ECOTRÓPICOS 22(1):23-36 2009
Sociedad Venezolana de Ecología

A MATRIX MODEL FOR THE POPULATION DYNAMICS OF *HYPTIS SUAVEOLENS*, AN ANNUAL WEED

UN MODELO MATRICIAL PARA LA DINÁMICA POBLACIONAL DE *HYPTIS SUAVEOLENS*, UNA MALEZA ANUAL

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ABSTRACT

Hyptis suaveolens is a neotropical annual weed that invades savanna agricultural systems. Although fire, grazing and soil disturbances have been proposed to cause its local dominance, these factors have not been experimentally tested. A field experiment was carried out in a savanna in the Venezuelan Llanos. Six treatments were meant to simulate proposed disturbances and explore underlying causes of the species' local dominance. A matrix population model was developed and for each treatment demographic and perturbation analyses were performed. Results indicate that population growth rate is promoted by all simulated disturbances but fire and nearby vegetation removal, increasing with disturbance intensity, especially under plowing. Demographic analyses show that the increase in population growth rate is mainly due to fecundity. However, germination is the most sensitive parameter. Fire and digging produced a strong reduction in germination, although this negative contribution is smaller than the positive contribution made by fecundity in the digging treatment. Matrix population model analyses allowed a better understanding of the processes leading to increases in the weed's growth rate, and allow development of more effective control measures. Some of them include avoiding soil disturbance and increasing control over germination. We also discuss the constraints of the developed model.

Key words: demography, disturbance, fecundity, life history traits, LTRE, seed, seed bank, sensitivity, analysis survival

RESUMEN

Hyptis suaveolens es una maleza anual de origen neotropical que invade los sistemas de cultivo en sabanas. Aunque el fuego, el pastoreo y las perturbaciones del suelo se han propuesto como causales de su dominancia local, éstas no se han determinado experimentalmente. Un experimento de campo se llevó a cabo en una sabana de los Llanos Venezolanos mediante seis tratamientos que simularon los disturbios mencionados y las posibles causas subyacentes de la dominancia local de la especie. Se desarrolló un modelo matricial de población y para cada tratamiento se realizaron análisis demográficos y de perturbación. Los resultados indican que la tasa de crecimiento poblacional aumenta bajo todos los tratamientos, con excepción del fuego y la remoción de la vegetación circundante, y que dicha tasa aumenta con la intensidad de la perturbación, especialmente bajo arado. Los análisis demográficos muestran que el aumento de la tasa de crecimiento poblacional se debe fundamentalmente a la fecundidad. Sin embargo, la germinación es el parámetro más sensible. El fuego y el arado produjeron una fuerte disminución de la germinación, sin embargo, esta contribución negativa es menor que la contribución positiva de la fecundidad. Los análisis de modelos matriciales de poblaciones contribuyeron a una mejor comprensión de los procesos que estimulan el crecimiento poblacional de la maleza y permitieron sugerir medidas efectivas para su control. Algunas de éstas incluyen evitar las perturbaciones del suelo e incrementar el control de la germinación. Se discuten las limitaciones del modelo desarrollado.

Palabras clave: análisis de sensibilidad, banco de semillas, características de historia de vida, demografía, fecundidad, LTRE, perturbaciones, semillas, supervivencia

INTRODUCTION

Matrix population models have shown to be of high value to study the dynamics of any population and for projection of its demographic behavior in natural or controlled conditions, including management and conservation purposes (Caswell 2001). Although this approach may be a valuable tool to understand and manage weed populations, very little has been done in this regard. With some exceptions matrix population models have not been used as a weed control analysis tool. Exceptions worth mentioning are the studies related to an invasive woody perennial (Sebert-Cuvillier *et al.* 2007), responses of weeds under different crop rotations (Martens 2002), and an annual native grass that becomes dominant after aboveground vegetation removal (Canales *et al.* 1994). However, the study of weed population dynamics in agricultural systems has been recognized as a valuable tool to understand population responses to disturbances (Freckleton and Watkinson 1998), and varying environmental conditions (Grigulis *et al.* 2001), as well as to contribute to the implementation of more effective and economically viable control strategies (Ghersa *et al.* 1994). Using experimental field data about *H. suaveolens*, a native savanna weed, we developed and applied matrix population models to improve understanding of its dynamics and suggest management strategies. Demographic analysis tools including Life Table Response Experiments (LTREs) and sensitivity analysis (Caswell 2001) were used to examine the population dynamics of *H. suaveolens* in the field under experimentally created disturbances in a Venezuelan savanna. These analytical approaches allow the quantification of population-level consequences of disturbances on population growth rates and individual life history parameters. These approaches also allow the projection of long-term population trends.

Hyptis suaveolens (Lamiaceae) is a minor component of undisturbed savannas that may become invasive after strong disturbances (Buzzi and Winder, 1986). Unfortunately, the economic losses due to the invasion of *H. suaveolens* in agricultural lands have not been assessed; however, substantial resources are invested annually in controlling this weed. Although the specific factors that lead to the local dominance of the species remain unclear, some possible causes have been proposed. González (1987) suggested that the removal of vegetation, fire, overgrazing and plowing could all contribute to the increase of *H. suaveolens* in savanna systems. Holmes (1969) proposed that the low palatability of this weed to cattle would provide a competitive advantage over more palatable plant species. Wulff and Medina (1971) proposed that soil disturbance (e.g. plowing) would favor the dominance of this weed, although no mechanism has been suggested for this effect.

Schwarzkopf (1992) studied the effects of experimentally-created disturbances under field conditions on growth, seed production and survival of the species. Her results provided a broad picture of the effect of these only on some life history traits. The consequences of disturbances on population dynamics and the ways to optimize management strategies for *H. suaveolens* still need to be assessed. Population growth models, which functionally relate population vital rates and dynamics, would allow addressing both aspects. Specifically, our analyses focused on the following questions: 1. What type of disturbance has the potential to significantly increase population growth of *H. suaveolens*? 2. Which demographic traits are more sensitive to specific disturbances? 3. What is the contribution of each demographic parameter to the population growth rate under different disturbance types? 4. How can the findings of this study improve management of *H. suaveolens*?

