FUDMA Journal of Sciences (FJS)
ISSN online: 2616-1370
ISSN print: 2645 - 2944
Vol. 3 No. 1, March, 2019, pp 65 – 71

TRANSIENT DYNAMIC ANALYSIS OF A MATHEMATICAL MODEL FOR WEED POPULATION DENSITY

[1]Abubakar, S. M. and [2]Nasir, M. O.

[1]Department of Mathematical Sciences, Faculty of Science, Kaduna State University, Kaduna, Nigeria.
[2]Department of Mathematics and Statistics, Federal Polytechnic, Nasarawa, Nigeria
Correspondence author: abu_magaji@kasu.edu.ng and nasomak@gmail.com

ABSTRACT
The transient population dynamics is the short-term behaviour of the population structure or the response of a model to changes in its parameters. This paper investigates transient sensitivity analysis of a density dependent mathematical model of a weed species for the purpose of short- term weed control plans as an alternative to sensitivity analyses of the steady-state equilibrium that rely on long-terms dynamics of the weed population. The analysis' result shows that the transient population growth is more sensitive to seedling survival (e) than germination rate (g_1). Hence, weed population control could be targeted at seed germination and seedling stages of the weed growth for effective control plan.

Keyword: Transient population, density-dependence, matrix calculus, staged-structured

INTRODUCTION
The transient population dynamics which is the short-term behaviour can differ in important ways from asymptotic dynamics, the long-term behaviour. It has long been recognized that a focus on the population growth rate alone can obscure these important transient effects (Caswell, 2007). Transient population growth rates and eventual population sizes differ sufficiently from asymptotic expectations (Dong *et a*l., 2013). Hence, Transient dynamics is a growing concern in population biology. This concern led to the development of a perturbation analysis of transient densities by Fox and Gurevitch (2000). The perturbation analysis of transient dynamics can reveal the determinants of short-term patterns (behaviours), just as perturbation analysis of (sensitivity and elasticity) of the asymptotic growth rate and steady state population density growth reveals the effects of the parameters (vital rates) on long-term growth.
Asymptotic dynamics always assume that environmental conditions will remain the same for a very long time, but this is often not the case, populations experience disturbances which either perturb the population structure or the parameters of the model.

Transient sensitivity analyses describe how parameters affect the transient (short-time) dynamics and can thus be used in management scenarios. Besides, it provides information more applicable in control compare to the long-time behaviour associated with eigenvalue sensitivity analyses (Burch *et al*., 2011). Transient dynamics can take place if a stage structured population is not at the steady stage distribution, that is, when the relative magnitude of life history stages has not reached stable values (Tenhumberg *et al.*, 2010). The transient analysis aims to understand the short-term dynamics exhibited following a disturbance which perturbs the population structure away from stable stage distribution. The steady state-type sensitivity analysis we carried out in the last section described how parameters affect the steady-state behaviour, but we are likely more interested in the behaviour soon before the steady-state for the purpose of control of annual weeds density (which we do not want to reach steady-state).

The Parameterized Model Equation
In this paper, we examine a stage structured population model for the abundant densities of seeds ($n_{1,t}$), established seedlings ($n_{2,t}$) and mature-weeds ($n_{3,t}$) described by Nasir et al (2015), given by the following system of difference equations:

$$n_{1,t+1} = d(1-g_1(n_{2,t}))n_{1,t} + bd(1-g_1(n_{2,t}))n_{3,t} \tag{1}$$

$$n_{2,t+1} = edg_1(n_{2,t})n_{1,t} + bedg_2(n_{2,t})n_{3,t} \tag{2}$$

$$n_{3,t+1} = m(n_{2,t})n_{2,t} \tag{3}$$

Biologically, any of the parameters g_i, e, m and b may experience density-dependence due to resource limitation (such as space, nutrient, water and light). The Beaverton-Holt density-dependence function type in (Alsharawi and Rhouma, 2010) is adopted for the functions $g_i(n_{2,t})$ and $m(n_{2,t})$ due to the assumption that seedling recruitment and the established seedling growth to mature weed are density dependent and there is competition among the weed for the available micro site. Thus;

