

WEED POPULATIONS AND CROP ROTATIONS: EXPLORING DYNAMICS OF A STRUCTURED PERIODIC SYSTEM

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Abstract. The periodic growing of a certain set of crops in a prescribed order, called a crop rotation, is considered to be an important tool for managing weed populations. Nevertheless, the effects of crop rotations on weed population dynamics are not well understood. Explanations for rotation effects on weed populations usually invoke the diversity of environments caused by different crops that a weed population encounters. Using a periodic matrix model, we show that the number of different crops is not the sole factor, and that the sequence of a given set of crops can play an important role. In the model the weed population is structured by seed depth in the soil, and plowing moves seeds between layers. For illustration of concepts, we use parameter values thought to be characteristic for *Polygonum persicaria* growing in carrots (crop A) and spring wheat (crop B) in the Netherlands. We systematically examine the population growth rates for *P. persicaria* and their sensitivity to changes for all rotations of 2–6 years based on crops A and B. We include eight scenarios that differ in the effects of plowing and seed survival over winter. Differences between rotations can be striking. For example the weed population growth rate in the baseline rotation AABB (assuming 100% winter survival) is nearly 25% lower than in rotation ABAB. The elasticity (a measure to quantify the effect of proportional changes in model parameters on population growth) to seedling survival is nearly 75% higher in the B years of rotation ABAB than in the B years of rotation AABB. Changing parameter values changes the relation between population dynamics and rotation organization, but not the conclusion that there are consequences for population dynamics and management due to choice of a rotation. While our example is an agronomic one, the question “Does sequence matter?” and the methods applied should be of interest to researchers and managers concerned with the periodic management of other ecosystems.

Key words: crop rotation; elasticity analysis; periodic matrix model; plant population management; *Polygonum persicaria*; population dynamics, weeds; rotational crops and weed abundance; weed population management.

INTRODUCTION

Crop rotation—the growing of different crops in recurring succession on the same land—has long been advocated as a method to increase crop yields and reduce inputs (Leighty 1938, Robinson 1949). Explanations for increased yields of crops grown in a rotation system rather than as a continuous monoculture crop include the periodic changes in the environment that prevent particular pests, diseases, and weeds from dominating, and the decreased stress on the soils by including crops that require less cultivation or that increase nutrient and organic-matter inputs (Crookston 1984, Crookston et al. 1991). The development of problematic weed populations is thought to be prevented by the diverse environments that weed populations encounter over the course of a crop rotation cycle (Liebman and Dyck 1993, Liebman and Gallandt 1997). For

example, sowing dates, weed-control methods, and competition from the crop will differ from season to season as the crop species change.

Each of the diverse environments is characteristic of a given crop. A crop rotation, by definition, extends over several cropping seasons. A rotation's organization includes the crop species, their proportion and order, and the length of the rotation (number of cropping periods). A natural question is whether the organization of a crop rotation, given a set of crops, will affect weed population growth rates. For example, would a rotation of alternating carrot and wheat crops result in a different weed population growth rate than a rotation consisting of two consecutive years of carrots followed by two consecutive years of wheat?

Up to now there have been few experimental or theoretical studies that directly and systematically address the effect of crop sequence on weed-population growth rates. Most studies have concentrated on comparing a continuous monoculture crop with one or more different rotations, usually in combination with different till-

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age or weed-control treatments (Martin and McMillan 1984, Schweizer et al. 1988, Blackshaw et al. 1994, Doucet et al. 1999, Kegode et al. 1999). Some modeling studies of weed population dynamics have included crop rotations, but did not systematically examine the effect of different crop rotations based on their set of crops (Gonzalez-Andujar and Fernandez-Quintanilla 1991, Jordan et al. 1995, Lindquist et al. 1995, Squire et al. 1997).

In a more general ecological setting, the realization of the importance of the timing of events in a periodic system is not new; Darwin and Williams (1964) found that the season of hunting affected the population growth rate of an age-structured population of rabbits. More recent studies have concentrated on the frequency of nominally periodic events, such as fire and drought (Gotelli 1991, Gross et al. 1998, Hoffman 1999), but have not examined the effect of systematically different orders of events on growth rates or on possibilities for management. Golubov et al. (1999) in their study of *Prosopis glandulosa* (honey mesquite) calculated the periodic growth rates for all combinations of their four, yearly transition matrices. However their aim was to obtain a confidence interval for the periodic growth rate. The population dynamics of annual weeds in a crop rotation represent a very simple periodic system, but one allowing multiple avenues for intervention, for example through changing the rotation itself or through changing the weed population's vital rates, through management, in a particular crop. A better understanding of weed population dynamics in crop rotations may contribute insights applicable to the understanding and management of species in other ecosystems.

Our purpose is the systematic examination of the effects of different crop rotations on weed population dynamics and on possibilities for management. Our questions pertain to how the proportion of crops, their order, and number affect the population growth rate of a depth-structured seed bank and the growth rate's sensitivity to changes in life-cycle processes. Answering these questions with field experiments, because of their long-term nature, is practically difficult. We therefore find answers through use of a mathematical model that captures essential features of our system but that is simple enough to allow in-depth investigation of the processes affecting weed population dynamics in crop rotations. Our investigation is restricted to a weed with a semelparous life history, growing in two crops, where its seed bank is structured by depth and seeds can be moved vertically in the soil by plowing. A particularly suitable description is a periodic matrix model. This choice also allows application of a considerable body of theory (de Kroon et al. 1986, Caswell 1989, Caswell and Trevisan 1994, Benton and Grant 1999, de Kroon et al. 2000). We illustrate concepts with parameter values characteristic for *Polygonum persicaria* L. (red-shank) growing in a variety of rotations, composed of carrots and spring wheat in the Netherlands.

METHODS

Model construction

The transition matrices.—As the ability of a seed to germinate and emerge varies with depth (Vleeshouwers 1997a), and as tillage operations redistribute seeds in the soil (Cousens and Moss 1990), a weed seed population can be considered as being structured by the depth at which seeds are located. We distinguish two soil layers, where the top layer is indexed 1 and the bottom layer indexed 2. The number of seeds in soil layers 1 and 2 at time t can be represented as a vector, $\mathbf{n}(t)$:

$$\mathbf{n}(t) = \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix}. \quad (1)$$

We regard time in discrete steps of 1 yr, where one crop is grown per year. Each time step the weed seed population in each soil layer can be calculated by applying a matrix of transition rules to the population vector resulting from the previous time step. The transition rules, also called "transitions," describe seed survival, reproduction, and movement between soil layers. These rules, and therefore the matrices, will be different depending on the particular crop grown each year. We consider two crops only, A and B, and assume that the transition rules only depend on the crop in question and not the crop that was grown, say, in the previous year. For a two-year rotation of crops A and B, the seeds will follow the transitions given in Fig. 1. These yearly transitions yield matrices \mathbf{A} and \mathbf{B} , for the respective crops, e.g., for crop A,

$$\mathbf{A} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \quad (2)$$

where the element a_{ij} of matrix \mathbf{A} is the contribution of one seed in layer j , at time t , to the population of seeds in layer i , at time $t + 1$. The population over a complete cycle of the rotation AB, is given as

$$\mathbf{n}(t + 2) = \mathbf{BAn}(t) \quad (3)$$

i.e., first apply the transition matrix \mathbf{A} and then the matrix \mathbf{B} (since crop A is grown first, followed by crop B).

In order to distinguish different years within a rotation cycle and in keeping with the terminology of Caswell and Trevisan (1994), we call each year of a rotation a "phase" and number the phases with respect to some "reference rotation." Defining rotation AB as the reference rotation, then crop A occurs in phase 1, denoted $A^{(1)}$, and crop B occurs in phase 2, denoted $B^{(2)}$. The rotation $B^{(2)}A^{(1)}$ is the cyclic permutation of AB, and starts with phase 2 of the reference rotation AB. Different cyclic permutations of some reference rotation will have the same population growth rate, but other properties, such as the distribution of seeds over soil layers at the end of the rotation, will differ for each

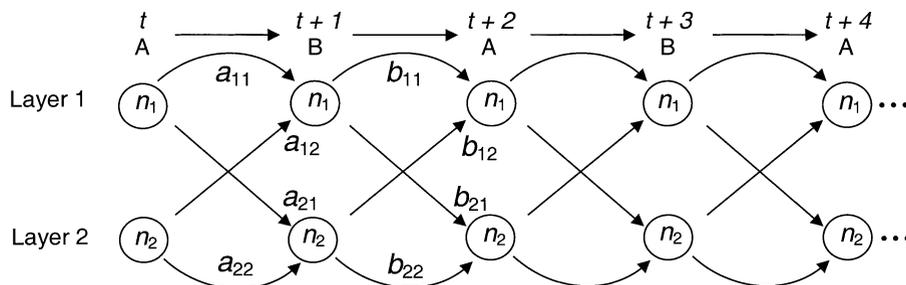


FIG. 1. Transitions in a two-year rotation of crops A and B. Weed seeds in soil are in either layer 1 or 2, and n = the number of weed seeds in layer 1 or 2 at time t ; a_{ij} = the contribution of one seed in layer j at time t to the population of seeds in layer i at time $t + 1$.

cyclic permutation of the reference rotation. Cyclic permutations of a given rotation will have identical population growth rates because in the long term the rotations are identical. Properties such as the depth distribution of seeds are expected to change because processes occurring during the previous crop act on the depth distribution present at the start of that crop. More details on these effects are given in following sections.

We also wish to distinguish rotations that cannot be cyclically permuted to give identical rotations. Rotations ABAB and AABB are such rotations, and we call them “essentially different.” Essentially different rotations are expected to produce different population growth rates.

In general, for some given rotation, the dynamics are:

$$\mathbf{n}(t + p) = \mathbf{M}^{(h)}\mathbf{n}(t) \tag{4}$$

where \mathbf{M} is the matrix product of the yearly transitions, starting in phase h , where h will be in $\{1, 2, 3, \dots, p\}$, and p is the length (period) of the rotation. We define reference rotations lexicographically, so that the largest block of consecutive A crops in the rotation occurs first. Thus, for example, rotations consisting of consecutive blocks of two A crops and two B crops will have the reference rotation AABB, whose matrix product is $\mathbf{M}^{(1)} = \mathbf{B}^{(4)}\mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}$. If the rotation starts with the last B crop, giving rotation BAAB, the matrix product is $\mathbf{M}^{(4)} = \mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}\mathbf{B}^{(4)}$.