Although the original aim of this investigation is to develop management strategies for *H. suaveolens* as a weed, our results may be applied to stimulate its population growth, since the species has also been regarded as a beneficial plant due to its contents of secondary products that have shown fungitoxic effects (Singh 1992; Pandey and Dubey1994), bacterial growth suppression (Fun *et al.* 1990; Rojas *et al.* 1992), and weed seed germination inhibition (Rao *et al.* 1987).

MATERIALS AND METHODS

The species

Hyptis suaveolens is a broad-leaved annual savanna herb of neotropical origin and tropical and subtropical distribution (Wulff and Medina 1971; Monasterio and Sarmiento 1976; Sarmiento 1984; Afolayan 1993). The species is quantitatively unimportant in savannas where human impact is low. However, in areas where mechanized agriculture and intensive cattle raising are practiced, the species has become prevalent and very difficult and expensive to control (Holmes 1969; Harrison 1973). Chemical and mechanical control measures are limited due to the overlapping growing season of the weed and crops. In fact, vegetative growth of *H. suaveolens* in Venezuelan savannas occurs during the rainy season, between May and November, largely because this species has a low tolerance to drought (Wulff 1987) and seed dispersal takes place at the beginning of the dry season, between December and January (Monasterio and Sarmiento 1976).

Epizoochory, a potential seed dispersal mechanism of *H. suaveolens* by means of the hooked calices containing the seeds (Van der Pijl 1972), might be important, particularly since small mammals and cattle are common in savannas. Following dispersal, seeds remain in soil and do not germinate until the arrival of the rainy season and the after-ripening process is complete (Wulff and Medina 1971). Seeds of *H. suaveolens* collected in a Venezuelan savanna, showed optimum germination temperatures between 25 and 30 ºC, and better germination rates under light (84 %) than in darkness (54 %) (Wulff and Medina 1971). The same paper reports on the photoblastic nature of these seeds and that for lab-stored seeds (20 ºC and 40% relative humidity) maximum germination rates are reached after 8 months of dispersal. Additionally, large seed size variability (0.5 – 50 mg) and lower germination rates in small seeds indicated that these are better adapted to germinate on bare soil and large seeds are capable of germinating under the canopy of competitors (Wulff 1973). Also, found that large and intermediate weight seeds produced more vigorous seedlings. Plants of *H. suaveolens* also show a high acclimation capacity to light and temperature with high photosynthesis rates. However, photosynthesis rates and leaf expansion are very sensitive to decreases in water potential (Wulff 1987).

The study site

The experiment was carried out in the Hato Paraima (120 m a.s.l.), located near San Carlos in the State of Cojedes, Venezuela (9º25’ N, 68º15’ W). The climate of the region where the study area is located is characterized by seasonal rainfall and fairly constant daily average temperatures of 26 to 27ºC. Mean annual rainfall (1982-1988) was 1404 mm. More than 80% of the rainfall occurs during the rainy season that begins in May and ends in November. Soils in the study area, classified as Haplustults, are relatively acidic clay-sandy textured with high aluminum availability (Bilbao 1988), developed on flat topography alluvial deposits.

The vegetation at the study site is an open savanna with scattered forest patches. The savanna has a continuous herbaceous layer dominated by perennial grasses, particularly *Trachypogon plumosus* (Humb.y Bonpl. ex Willd.) Nees and *Thrasya petrosa* (Trin.) Chase and a very open tree stratum dominated by *Curatella americana* L., *Byrsonima crassifolia* (L.) Kunth and *Bodwichia virgiloides* Kunth.

Intensive agriculture, especially corn and soybean, and more locally, non-native grass seed production, and extensive cattle rising were the most common agricultural practices in farms near the study area. Agriculture was highly mechanized with heavy equipment, including tillage, planting

Table 1. Averages and standard errors of field data by treatment. Superscripts correspond to results of ANOVA and paired t-test post hoc comparisons. Different letters indicate significant differences at $p < 0.05$.

TREATMENT	*Initial number*	*Final number*	*Survival rate*	*Fecundity (seeds/plot)*	*Average seeds per plant*
Control	30.33 ± 6.12^{a}	17.89 ± 4.87^{a}	0.51 ± 0.11^{a}	2202 ± 789^{a}	123
Fire	12.00 ± 5.68^{a}	11.60 ± 5.71^{a}	0.67 ± 0.16^{ab}	2033 ± 945^{a}	175
Clipping	31.86 ± 6.94^{a}	20.29 ± 5.40^{a}	0.64 ± 0.05^{ab}	4710 ± 865^{ab}	232
Removal	39.11 ± 12.82^{a}	26.00 ± 7.87^{a}	0.78 ± 0.05^{bc}	5293 ± 1415^{ab}	204
Digging	14.29 ± 3.43^{a}	12.14 ± 2.80^{a}	0.85 ± 0.04^{c}	9302 ± 2028^{b}	766
Digging-removal	19.43 ± 3.44^{a}	16.29 ± 3.00^{a}	0.85 ± 0.05^{bc}	18343 ± 1663^{c}	1126

