an application building a mathematical model based on previously reported seedling emergence and population dynamics data to simulate cohort-dependent population dynamics of wild oat is given. Three management scenarios (S₁, S₂, S₃) were considered. In S₁, farmers are not aware of the time of weed emergence make control decisions as a stochastic process. Under S₂, farmers are aware of the time of weed emergence and make decisions considering the time of emergence. The effect of 100% control when 80, 90, 95 and 100% of wild oats had emerged was examined. In S₁, there was «no control». In the absence of control the wild oat population grew in a sigmoid manner and reached an equilibrium density at about 16,000 seeds m⁻² in the soil seed bank. In S₁, simulation resulted in an average population equilibrium at about 13,000 seeds m⁻². This equilibrium position represented only a 19% reduction of the carrying capacity of the system. In S₂, the 95% and 100% emerged weeds, produced population extinction after 16 and 6 years, respectively. In S₂ with 90% and 80% of emerged weeds the carrying capacity of the system was reduced by 95% and 28%, respectively. Scenario S₂ with minimum uncertainty always gave better results than S₁. Integrating simple population models with emergence models would help farmers in long-term decision making for weed management.

Additional key words: degree-days, Gompertz model, life-cycle model, logistic model, simulation, weed control.

Resumen

Comunicación corta. Integración de modelos de dinámica de poblaciones y de emergencia para el manejo a largo plazo de malas hierbas: la avena loca (*Avena fatua* L.) como ejemplo

Se construyó un modelo matemático basado en datos de emergencia y demografía para simular la dinámica de poblaciones de la avena loca (*Avena fatua* L.). Tres escenarios de manejo fueron considerados (S₁, S₂ y S₃). En S₁, los agricultores carecen de conocimiento sobre el proceso temporal de la emergencia de la avena loca y toman sus decisiones de manera aleatoria. En S₂, los agricultores tienen conocimiento del proceso temporal de la emergencia de la mala hierba. Consideramos el efecto sobre la dinámica de poblaciones de un control del 100% cuando han emergido el 80, 90, 95 y 100% de las plantas. El S₁ fue el correspondiente a la no aplicación de medidas de control. En S₁, la población creció sigmoidalmente, alcanzando una densidad de equilibrio de aproximadamente 16.000 semillas m⁻² en el suelo. La simulación correspondiente a S₁ dio lugar a un equilibrio de la población de 13.000 semillas m⁻². Este equilibrio supone solamente una reducción del 19% de la capacidad de carga del sistema. En S₂, con las medidas de control aplicadas con el 95% y 100% de la población emergida, se produjo una extinción de la población después de 16 y 6 años, respectivamente. Sin embargo, S₂ con el 90% y el 80% de la población emergida dio lugar a un banco de semillas que representó el 95% y 28%, respectivamente, de la capacidad de carga del sistema. S₂ supone una reducción de la incertidumbre del agricultor y produjo siempre resultados mejores que el S₁. La integración de modelos de dinámica de poblaciones con modelos de emergencia pueden ser una herramienta de ayuda para los agricultores en la toma de decisiones a largo plazo.

Palabras clave adicionales: control de malas hierbas, grados días, modelo de ciclo de vida, modelo de Gompertz, modelo logístico, simulación.
Prediction of weed populations in production systems is a crucial objective in weed science, since it helps to optimize long-term weed control tactics and strategies (Cousens and Mortimer, 1995). One of the key issues in modelling weed populations is the recruitment of seedlings from the seed bank and the dynamics of these plants. Although weed emergence patterns have been studied since the early 1960’s (Roberts, 1964; Stoller and Wax, 1973; Leguizamón, 1986; Egley and Williams, 1991; González-Andújar et al., 2001), there has only been recent interest in developing emergence models (Grundy and Mead, 2000; González-Andújar et al., 2001; Leguizamón et al., 2005). This semi-empirical approach has proved highly successful for forecasting weed emergence. However, emergence models lack inputs from long-term predictions.