For our example crops, A and B, we systematically examine all essentially different cropping sequences of two to six years, as well as monocultures of both crops. In practice crop rotations do not usually exceed six years. For each rotation length, all possible ratios of the two crops and all essentially different orders are investigated. We also examine the effect of increasing rotation length while keeping the proportion of each crop the same for the series AB, AABB, AAABBB, and so on.

Life history underlying the transitions.—As it is difficult to directly measure the transitions a_{ij} and b_{ij} , and as it is not possible to directly manipulate them because they are composed of a variety of biological and management processes, we must consider a weed’s life cycle and the parameters that underlie transitions from one stage to the next. Fig. 2 illustrates the life cycle for a summer annual weed growing in a crop, where tillage occurs in the fall. By following the paths seeds take over their life, one arrives at the transition values. For example, the contribution of this year’s seeds in layer 1 to next year’s population in layer 1, i.e., a_{11} or b_{11} , can be broken down as follows: at time t a certain fraction α_1 emerge from the top layer, of which a fraction v plants survive, with each surviving plant producing γ seeds. The newly produced seeds are added to the fraction of seeds that did not emerge and that survived, $(1 - \mu_1)(1 - \alpha_1)$, where μ_1 is the fraction of seeds in the top layer that died or were lost. The seeds

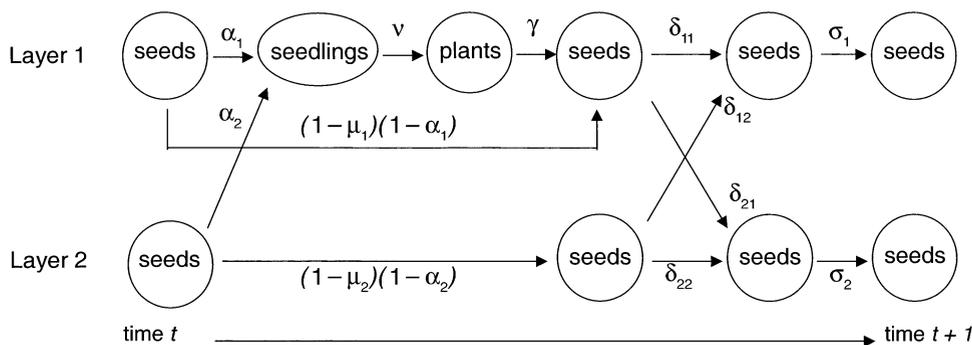


FIG. 2. Weed life history used in defining the transition rules. See *Methods: Life history underlying transitions* and Table 1 for explanation of symbols. The life cycle begins in the spring of one year and ends in the spring of the following year.

TABLE 1. Baseline ($\sigma_1 = 1$) parameter values based on *Polygonum persicaria* growing in carrots and spring wheat under non-herbicide weed-management regimes in the Netherlands.

Parameter	Description	Crop A	Crop B
α_1	seedling emergence from layer 1	0.45	0.15
α_2	seedling emergence from layer 2	0.00	0.00
μ_1	seed mortality layer 1	1.00	0.30
μ_2	seed mortality layer 2	0.20	0.20
ν	fraction of seedlings surviving weed control	0.001	0.60
γ	seed production per surviving plant	400.00	90.00
σ_i	survival over winter	1.00	1.00
δ_{11}	fraction of seeds remaining in layer 1	0.02	0.02
δ_{12}	fraction of seeds moving from layer 2 to layer 1	0.29	0.29
δ_{21}	fraction of seeds moving from layer 1 to layer 2	0.98	0.98
δ_{22}	fraction of seeds remaining in layer 2	0.71	0.71

are then moved between layers by plowing in the fall, with a fraction δ_{11} remaining in layer 1, i.e., moving from layer 1 back to layer 1, and then a fraction σ_1 survive over the winter to time $t + 1$. In short, the transition rule for remaining in layer 1 of crop A is $a_{11} = \alpha_1 \nu \gamma \delta_{11} \sigma_1 + (1 - \mu_1)(1 - \alpha_1) \delta_{11} \sigma_1$. The other transitions can be calculated in a similar fashion, giving for crop A:

$$\begin{aligned} a_{12} &= \alpha_2 \nu \gamma \delta_{11} \sigma_1 + (1 - \mu_2)(1 - \alpha_2) \delta_{12} \sigma_1 \\ a_{21} &= \alpha_1 \nu \gamma \delta_{21} \sigma_2 + (1 - \mu_1)(1 - \alpha_1) \delta_{21} \sigma_2 \\ a_{22} &= \alpha_2 \nu \gamma \delta_{21} \sigma_2 + (1 - \mu_2)(1 - \alpha_2) \delta_{22} \sigma_2. \end{aligned} \quad (5)$$

Each transition consists of two terms, the first one representing reproduction, and the second representing survival. The subscripts on the parameters for seed movement (δ_{ij}) indicate transfer of seeds from layer j to layer i . All parameter values can depend on the crop and can therefore be different for crops A and B.

Parameter values used.—For the purposes of illustration we have used parameter values that resemble those for *Polygonum persicaria*, growing in crops similar to carrots (crop A) and spring wheat (crop B), under non-herbicide weed-management regimes in the Netherlands (Table 1). The life cycle begins 1 April and continues until 31 March the following year. The depths of the soil layers are 0–5 cm for layer 1 and 5–20 cm for layer 2. Vleeshouwers (1997a) has shown that *P. persicaria* does not usually emerge from depths >5 cm. The parameters for seed movement are based on a plowing matrix experimentally measured by Cousens and Moss (1990).

The values of the parameters for emergence and mortality are derived from experiments by Vleeshouwers (1997b) on the emergence and fate of *P. persicaria* seeds in relation to the timing of disturbance (e.g., seedbed preparation, shallow cultivation). The timings of disturbances used by Vleeshouwers (1997b) are similar to those that would occur for seedbed preparation of carrots (crop A) and spring wheat (crop B). Experiments by Roberts and Neilson (1980) indicate that seed age does not have an important effect on the probability of emergence of *P. persicaria* seedlings. Under a non-

herbicide weed-management regime, the fraction of seedlings surviving control (ν) is much lower for carrots than for spring wheat, because of the increased efficacy of mechanical and hand control in carrot crops. The number of seeds produced per surviving weed (γ) is much higher in carrots than in wheat because a carrot crop is less competitive than a wheat crop. As there is no information concerning winter survival of *P. persicaria* seeds these parameters (σ_i) have been set to 1.

Using the parameter values for crops A and B in the above setting (the “baseline ($\sigma_1 = 1$)” parameter set) and the equations for the transition elements (Eqs. 5), we obtain the following matrices:

$$\begin{aligned} \mathbf{A} &= \begin{pmatrix} 0.0036 & 0.2320 \\ 0.1764 & 0.5680 \end{pmatrix} \\ \mathbf{B} &= \begin{pmatrix} 0.1739 & 0.2320 \\ 8.5211 & 0.5680 \end{pmatrix}. \end{aligned} \quad (6)$$

In the analysis of different rotations it is useful to appreciate that in the top layer of crop A, before plowing, about 0.2 seeds are produced per seed ($a_{11} + a_{21}$), while in the top layer of crop B, also before plowing, about 9 seeds are produced per seed ($b_{11} + b_{21}$). In the bottom layer of both crops, 0.8 seeds per seed are produced before plowing ($a_{12} + a_{22}$, $b_{12} + b_{22}$).

We also investigated the effect of changing the values for winter survival in the top layer (σ_1) and for seed movement (δ_{ij}). These two parameters were chosen because there is great uncertainty in the values for survival over winter, and because in many agricultural regions minimum-tillage cropping systems are used. In such systems plowing is carried out less frequently or plow types are used that do not invert the soil. Not plowing is expected to decrease seed survival over winter because crop residues left on the soil surface may, for example, increase microbial activity or populations of seed predators. The values for these seven additional scenarios are given in Table 2. Throughout this paper we use the terms “plowing” and “tillage” interchangeably. We label the scenarios, for example, as no-till A ($\sigma_1 = 0.5$), to indicate the scenario where plowing is not carried out at the end of the A phases so that most

TABLE 2. Parameter values used for each crop in each scenario.

Parameter	Scenario															
	Baseline				No-till A				No-till B				No-till A and B			
	$\sigma_1 = 1$		$\sigma_1 = 0.8$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$	
	A	B	A	B	A	B	A	B	A	B	A	B	A	B	A	B
δ_{11}	0.02	0.02	0.98	...	0.98	0.98	...	0.98	0.98	0.98	0.98	0.98
δ_{21}	0.98	0.98	0.02	...	0.02	0.02	...	0.02	0.02	0.02	0.02	0.02
δ_{12}	0.29	0.29	0.02	...	0.02	0.02	...	0.02	0.02	0.02	0.02	0.02
δ_{22}	0.71	0.71	0.98	...	0.98	0.98	...	0.98	0.98	0.98	0.98	0.98
σ_1	1.00	1.00	0.80	0.80	0.50	0.50	0.50	0.50

Notes: For convenience we repeat the relevant baseline ($\sigma_1 = 1$) parameter values, and for the other scenarios we show only differences with respect to the baseline ($\sigma_1 = 1$) scenario. The name of each scenario indicates in which crop tillage (plowing) is not carried out and the level of winter survival in the top soil layer. See Table 1 for description of parameters.

seeds remain in each layer, and where only half of the seeds in the top layer of the A phases survive over the winter. We examine the population growth rates and elasticities for all essentially different rotations up to six years long.

Model analysis

Growth rate.—When examining different crop rotations, a question of primary importance is how fast a weed population grows in each crop rotation. The growth rate over a complete rotation cycle is given by the dominant eigenvalue (λ) of the matrix product $\mathbf{M}^{(h)}$ (Luenberger 1979, Caswell 1989, Caswell and Trevisan 1994). For $\lambda > 1$ the population will eventually increase geometrically, for $\lambda < 1$ the population will eventually decrease geometrically. In order to compare rotations of different lengths, we need a mean growth rate per year. This is given by the geometric mean of the cycle growth rate,

$$\hat{\lambda} = \lambda^{(1/p)} \tag{7}$$

where p is again the length of the rotation cycle.

Stable depth distribution and reproductive value.—Insight into differences in the growth rates and their sensitivities to changes is gained through examining the stable depth distribution and reproductive value. The stable depth distribution is the distribution of seeds over the various soil layers, approached over the long term. The reproductive value is a measure of the contribution of seeds in a given layer to future population growth, and is also approached over the long term. For an annual weed, when emergence and reproduction does not depend on seed age, the reproductive value will depend on a seed’s probability of surviving until able to reproduce, and the amount of future reproduction (cf. Caswell 1989). In a periodic system the stable depth distribution and reproductive values are cyclically stable. When examined from one projection period to the next these quantities do not change. They will, however, differ from one phase to the next.

