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The Population Ecology of *Datura ferox* in Soybean Crops. A Simulation Approach Incorporating Seed Dispersal

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ABSTRACT

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A numerical model for simulating the population dynamics of *Datura ferox* L. (chamico, chinese thornapple) has been built based on previously reported data. In the model, a soybean field is divided into 0.7×0.7-m conceptual modules. A seed production sub-model simulates the annual seed output of each module, and a seed dispersal sub-model simulates the distribution of these propagules within the field in accordance to a specified dispersal pattern. Different model scenarios were generated by varying the proportion of seeds lost from the soil bank, the annual recruitment, the seedling mortality and the proportion of seeds exported from the field during crop harvest. The results obtained by simulation suggest that (1) seed dispersal due to crop harvesting tends to produce an exponential growth of weed seed production, (2) limited or no success could be attained in the control of *D. ferox* using procedures that kill the seedlings efficiently if combine harvesters are not adjusted so as to maximize the proportion of weed seeds that are exported from the field and (3) if cleaning debris continues to be returned to the ground during crop harvesting, the improvement in the efficiency of the grain/weed separating mechanisms does not provide an effective long-term strategy to avoid grain contamination problems.

INTRODUCTION

The effectiveness of any weed control program depends to a large extent on the understanding of the life cycle of the weeds and their population dynamics (Mortimer et al., 1978). There is considerable information about factors and processes involved in the population dynamics of *Datura ferox* L. (chamico, chinese thornapple) which is an important weed, particularly in soybean crops. *Datura ferox* is a semelparous, and its seeds show germination blockage when the capsules are ripe (Soriano et al., 1964). In the field, germination takes

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place in spring or summer if, after a period of burial of some months, the seeds are carried back near the soil surface. Soriano et al. (1971), reported $<20\%$ in situ germination when seeds were returned to the surface during the first spring after being buried, but 40–50% for the second spring. In soybean-growing fields, the emergence of seedlings of *D. ferox* is concentrated generally within a few days after crop drilling, and virtually ceases by late December (Ballaré et al., 1987). Scopel (unpublished data, 1985) found that ca. 17% of seeds of the soil bank gave rise to seedlings in this time span. Seedling mortality of *D. ferox* is generally high (ca. 95%) in commercial soybean crops due to control procedures (Ballaré et al., 1987). However, since seed output is high (ca. 500–1500 seeds/plant) at low population densities (Ballaré et al., 1987), serious contamination of grain with its seeds is a common problem (Junta Nacional de Granos, 1982). Seed production per plant is negatively correlated with seedling density, even when control procedures effect major changes in the number of individuals early on in the growing season (Ballaré et al., 1987). Weed seeds are dispersed primarily by the combine harvesters, and mechanical harvesting is likely to increase the annual seed production of this weed because the individuals would be less affected by intraspecific density regulation (Ballaré et al., 1987).

The construction of weed population models is a technique that can be used to analyze the processes and rates of weed population growth in a given cropping environment, to design weed control strategies and to evaluate the economic implications of a given control program (Ghersa and Satorre, 1981; Mortimer, 1983; Doyle et al., 1984, 1986). This paper explores the population dynamics of *D. ferox* under the conditions imposed by a soybean crop system using a simulation model. The model was constructed to quantify the effects of various recruitment, mortality and dispersal schedules on the amount of seeds produced by a simulated population of the weed. The model provides an integral view of the demographic data, thus constituting a useful mean to determine which parts of the weed's life cycle could be manipulated in attempts to reduce the incidence of the weed.

THE MODEL

In the model, a soybean field is divided into m 0.7×0.7-m conceptual land units (modules). A seed production sub-model simulates the annual seed output of each module and a seed dispersal sub-model simulates the distribution of the propagules within the system following a specified dispersal pattern. A generalized schematic for the model is given in Fig. 1.