$$g_i(n_{2,t}) = \lambda g_i \quad (4)$$

$$m(n_{2,t}) = \lambda m \quad (5)$$

Where $\lambda = \dfrac{1}{1+\alpha n_{2,t}}$

Substituting (4) and (5) into (1) – (3) gives a density–dependence stage-structured model for non-homogeneous population density of an annual weed, thus

$$n_{1,t+1} = d(1-\lambda g_1)n_{1,t} + bd(1-\lambda g_2)n_{3,t} \quad (6)$$

$$n_{2,t+1} = de\lambda g_1 n_{1,t} + bde\lambda g_2 n_{3,t} \quad (7)$$

$$n_{3,t+1} = \lambda m n_{2,t} \quad (8)$$

The system of difference equations (6) – (8) is a density–dependence stage-structured model for non-homogeneous population density of an annual weed.

Where

$\boldsymbol{n_{1,t}}$ Density of seeds in the seed bank

$\boldsymbol{n_{2,t}}$ Density of the established seedling

$\boldsymbol{n_{3,t}}$ Density of mature weeds

g_i The maximum value of $g_i(n_{2,t})$ at a low density of established seedling $(n_{2,t})$.

d Fraction of dormant seeds surviving in the seed bank

g_2 Fraction of viable new (fresh) seeds germination within the growing season

g_1 Fraction of seeds older than one year germination out of the seed bank.

e Fraction of germinated seeds that become established seedlings

m Fraction of the established seedlings that survive to mature weeds

b Average number of seeds produced by the mature weed per unit area.

α Intra-specific coefficient of the established seedling

The variables units are density per unit area.

Note: Mature weed density is not consider to be density–dependence, because after seed production they will die been monocarpic annual weed.

Transient Dynamic Analysis

In order to investigate the transient dynamic of the model equations (6) – (8) for weed population density, the matrix calculus approach in Caswell (2008) is employed to carry out the transient sensitivity analysis for the model. To study the sensitivity of each parameter in the population growth model, the model equation is differentiated partially with respect to each identified vital parameter in the model. Since the state variables and parameters of a given population model may take on a wide range of values, it is imperative to evaluate how these parameters influence the population (Omony, 2014).

The model equations (6) – (8) is stated in the form of matrix equation thus;

$$\mathbf{n}_{t+1} = \mathbf{P}(\theta, n_t)\mathbf{n}_t \quad (9)$$

Where $\mathbf{n}_{t+1} = (n_{1,t+1} \quad n_{2,t+1} \quad n_{3,t+1})^T$, $\mathbf{n}_{i,t} = (n_{1,t,} n_{2,t}, n_{3,t})$ and

$$\mathbf{P}(\theta,n_t)=\begin{pmatrix} d\left(1-\dfrac{g_1}{1+\alpha n_{2,t}}\right) & 0 & bd\left(1-\dfrac{g_2}{1+\alpha n_{2,t}}\right) \\ de\dfrac{g_1}{1+\alpha n_{2,t}} & 0 & bde\dfrac{g_2}{1+\alpha n_{2,t}} \\ 0 & \dfrac{m}{1+\alpha n_{2,t}} & 0 \end{pmatrix} \tag{9a}$$

Differentiating both sides of the matrix equation (9) (instead of its steady-state solution), multiplying by $\mathbf{I}_3$ (identity matrix), applying the vec operator and chain rule to gives;

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T}=\mathbf{P}(\theta,\mathbf{n}_t)\frac{d\mathbf{n}_t}{d\theta^T}+\mathbf{I}_3 d\mathbf{P}(\theta,\mathbf{n}_t)\mathbf{n}_t^T \;=\mathbf{P}(\theta,\mathbf{n}_t)\frac{d\mathbf{n}_t}{d\theta^T}+(\bar{\mathbf{n}}^T\otimes\mathbf{I}_3)\frac{dvec\mathbf{P}}{d\theta^T} \tag{10}$$