Mathematically, the stable depth distribution and reproductive value correspond, respectively, to the right ($\mathbf{w}^{(h)}$) and left ($\mathbf{v}^{(h)}$) eigenvectors associated with the

dominant eigenvalue (λ) of $\mathbf{M}^{(h)}$. Usually the right eigenvector is normalized so that the elements sum to 1, while elements in the left eigenvector are divided by the value of the first element so that the reproductive values of lower layers are relative to that in the top layer. The eigenvectors are defined as

$$\mathbf{M}^{(h)}\mathbf{w}^{(h)} = \lambda\mathbf{w}^{(h)} \quad \mathbf{v}^{(h)\top}\mathbf{M}^{(h)} = \lambda\mathbf{v}^{(h)} \tag{8}$$

where \mathbf{T} indicates the transpose and h indicates a phase in the rotation and is in $\{1, 2, \dots, p\}$ and p is the length of the rotation. The phase index on the eigenvectors indicates the rotation matrix with which they are associated. The eigenvectors, though, are achieved at the end of a rotation starting with phase h . We therefore display the eigenvectors with the final phase with which they were achieved rather than with the starting phase of the rotation from which they were calculated. Thus in rotation AABB, the stable depth distribution after phase $\mathbf{B}^{(3)}$ is the right eigenvector $\mathbf{w}^{(4)}$, associated with the matrix $\mathbf{M}^{(4)} = \mathbf{B}^{(3)}\mathbf{A}^{(2)}\mathbf{A}^{(1)}\mathbf{B}^{(4)}$. The left eigenvector $\mathbf{v}^{(4)}$ indicates the reproductive value of seeds in each layer at the end $\mathbf{B}^{(3)}$ and gives the contribution of seeds to future generations starting with phase $\mathbf{B}^{(4)}$.

Elasticity analysis.—The response of λ to perturbations in the transition elements and the underlying parameters is likely to depend on the composition of the crop rotation. These responses are usually represented as either sensitivities or elasticities. Sensitivities give the absolute change in λ in response to an absolute change in a transition element or underlying parameter. Elasticities give the proportional change in λ in response to a proportional change in a transition elements or underlying parameter (de Kroon et al. 1986). We focus on elasticities, as in a weed-management context it is more typical to consider proportional rather than absolute changes in parameters. See Caswell (2001) for further discussion of differences between sensitivities and elasticities.

The calculation of elasticities is based on that for sensitivities. An elasticity is the product of the ratio of a transition element or parameter to the growth rate and of its sensitivity. Caswell and Trevisan (1994) pro-

vide an equation for calculating the sensitivity matrices for the phases in a periodic matrix model:

$$\mathbf{S}_C^{(h)} = [\mathbf{C}^{(h-1)}\mathbf{C}^{(h-2)} \dots \mathbf{C}^{(1)}\mathbf{C}^{(p)}\mathbf{C}^{(p-1)} \dots \mathbf{C}^{(h+1)}]^T \mathbf{S}_M^{(h)}. \tag{9}$$

$\mathbf{S}_C^{(h)}$ is the matrix of sensitivities, with elements $\partial\lambda/\partial c_{ij}^{(h)}$, of either crop A or B in phase h . $\mathbf{C}^{(h)}$ is either matrix $\mathbf{A}^{(h)}$ or $\mathbf{B}^{(h)}$, and $c_{ij}^{(h)}$ is an element corresponding to one of these two matrices in phase h . The first term on the right-hand side is obtained as follows: cyclically permute the crop matrices of the rotation so that the h th crop matrix ($\mathbf{C}^{(h)}$) occurs first, then exclude this matrix, and transpose the resulting product. The second term, $\mathbf{S}_M^{(h)}$, is the sensitivity matrix of the product matrix \mathbf{M} , rotated to phase h . The elements, $\partial\lambda/\partial m_{ij}^{(h)}$, of $\mathbf{S}_M^{(h)}$ are calculated using the right ($\mathbf{w}^{(h)}$) and left ($\mathbf{v}^{(h)}$) eigenvectors:

$$\frac{\partial\lambda}{\partial m_{ij}^{(h)}} = \frac{v_i^{(h)}w_j^{(h)}}{\mathbf{w}^{(h)} \cdot \mathbf{v}^{(h)}} \tag{10}$$

where $m_{ij}^{(h)}$ are the elements of $\mathbf{M}^{(h)}$, and $\mathbf{w}^{(h)}, \mathbf{v}^{(h)}$ is the inner product of the right and left eigenvectors of $\mathbf{M}^{(h)}$ (Caswell 1989). The elasticities associated with the transitions in each phase of a crop rotation can then be calculated as

$$e_{ij}^{(h)} = \frac{c_{ij}^{(h)}}{\lambda} \frac{\partial\lambda}{\partial c_{ij}^{(h)}} \tag{11}$$

where $\partial\lambda/\partial c_{ij}^{(h)}$ are the elements of $\mathbf{S}_C^{(h)}$, given in Eq. 9. The elasticities in each phase sum to 1, thus the element containing the largest elasticity must always have an elasticity >0.25 .

The elasticities to the transition elements are a useful guide in pointing out, in a general way, how the growth rate will respond to changes. However, changes in the transition elements can only be made by adjusting the parameter values. Therefore it is of practical interest to examine the elasticities to the parameters, for each phase of the rotation. The general expression for calculating the elasticity to the underlying parameters is obtained by applying the chain rule for differentiation, giving

$$\frac{x}{\lambda} \frac{\partial\lambda}{\partial x} = \frac{x}{\lambda} \sum_{ij} \frac{\partial\lambda}{\partial g_{ij}} \frac{\partial g_{ij}}{\partial x} \tag{12}$$

for some parameter x in a matrix \mathbf{G} with elements g_{ij} (Caswell 1989). In a periodic system, as with the transition elements, one must consider the phase in which the parameters occur, so that the elasticity to a parameter in the h th phase is

$$\frac{x^{(h)}}{\lambda} \frac{\partial\lambda}{\partial x^{(h)}} = \frac{x^{(h)}}{\lambda} \sum_{ij} \frac{\partial\lambda}{\partial c_{ij}^{(h)}} \frac{\partial c_{ij}^{(h)}}{\partial x^{(h)}}. \tag{13}$$

Again, $\partial\lambda/\partial c_{ij}^{(h)}$ are given by elements of $\mathbf{S}_C^{(h)}$ (Eq. 9).

Simulation and yearly growth rates.—With the models considered here, most of the characteristics of a

weed’s population dynamics can be obtained through direct analysis of the matrices. The iterated solution to the model, however, aids understanding through the possibilities of graphical representation and calculation of yearly growth rates given an initial population. Each simulation started with 10 seeds per layer. The yearly growth rates were calculated by dividing the population size at time $t + 1$ by the population size at time t , once the rotation growth rate and stable depth distribution were 99.99% of the analytically calculated quantities.

RESULTS

Having the basic crop matrices and a means of analyzing periodic matrix models, we can now systematically examine a variety of crop rotations. First we present results of the effects of different crop rotations on mean weed population growth rates per year ($\hat{\lambda}$) and of effects on the elasticity of the growth rate to transition elements and parameters. Then, using the stable depth distributions and reproductive values, we give a biological explanation for the differences in growth rates and elasticities, between rotations and between the scenarios indicated in Table 2.

Effects of crop rotation on growth rate

We first examine, for all scenarios, general patterns in the relationship between $\hat{\lambda}$ and the proportion of each crop. Subsequently we consider the effect of crop order and increasing rotation length.

General patterns in $\hat{\lambda}$.—For each scenario, $\hat{\lambda}$ decreases as the fraction of crop A increases (Fig. 3a–d). The mean annual population growth rate of the baseline ($\sigma_1 = 1$) monoculture B is about 1.79 and that of the baseline A monoculture is about 0.63. The form of the decrease varies between scenarios. For example, scenarios that do not include plowing at the end of the B years result in a more concave pattern in the relationship between $\hat{\lambda}$ and the fraction of crop A compared to the baseline and no-till A scenarios. In the no-till A ($\sigma_1 = 0.5$) scenario, rotations with a low fraction of B have a $\hat{\lambda}$ lower than that of a monoculture of A (Fig. 3b). In the scenarios where plowing is not carried out in the B years, the $\hat{\lambda}$ of the monoculture B is much higher than the baseline situation. Adding a low proportion of crop A, though, causes a large decrease in $\hat{\lambda}$ (Fig. 3c–d). Decreasing survival over winter in the top layer tends to decrease $\hat{\lambda}$, but the effect is less in rotations with a high proportion of crop A.

Effects of crop order.—For all scenarios except where plowing is not carried out in both crops, the $\hat{\lambda}$ for a given fraction of crop A can differ substantially depending on crop order (Table 3). For example, in the baseline ($\sigma_1 = 1$) scenario, rotation ABAB has a $\hat{\lambda}$ of 1.52, while rotation AABB has a $\hat{\lambda}$ of 1.15. For certain scenarios and fractions of crop A, crop order can mean the difference between an increasing or a decreasing population. For example in the no-till B ($\sigma_1 = 0.5$) scenario, rotation ABABB has a $\hat{\lambda}$ of 0.98 while ro-