Seed production sub-model

Seedling emergence

Let W_j=size of seed bank in winter in the jth module (seeds/module), S_j=number of seedlings emerged in the jth module in late spring and early

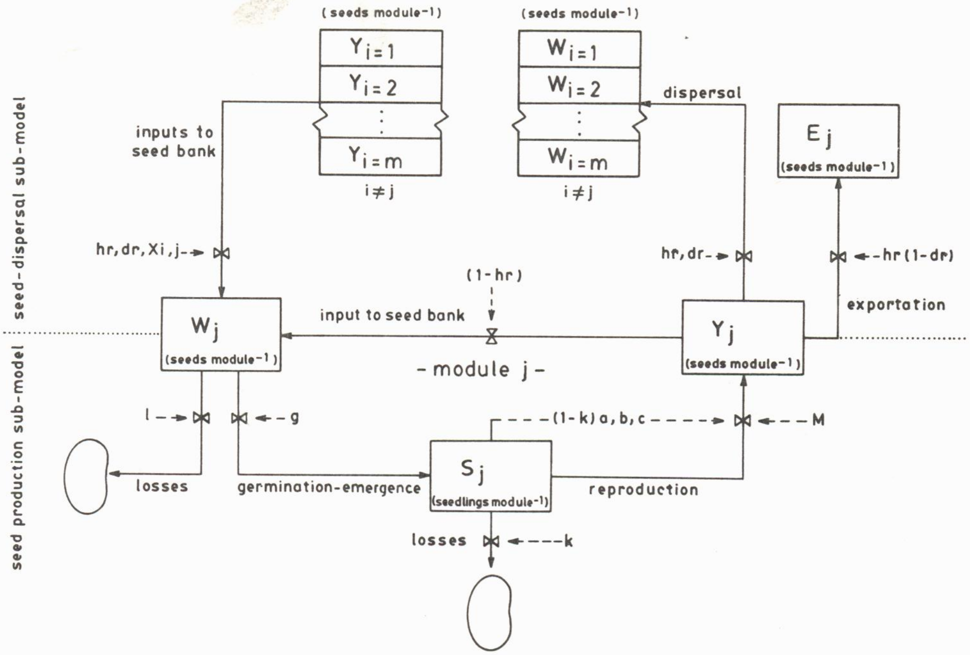

Fig. 1. A generalized schematic diagram for the model. W=bank of seeds in winter, S=seedling population in early summer, Y=newly formed seeds, E=seeds exported as grain contaminants. Other terms are explained in the text.

summer during the 3-week period following crop seeding date (seedlings/module), l=proportional loss of seeds from the seed bank during winter and early spring due to decay, death and untimely germination and g=proportion of seeds in the seed bank giving rise to seedlings in late spring and early summer (after crop drilling).

Then S_j in the yth year is calculated as follows:

$$S_{j,y} = W_{j,y}(1-l_y)g_y \tag{1}$$

In a trial in which seeds of *D. ferox* were buried 20 cm deep in winter and carried back to the surface soil at different times of the year, Soriano et al. (1971) reported seed losses during winter and spring of between 20–50%, depending upon the amount of in situ germination that occurred in early spring. Accordingly, two values for l, 0.2 and 0.5, have been chosen for simulations. On the other hand, g has been assumed to be 0.2 or 0.3, in agreement with available information (Soriano et al., 1971; Scopel, unpublished data, 1985).

Seedling establishment and reproduction

Let Y_j=total seed production in the jth module (seeds/module), k=proportion of seedlings which are killed during the growing season due to control procedures and M = maximum seed production per plant, representing the average yield of mature plants generated from seedlings grown in the absence of any density dependent regulation (seeds/plant).

Then, Y_j in a particular year is given by

$$Y_{j,y} = S_{j,y}(1-k_y)M_y(a+b\,S_{j,y})^c \tag{2}$$

where a, b and c are constants relating the production of seeds per plant to seedling density. The values used for simulation were: $a=0.9747$; $b=0.0253$; $c=-0.9537$ (Ballaré et al., 1987). The value of M has been estimated to equal 1050, which is consistent with our previous observations. Two levels of k have been used for simulations: 0.95 and 0.99. The first one is a frequent value in soybean crops whenever rigorous control practices are applied (Ballaré et al., 1987), while the second has been selected to explore the effects of more sophisticated control techniques on the population dynamics of *D. ferox.*

Seed dispersal sub-model

Once the seeds are produced in a given module they can be allocated to three different sinks, according to a distribution pattern which is largely dependent on the process of crop harvest: (1) seeds may be collected by combines and exported from the field as a grain contaminant; (2) seeds collected by the machines may be returned to the ground (i.e. primary dispersal), (3) some are not collected and remain in the capsules in the same module where they were produced (Ballaré et al., 1984, 1987).