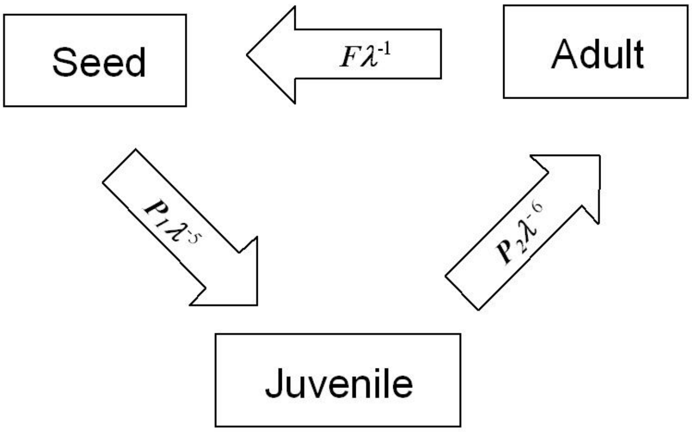

Figure 1. Z-transformed life cycle graph for *H. suaveolens*. P_1, P_2 and F are transition probabilities between stages: seed, juvenile and adult. P_1 is the probability of survival from seed to juvenile stage (germination), P_2 survival probability from juvenile to adult stage (survival) and F fecundity. The negative exponent of λ represents the number of months required for the transition.

and harvesting devices. Tillage was practiced mainly with tandem disk and moldboard plows as well as spike tooth harrow equipment. Fires during the dry season and extensive grazing by cattle were common events in the area. However, the study site had not been cultivated for several years before the experimental plots were established and livestock and fire were excluded one year prior to the start of trials.

Experimental set-up

Plots were established in an open savanna area where senesced plants of *H. suaveolens* from the previous growing season were fairly abundant. Sixty 1.5 × 1.5 m square plots were marked using wire and metal pins. A 1 × 1 m sub-plot was also established at the center of each plot. Treatments were applied to the 1.5 × 1.5 m plots, while data were obtained from the 1 × 1 m sub-plots, thus leaving a 0.5 m buffer zone around each plot.

At the beginning of the wet season, in May 1989, prior to germination of *H. suaveolens*, six different treatments were randomly assigned to the plots. Each treatment consisted of 10 replicates, unfortunately 1-5 were accidentally lost. Treatments, listed in an assumed order of increasing intensity, were as follow:

1. Control. Plots not disturbed during the experiment. This treatment would simulate undisturbed savanna conditions (with fire and grazing excluded). *2. Fire*. Plots burned once at the end of the dry season. This treatment is meant to measure the impact of dry season fires on the demographic behavior of the weed. *3. Clipping.* In May and June all above ground vegetation but *H. suaveolens* was cut at ground level. The clipped biomass was removed from plots. This treatment would allow testing the effect of shoot competition and partially test the impact of selective grazing. *4. Vegetation removal.* All plants in the plot, with the exception of *H. suaveolens*, were carefully removed by hand, attempting to minimize soil disturbance. This treatment was also applied twice, at the beginning of the experiment in May and again in June. This treatment would allow singling out the effect of root and shoot competition as opposed to shoot competition only. *5. Digging.* At the beginning of the rainy season, soil was manually inverted to a depth of 10-15 cm using manual tools. This treatment is meant to assess soil disturbances caused by tillage practices or similar procedures. *6. Digging and vegetation removal.* Both treatments (4 and 5) were applied together. This would allow comparisons with the two single treatments.

In July 1989, after no newly emerged *H. suaveolens* juvenile plants were detected for the past month, their number was determined for each plot. Seedling mortality during this period was negligible. In January 1990, before *H. suaveolens* seed dispersal was initiated, all plants of the target species in the sub-plots were harvested, counted and taken to the lab. Reproductive tissues were separated by plot, dried to constant weight at 70 ºC, and weighted. The number of seeds produced in each plot ($\boldsymbol{s}$) was estimated by its linear response to the reproductive biomass ($\boldsymbol{w}$ in g) per plot. The equation ($\boldsymbol{s} = -232.65 + 218.03\ \boldsymbol{w}$, for $\boldsymbol{w} > 1.53$ g) was based on samples from 15 plots randomly selected among the different treatments (r=0.99).

In order to calculate seed survival, the actual number of *H. suaveolens* seeds in the soil when the experiment was initiated had to be determined. Unfortunately, it was not possible to count the seeds in the soil without large disturbances or error. Therefore, the initial seed count for the six treatments had to be estimated. Average seed production of plants in the control plots at the end of the experiment was used as the initial number of seeds dispersed at all plots when the experiment initiated in 1989. This estimation was based on two assumptions: 1. At the end of the experiment, plants in control plots produced the same quantity of seeds as plants growing under undisturbed conditions the year prior to treatment application. Consequently, and since contributions from the seed bank are nil (Schwarzkopf 1992), population is stable under undisturbed (control) savanna conditions, hence, population growth rate is equal to one; 2. Spatially random treatment assignment prevents bias due to seed shadow spatial autocorrelation. Moreover, the fact that juvenile and adult weed density was not significantly different among disturbance treatments (ANOVA, $p < 0.05$) (Schwarzkopf 1992) also suggests a fairly similar seed shadow. Our assumptions are additionally justified by the fact that our interest is to assess the relative effect of different disturbances on the life cycle parameters of *H. suaveolens* as opposed to undisturbed savanna conditions and, therefore, the control treatment represents the reference to which each treatment will be compared.

Based on the estimated initial number of seeds, the juvenile count by the end of July, the adult count by the end of the growing season, and the estimated seed production per plot, seed and seedling survival average and individual fecundity were calculated for each plot and used to estimate the transition probabilities between stages in the demographic model described below. ANOVA tests ($p < 0.05$) were performed on the initial and final number of plants, survival and fecundity per plot. Where ANOVA was significant, pair wise t-tests ($p < 0.05$) were carried out as post hoc tests to determine which treatments were different.

Demographic Analysis

To study the dynamics of *H. suaveolens*, we applied the analytical tools of life cycle graphs, the z-transform of graphs and matrix population models (Caswell 2001). A linear time-invariant stage-classified model is used to describe the dynamics of populations of this species. This model is expressed initially in terms of the life cycle graph that corresponds to the population projection matrix. The life cycle of *H. suaveolens* is described as an annual plant without a permanent seed bank, which flowers in November and one month later produces seeds that remain dormant until May (five months), at which time they germinate and begin vegetative growth.