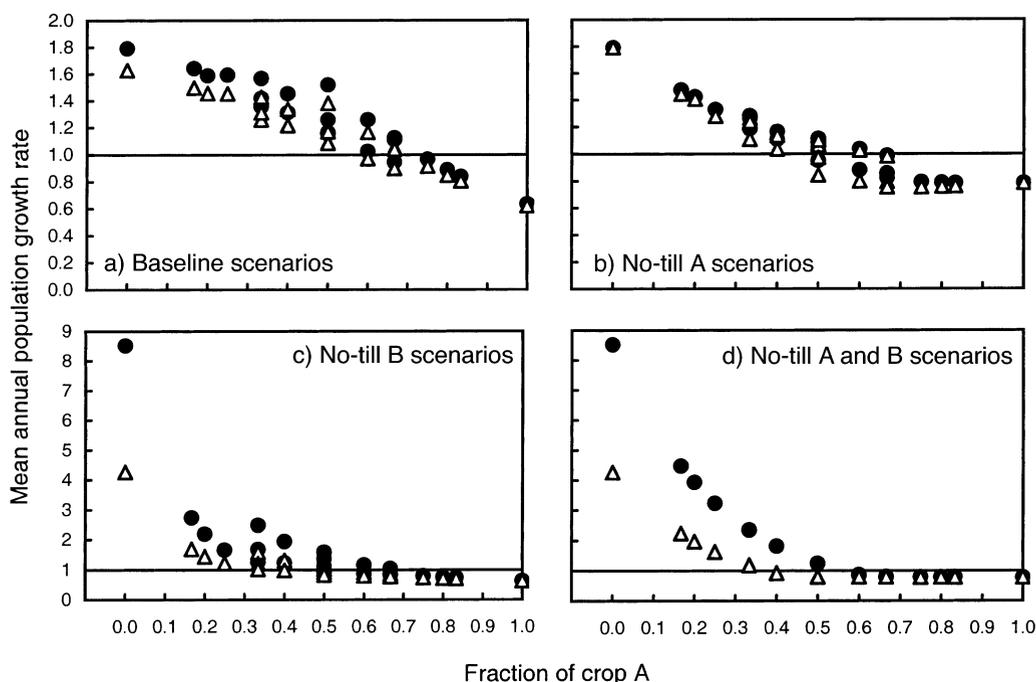


FIG. 3. Mean annual population growth rates ($\hat{\lambda}$) for all four scenarios and all essentially different rotations of up to six years of crops A and B. Solid circles indicate scenarios with seed survival over winter $\sigma_1 = 1$; open triangles indicate scenarios with (a) $\sigma_1 = 0.8$, and (b)–(d) $\sigma_1 = 0.5$. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and *Methods: Model construction: Parameter values used* for a complete explanation of the parameter values used in the scenarios.

tation AABBB has a $\hat{\lambda}$ of 1.31. In the baseline scenarios, patterns in which each crop is in a consecutive block have a lower $\hat{\lambda}$ than patterns that have alternating years of crops A and B. In the other scenarios, patterns with each crop in a consecutive block have the highest growth rate for a given rotation length and fraction of each crop.

Effects of rotation length.—When rotations increase in length following the pattern AB, AABB, AAABBB, and so on, the trend in $\hat{\lambda}$ tends to decrease in the baseline scenarios (Fig. 4a). In the no-till A scenarios, the $\hat{\lambda}$ appears to level off at 1.82, which is close to the $\hat{\lambda}$ for a monoculture of B in the baseline scenario (Fig.

4b). In scenarios where tillage does not occur in the B years, the $\hat{\lambda}$ increases and there is a large effect of decreased survival over winter (Fig. 4c–d).

Effects of crop rotation on elasticity of growth rate

We first examine elasticities of $\hat{\lambda}$ to transitions and underlying parameters for the baseline ($\sigma_1 = 1$) monocultures and rotations ABAB and AABB. We then examine patterns in the highest elasticities found for each rotation of all eight scenarios.

Elasticities to baseline transitions per phase.—In the A monoculture, the highest elasticity value is to transition a_{22} , which is the transition related to remaining

TABLE 3. Effect of the order of crops (A and B) on $\hat{\lambda}$, the mean weed population growth rate per year.

Rotation	Fraction crop A	Baseline		No-till A		No-till B		No-till A and B	
		$\sigma_1 = 1$	$\sigma_1 = 0.8$	$\sigma_1 = 1$	$\sigma_1 = 0.5$	$\sigma_1 = 1$	$\sigma_1 = 0.5$	$\sigma_1 = 1$	$\sigma_1 = 0.5$
B	0.00	1.791	1.629	1.791	1.791	8.521	4.261	8.521	4.2610
ABABBB	0.33	1.568	1.429	1.185	1.108	1.674	1.209	2.345	1.1820
ABBABB	0.33	1.419	1.312	1.263	1.239	1.242	1.014	2.342	1.1730
AABBBB	0.33	1.356	1.258	1.282	1.267	2.480	1.586	2.342	1.1821
AABBB	0.40	1.312	1.217	1.164	1.135	1.940	1.310	1.812	0.9217
ABABB	0.40	1.455	1.338	1.106	1.037	1.227	0.981	1.809	0.9106
ABAB	0.50	1.520	1.383	0.949	0.844	0.912	0.831	1.228	0.7868
AABB	0.50	1.154	1.084	1.112	1.100	1.358	1.017	1.231	0.7903
AABAAB	0.67	1.110	1.041	0.820	0.756	0.863	0.779	0.788	0.7848
AAABAB	0.67	1.124	1.051	0.858	0.794	0.823	0.765	0.790	0.7850
AAAABB	0.67	0.945	0.900	0.988	0.982	1.041	0.862	0.799	0.7867
A	1.00	0.633	0.621	0.784	0.784	0.633	0.633	0.784	0.7840

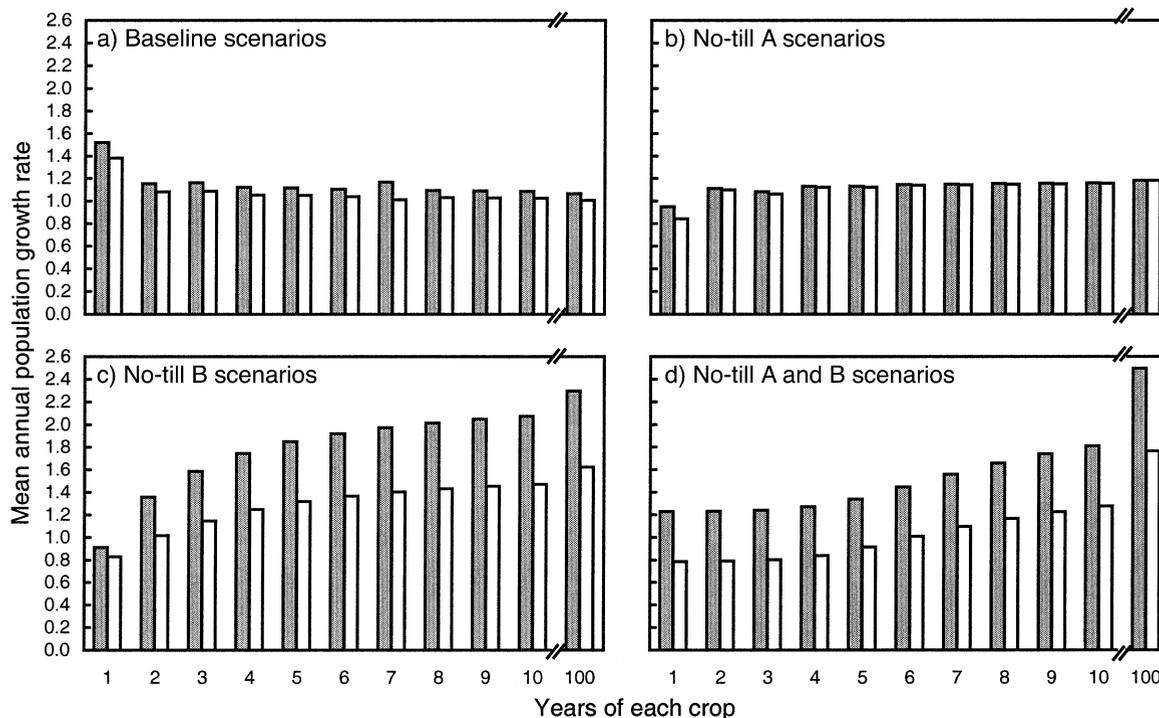


FIG. 4. Effect of increasing crop rotation length on mean annual population growth rate, $\hat{\lambda}$, where equal amounts of each crop are used and the rotations use the simplest pattern, giving the sequence AB (one year of each crop), AABB (two years of each crop), AAABBB, and so on. Dark gray bars indicate scenarios with $\sigma_1 = 1$; open bars indicate scenarios with (a) $\sigma_1 = 0.8$, and (b)–(d) $\sigma_1 = 0.5$. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and *Methods: Model construction: Parameter values used for a complete explanation of the scenarios*.

in the bottom layer (Fig. 5a). With a value of ~ 0.8 , it is much higher than the elasticities to the other transitions. The elasticity values found for the B monoculture (Fig. 5b) are more evenly spread, with transitions b_{12} and b_{21} having the highest value. Rotation ABAB (Fig. 5c) has a regular pattern of elasticities, with the highest elasticity alternating between the transitions $a_{12}^{(1,3)}$ and $b_{21}^{(2,4)}$, governing movement between layers. (see *Methods: Model construction: Elasticity analysis* for explanation of symbols.) The pattern of elasticities for rotation AABB is more complicated (Fig. 5d). Overall the highest elasticity is for transition $a_{22}^{(1)}$, that of remaining in the bottom layer during the first A crop. In the other phases, the transitions governing movement of seeds between layers and of remaining in the bottom layer tend to have the highest elasticity values.

Elasticities of underlying parameters.—As with the elasticities for the transitions, the crop rotation influences the impact of changes in a particular parameter on the growth rate (Table 4). We again focus on the baseline ($\sigma_1 = 1$) rotations ABAB and AABB, and also compare them with the monocultures of A and B. In the next section we will investigate the reasons for differences in elasticities.

The highest elasticity values tend to be to the pa-

rameters for survival over winter (σ_i), in either or both of the soil layers. In monocultures of A and B, winter survival in the bottom layer is most important, but in crop A it has a much larger elasticity than in crop B. In phase A of rotation ABAB, survival over winter in the top layer is most important, while in phase B winter survival in the bottom layer is most important, and has a much larger elasticity than a B monoculture. For rotation AABB, winter survival in the bottom layer has a higher elasticity in the first and the last phases than in the middle two phases.