But $dvec\mathbf{P}$ in (10) include both direct effects of θ and indirect effects of $\mathbf{n}_t$ on the dynamics of (9), so

$$\frac{dvec\mathbf{P}}{d\theta^T}=\frac{\partial vec\mathbf{P}}{\partial\theta^T}+\frac{\partial vec\mathbf{P}}{\partial\mathbf{n}^T}.\frac{d\mathbf{n}_t}{d\theta^T} \tag{11}$$

Substituting (11) into (10) gives

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T}=\mathbf{P}(\theta,\mathbf{n}_t)\frac{d\mathbf{n}_t}{d\theta^T}+(\mathbf{n}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\theta^T}+\left[(\mathbf{n}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\mathbf{n}^T}\right]\frac{d\mathbf{n}_t}{d\theta^T} \tag{12}$$

Rearranging the terms gives the transient sensitivity as

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T}=\left[\mathbf{P}(\theta,\mathbf{n}_t)+(\mathbf{n}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\mathbf{n}^T}\right]\frac{d\mathbf{n}_t}{d\theta^T}+(\mathbf{n}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\theta^T} \tag{13}$$

In other to solve equation (13) we obtained the derivatives of $\mathbf{P}(\theta,\mathbf{n}_t)$ with respect to the parameters $\theta=(g_1\;\;g_2\;\;b\;\;e\;\;m)^T$ and to the densities $\mathbf{n}_{i,t}=(n_{1,t,}n_{2,t},n_{3,t})$ and substituting these derivatives into equation (13) give the transient sensitivities of our model.

Express $\mathbf{n}_t$ as in (9) and find $\dfrac{d\mathbf{n}_t}{d\theta^T}$ by taking the differential of both sides applying both Roth's theorem and chain rule to obtain (14) after the rearrangement.

$$\frac{d\mathbf{n}_t}{d\theta^T}=\left(\mathbf{I}_3-\mathbf{P}-(\mathbf{n}_t{}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\mathbf{n}^T}\right)^{-1}(\mathbf{n}_t{}^T\otimes\mathbf{I}_3)\frac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\theta^T} \tag{14}$$

Using (9a) to obtain $\dfrac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\theta^T}$ and $\dfrac{\partial vec\mathbf{P}(\theta,\mathbf{n}_t)}{\partial\mathbf{n}^T}$, thus

$$\frac{\partial vecP(\theta,\mathbf{n})}{\partial\theta}=\begin{pmatrix} -(1+\alpha n_2)^{-1} & 0 & 0 & 0 & 0 \\ e(1+\alpha n_2)^{-1} & 0 & 0 & g_1(1+\alpha n_2)^{-1} & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & (1+\alpha n_2)^{-1} \\ 0 & -b(1+\alpha n_2)^{-1} & 1-g_2(1+\alpha n_2)^{-1} & 0 & 0 \\ 0 & be(1+\alpha n_2)^{-1} & eg_2(1+\alpha n_2)^{-1} & bg_2(1+\alpha n_2)^{-1} & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \quad (15)$$

And

$$\frac{\partial vecP(\theta,\mathbf{n})}{\partial\mathbf{n}^T}=\begin{pmatrix} 0 & g_1\alpha(1+\alpha n_2)^{-2} & 0 \\ 0 & -eg_1\alpha(1+\alpha n_2)^{-2} & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & -m\alpha(1+\alpha n_2)^{-2} & 0 \\ 0 & bg_2\alpha(1+\alpha n_2)^{-2} & 0 \\ 0 & -beg_2\alpha(1+\alpha n_2)^{-2} & 0 \\ 0 & 0 & 0 \end{pmatrix} \quad (16)$$