Table 2. Transition coefficients and population parameters of *H. suaveolens* based on the population model depicted in Fig. 1, corresponding to the different field treatments. Meaning of variables indicated in the text.

TREATMENT	P_1	P_2	F	λ_1	r	R_0
Control	0.0135	0.6500	113.90	1.0000	0.0000	1.0000
Fire	0.0056	0.8325	165.13	0.9784	-0.0218	0.7698
Clipping	0.0112	0.6414	330.21	1.0746	0.0719	2.3721
Removal	0.0138	0.7789	296.85	1.1015	0.0967	3.1908
Digging	0.0050	0.8500	846.55	1.1126	0.1067	3.5978
Digging-removal	0.0068	0.8457	1453.00	1.1935	0.1769	8.3559

The life cycle graph is constructed by dividing the population in three stages. The transition probability for an individual to pass from the seed stage (*S*) to the juvenile stage (*J*) is *P*1, here called germination. Each individual plant needs six months to complete the vegetative stage and flower, and *P*2, here called survival, represents this transition from juvenile to reproductive adult (*A*). The transition that refers to the number of seeds produced by an adult is given by the fecundity value *F*.

The demographic analysis will rely on the characteristic equation, which can be directly obtained from the z-transformed life cycle graph (Fig.1). This graph is obtained by multiplying the corresponding transition coefficient in the life cycle graph by $\lambda^{-\alpha}$, whwere α indicates the number of months required for that transition. The method of z-transforms applied to the graph produces the characteristic equation:

$$1 - P_1 P_2 F \lambda^{-12} = 0$$

or its equivalent

$$\lambda^{-12} - P_1 P_2 F = 0 \qquad (1)$$

in which the power 12 indicates that there are twelve-month transitions as shown by the exponents of λ in the z-transformed graph The roots of this equation are the eigenvalues of the population projection matrix. The projection matrix from life cycle graphs given by a single loop is imprimitive with all eigenvalues equal in magnitude.

In fact, equation (1) has twelve roots of same magnitude. We denote by λ_1 the unique positive eigenvalue:

$$\lambda_1 = R_0^{1/2} \qquad (2)$$

where $R_0 = P_1 P_2 F$ is the net reproductive rate, or expected number of surviving offspring per generation as given by the Euler equation relating survivals and fecundities.

Since there is no dominant eigenvalue, the population does not converge to a stable stage distribution, but it oscillates with a period of 12 months. However, on a year-to-year time scale, the mean population structure does converge to stability (Cull and Vogt 1974), and therefore, any class grows from one year to the next at a rate given by λ_1^{12} (see Canales *et al*. 1994). Hence, the annual population growth rate is given by λ_1^{12}, so that, if $\lambda_1 < 1$ the population decays to extinction and if $\lambda_1 > 1$ the population grows exponentially.

A two-tailed randomization test

To test the statistical significance of the treatment effects on λ_1, we used a two-tailed randomization test as described in Manly (1991) and Caswell (2001). As a test statistic we chose $|\Delta\lambda_1^{(j)}| = |\lambda_1^{(j)} - \lambda_1^{(c)}|$ where $\lambda_1^{(j)}$ and $\lambda_1^{(c)}$ denote the values of λ_1 for treatment *j* and the control, respectively. Then, from the data we calculated the observed value $|\Delta\lambda_{1obs}|$ of that difference for each treatment. All sets of demographic parameters in the control and treatment j plots were randomly permuted 3000 times, and a normal distribution of the data was obtained. Transition coefficients P_1, P_2, and *F*, and the treatment effect $|\Delta\lambda_1^{(j)}| = |\lambda_1^{(j)} - \lambda_1^{(c)}|$ were calculated for each permutation in each treatment, generating a distribution of $|\Delta\lambda_{.1}|$ under the null hypothesis (p $\{|\Delta\lambda_1| \geq |\Delta\lambda_{1obs}| \mid H_0\}$). The null hypothesis H_0 is that the treatment received by a plot has no effect on the population's fate. We obtained the significance level of this test comparing the observed $|\Delta\lambda_{1obs}|$ and the randomly generated $|\Delta\lambda_1|$. The statistical significance of the observed difference is given by the probability of an equal or greater effect under the null hypothesis. Multiple comparisons among the different treatments were also performed using the same methodology.

Sensitivity and Life Table Response Experiment (LTRE) analyses

To investigate how variations of P_1, P_2, and *F*, affect the growth rate (λ_1), sensitivities are derived by implicit differentiation of equation (1) with respect to each of its coefficients:

$$\delta\lambda_1 / P_i = (1/12)\,(\lambda_1/P_i) \qquad i = 1,2 \qquad (3)$$

$$\delta\lambda_1 / F = (1/12)\,(\lambda_1/F) \qquad (4)$$

To measure the contribution of germination, survival and fecundity parameters we used the LTRE (Life Table Response Experiments) method of Caswell (2001). A first approximation to $\Delta\lambda_1^{(j)}$ is given by:

$$\Delta\lambda_1^{(j)} \approx \Delta P_1^{(j)}\,(\delta\lambda_1^{(c)}/\delta P_1) + \Delta P_2^{(j)}\,(\delta\lambda_1^{(c)}/\delta P_2)$$

$$+ \Delta F^{(j)} (\delta\lambda_1^{(c)}/\delta F) \qquad (5)$$

where

$$\Delta P_1^{(j)} = P_1^{(j)} - P_i^{(c)} \qquad i = 1,2$$

$$\Delta F^{(j)} = F^{(j)} - F^{(c)}$$

and the sensitivities are calculated by equations (3) and (4) evaluated at the mean of the parameters. Each term in the summation of equation (5) is the contribution of the differences in the vital rates to the overall effect of treatment *j* on $\lambda_1^{(c)}$.