Weed population models are well established in weed science and have been used to simulate long-term population trends and evaluate control strategies (Doyle et al., 1984; González-Andújar and Fernández-Quintanilla, 1991, 2004; Jordan et al., 1995). Such models are more appropriate to qualitative than quantitative predictions. However, as far as we are aware, there have been no attempts to integrate a weed emergence model with a population dynamics model in a combined approach to build an improved model with increased predictive capacity.

In this paper a method of integrating seedling emergence and population dynamics models is developed, using an important annual weed species, *Avena fatua* L., as an example.

The relationship between daily soil temperature (soil degree-days, *SD*) at 5 cm between 1 April (crop seeding) and 1 July (92 days) and time (*d*) in days was modelled using a Gompertz model:

\[
SD = \phi \exp \{- \exp \left[ -\phi \left( d - \gamma \right) \right]\} \quad [1]
\]

where \( \phi \), \( \varphi \) and \( \gamma \) are parameters. The model was fitted to the data set (soil temperature, unpublished) using generalized non-linear least squares. Goodness of fit was judged by residual mean square (RMS), estimation of parameters, \( R^2 \), and visual examination of the residuals (\( R^2 = 0.85 \), RMS = 6.71, \( df = 89 \)). The estimated values of these parameters were \( \phi = 24.69 \) (SE = 1.74), \( \varphi = 0.033 \) (SE = 0.005), and \( \gamma = 25.48 \) (SE = 2.74).

Daily fluctuations in soil temperatures (\( SD_\varepsilon \)) was represented by a normal distribution, with each predicted mean temperature value being generated using the RMS of the Gompertz regression as an unbiased estimate of the variance (\( \sigma^2 \)):

\[
SD_\varepsilon = SD + \varepsilon \quad [2]
\]

where \( \varepsilon \sim N (0, 6.71) \). Accumulated soil degree-days (\( ASD \)) at 5 cm were calculated by:

\[
ASD = \sum_{d=1}^{92} SD_\varepsilon \quad [3]
\]

Accumulated wild oat emergence (\( y_d \)) was modelled as a function of \( ASD \) using a simple logistic model (González-Andújar et al., 2001):

\[
y_d = \frac{\alpha}{1 + e^{-\beta \left( ASD - \delta \right)}} \quad [4]
\]

where \( \alpha \) is the asymptote, \( \beta \) is the rate of emergence at the beginning of the season and \( \delta \) is the inflection point (corresponding to 50% total emergence). The model was fitted to the wild oat emergence data set (unpublished), using the same statistical method as used to fit the Gompertz model (\( R^2 = 0.99 \), RMS = 1, \( df = 15 \)). Values of the estimated parameters were \( \alpha = 99.66 \) (SE = 0.21), \( \beta = 0.16 \) (SE = 0.005), and \( \delta = 106.36 \) (SE = 0.178).

The model describing the wild oat life-cycle is similar to the model proposed by different authors for other annual weed populations (González-Andújar and Fernández-Quintanilla, 1991, 1993; Cousens et al., 1986).

**Seedling emergence**

The total number of seedlings m\(^{-2}\) emerging in year \( t \) (\( S_t \)) is given by:

\[
S_t = e^{B_t} \quad [5]
\]

where \( e \) is the proportional emergence of the seed bank and \( B_t \) is the seed bank (seeds m\(^{-2}\)) at time \( t \). Using the previously developed logistic model (\( y_d \)), the number of seedlings emerged until day \( d \) can be established as:

\[
S_{t,d} = \left( \frac{y_d}{100} \right) S_t \quad [6]
\]

**Seedling survival after control**

A proportion of emerged seedlings can be controlled by the farmer depending on which day control decisions are made. All emerged weed seedlings on that day \( d \) are assumed to be controlled, but seedlings which have not yet emerged would not be controlled. Total surviving seedlings after day \( d \) was computed as:

\[
S_{t,d} = (1 - y_d / 100) S_t \quad [7]
\]
Mature plants

Survival of emerged, non-controlled seedlings to maturity \((M, \text{ mature plants m}^{-2})\) is density-dependent (Cousens \textit{et al.}, 1986):

\[ M_t = S_{t,d} / (1 + a S_{t,d}) \]  \[8\]

where \(a\) is the reciprocal of the asymptotic value of \(M\).