Dispersal of seeds

Let R_i = the number of seeds dispersed from the ith module to other modules of the system (seeds/module), hr = proportion of seeds collected by the combine harvester and dr = proportion of the collected seeds which are delivered to other modules (dispersal rate).

Then

$$R_{i,y} = Y_{i,y}hr_y dr_y \tag{3}$$

Conversely, the number of seeds produced in i which are exported as grain contaminants is given by

$$E_{i,y} = Y_{i,y}hr_y(1-dr_y) \tag{4}$$

For convenience, hr has been set at 1, thus assuming that all seeds are collected during soybean harvest. For these simulations we did not consider the case in which the debris of grain cleaning (and the weed seeds in it) is exported from the field. These assumptions were made on the basis of results from field experiments with commercial farm combines (Ballaré et al., 1987). Since the proportion of the collected seeds that are returned to the ground during crop harvest is widely variable among combines (Ballaré et al., 1987), we included various levels of dr in the simulations.

Inputs to seed bank

The input of seeds to each seed bank is calculated as follows:

$$I_{j,y} = Y_{j,y}(1-hr_y) + \sum_{\substack{i=1 \\ i \neq j}}^{m} R_{i,y} X_{i,j,y} \tag{5}$$

where $I_{j,y}$ is the number of seeds entering in the jth module at the end of the yth growing season (seeds/module) and $X_{i,j,y}$ is the proportion of seeds dispersed from the ith module entering the jth land unit.

The value of $X_{i,j}$ is dependent upon the pattern of seed dispersal and the pair of modules considered (see Appendix 1). We used only one dispersal pattern for all the simulations which has been described in Ballaré et al. (1987). Additionally, we assumed that owing to soil disturbance 10% of the seeds present in a given module are moved each year to a contiguous one (i.e. secondary dispersal).

Calculation of the number of seeds in each seed bank

The output of the sub-model is the size of the seed bank in each module of the system at the beginning of the next winter (eqn. 6).

$$W_{j,y+1} = W_{j,y}(1-l_y)(1-g_y) + I_{j,y} \tag{6}$$

Contamination of the harvested grain

The contamination of the harvested grain is calculated based on the number of seeds exported as contaminants ($E_{i,y}$) and soybean yields (eqn. 7).

$$C_y = \sum_{i=1}^{m} E_{i,y}(S_y A)^{-1} \tag{7}$$

where C_y = contamination of the harvested soybean (seeds per 100 g grain), S_y = soybean yield in the yth year (t ha^{-1}) and A = area of the conceptual field: $0.49 \times m$ (m^2).

In all cases, the initial value of the seed bank used for simulation was 500 seeds. These seeds were assumed to be distributed into 10 modules belonging to a conceptual area of 24×160 land units (0.1882 ha). The soybean yield was fixed at 2 t ha^{-1} (Bolsa de Cereales de Buenos Aires, 1984).

Using the model, the whole seed production derived from the original 500 D.