The value of the parameter for seedling survival (ν) is likely to depend heavily on weed-control methods and is therefore the process over which a farmer usually has the most influence. It also has the same elasticity as the parameter for seed production (γ) because in this model γ is density independent and multiplication with ν yields a single parameter—seeds produced per emerged seedling. The elasticity of ν differs between rotations and between phases in a rotation. In a monoculture of A the elasticity of ν is low compared to the elasticities of the other parameters, while in a monoculture of B, ν has an elasticity similar to many of the other parameters. In rotation ABAB the elasticity of ν is lower in the A phases compared to an A monoculture. In the B phases the elasticity of ν is larger relative to

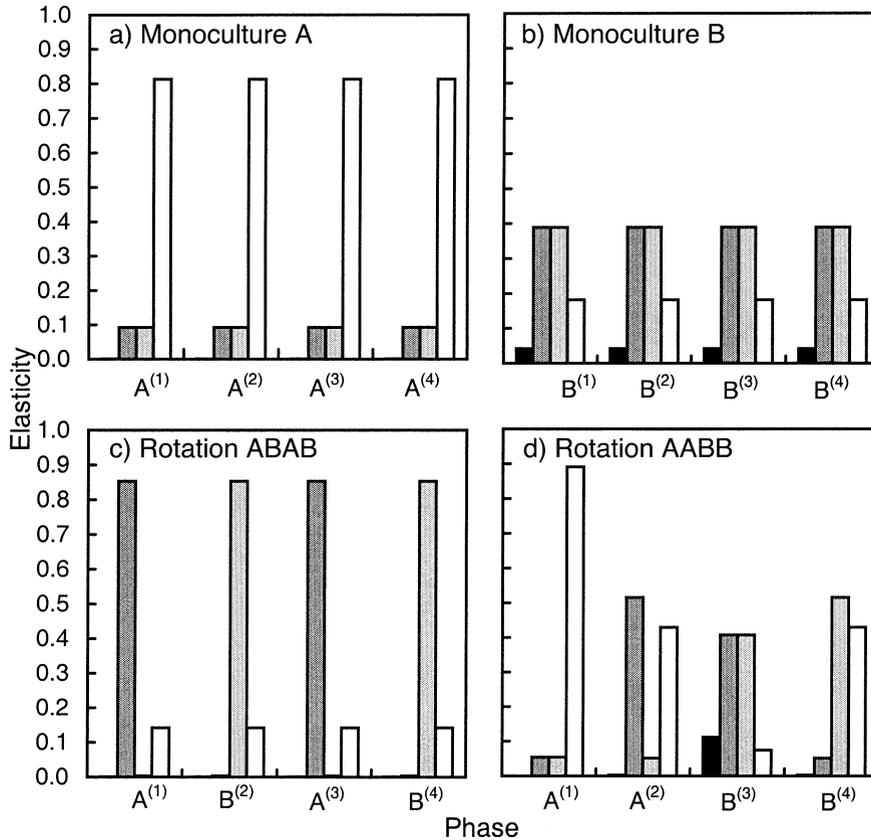


FIG. 5. Elasticities of transition elements in the baseline ($\sigma_1 = 1$) scenario. The transitions $c_{ij}^{(h)}$ for crop A or B of phase h are indicated as follows: $c_{11}^{(h)}$, black; $c_{12}^{(h)}$, dark gray; $c_{21}^{(h)}$, light gray; $c_{22}^{(h)}$, open bars.

a B monoculture. In rotation AABBB the elasticities of ν during the A phases are also very low, while during the B phase they are somewhat larger than in a B monoculture but not nearly as large as during the B phase of rotation ABAB. The elasticities for ν do not necessarily remain the same for the same crop in different phases within a rotation. For example in the baseline ($\sigma_1 = 1$) rotation AABABB, the elasticity of ν is much

greater during phase B⁽³⁾ than during any other phase (Fig. 6).

Elasticity patterns in all scenarios.—An overview of the effect of changing parameter values can be seen in graphs of the highest elasticity to a transition per rotation against the fraction of crop A (Fig. 7a–d). As it is not possible to include the rotation or phase in the graphs, we give these results in the Appendix. In the

TABLE 4. Elasticity of weed growth rate to baseline ($\sigma_1 = 1$) parameter values.

Parameter	Monoculture		ABAB		AABB			
	A	B	A ⁽¹⁾ , A ⁽³⁾	B ⁽²⁾ , B ⁽⁴⁾	A ⁽¹⁾	A ⁽²⁾	B ⁽³⁾	B ⁽⁴⁾
α_1	0.0936	0.3959	0.0044	0.7855	0.0546	0.0546	0.4772	0.4772
α_2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
μ_1	-0.2861	-0.0126	-0.0133	-0.0251	-0.1668	-0.1668	-0.0152	-0.0152
μ_2	-0.2266	-0.1423	-0.2489	-0.0364	-0.2364	-0.2364	-0.1203	-0.1203
ν	0.0936	0.4011	0.0044	0.7958	0.0546	0.0546	0.4835	0.4835
γ	0.0936	0.4011	0.0044	0.7958	0.0546	0.0546	0.4835	0.4835
δ_{11}	0.0005	0.0418	0.0010	0.0010	0.0002	0.0031	0.1119	0.0031
δ_{12}	0.0931	0.3888	0.8533	0.0034	0.0544	0.5159	0.4071	0.0515
δ_{21}	0.0931	0.3888	0.0034	0.8533	0.0544	0.0515	0.4071	0.5159
δ_{22}	0.8133	0.1806	0.1424	0.1424	0.8910	0.4295	0.0740	0.4295
σ_1	0.0936	0.4306	0.8543	0.0044	0.0546	0.5190	0.5190	0.0546
σ_2	0.9064	0.5694	0.1457	0.9956	0.9454	0.4810	0.4810	0.9454

Notes: For rotation ABAB, only values for years 1 and 2 are given, as years 3 and 4 are the same as years 1 and 2, respectively. See Table 1 for explanation of parameters.

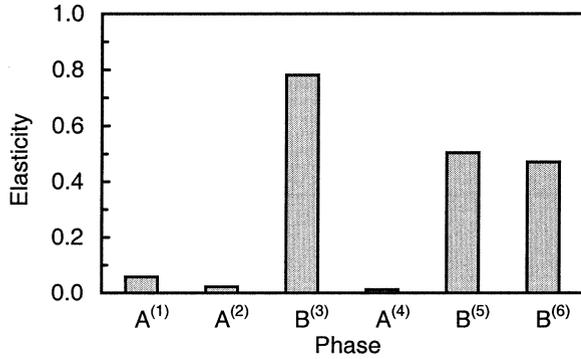


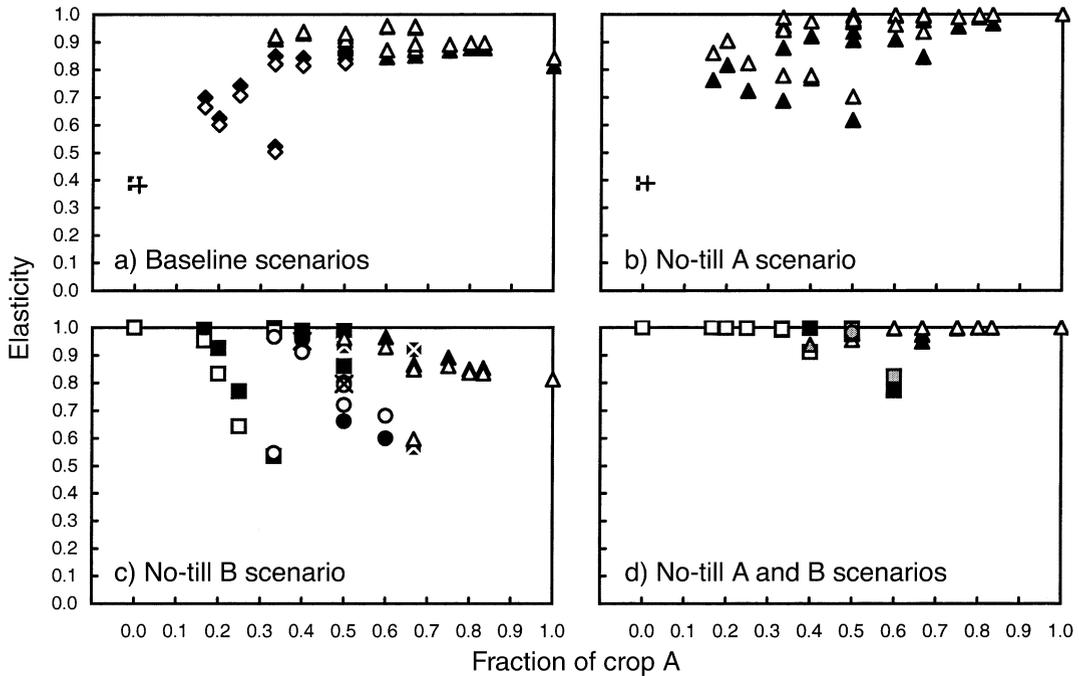
FIG. 6. Elasticities of the parameter for seedling survival (ν) in rotation AABABB (baseline [$\sigma_1 = 1$] scenario).

baseline scenarios the values of the highest elasticities appear to increase with the fraction of crop A (Fig. 7a). Crop order, however, can cause differences in the values as well as the transition and phase in which they occur. For the baseline rotations where consecutive A crops occur, then the highest elasticities are to a_{22} . When A and B crops alternate, then the highest elas-

ticities are to transitions a_{12} and b_{21} . In the no-till A scenarios, the highest elasticity values are to transition a_{22} for all rotations (Fig. 7b). As the fraction of crop A increases, then the elasticity values approach 1. In the no-till B scenarios the relation is more complicated (Fig. 7c). There is some pattern: Rotations with a majority of crop B tend to have the highest elasticity to transition b_{11} , while those with a majority of crop A have the highest elasticity to transition a_{22} . In between, the dominant elasticity is to transition b_{22} , but other transitions may also carry the highest elasticity. In the no-till in both the A and B scenarios, the pattern of transitions carrying the highest elasticity is similar to that for the no-till B scenarios but the values tend to be close to 1 (Fig. 7d).

Causes of differences in growth rates and elasticities

Using the baseline ($\sigma_1 = 1$) monocultures and rotations ABAB and AABB, we elucidate the causes of some of the differences described in the preceding subsections. Because we have examined a small set of the infinite number of theoretically possible rotations, some points may appear as outliers in the figures of



Winter survival	Transition							
	a_{12}	a_{22}	b_{11}	b_{22}	$a_{12}-b_{21}$	$b_{12}-b_{21}$	$a_{11}-b_{11}$	$a_{22}-b_{22}$
$\sigma_1 = 1.0$	⊗	▲	■	●	◆	⊞	◻	
$\sigma_1 < 1.0$	×	△	□	○	◇	+	▲	●

FIG. 7. Highest values of elasticities to transition elements for all scenarios and all essentially different rotations up to six years long. For panel (a) the weed seed survival over winter $\sigma_1 = 0.8$, and for (b)–(d) $\sigma_1 = 0.5$. In the no-till scenarios for a particular crop, the values for the parameters governing seed movement are such that very little movement of seeds between layers occurs. See Tables 1 and 2, and *Methods: Model construction: Parameter values used* for a complete explanation of the scenarios. This figure is based on the data in the Appendix.