Putting (15). (16). $\mathbf{n}_{i,t}$ and $P(\theta,\mathbf{n})$ in (14) and simplified to obtain

$$\frac{d\mathbf{n}_t}{d\theta^T}=\begin{pmatrix} \frac{k_{12}en_1-k_{11}n_1}{1+\alpha n_2} & \frac{k_{12}ben_3-k_{11}bn_3}{1+\alpha n_2} & \frac{k_{12}eg_2n_3+k_{11}m[(1+\alpha n_2)-g_2]}{1+\alpha n_2} & \frac{k_{12}(g_1n_1+bg_2n_3)}{1+\alpha n_2} & \frac{k_{13}n_2}{1+\alpha n_2} \\ \frac{k_{22}en_1-k_{21}n_1}{1+\alpha n_2} & \frac{k_{22}ben_3-k_{21}bn_3}{1+\alpha n_2} & \frac{k_{22}eg_2n_3+k_{21}m[(1+\alpha n_2)-g_2]}{1+\alpha n_2} & \frac{k_{22}(g_1n_1+bg_2n_3)}{1+\alpha n_2} & \frac{k_{23}n_2}{1+\alpha n_2} \\ \frac{k_{32}en_1-k_{31}n_1}{1+\alpha n_2} & \frac{k_{32}ben_3-k_{31}bn_3}{1+\alpha n_2} & \frac{k_{32}eg_2n_3+k_{31}m[(1+\alpha n_2)-g_2]}{1+\alpha n_2} & \frac{k_{32}(g_1n_1+bg_2n_3)}{1+\alpha n_2} & \frac{k_{33}n_2}{1+\alpha n_2} \end{pmatrix} \quad (17)$$

where,

$$k_{11}=\frac{(1+\alpha n_2)^2(1+eg_1\alpha n_1+beg_2\alpha n_3)-beg_2[m-m\alpha n_2(1+\alpha n_2)]}{g_1[(1+\alpha n_2)-bem(1+\alpha n_2)]}$$

$$k_{12}=\frac{(1+\alpha n_2)^2(1+g_1\alpha n_1+bg_2\alpha n_3)-b[(1+\alpha n_2)-g_2][m-m\alpha n_2(1+\alpha n_2)]}{g_1[(1+\alpha n_2)-bem(1+\alpha n_2)]}$$

$$k_{13}=\frac{beg_2(g_1\alpha n_1+bg_2\alpha n_3)-b[(1+\alpha n_2)-g_1][(1+eg_1\alpha n_1+beg_2\alpha n_3)]}{g_1[(1+\alpha n_2)-bem(1+\alpha n_2)]}$$

$$k_{21}=\frac{e(1+\alpha n_2)}{[(1+\alpha n_2)-bem(1+\alpha n_2)]}$$

$$k_{22} = \frac{(1+\alpha n_2)}{[(1+\alpha n_2) - bem(1+\alpha n_2)]}$$

$$k_{23} = \frac{be(1+\alpha n_2)}{[(1+\alpha n_2) - bem(1+\alpha n_2)]},$$

$$k_{31} = \frac{e[m - m\alpha n_2(1+\alpha n_2)]}{[(1+\alpha n_2) - bem(1+\alpha n_2)]}$$

$$k_{32} = \frac{[m - m\alpha n_2(1+\alpha n_2)] + e(g_1\alpha n_1 + bg_2\alpha n_3)(1+\alpha n_2)}{[(1+\alpha n_2) - bem(1+\alpha n_2)]}$$

$$k_{33} = \frac{(1+\alpha n_2)}{[(1+\alpha n_2) - bem(1+\alpha n_2)]}$$

Simplifying (13) subsequently, gives

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T} = \left[\begin{pmatrix} \frac{(1+\alpha n_{2,t}) - g_1}{1+\alpha n_{2,t}} & 0 & \frac{b[(1+\alpha n_{2,t}) - g_2]}{1+\alpha n_{2,t}} \\ \frac{eg_1}{1+\alpha n_{2,t}} & 0 & \frac{beg_2}{1+\alpha n_{2,t}} \\ 0 & \frac{m}{1+\alpha n_{2,t}} & 0 \end{pmatrix} + \begin{pmatrix} 0 & \frac{g_1\alpha n_1 + bg_2\alpha n_3}{(1+\alpha n_2)^2} & 0 \\ 0 & \frac{-eg_1\alpha n_1 - beg_2\alpha n_3}{(1+\alpha n_2)^2} & 0 \\ 0 & \frac{-m\alpha n_2}{(1+\alpha n_2)^2} & 0 \end{pmatrix}\right] \frac{d\mathbf{n}_t}{d\theta^T} +$$