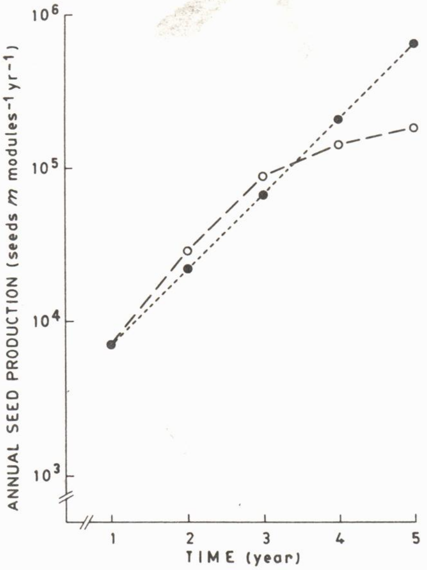

Fig. 2. Annual progress of seed production without primary dispersal (○ — — ○) and with primary dispersal caused by crop harvest (● — — ●). Other conditions are: dispersed fraction (dr) = 0.2; fractional loss of seeds from the soil bank (l) = 0.2; annual recruitment (g) = 0.3; seedling mortality (k) = 0.95.

ferox seeds was simulated through five growing seasons. This time span has been chosen since in northern Buenos Aires the same field is rarely planted with soybeans for more than 5–6 consecutive years. Additionally, grain contamination was calculated each year, and the resultant value compared against the maximum allowed for soybeans in commercial transactions (two *D. ferox* seeds per 100 g grain, Junta Nacional de Granos, 1982).

RESULTS AND DISCUSSION

The annual progress of seed production was simulated under various mortality, recruitment and dispersal schedules. The same distribution of seed-containing modules was used to start all the simulations, and the trajectories of the combine harvesters were chosen arbitrarily.

The model produced an exponential growth of seed production over 5 years when forced to mimic typical field conditions (Fig. 2). Conversely, when primary dispersal was not included in the simulations, seed production of the weed tended to stabilize after the 3rd year. The former result is explained by the continual redistribution of seeds to new land units by the process of combining, thus not allowing high densities to be reached in any module of the system (Fig. 3). All other things being equal, only if the proportion of seeds that return to the field during combining is high (i.e. $dr = 0.4$) does the growth

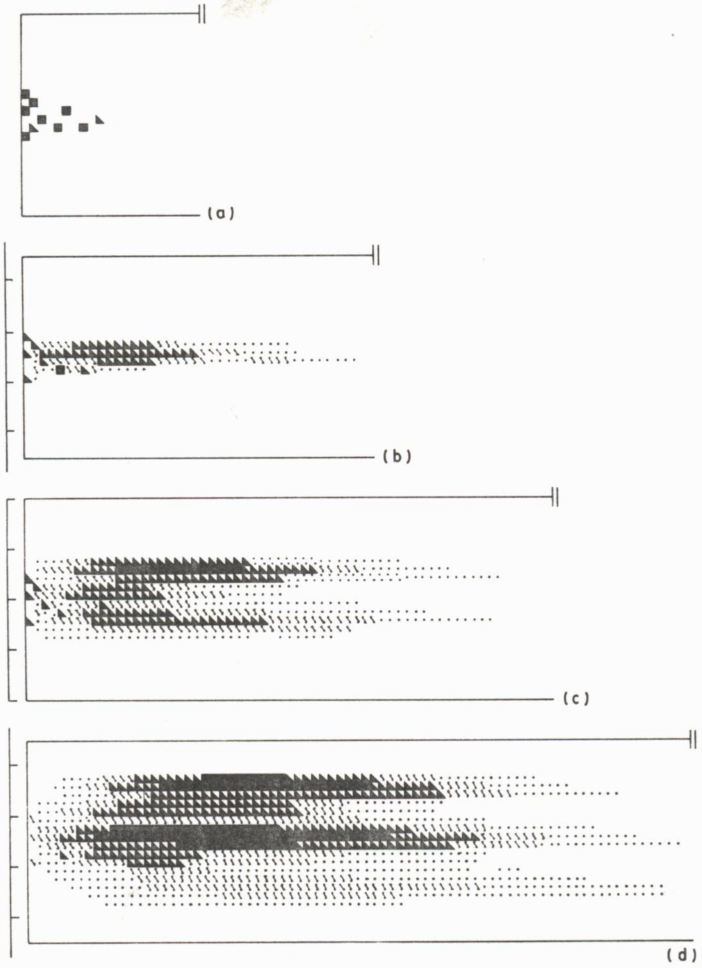

Fig. 3. The distribution of seeds among the modules of the field. (a) = initial seed bank, (b–d) = the seed bank at the end of the 1st, 2nd and 3rd growing seasons, respectively. The beginning of the imaginary runs of the combine harvesters are indicated by braces. □ = 0, ⊡ = 1–5, ⧅ = 6–15, ◣ = 16–45 and ■ = 46–130 seeds/module.