The developed demographic model for *H. suaveolens* is based on the following assumptions: 1. Interannual biotic and climatic variation is negligible compared to the impact of the tested treatments on population dynamics. 2. Since population growth rate in plants varies with habitat (Werner y Caswell 1977), the developed models would project the demographic behavior of the weed in similar conditions, i.e. savannas where the species is not dominant, and, water, nutrient, and disturbance history are similar. 3. All individuals in each life cycle stage have the same transition probabilities. 4. Density effects are not considered since a parallel experiment (Schwarzkopf 1992) showed that densities observed in the plots´ vicinity were below density dependent values. 5. Seed rain was independent of treatments, since seed sources were similar among plots. 6. Population is assumed to have a stable population size under the control treatment and on any site not disturbed during the previous year.

RESULTS

Field Data

Table 1 summarizes the data obtained from the experimental plots. Initial and final number of plants did not differ between treatments. Survival rates in the treatments that included removal and/or digging differed significantly from the control, whereas fire and clipping did not. Only the treatments of digging and digging-removal differed from the control in fecundity per plot. Seed counts were estimated from seed weight. Average individual seed mass was not affected by treatment since seed weight/seed number ratios per plot were not significantly different among treatments (ANOVA, $p<0.05$). Juvenile and adult weed densities were independent of disturbance treatments (ANOVA, $p< 0.05$).

Population growth rates and demographic parameters

Three transition coefficients were calculated using the field data to generate specific models for each treatment, based on the general model (Fig. 1). These coefficients (P_1, P_2, and F) and the resulting growth rates (λ_1), the instantaneous growth rates ($r = ln\ \lambda_1$) and the net reproductive rate (R_0) for the populations under the different treatments are shown in Table 2. Instantaneous population growth rate of the control treatment is zero as a result of the assumption that seed production at the end of the growing season is equal to the amount of seeds dispersed at the beginning of the experiment. The population growth rate and the life history traits responses to treatments were variable, depending upon the type of disturbance. Germination (P_1) and fecundity (F) are the traits most affected by the tested disturbances. Although average growth rate increases with disturbance intensity, the randomization test indicates that not all paired treatment comparisons are significantly different (Table 3). All treatments but fire and clipping had a positive effect on the population growth rate compared to the control. Growth rate on digging-removal treatment is significantly different to all other treatments, but removal. Burning is significantly different than all other treatments except control and removal treatments. Clipping, removal and digging treatments are not statistically different among each other.

Sensitivity and LTRE analyses

Two types of perturbation analysis (Caswell 2001) useful in the study of population dynamics and the identification of management targets were performed: prospective analysis through sensitivity analysis and retrospective analysis by means of LTRE analysis.

Sensitivity analysis allows assessing responses of λ_1 to potential changes in life history traits by means of their functional relationships. Sensitivities allow a better understanding of the impact of changes on single vital rates on the population growth rates. Sensitivities of λ_1 for the six models (Fig. 2) indicate that the parameter to which the population growth rate is most sensitive under any of the treatments is by far P_1. In fact,

Table 3. Results of statistical test (randomization), showing significance level of differences in population growth rate (λ_1) of *H. suaveolens* among field treatments. Numbers shown are probabilities. * marked values are significant at $p < 0.05$.

TREATMENT	***Control***	***Fire***	***Clipping***	***Removal***	***Digging***
Fire		0.9700			
Clipping		0.0640	0.0425*		
Removal		0.0110*	0.0640	0.4600	
Digging		0.0005*	0.0019*	0.1187	0.8078
Digging-removal	0.0002*	0.0027*	0.0005*	0.0785	0.0055*

sensitivities to P_1 are at least 50 times greater than sensitivities to P_2. The treatments where the growth rate is most sensitive to P_1 are fire and those that included digging. These sensitivities are at least twice as big as the sensitivities shown by the remaining treatments (control, clipping, and removal). On the other hand, sensitivity of λ_1 to F is negligible compared to the sensitivities to survival and declines from fire to digging, except in the control treatment, where these parameters are fairly similar.

The LTRE approach allows assessing the contribution of each life cycle parameter to the difference in the population growth rate between the control and the remaining treatments. Following Caswell (2001), the quantities in parentheses in equation (5) are referred as differences, and the product between them and the corresponding sensitivities as contributions. Differences and contributions for all treatments are shown in Figure 3. It is important to mention that germination, survival and fecundity are measured on different scales, but their contributions to effects on λ_1 are all expressed in the same scale, and thus are directly comparable. The contributions to λ_1 from survival and fecundity in each treatment follow the same pattern as the differences. Except for removal, all treatments have a negative effect on germination, and except for clipping, all treatments have a positive effect on survival (Fig. 3). The effects on fecundity were positive in all treatments, but much smaller under fire, clipping and removal than in digging and digging-removal. The relatively large negative contribution of P_1 to λ_1 under those treatments that included soil disturbance was exceeded by the positive contribution of fecundity.

Interestingly, treatments with no statistically different population growth rates may show large differences in single parameter contributions. For example, demographic traits (P_1, P_2 and F) made quite different contributions to λ_1 under removal, clipping or digging, in spite of non significant differences in their growth rates.

DISCUSSION

Overall responses of H. suaveolens' growth rates to treatments

The population responses discussed here, based on the results of the population model analysis, can only be interpreted as projections and not as forecast, since matrix population models are developed under the assumption that all other variables are kept constant (Caswell 2001). Densities at which the weed grew in the experiment were below density-dependent levels (Schwarzkopf 1992), and treatments did not significantly affect weed densities. Our demographic models developed for *H. suaveolens* under different field treatments showed that the weed's population growth rate increases significantly only under removal or digging (Table 3). Neither fire nor clipping had a significant impact on the population growth of the weed. Removal and digging had about 10% larger growth rates and both treatments combined reached almost a 20% larger growth rate (Table 2). It is apparent that the population growth rate increases with the severity of the damage caused to the surrounding vegetation. Sebert-Cuvillier *et*