Seed production

Fecundity \((F, \text{ seeds plant}^{-1})\) is density-dependent and follows a hyperbolic model (Cousens \textit{et al.}, 1986):

\[ F = f / (1 + b M_t) \]  \[9\]

where \(f\) is the number of seeds produced by an isolated mature plant \((M \rightarrow 0)\), and \(b\) is the area required by a plant to produce \(f\) seeds (Watkinson, 1980; González-Andújar and Fernández-Quintanilla, 1991). Total seed production \((T, \text{ seeds m}^{-2})\) is given by:

\[ T_t = F M_t \]  \[10\]

Seed rain losses

The seed rain produced can be lost in different ways (predators, harvest, etc.). The residual seed rain \((R, \text{ seeds m}^{-2})\) entering the soil seed bank is given by:

\[ R_t = T_t (1 - l) \]  \[11\]

where \(l\) represents the proportion of seeds lost by biotic and abiotic factors.

Seed bank

The seed bank \((B, \text{ seeds m}^{-2})\) is reduced through seed death and germination and is increased by the residual seed rain entering the seed bank. The size of the seed bank in any year is given by:

\[ B_{t+1} = B_t (1 - e) (1 - m) + R_t \]  \[12\]

where \(m\) is proportional mortality.

When farmers make weed management decisions to either spray a herbicide or cultivate, they are immediately faced with the question: At what level and time of weed emergence should control be implemented to simultaneously maximize crop yield and minimize weed density? To answer the question, farmers can consider two scenarios:

Scenario 1: Random decision

After sowing the crop (1 April in the simulations) the farmer chooses the most appropriate date to control weeds. All emerged weed seedlings on that date are assumed to be controlled, but seedlings that had not emerged would not be controlled.

The farmer’s decision was modelled as a stochastic process following a rectangular distribution. Its density function \(g(d)\) is:

\[ g(d) = \begin{cases} 
1 / (\beta - \alpha) & \text{when } \alpha < d < \beta \\
0 & \text{otherwise} \end{cases} \]  \[13\]

The guess values for \(\alpha\) and \(\beta\) that were used to generate a random value of \(d\) (decision day) were, respectively, \(\alpha = 13\) and \(\beta = 30\). In this way, time of control ranged randomly between 13 and 30 days after crop sowing.

Scenario 2: Time of emergence

Knowing the extent of seedling emergence provides some triggers for effective weed control decisions. Under this scenario farmers make decisions considering the time of emergence (trying to maximize the proportion of emerged weed seedlings destroyed by the control), using the emergence model developed. However, if farmers wait too long (until weed emergence reaches 100%), there will be some yield reduction expected either due weed competition from early germinated weeds and/or a shorter crop growth cycle. On the other hand, if farmers decide to control weeds very early during crop growth with a non-residual post-emergence herbicide, some weeds will escape control because they will emerge after the herbicide was applied. Therefore, we also simulated the consequences of initiating weed control at times other than 100% emergence. Thus, the effect of 100% control when 80, 90, 95 and 100% of wild oats were predicted to have emerged was also examined.

Initial conditions

The model was run over 30 years or until an equilibrium density was reached. For each run, results from 50 repetitions were recorded and the arithmetic mean calculated. The initial seed bank \((B_0)\) was set at 100 seeds m\(^{-2}\). Parameters to initiate the life cycle model were from Cousens \textit{et al.} (1986) (Table 1).
Three management scenarios (S1, S2, S3) were tested by the runs of the model. Scenarios S1 and S2 corresponded to farmer control decisions described above, i.e., (1) no consideration of the time of weed emergence and (2) a consideration of time of weed emergence. Scenario S3 represented «no control».