of seed production depart from the exponential model (not shown). Therefore, it may be postulated that the spatial scattering of the propagules that occurs during crop harvest, plus the exportation of some seed, is generally sufficient to avoid a strong density-dependent control of seed output. In commercial farms, the spatial distribution of seeds is likely to be even more random than in the base case modelled because different combines are frequently used to harvest the same field. Clearly, the main difference between this and other models of weed population dynamics (e.g. Mortimer et al., 1978; Mortimer, 1983) arises at this point. In earlier models the spatial dynamics of the weeds was not considered and, therefore, after a few growing seasons, the size of the simulated populations become stable as a result of intraspecific density regulation. Conversely, the results of our model of *D. ferox* suggest that the importance of density-dependent regulation is confined to the cases in which the annual input of seeds is very high and/or in highly infested fields.

The effect of varying the dispersal rate

Since we assumed that $hr=1$ (i.e. all weed seeds are collected during crop harvest), the annual input of seeds to the field is, for a given seed production, solely dependent on the dispersal rate (dr) chosen (eqns. 3 and 5). We investigated the effect of varying the dispersal rate on seed production growth. Simulations were carried out under different levels of the coefficient l (fractional loss from the seed bank) and g (proportion of seeds that produce seedlings). The output variable was the relative growth rate of seed production (R). Since the seed production growth is exponential, R may be calculated from any pair of consecutive years as follows:

$$R=(YF_{y+1}-YF_{y})\,YF_{y}^{-1} \tag{8}$$

where YF is the total seed production of the field in a particular year (seeds/year).

The results show that if only 1% of the seeds produced are returned to the field each year ($dr=0.01$) the weed seed production diminishes over time (i.e. R is negative) (Fig. 4). The relative annual reduction of YF is strongly dependent on the fractional loss of seed from the soil bank (in the interval $l=0.2$–0.5), but almost insensitive to variations in the germination rate between $g=0.2$–0.3. A remarkable point is that the critical values of the dispersal rate (those which determine the seed production growth rate to be zero) are very low (ca. $\leqslant 10\%$), and generally smaller than those estimated from field experiments with commercial farm combines (Ballaré et al., 1984, 1987).

The effect of increasing the efficiency of weed control

An increase in the efficiency of weed control (k) from 0.95 to 0.99 results in a general reduction in the seed production growth rate (R) (Fig. 5). As in the cases presented above, if only 1% of the seeds are returned to the field during crop harvest ($dr=0.01$), R is always negative. Moreover, at this low value of dr, there is only little response in the growth rate of seed production to the increase in control efficiency from 0.95 to 0.99 (see Figs. 4 and 5). If the loss of seeds from the soil bank is important ($l=0.5$) the projected growth rate of seed production is zero or negative for the values of the dispersal rate examined. Otherwise, the simulated value of R becomes positive whenever relatively low levels of dr are exceeded. For instance, if 99% of the seedlings are killed

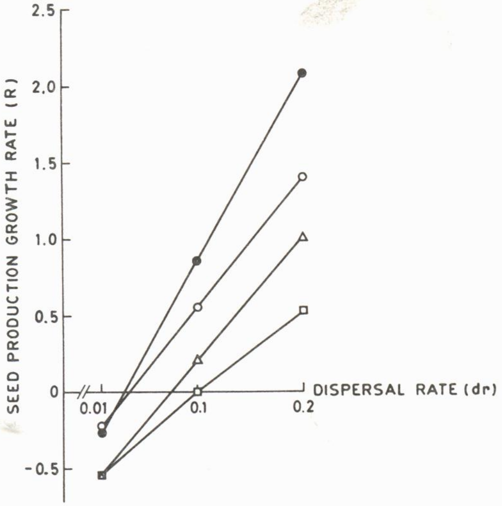

Fig. 4. Relative growth rate of seed production over a 5-year period in relation to *dr*. The efficiency of weed control procedures (k) = 0.95. (●), fractional loss of seeds from the soil bank (l) = 0.2, annual recruitment (g) = 0.3; (○), $l=0.2$, $g=0.2$; (△), $l=0.5$, $g=0.3$; (□), $l=0.5$, $g=0.2$