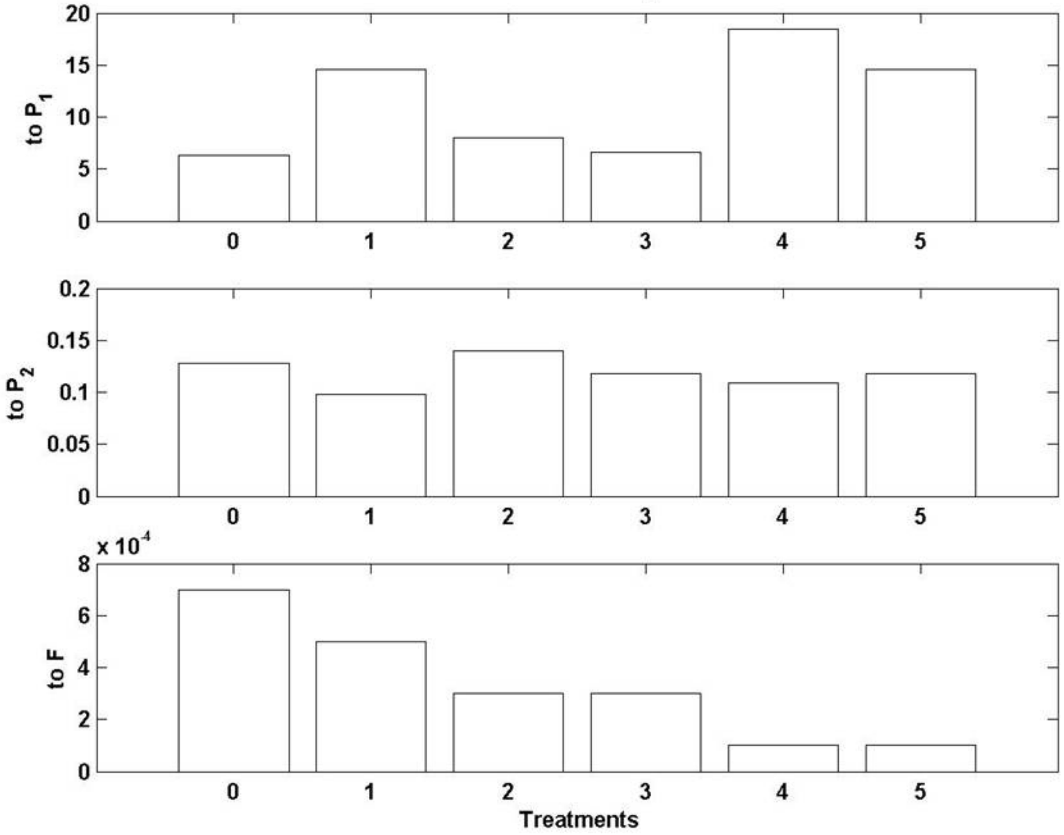

Figure 2. Sensitivities of λ_1 to changes in germination and survival probabilities P_1, P_2 and fecundity F for the six models corresponding to field treatments of *H. suaveolens* : 0 control, 1 fire, 2 clipping, 3 removal, 4 digging, 5 digging-removal.

al. (2007) found an increase in population growth rates with increased light availability, which may also be our case, however, we did not measure light. It is likely that fire and clipping promote growth of the remaining savanna vegetation, limiting the development of *H. suaveolens*, similarly to the control treatment. This may be related to the fact that fire and grazing are common features of these savannas where most of the species are perennial and show adaptations to fire, which may be advantageous under grazing as well. However, these traits make perennial species more susceptible to disturbances at the root zone.

Earlier studies suggested that the local dominance of the weed in savannas is associated with anthropogenic disturbances, namely, fire, grazing and tillage (Holmes 1969; Wulff and Medina 1971; González 1987). Our results indicate that fire does not improve population performance, since population growth rate is not significantly different compared to the control treatment. This lack of effect is the result of a compensation of the increased fecundity and survival by the substantial reduction in germination. This suggests that, although the species is common in savanna environments, its seeds lack effective mechanisms of resistance to fire. In fact, González (1987) found 7.2% of germination after exposure to fire at soil surface under field conditions against 49% for the control treatment. In addition, this species has large amounts of essential oils that make its dry biomass highly flammable and burning temperatures of *H. suaveolens* dry standing biomass may reach 770ºC while temperatures under fire at the ground are around