$$\begin{pmatrix} \frac{-n_1}{1+\alpha n_2} & \frac{-bn_3}{1+\alpha n_2} & \frac{[(1+\alpha n_{2,t}) - g_2]n_3}{1+\alpha n_2} & 0 & 0 \\ \frac{en_1}{1+\alpha n_2} & \frac{ben_3}{1+\alpha n_2} & \frac{eg_2}{1+\alpha n_2} & \frac{g_1 n_1 + bg_2 n_3}{1+\alpha n_2} & 0 \\ 0 & 0 & 0 & 0 & \frac{n_2}{1+\alpha n_2} 0 \end{pmatrix} \quad (18)$$

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T} = \begin{pmatrix} \frac{(1+\alpha n_{2,t}) - g_1}{1+\alpha n_{2,t}} & \frac{g_1\alpha n_1 + bg_2\alpha n_3}{(1+\alpha n_2)^2} & \frac{b[(1+\alpha n_{2,t}) - g_2]}{1+\alpha n_{2,t}} \\ \frac{eg_1}{1+\alpha n_{2,t}} & \frac{-eg_1\alpha n_1 - beg_2\alpha n_3}{(1+\alpha n_2)^2} & \frac{beg_2}{1+\alpha n_{2,t}} \\ 0 & \frac{m(1+\alpha n_2) - m\alpha n_2}{(1+\alpha n_2)^2} & 0 \end{pmatrix} \frac{d\mathbf{n}_t}{d\theta^T} +$$

$$\begin{pmatrix} \frac{-n_1}{1+\alpha n_2} & \frac{-bn_3}{1+\alpha n_2} & \frac{[(1+\alpha n_{2,t}) - g_2]n_3}{1+\alpha n_2} & 0 & 0 \\ \frac{en_1}{1+\alpha n_2} & \frac{ben_3}{1+\alpha n_2} & \frac{eg_2}{1+\alpha n_2} & \frac{g_1 n_1 + bg_2 n_3}{1+\alpha n_2} & 0 \\ 0 & 0 & 0 & 0 & \frac{n_2}{1+\alpha n_2} 0 \end{pmatrix} \quad (19)$$

Then substituting (17) into (19), and after several algebraic calculation and rearrangement, it gives

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T} = \begin{pmatrix} \frac{R_{11}(1+\alpha n_2)-n_1}{1+\alpha n_2} & \frac{R_{12}(1+\alpha n_2)-bn_3}{1+\alpha n_2} & \frac{R_{13}(1+\alpha n_2)+[(1+\alpha n_{2,t})-g_2]n_3}{1+\alpha n_2} & R_{14} & R_{15} \\ \frac{R_{21}(1+\alpha n_2)+en_1}{1+\alpha n_2} & \frac{R_{22}(1+\alpha n_2)+ben_3}{1+\alpha n_2} & \frac{R_{23}(1+\alpha n_2)+eg_2}{1+\alpha n_2} & \frac{R_{24}(1+\alpha n_2)g_1 n_1+bg_2 n_3}{1+\alpha n_2} & R_{25} \\ R_{31} & R_{32} & R_{33} & R_{34} & \frac{R_{35}(1+\alpha n_2)+n_2}{1+\alpha n_2} \end{pmatrix} \tag{20}$$