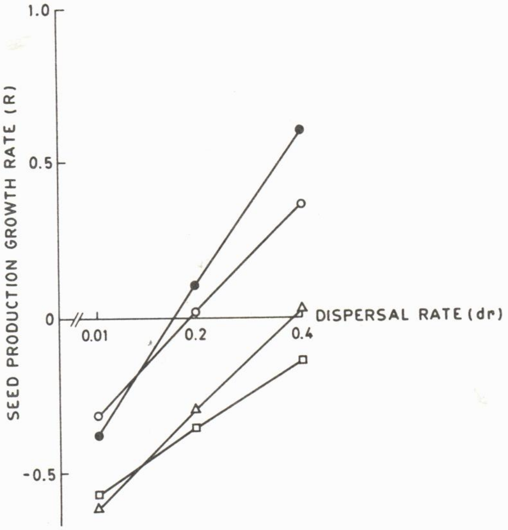

Fig. 5. Relative growth rate of seed production over a 5-year period in relation to *dr*. The efficiency of weed control procedures (k) = 0.99. Symbols as for Fig. 4.

during the growing season but the combine harvester returns to the ground > 20% of the weed seeds produced, the model predicts no effect of the control technique in reducing future seed production (Fig. 5). Consequently, the success of a new control strategy will be strongly dependent on the fate of seeds during crop harvest. It is important to note that the actual values of l could

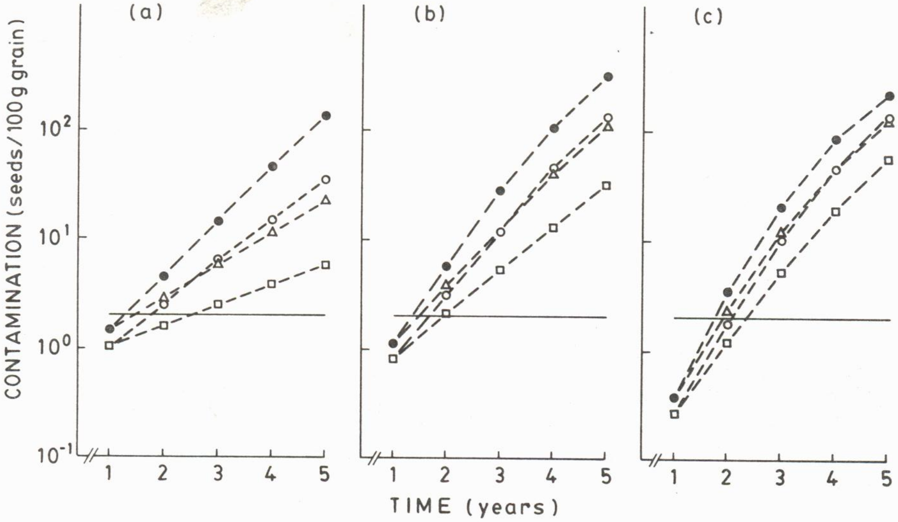

Fig. 6. Projected annual progress of grain contamination with seeds of *D. ferox* (broken line). The solid line indicates the commercial allowance. (a), $dr=0.2$; (b), $dr=0.4$; (c), $dr=0.8$. (●), $l=0.2$, $g=0.3$; (○), $l=0.2$, $g=0.2$; (△), $l=0.5$, $g=0.3$; (□), $l=0.5$, $g=0.2$. In all cases the weed control efficiency $(k)=0.95$.

vary with the tillage regime performed (Soriano et al., 1971) and the degree of maturity attained by the seeds of *D. ferox* when they are dispersed to the ground. Data not presented in this paper suggest that the degree of seed ripeness depends on the timing of the soybean harvest and that most of the immature seeds are lost from the soil bank within a few months by germination and death.