In the absence of control, the seed bank population growth followed a sigmoidal curve (Fig. 1). Population equilibrium was reached at a density of 16,435 seed m–2 in the soil seed bank. This can be considered as the carrying capacity of wild oats growing in association with wheat. These large populations can be expected to cause substantial crop yield losses and, therefore, should be controlled before reaching these high levels.

For S1, simulation gave an average population equilibrium of 13,338 seeds m –2 (4.12 in a logarithmic scale, Fig. 2). This equilibrium was only a 19% reduction in the carrying capacity of the system. This small population reduction, despite a high weed control level (100%), is a consequence of not considering weed emergence patterns. Control applied at random timing did not destroy a significant proportion of population. This simulation result agrees with the common observation that, although many grass herbicides are very effective in controlling populations of wild oat seedlings, the weed tends to persist year after year.

As expected, in S2 with 100% control of emerged wild oat seedlings there was a long-term reduction in the seed bank compared with the no control option (Figs. 1 and 2). Based on this scenario, the effect of the optimum time of wild oat seedling control can be estimated to give nearly a 100% reduction in the carrying capacity of the system after 6 years. Similar results were obtained in S2 with 95% of emerged seedlings being controlled, giving a 100% reduction of the seed bank population after 16 years. Simulations under S2 with 90% and 80% of emerged seedlings being controlled increased the wild oat population, with a population equilibrium at 775 and 11,690 seeds m–2, respectively (Fig. 2). These equilibrium densities represent seed bank reductions of 95.2% and 28.6%, respectively, of the carrying capacity of the system.

Scenario S2 with reduced uncertainty of farmer’s decisions, gave better control than the use of random treatment dates (S1). The reduction in carrying capacity of the system under $S_2$ with total control of 80% of emerged seedlings (28.6%), was better than that obtained under S1 (19%) with 100% control. Farmers’ decisions are improved under S2 because it reduces uncertainty associated with weed control decisions. The simulations indicate that integration of emergence with simple population dynamics models might substantially improve predictive capacity. Thus, farmers should be able to make better weed control decisions.

It is eighteen years since Mortimer et al. (1989) reviewed the use of simple models to describe weed population dynamics and the utility of such modelling in the design of weed control programs for annual crops. Their motivation was stated as: «A primary and strategic aim of weed ecology is to be able to explain and ultimately predict which weed species may become abundant and, moreover, the levels of abundance they

### Table 1. Parameter values for parameters for the life cycle model

| Parameter                          | Value |
|------------------------------------|-------|
| Emergence                          | 0.10  |
| Density-dependent seedling death   | 0.002 |
| Density-dependent seed production  | 0.0034|
| Fecundity (seed plant⁻¹)           | 75    |
| Seed losses                        | 0.10  |
| Seed-bank deaths                   | 0.55  |

Figure 2. Simulated average population trends. Scenario 1 (○) and scenario 2, 100% control of: 80% emerged seedlings (■), 90% emerged seedlings (●), 95% emerged seedlings (●) and 100% emerged seedlings (□).

Figure 1. Simulated wild oat population trend with no control.
may achieve under particular management practices». Despite the success of simple models in characterizing weed population dynamics of weed populations and interpreting the major processes involved in weed population change (Fernández-Quintanilla and González-Andújar, 2001), the utility of these models in predicting weed dynamics have been questioned (Cousens, 1995). Some authors advocate the development of mechanistic models (Kropff, 1988) that explicitly relate plant growth and competition to the environment. However, a problem of mechanistic models is their high complexity and the difficulties involved in gathering the data required to estimate the parameters. This paper suggests an intermediate way, integrating simple population models with emergence models that would help farmers in long-term decision making about weed management.

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