We consider an initial population of dormant seeds; $\mathbf{n}_0 = (1\ \ 0\ \ 0)^T$, So

$$R_{11} = \frac{e^2 g_1{}^2 \alpha b(1-g_2)+(1-g_1)e-(1+bem)}{g_1(1-bem)}, \quad R_{12} = 0$$

$$R_{13} = \frac{m(1-g_2)[(1-g_1(e\alpha+1)]-bem[(g_1+g_2)-g_1g_2]}{g_1(1-bem)},$$

$$R_{14} = \frac{1+g_1(\alpha-g_1)-(1-g_2)[bm+beg_1{}^2\alpha]}{(1-bem)}, \quad R_{15} = 0, \quad R_{21} = \frac{be^3\alpha g_1 g_2 + e^2 - (1+bem)e}{(1-bem)},$$

$$R_{22} = 0, \quad R_{23} = \frac{em(1-g_2)}{(1-bem)}, \quad R_{24} = \frac{eg_1(1+2bmg_2+beg_2g_1\alpha-bm)}{(1-bem)}$$

$$R_{25} = 0, \quad R_{31} = 0, \quad R_{32} = 0, \quad R_{33} = \frac{em^2[(1-g_2]}{(1-bem)}, \quad R_{34} = \frac{mg_1}{(1-bem)}, \quad R_{35} = 0$$

Substituting R_{ij} and the initial population density $n_0 = (1\quad 0\quad 0)^T$ into (20), gives

$$\frac{d\mathbf{n}_{t+1}}{d\theta^T} = \mu \begin{pmatrix} \frac{r_{11}}{g_1} & 0 & \frac{r_{13}}{g_1} & r_{14} & 0 \\ r_{21} & 0 & r_{23} & r_{24} & 0 \\ 0 & 0 & r_{33} & r_{34} & 0 \end{pmatrix} \tag{21}$$

where,

$$r_{11} = e^2 g_1{}^2 \alpha b(1-g_2)+(1-g_1)e-(1+bem)-g_1(1-bem),$$

$$r_{13} = m(1-g_2)[(1-g_1(e\alpha+1)]-bem[(g_1+g_2)-g_1g_2],$$

$$r_{14} = 1+g_1(\alpha-g_1)-b(1-g_2)[m+eg_1{}^2\alpha]$$

$$r_{21} = e^2(1+be\alpha g_1 g_2 - 2bm),$$

$$r_{23} = em(1-g_2)+eg_2(1-bem),$$

$$r_{24} = eg_1^2(1+2bmg_2+beg_2g_1\alpha-bm)$$

$$r_{33} = em^2(1-g_2), \quad r_{34} = mg_1$$

$$\mu = \frac{1}{(1-bem)}$$

Equation (21) gives the transient sensitivity of weed population density to perturbation in the vital parameters. Compactly written as

$$\frac{d\mathbf{n}_{t+1}}{d\theta} = \left(\frac{d\mathbf{n}_{t+1}}{dg_1} \quad \frac{d\mathbf{n}_{t+1}}{dg_2} \quad \frac{d\mathbf{n}_{t+1}}{db} \quad \frac{d\mathbf{n}_{t+1}}{de} \quad \frac{d\mathbf{n}_{t+1}}{dm} \right) \tag{22}$$

Each column of (22) indicates changing rate of the $\mathbf{n}_{t+1}$ to each of the parameter θ. Thus, transient weed population density is susceptible to alteration in established seedling survival (*e*) and recruitment rate from the seed bank (g_1) than any other parameter. However, the transient population growth is more sensitive to seedling survival (*e*) than germination rate (recruitment) (g_1), since $r_{24} > r_{11}$. Sensitivity of the transient population to establish seedling implies that whenever, the seedling population is disturbed by cutting or fire, this creates micro-site space for more seeds to germinate from the seed bank, which create unstable population system as response of weed population to disturbances. This result is contrary to that obtained in Nasir et al (2015), that, equilibrium population density of a weed is susceptible to maturation rate (*m*) and seedling survival rate (*e*),

CONCLUSION

Transient dynamics of a weed population was examined by carrying out the sensitivity analysis on a parameterized model of the transient population growth to changes in the identified parameters for the purpose of short-term weed control plans. Besides, it articulates the responses of the weed population to disturbance through mowing. From the analysis of this model, the transient population growth is more sensitive to seedling survival (*e*) than germination rate (g_1). Hence, weed population control could be targeted at these two stages of the weed growth, which are seed germination and seedling. However, further research work is going on in the area of transient elasticity and its application to some weeds species

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