TABLE 5. Baseline ($\sigma_1 = 1$) depth distribution of weed seeds (fraction in each layer), seed reproductive values (relative to value in layer 1) at the end of the indicated phase, and growth rates per phase in both layers and for the total population.

Crop rotation	Phase	Seed depth distribution		Reproductive value, layer 2	Annual population growth rate		
		Layer 1	Layer 2		Layer 1	Layer 2	Total
Monoculture	A	0.269	0.731	3.568	0.633	0.633	0.633
	B	0.125	0.875	0.190	1.791	1.791	1.791
ABAB	A ⁽¹⁾ , A ⁽³⁾	0.285	0.715	0.068	3.060	0.581	0.756
	B ⁽²⁾ , B ⁽⁴⁾	0.071	0.929	17.33	0.755	3.972	3.054
AABB	A ⁽¹⁾	0.279	0.721	6.686	1.183	0.603	0.698
	A ⁽²⁾	0.268	0.732	0.340	0.604	0.636	0.627
	B ⁽³⁾	0.074	0.926	0.074	0.806	3.694	2.919
	B ⁽⁴⁾	0.164	0.836	3.406	3.071	1.250	1.385

the population growth rates and elasticities (Figs. 3 and 7). Such points are not outliers in a statistical sense because values are due to the same deterministic processes at work for any other point. Therefore the reasoning applied below to differences between rotations ABAB and AABB can be used to explain differences between other rotations, as well as to differences between scenarios.

Depth distributions and baseline ($\sigma_1 = 1$) growth rates.—In both monocultures, the bottom layer has a higher proportion of seeds than the top layer (Table 5), reflecting how plowing moves almost all seeds from the top layer to the bottom layer and moves only about a third of the seeds in the bottom layer to the top layer. The fraction of seeds in the top layer of A is, however, about twice that found in the top layer of crop B. In crop B, due to high seedling survival and reproduction by seeds in the top layer, a greater proportion of the total population ends up in the bottom layer compared to crop A.

In the modeled crop rotations, the depth distribution of seeds achieved after each phase only approaches that of the corresponding monoculture crop. This occurs because the distribution resulting after each phase depends on the preceding distribution as well as on the transition values of the current phase (Table 5).

For example, when a baseline A crop precedes a baseline B crop, there will be a greater proportion of seeds in the top layer before the B phase compared to a B monoculture (Table 5). Therefore more seeds will be produced during the B phase compared with a B monoculture and they will be on the top layer before plowing. After plowing the proportion of seeds on the bottom layer is greater than in a B monoculture. This is because before plowing there was a greater proportion and number of seeds in the top layer than in a B monoculture. Plowing moved more seeds to the bottom layer and fewer seeds to the top layer, leading to a decline in the number of seeds in the top layer and a very large increase in the bottom layer. The overall growth rate for a B phase following an A phase is thus larger than the yearly growth rate in a B monoculture (Table 5). Similar reasoning can be used to show that,

after an A phase, if the initial distribution of seeds is higher in the bottom layer compared with an A monoculture, then the proportion and absolute number of seeds in the top layer will increase, as will the total number of seeds over both layers. Such a situation occurs when the preceding phase is crop B. The stable depth distribution for a given phase in a rotation can be thought of as a transient distribution when compared to a monoculture situation.

For the baseline rotations ABAB and AABB, the different values of $\hat{\lambda}$ can be explained as follows. Compared with the A phases of rotation AABB, the A phases of ABAB result in a higher proportion of seeds in the top layer and thus also a greater population in the top layer (Table 5). These seeds can then produce many more seeds during the following B phase. Similarly, the B phases of ABAB result in a higher proportion and number of seeds in the bottom layer than the B phases of AABB. Therefore, before plowing in the following A year, fewer seeds are lost from the bottom layer than from the top layer. Consequently during each phase of ABAB, the population will grow faster than in the same crop in rotation AABB, leading to a higher growth rate over the entire rotation cycle. The alternating pattern of crops thus increases the population of the top layer by the end of an A year, and sets the population up for another round of high reproduction in the next B year (Fig. 8a). In contrast, at the end of phase A⁽¹⁾ in rotation AABB, while the proportion of seeds in the top layer is similar to that of the A phases of ABAB, during the second phase very few seeds will be produced because it is an A phase. In fact, the population declines more than in an A monoculture (Table 5). Phase A⁽²⁾ acts as a brake, slowing the yearly growth rate in each of the following phases compared to the corresponding crop growth rates in rotation ABAB (Fig. 8b).

Reproductive values, depth distributions, and baseline elasticities.—Unlike the growth rates, the elasticity of the growth rate to changes in transitions depends on what will happen to a seed in the future as well as the probability of which layer it will end up in at the end of the previous crop. Elasticity values therefore depend

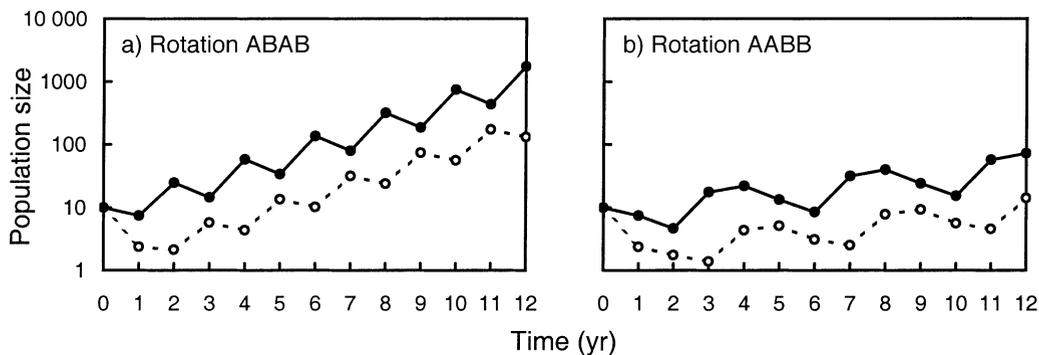


FIG. 8. Simulated population dynamics of baseline ($\sigma_1 = 1$) scenario. Broken lines and open circles indicate the population in the top layer, and thick lines and solid circles indicate the population in the bottom layer.

both on the reproductive value and the depth distribution of seeds. While reasons for differences in the stable depth distributions depend on previous distributions and transitions, differences in the reproductive values are due to differences in future environments.

In an A monoculture the reproductive value of the lower layer is more than 3.5 times that of an individual in the top layer, i.e., most contributions to future generations come from seeds in the bottom layer (Table 5). This is because prior to plowing in crop A, the seed population decreases less in the bottom layer. On the other hand, in a B monoculture, because of high seed survival and reproduction in the top layer before plowing, the reproductive value of a seed in the top layer is ~ 5 times that of seed in the bottom layer. In a rotation, the different sequences of following crops will alter the reproductive values of each phase.

For example, after phase A of rotation ABAB, the reproductive value of the top layer is almost 15 times that of the bottom layer, which contrasts sharply with that found in a monoculture of A (Table 5). In the ABAB rotation, the seeds in the top layer at the end of an A phase can produce many new offspring during the following B year. Furthermore the newly produced seeds will be moved to the bottom layer prior to the next A phase where their chances of survival are higher than in the top layer. Such reasoning can be used to explain the different reproductive values in the B phase and in other rotations.

Understanding the causes of differences in reproductive values, we can now explain the differences in the elasticities. The high elasticity found in transition a_{12} of rotation ABAB, for example, can be accounted for by the high reproductive value of seeds in the top layer and because most of the seeds that are in the top layer came from the bottom layer. Likewise, the transition b_{21} has a high elasticity because most of the seeds in the bottom layer were in the top layer before plowing, and once in the bottom layer they have a high reproductive value. Therefore management practices that decrease the proportion of seeds in the top layer at the end of an A phase or the amount of reproduction

during the B phase are likely to have the largest impact on the growth rate. This result concurs with that of the elasticities of the parameters, where, for example, winter survival in the top layer of A and in the bottom layer of B both have high elasticities. Through considering the stable depth distribution, and reproductive and parameter values, the transition and parameter elasticities for other rotations can similarly be explained.

Explaining differences between scenarios.—The different patterns found between scenarios in the growth rates and elasticities can broadly be understood by considering the analysis of the baseline monocultures and simple rotations presented in the last section. As examples we consider why rotations with alternating years of A and B have lower growth rates in the no-till scenarios than in the baseline scenarios, why not plowing in both crops leads to little effect of crop order and why growth rates of certain rotations in the no-till A ($\sigma_1 = 0.5$) scenarios can be lower than that of the crop A monoculture. Finally we examine reasons for the effects of increasing rotation length on $\hat{\lambda}$. Differences in elasticity patterns between and within scenarios can be explained by considering how seeds are distributed over the soil layers and their capacity for future reproduction. Such an exercise follows the reasoning used earlier for the baseline ($\sigma_1 = 1$) ABAB and AABB rotations and therefore we do not devote space to it here.

In rotations in which tillage is not carried out for either crops A or B, the $\hat{\lambda}$ are lower for those rotations in which crops A and B alternate. In the no-till B scenarios, this is because, for an alternating pattern of crops A and B, seeds produced in a B crop remain in the top layer and then are mostly removed during the following A phase. In the no-till A scenarios, seeds that were buried at the end of the B year are not brought back to the surface before the next B year and so cannot reproduce. The effect of consecutive blocks of crops in the no-till scenarios is to either store seeds until they can be brought back to the surface after the first B phase (no-till A scenarios) or to cause a large build up in the population during the B years that is not offset

by decreases during the A phases (no-till B scenarios). Considering the elasticity patterns found in the analysis of the baseline ($\sigma_1 = 1$) ABAB rotation (Fig. 5a), this is not a surprising result.

When plowing is not carried out in both crops, the lack of difference between $\hat{\lambda}$ for rotations that differ only in crop sequence is because not plowing effectively decouples the dynamics of the two layers. Thus two, nearly separate populations are created and therefore order of multiplication of matrices and crop order does not have a large effect. Structure, however, still does play a role as $\hat{\lambda}$ for each rotation is not a simple (geometric) average of the monoculture growth rates. The decoupling of the layers also causes the highest elasticity of each phase to be close to 1 because the annual growth rates are dominated by a single transition.