Contamination of grain lots

It was assumed in the simulations that those seeds that are collected by the combine harvesters and not exported from the field as grain contaminants are returned to the ground (eqns. 3 and 4). The results presented above indicate that, with typical control efficiencies, the seed production of *D. ferox* is very likely to increase in soybean fields if the dispersal rate is not drastically reduced. Using the model, an investigation of the effects of various grain cleaning strategies on the contamination of the harvested soybean was attempted. Figure 6 (a–c) shows the simulation results of soybean contamination over time under medium or high levels of the dispersal rate ($dr \geqslant 0.2$), and under different assumptions about the dynamics of the seed population in the soil. From these simulations, the contamination of soybean grain may be expected to exceed the commercial allowance after a few years, even if the initial size of the seed bank is as small as that used here. For the cases modelled, the worst harvesting strategy is that in which about half of the collected seeds are returned to the ground ($dr=0.4$). In such a case, no matter what the assumptions about g and l, the tolerance is exceeded after 2 years (Fig. 6b). On the other hand, the use of a combine harvester with an efficient weed/grain separating mechanism merely delays, in some of the cases considered ($g=0.2$), the moment when grain contamination becomes greater than the tolerated value (Fig. 6c). In other words, if the combines efficiently separate the weed seeds from the grain but return them to the ground, the concomitant increase in future weed seed production will rapidly exceed the capacity of the cleaning unit.

CONCLUSIONS

The model was constructed with the aim of investigating the population dynamics of *D. ferox* under various combinations of the variables that, a priori, were considered to be most relevant. The simultaneous consideration of these variables suggests the following:

(1) The spatial dispersal of the propagules that occurs during crop harvest tends to produce an exponential growth of seed production. The seed production growth rate is strongly conditioned by density-independent variables.

(2) If the combine harvesters are not adjusted so as to reduce the dispersed fraction of newly formed seeds, a procedure that kills the seedlings efficiently (ca. control=95–99%) may be worthless if the objective pursued is to reduce the annual production of weed seeds. A greater impact on weed population could be obtained by combining seedling control with exportation of a large proportion of the produced seeds (ca. 80–90%) during crop harvest.

(3) Continued soybean cropping without grain contamination problems may not be achieved merely by increasing the efficiency of the cleaning mechanisms of the combine harvesters if the cleaning debris is returned to the field. Rather, a dramatic rise in weed seed production should be expected.

These results may provide a useful framework for planning control strategies.

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APPENDIX

Whenever a harvesting episode is simulated, the conceptual field is divided into a certain number of $c \times r$ matrices of 0.7×0.7-m modules. For the simulations reported here, the number of columns (c) of each matrix has been taken to be 6, as defined by the number of modules that an imaginary combine with a cutter-bar of 4.2 m would meet in a single run, and the number of rows

(r) has been taken to be 160, according to the length of the simulated field. For two modules, j and i, belonging to the same matrix, the probability that a seed dispersed from i lands in j is given in Table AI.

TABLE AI

Values of $X_{i,j}$ used in the simulations. Assuming that i is any module of the row r, the values are defined with reference j

Row	Column					
	1	2	3	4	5	6
$r+1$-$r+5$	0	6.3×10^{-3}	8.8×10^{-3}	2.4×10^{-2}	1.1×10^{-2}	0
$r+6$-$r+10$	0	1.1×10^{-3}	1.3×10^{-2}	4.2×10^{-2}	3.2×10^{-2}	0
$r+11$-$r+15$	0	0	1.1×10^{-2}	1.6×10^{-2}	3.1×10^{-3}	0
$r+16$-$r+20$	0	0	5.0×10^{-3}	1.2×10^{-2}	0	0
$r+21$-$r+25$	0	0	0	2.5×10^{-3}	1.8×10^{-3}	0
$r+26$-$r+30$	0	0	9.1×10^{-3}	0	0	0
$r+\geqslant 31$	0	0	0	0	0	0

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