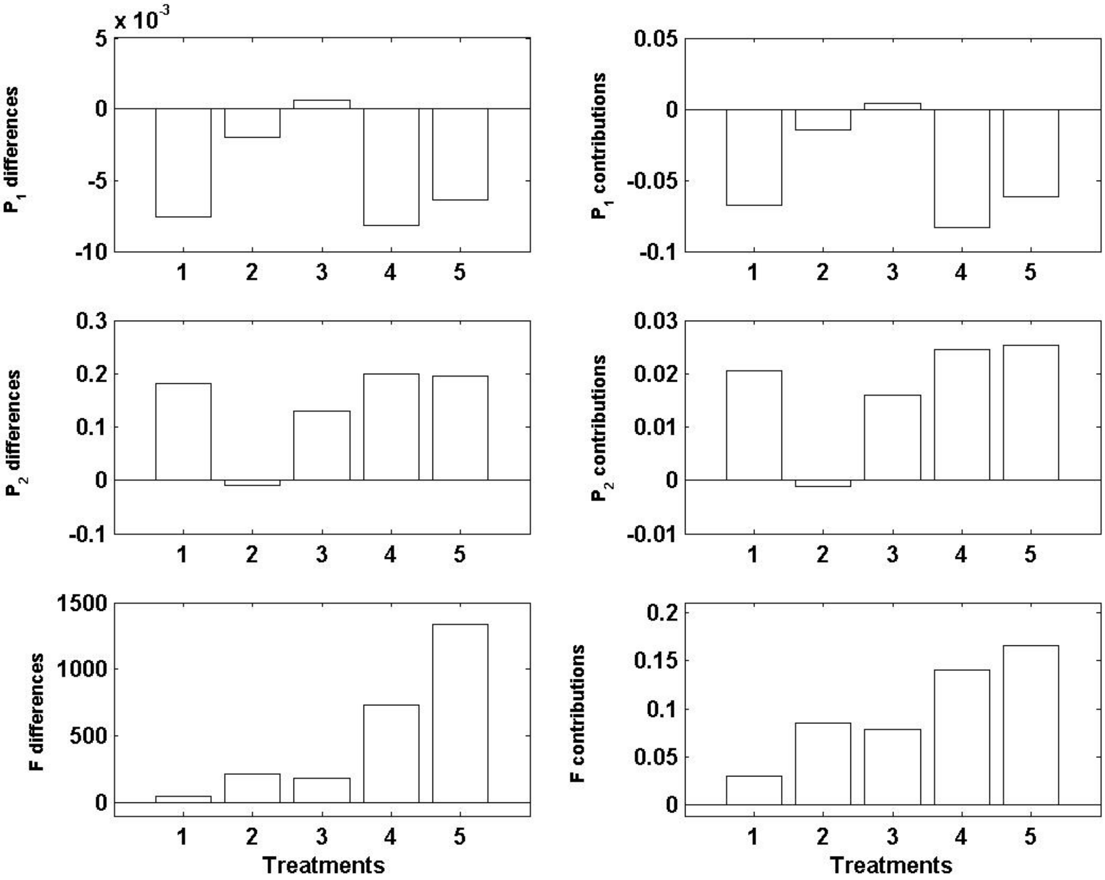

Figure 3. Left: differences in demographic transitions P_1 (germination), P_2 (plant survival) and F (fecundity) between the control and the treatments. Right: contributions of each transition to the differences in population growth rate λ_1 between the control and the treatments. Treatments are: 1 fire, 2 clipping, 3 removal, 4 digging, 5 digging-removal. Notice change of scale with parameters.

90 ºC (Vareschi 1962). Population growth rate has also shown a high sensitivity to germination. Therefore, burning before dispersal, when the seeds are still in their capsules is particularly critical. However, by the time the fire treatment was applied in our experiment, most seeds had already reached the ground, hence, pre-dispersal effect of fire on germination was not assessed in this study, although no survival is likely.

As mentioned earlier, it has been hypothesized that selective grazing, as a result of low palatability of *H. suaveolens*, may favor its population growth. Our selective clipping experiment showed that this treatment has no significant impact on the weed's population growth rate, compared to the control treatment. This is the result of the compensation of the negative contributions of germination and survival, and the positive contributions of fecundity to the difference in growth rate. Although it is unlikely that selective grazing promotes *H. suaveolens* invasion, other effects of grazing like seed dispersal, nutrient input and trampling were not assessed.

Neotropical savanna grasses, potentially the most important competitor for *H. suaveolens*, are better adapted to fire (Medina and Silva 1990) than to grazing (Sarmiento 1992), although the response of perennial grasses might depend on the nature, intensity, and timing of the disturbance (Medina and Silva 1990). Therefore, it might be expected that removal of aboveground competition by clipping savanna perennials may stimulate local dominance of *H. suaveolens*. Nevertheless, clipping and fire, two different ways of aboveground biomass removal, did not significantly improve population growth rates. Furthermore, the LTRE analysis reveals that these two treatments make negative contributions to germination and positive contributions to fecundity, while opposite contributions were only found in survival, positive in fire and negative in clipping, suggesting a quicker vegetation recovery under clipping. Moreover, clipping has small negative contributions to germination and survival, which may be due to the increase in shade at the earlier stages, similar to the control treatment.

Growth rate in the removal treatment is significantly larger than that in the control. The effects of removal are peculiar since this is the only treatment where all demographic parameters make positive contributions to the differences in λ_1. Similar positive contributions of survival under fire and vegetation removal confirm our previous suggestion about the quicker recovery of the vegetation under clipping.

Digging had the largest, positive and significant impact on population growth rate, in spite of its negative effect on germination most likely as a consequence of seed burial. Large seed mortality under tillage due to seed burial or soil temperature has been reported by Lal (1987). In species with a permanent seed bank, tillage usually stimulates the germination of weeds due to seed exposure to better conditions for germination (Ross and Lembi 1985). However, Mohler (2006) showed that, independently of seed size and surface, tillage implements move surface seeds downwards and smaller amounts of seeds from deeper in the soil to the surface. Therefore, the negative effect of digging on germination seems to be associated with the lack of a permanent seed bank (Smith *et al.* 1999). Wulff and Medina (1971) found 50% survival of seeds that had been stored in containers for more than one year under laboratory conditions (plastic containers, 20 °C and 40% relative humidity). However, no seed survival was found by Schwarzkopf (1992) under field conditions at the study site one year after dispersal in 40 soil samples (1125 cm^3 each, 0-5 and 5-10 cm depth) taken right before the next dispersal event. These were randomly taken from two 10x10 m plots, one with high and one with low *H. suaveolens* density. To our knowledge, there is no published evidence of a persistent seed bank of *H. suaveolens*. Schwarzkopf (1992) also found that seed survival in plastic mesh bags (1mm mesh) in a savanna soil was about 33% one year after dispersal. The conflicting results between the soil sample test and the mesh bag test as well as Wulff and Medina´s lab study may be due to seed mortality as a result of soil conditions favoring fungal attack and seed predation by insects. This is consistent with the fact that seed longevity seems to be a less common feature in tropical weeds than in temperate weeds (Marks and Nwachuku 1985) and that native tropical savanna grasses also lack a permanent seed bank (Silva and Ataroff 1985). Digging, however, produced a large increase in population growth through seed production, making *F* the parameter determinant of the large increase in population growth rate. Population growth rate does not differ significantly between removal and digging treatments. However, the LTRE analysis indicates that this similarity is the result of the compensation of the negative effect of germination by the positive effects on survival and fecundity on λ_1 in the case of digging, compared to the removal treatment, where all effects are positive.