Rotations with $\hat{\lambda}$ lower than that of the lowest monoculture may occur when introduction of another crop with a higher monoculture $\hat{\lambda}$ moves seeds to a layer where they will be removed faster than they will be replaced by the increase caused by the crop with a higher monoculture $\hat{\lambda}$. For the no-till A, ($\sigma_1 = 0.5$) scenarios, the majority of seeds in a monoculture of crop A will be in the bottom layer. The inclusion of a single B crop in rotations of 3 to 5 A crops, permits plowing so that many seeds are moved to the top layer where they are removed from the population. The low survival over winter compensates for the slight increase in population during the B year.

The patterns observed in Fig. 4, for the effects of increasing rotation length, can also be explained by the same reasons for the differences in crop order. When rotations are extended to a common rotation length, the shorter rotations just have more repeating units. Conversely, longer rotations have longer spans of each crop in a consecutive block. In the baseline scenarios, rotations with each crop in a block had the lowest $\hat{\lambda}$ for a given number and fraction of each crop. For the other scenarios the opposite was the case. It is not clear, however, whether the $\hat{\lambda}$ will reach a limit if rotation length were further extended. In the no-till A scenarios, $\hat{\lambda}$ appears to level off, but it may also be increasing very slowly.

DISCUSSION

Our goal has been to show how different types of crop rotations affect weed population dynamics. We have used a periodic matrix model and examined a variety of crop rotations, and the effects of crop order, rotation length, and proportion of each crop. Of prime importance is the conclusion that the order of crops will affect the population growth rate. Our conclusion rests on the form of the model, i.e., that the population is structured, and that life-cycle parameters change with the crop being grown. Only when life-history parameter values lead to a non-structured population,

does the order have little effect on the population growth rate.

The sequence of crops in rotation also affects the sensitivity of the growth rate to changes, at both the levels of the transition elements and the underlying parameters. The differences in growth rates and elasticities between rotations, and between phases within rotations, are in general due to how mixtures of crops, in comparison to monocultures of each crop, alter both the distribution of seeds over soil layers and the contribution of a seed in a particular layer to future generations. Below we consider extensions of our approach, and the implications for weed management and understanding of crop rotations.

Extension of the method

The approach we have taken in this paper can be extended to include aspects such as density dependence, effects of environmental variation on vital rates, and increasing the number of soil layers. Doing so is not likely to change our qualitative conclusion and comes at the expense of analytical tractability, therefore complicating the interpretation of results. For example, aperiodically fluctuating populations due to density-dependent vital rates may obscure the effects of the crop rotation cycle. Our interest is not in forecasting what the population will be, rather it is in projecting what the population would be should the given conditions (parameter values) remain constant (Caswell 1989). Understanding population projections provides a sound basis for developing more complex models, while in the empirical arena it results in more precise hypotheses and thus in better experimental designs.

Division of the soil column into more layers is likely to lower weed population growth rates over a rotation cycle because seeds will reside much longer in layers from where they cannot emerge and thus have a greater chance of losing viability. In situations where accurate quantitative prediction of the future population is of interest, division of the soil into more layers or use of an integral projection model would most likely be necessary (Easterling et al. 2000).

Because weed populations can be structured in many other ways, such as by seed age, size of rhizomes, or seed position relative to a ridge, our approach can be applied to other situations besides those where the seed population is structured by depth in the soil and the seeds are moved by plowing.

Implications for management

The outcomes of decisions concerning crop rotation sequences have implications for weed management, in both the long and short term. As different rotations can have different growth rates, the amount of time to reach a target weed population will be different for each rotation. If other, non-weed-management aspects are equal, then the rotation with the lowest weed popula-

tion growth rate would be the most sensible. One way of thinking about the difference in growth rates between rotations is, e.g., to imagine how much seedling survival (v) needs to be changed in order to achieve the same growth rate of another rotation. In crop B of the baseline (σ_1 [weed seed survival over winter] = 1) rotation ABAB, seedling survival would have to be decreased from 0.6 to 0.28 in order to achieve the same growth rate found for the population in rotation AABB. This would require an 80% increase in effectiveness of weed control. Thus rotation AABB provides the equivalent of an extra, efficient weed-control operation without the effort.

Short-term management decisions will also be affected by the choice of a particular rotation because of different elasticity patterns resulting from different rotations. As a rule of thumb the largest impact on the population growth rate is achieved by changing the values of the parameters with the largest elasticities. Decreasing seedling survival in a given crop may be more effective in one rotation than in another rotation. Furthermore, within a rotation, the strategy may be more effective in one phase than in another phase (each year of a rotation is called a "phase"). This not to say that the process with the highest elasticity is necessarily the best or most convenient one to manipulate. As de Kroon et al. (2000) point out, there may be limits to the degree of change that can be induced in a particular process.

Our model, as with any periodic linear model, shows that the population growth rate, given by the dominant eigenvalue, will not be affected by the starting phase of the rotation. The size of a future population will, however, be affected by the starting crop and the initial distribution of seeds over the soil column. Taking the baseline ($\sigma_1 = 1$) rotation AB as an example, if most of the seeds are in the top layer, then it may be beneficial to start with the A phase of the rotation. Few seeds will be produced and then most of them will be moved to the bottom layer, where their reproductive value will be low. Therefore the amount of new seeds produced in the following B phase will be less than if the B phase occurred first. As the size of the weed population can affect the costs of control and can reduce crop yield, it may be important to consider the initial seed distribution and starting crop when a change to another rotation is contemplated. The starting distribution of seeds also has practical consequences for empirical studies of long-term weed growth rates in crop rotations. Experiments should be carried out long enough to overcome any transient effects and the starting distribution of seeds over the soil column should be measured, an observation also made by Mohler (1993).

From a management perspective, it is tempting to ask whether there are critical values of the monoculture growth rates for which order would not affect the population growth rate over a rotation cycle. Such reason-

ing, though, ignores the crucial role of population structure. For a structured periodic system the population growth rate is not the product of the monoculture growth rates because the order of crops changes the population structure, which in turn affects the growth rate the following year. Consequently rotation population growth rates may show little relation to the product of the monoculture population growth rates. In a structured periodic system, order will not matter only when there is no difference in right eigenvectors between the yearly transition matrices (Caswell 2001) or when processes in one crop yield a matrix that is the inverse of the other crop or the inverse of the product of the other matrices. Such situations are unlikely to occur. The only other possibility is if the life history for the weed species in each of the crops leads to transition matrices that are similar. The elasticity of the population growth rates to the underlying parameters may differ though, because the sums and products of parameter values determining the value of a particular transition may be the same for each crop, but the values of corresponding parameters in each crop may be different.

Toward an improved understanding of crop rotations

As stated at the outset, impacts of crop rotations on weed populations are typically attributed to the diversity of environments, which are thought to prevent a weed population from becoming unmanageably large. While there is undoubtedly much truth in this explanation, it is now possible to specify underlying processes more precisely as well as to provide some qualifications. Critically, not just the diversity of environments matters, but also the sequence of environments interacting with the population structure. Two rotations can be equally diverse, i.e., having the same number and proportion of crops, but still can have different weed population growth rates depending on their order. Furthermore, one can now begin to imagine rotations that could increase a weed problem compared to a monoculture of any of the component crops. This could perhaps happen when germination and emergence depend on seed age and the population is structured by position in the soil. Particular sequences could enhance the fraction of seeds emerging beyond that found in a monoculture. The observation of how growth rates change as rotation length increases is perhaps interesting from a mathematical perspective but has less practical relevance for weed populations.

Use of simple, analytically tractable models to examine crop rotations goes far in giving the ability to explain how biological processes and effects of management interact differently under different rotations. Jordan et al. (1995) observed, in simulations of a structured weed population with a four-year rotation (oats/clover, corn, soybean, corn), that different sensitivities resulted between the first and second corn years. While these could have been due to differences in the plowing

regimes between the two corn crops, some of the differences could be due to the rotation itself. They were not able, however, to explain the processes underlying the differences in sensitivities and concluded that "crop rotations are complicated historical sequences, and effects of an event or process on weed population dynamics may be very different depending on timing within the rotation" (Jordan et al. 1995:395). In this paper we have been able to explain such effects.

The present analysis raises the question of why a particular crop rotation is being used and whether the arguments given for this choice actually hold. In the Netherlands, for example, crop rotations tend to follow an ABAB pattern, alternating competitive crops (grains, potatoes) with non-competitive crops (sugar beets, onions), and plowing is done after each crop. Typical reasons for the alternating pattern relate to soil, weed, and disease management. Given our findings we wonder whether the ABAB pattern, with tillage occurring after each crop, is the ideal one, at least as far as weed management is concerned. With regard to soil and disease management there has been no systematic investigation of the effects of crop order, number, and proportion on these aspects of crop production. It is possible that they may show dynamics qualitatively similar to the results presented here for weed populations.

Taking a theoretical approach frees one to ask apparently absurd questions, such as what would happen if plowing did not occur prior to a carrot crop. From a standard agronomic perspective there may be little sense in not tilling before a carrot crop. From a weed-management perspective, such a practice may be beneficial and should, for example, stimulate investigation of new crop husbandry methods or development of varieties that grow well without tillage. An improved theoretical approach to crop rotations we hope will contribute to more creativity in finding solutions for managing weed populations.

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APPENDIX

SUPPLEMENTARY RESULTS ON HIGHEST ELASTICITIES

For each crop rotation scenario, the highest elasticity value occurring in each rotation is given, along with the transition and phase in which it occurs. Fig. 7 is based on the elasticity values and transitions shown below.

Rotation	Fraction crop A	Baseline				No-till A			
		$\sigma_1 = 1$		$\sigma_1 = 0.8$		$\sigma_1 = 1$		$\sigma_1 = 0.5$	
		Elasticity	Transition	Elasticity	Transition	Elasticity	Transition	Elasticity	Transition
B	0.00	0.389	$b_{21}^{(1)}, b_{21}^{(1)}$	0.380	$b_{12}^{(1)}, b_{21}^{(1)}$	0.389	$b_{12}^{(1)}, b_{21}^{(1)}$	0.389	$b_{12}^{(1)}, b_{21}^{(1)}$
ABBBBB	0.17	0.698	$a_{12}^{(1)}, b_{21}^{(6)}$	0.664	$a_{12}^{(1)}, b_{21}^{(6)}$	0.762	$a_{22}^{(1)}$	0.860	$a_{22}^{(1)}$
ABBBB	0.20	0.625	$a_{12}^{(1)}, b_{21}^{(5)}$	0.601	$a_{12}^{(1)}, b_{21}^{(5)}$	0.817	$a_{22}^{(1)}$	0.904	$a_{22}^{(1)}$
ABBB	0.25	0.743	$a_{12}^{(1)}, b_{21}^{(4)}$	0.708	$a_{12}^{(1)}, b_{21}^{(4)}$	0.723	$a_{22}^{(1)}$	0.824	$a_{22}^{(1)}$
AABBBB	0.33	0.910	$a_{22}^{(1)}$	0.922	$a_{22}^{(1)}$	0.957	$a_{22}^{(1)}$	0.988	$a_{22}^{(1)}$
ABABBB	0.33	0.850	$a_{12}^{(1)}, b_{21}^{(2)}$	0.820	$a_{12}^{(1)}, b_{21}^{(2)}$	0.688	$a_{22}^{(3)}$	0.779	$a_{22}^{(3)}$
ABB	0.33	0.522	$a_{12}^{(1)}, b_{21}^{(3)}$	0.503	$a_{12}^{(1)}, b_{21}^{(3)}$	0.879	$a_{22}^{(1)}$	0.944	$a_{22}^{(1)}$
AABBB	0.40	0.931	$a_{22}^{(1)}$	0.938	$a_{22}^{(1)}$	0.920	$a_{22}^{(1)}$	0.975	$a_{22}^{(1)}$
ABABB	0.40	0.843	$a_{12}^{(1)}, b_{21}^{(2)}$	0.814	$a_{12}^{(1)}, b_{21}^{(2)}$	0.768	$a_{22}^{(3)}$	0.779	$a_{22}^{(1)}$
AAABBB	0.50	0.862	$a_{22}^{(1)}, a_{22}^{(2)}$	0.884	$a_{22}^{(1)}, a_{22}^{(2)}$	0.980	$a_{22}^{(1)}$	0.996	$a_{22}^{(1)}$
AABBB	0.50	0.920	$a_{22}^{(1)}$	0.931	$a_{22}^{(1)}$	0.906	$a_{22}^{(1)}$	0.971	$a_{22}^{(1)}$
AABB	0.50	0.891	$a_{22}^{(1)}$	0.907	$a_{22}^{(1)}$	0.975	$a_{22}^{(1)}$	0.994	$a_{22}^{(1)}$
AABBAB	0.50	0.920	$a_{22}^{(1)}$	0.931	$a_{22}^{(1)}$	0.936	$a_{22}^{(1)}$	0.980	$a_{22}^{(1)}$
AB	0.50	0.853	$a_{12}^{(1)}, b_{21}^{(2)}$	0.824	$a_{12}^{(1)}, b_{21}^{(2)}$	0.617	$a_{22}^{(1)}$	0.702	$a_{22}^{(1)}$
AAABB	0.60	0.846	$a_{22}^{(1)}, a_{22}^{(2)}$	0.871	$a_{22}^{(1)}, a_{22}^{(2)}$	0.994	$a_{22}^{(1)}$	0.999	$a_{22}^{(1)}$
AABAB	0.60	0.955	$a_{22}^{(1)}$	0.958	$a_{22}^{(1)}$	0.909	$a_{22}^{(1)}$	0.962	$a_{22}^{(1)}$
AAAABB	0.67	0.851	$a_{22}^{(1)}, a_{22}^{(3)}$	0.874	$a_{22}^{(1)}$	0.998	$a_{22}^{(1)}$	0.999	$a_{22}^{(1)}$
AAABAB	0.67	0.871	$a_{22}^{(1)}, a_{22}^{(2)}$	0.892	$a_{22}^{(1)}, a_{22}^{(2)}$	0.978	$a_{22}^{(1)}$	0.994	$a_{22}^{(1)}$
AAB	0.67	0.952	$a_{22}^{(1)}$	0.957	$a_{22}^{(1)}$	0.845	$a_{22}^{(1)}$	0.936	$a_{22}^{(1)}$
AAAB	0.75	0.870	$a_{22}^{(1)}, a_{22}^{(2)}$	0.891	$a_{22}^{(1)}, a_{22}^{(2)}$	0.955	$a_{22}^{(1)}$	0.990	$a_{22}^{(1)}$
AAAAB	0.80	0.878	$a_{22}^{(1)}, a_{22}^{(3)}$	0.896	$a_{22}^{(1)}, a_{22}^{(3)}$	0.988	$a_{22}^{(1)}$	0.997	$a_{22}^{(1)}$
AAAAAB	0.83	0.878	$a_{22}^{(1)}, a_{22}^{(3)}$	0.896	$a_{22}^{(1)}, a_{22}^{(3)}$	0.996	$a_{22}^{(1)}$	0.999	$a_{22}^{(1)}$
A	1.00	0.813	$a_{22}^{(1)}$	0.842	$a_{22}^{(1)}$	1.000	$a_{22}^{(1)}$	1.000	$a_{22}^{(1)}$

Rotation	Fraction crop A	No-till B				No-till A and B			
		$\sigma_1 = 1$		$\sigma_1 = 0.5$		$\sigma_1 = 1$		$\sigma_1 = 0.5$	
		Elasticity	Transition	Elasticity	Transition	Elasticity	Transition	Elasticity	Transition
B	0.00	1.000	$b_{11}^{(1)}$	1.000	$b_{11}^{(1)}$	1.0000	$b_{11}^{(1)}$	0.9998	$b_{11}^{(1)}$
ABBBBB	0.17	0.992	$b_{11}^{(3)}$	0.954	$b_{11}^{(3)}$	0.9999	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9996	$b_{11}^{(3)}, b_{11}^{(4)}$
ABBBB	0.20	0.926	$b_{11}^{(2)}$	0.834	$b_{11}^{(2)}$	0.9997	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9994	$b_{11}^{(3)}$
ABBB	0.25	0.770	$b_{11}^{(2)}$	0.644	$b_{11}^{(2)}$	0.9997	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9982	$b_{11}^{(3)}, b_{11}^{(4)}$
AABBBB	0.33	0.998	$b_{11}^{(4)}$	0.986	$b_{11}^{(4)}$	0.9997	$b_{11}^{(4)}$	0.9905	$b_{11}^{(4)}$
ABABBB	0.33	0.986	$b_{11}^{(4)}$	0.966	$b_{11}^{(2)}$	0.9996	$b_{11}^{(4)}, b_{11}^{(5)}$	0.9941	$b_{11}^{(4)}, b_{11}^{(5)}$
ABB	0.33	0.535	$b_{11}^{(2)}$	0.547	$b_{22}^{(3)}$	0.9994	$b_{11}^{(2)}$	0.9938	$b_{11}^{(2)}$
AABBB	0.40	0.988	$b_{11}^{(3)}$	0.952	$a_{12}^{(2)}$	0.9985	$b_{11}^{(3)}, b_{11}^{(4)}$	0.9112	$b_{11}^{(3)}, b_{11}^{(4)}$
ABABB	0.40	0.956	$b_{22}^{(2)}$	0.911	$b_{22}^{(2)}$	0.9992	$b_{11}^{(4)}$	0.9378	$a_{11}^{(3)}, b_{11}^{(5)}$
AAABBB	0.50	0.987	$b_{11}^{(4)}$	0.962	$a_{22}^{(2)}$	0.9897	$b_{11}^{(4)}, b_{11}^{(5)}$	0.9552	$a_{22}^{(1)}, a_{22}^{(2)}$
AABBB	0.50	0.861	$b_{11}^{(5)}$	0.802	$b_{11}^{(3)}$	0.9956	$b_{11}^{(5)}$	0.9807	$a_{22}^{(1)}$
AABB	0.50	0.934	$a_{12}^{(2)}$	0.797	$a_{12}^{(2)}$	0.9940	$b_{11}^{(2)}$	0.9761	$a_{22}^{(1)}$
AABBAB	0.50	0.860	$b_{11}^{(3)}$	0.792	$b_{11}^{(5)}$	0.9956	$b_{11}^{(3)}$	0.9807	$a_{22}^{(1)}$
AB	0.50	0.662	$b_{22}^{(2)}$	0.721	$b_{22}^{(2)}$	0.9934	$a_{11}^{(1)}, b_{11}^{(2)}$	0.9815	$a_{22}^{(1)}, b_{22}^{(2)}$
AAABB	0.60	0.965	$a_{22}^{(2)}$	0.930	$a_{22}^{(2)}$	0.7739	$b_{11}^{(4)}$	0.9966	$a_{22}^{(1)}, a_{22}^{(2)}$
AABAB	0.60	0.600	$b_{22}^{(3)}$	0.682	$b_{22}^{(3)}$	0.8236	$b_{11}^{(3)}, a_{11}^{(4)}$	0.9983	$a_{22}^{(1)}$
AAAABB	0.67	0.920	$a_{12}^{(4)}$	0.867	$a_{22}^{(3)}$	0.9497	$a_{22}^{(2)}$	0.9978	$a_{22}^{(1)}, a_{22}^{(3)}$
AAABAB	0.67	0.865	$a_{22}^{(2)}$	0.849	$a_{22}^{(2)}$	0.9717	$a_{22}^{(1)}, a_{22}^{(2)}$	0.9993	$a_{22}^{(1)}$
AAB	0.67	0.566	$a_{12}^{(2)}$	0.598	$a_{12}^{(2)}$	0.9748	$a_{22}^{(1)}$	0.9990	$a_{22}^{(1)}$
AAAB	0.75	0.892	$a_{22}^{(2)}$	0.862	$a_{22}^{(2)}$	0.9962	$a_{22}^{(1)}, a_{22}^{(2)}$	0.9995	$a_{22}^{(1)}, a_{22}^{(2)}$
AAAAB	0.80	0.849	$a_{22}^{(2)}$	0.837	$a_{22}^{(2)}$	0.9987	$a_{22}^{(2)}$	0.9998	$a_{22}^{(2)}$
AAAAAB	0.83	0.853	$a_{22}^{(4)}$	0.835	$a_{22}^{(2)}$	0.9992	$a_{22}^{(2)}, a_{22}^{(3)}$	0.9998	$a_{22}^{(2)}, a_{22}^{(3)}$
A	1.00	0.813	$a_{22}^{(1)}$	0.813	$a_{22}^{(1)}$	0.9997	$a_{22}^{(1)}$	0.9999	$a_{22}^{(1)}$

Notes: In order to distinguish different years within a rotation cycle, each year of a rotation is called a ‘‘phase,’’ and the phases for each crop in a rotation are numbered chronologically and denoted by a superscript in parentheses. For crop A the element a_{ij} of transition matrix **A** is the contribution of one weed seed in soil layer j at time t to the population of seeds in layer i at time $t + 1$. Weed seed survival over winter is σ_i .