Population growth rate difference between digging and digging-removal treatments is highly significant and fairly high (Table 2 and 3). Moreover, when the perennial savanna vegetation is removed in addition to digging, fecundity is mainly responsible for the large increase in population growth rate (Fig. 3). We conclude that removal of competitors exerts its effect trough fecundity enhancement and digging has an additional effect on fecundity, presumably due to improvement of soil conditions.

Prospective and retrospective analyses have not only shown that population growth rates are not very sensitive to survival (P_2) under the tested conditions, but also made clear that the effect of disturbances on population growth rates of *H. suaveolens* does not necessarily follow the patterns of their individual transition coefficients. These facts indicate that assessing single life history parameters without an appropriate functional connection may be misleading in terms of understanding its dynamics and developing appropriate management strategies. This study also reveals that population level processes are crucial to a better understanding of the behavior of weeds, which is also related to the selection process of weediness (Clements *et al.* 2004).

Management targets and constraints

Our results are useful to analyze practical situations related to the control of *H. suaveolens* that may arise in savannas used for agricultural purposes. Some of these situations, together with limitations and suggestions, are summarized here: 1. Sensitivity of λ_1 to germination (P_1) under any treatments suggests the convenience of this parameter as a target for control. Consequently, using herbicides, which would reduce survival, would be less effective than decreasing germination, at similar rates, although this may be difficult to achieve in the field. However, any procedure that may favor germination should be avoided and the seeds' photoblastic nature should be taken into account. 2. Trying to control the weed by means of plowing before crop planting has a positive effect on the population growth rate since plowing reduces germination but enhances fecundity. Therefore, plowing would be recommendable only if fecundity (seed production) is controlled (i.e. removal of the weed before seed set). Agricultural practices able to reduce *H. suaveolens´* seed set (i.e. a crop harvested in mid to end of rainy season) would enhance the control of the weed, since no seeds are added to the seed bank, which is depleted yearly. Also no till practices would enhance control of the weed. 3. Early dry season or pre-dispersal fire would improve weed control, since *H. suaveolens*' germination is very sensitive to fire, and plant dry biomass is highly flammable and reaches very high temperatures. 4. Although the life cycle models presented here are useful to study the population dynamics of *H. suaveolens*, its use is limited to conditions similar to those in the study area. The following are situations in which the general model presented here may need to be structurally adjusted: a. The life cycle of the studied populations lacks a permanent seed bank. However, the species has the potential for significant seed survival after more than one year (Wulff and Medina 1971; Schwarzkopf 1992). Therefore, if predators and fungal attack were negatively affected, a permanent seed bank would build up, changing significantly the dynamics of the population (Thrall *et al.* 1989; Caswell 2001). b. Part of the success of *H. suaveolens* as a weed relies on the fact that the cultivation period in savannas matches with the active growth period of the weed, the rainy season. This is mainly due to its low tolerance to drought (Wulff 1987). Therefore, the potential of the weed to grow under irrigation during the dry season might allow generations overlapping, thus substantially changing its population dynamics (Caswell 2001).

ACKNOWLEDGMENTS

We would like to thank Mr. Luis Nieto, M.Sc. Josune Canales, Dr. José Raventós and Dr. Pedro Jiménez for their assistance in the field, SEMBRA for allowing us to perform our experiments in their land (Hato Paraima) and Dr. Antonio DiTommaso for encouragement and great suggestions on an early version of this paper.

LITERATURE CITED

AFOLAYAN, A. J. 1993. Germination and growth features of seed of different sizes in Hyptis suaveolens (L.) Poit. Range Management and Agroforestry 14: 139-145.

BILBAO, B. A. 1988.. Eficiencia de uso de nitrógeno por una especie nativa: Paspalum plicatulum y una africana: Andropogon gayanus. Caracas, Universidad Central de Venezuela. Tesis de Licenciatura.

BUZZI, Z. J. and J. A. WINDER. 1986. Stages and life cycle of Drepanocasis profana (Boh., 1855) (Coleoptera, Chrysomelidae, Cassidinae) on Hyptis suaveolens (L.) Poit. (Labiatae) in Brazil. Revista Brasileira de Entomologia 30: 31-41.

CANALES, J., M. C. TREVISAN, J. F. SILVA and H. CASWELL. 1994. A Demographic Study of an Annual Grass (Andropogon brevifolius Schwarz) in Burnt and Unburnt Savannas. Acta Oecologica 15(3): 261-273.

CASWELL, H. (2001). Matrix Population Models, Construction, Analysis, and Interpretation. 2nd ed. Sinauer, Massachussets.

CLEMENTS, D. R., A. DITOMMASO, N. JORDAN, B. D. BOOTH, J. CARDINA, D. DOOCHAN, C. L. MOHLER, S. D. MURPHY, C. J. SWANTON. 2004. Adaptability of plants invading North American cropland. Agriculture, Ecosystems and Environment 104: 379-398.

CULL, P. and A. VOGT. 1974. The periodic limit for the Leslie model. Biosciences 21: 39-54.

FRECKLETON, R. P., A. R. WATKINSON. 1998. Predicting the determinants of weed abundance: A model for the population dynamics of Chenopodium album in sugar beet. Journal of Applied Ecology 35: 904-920.

FUN, C. E., A. BAERHEIM, and A. SVENDSEN. 1990. The essential oils of Hyptis suaveolens Poit. grown on Aruba, West Indies. Flavor and Fragance Journal 5: 161-164.

GHERSA, C. M., M. L. ROUSH, S. R. RADOSEVICH and S. M. CORDRAY. 1994. Coevolution of agroecosystems and weed management. Bioscience 44: 85-94.

GONZALEZ, V. C. 1967. Efectos del fuego sobre la reproduccion de algunas plantas de las Llanos de Venezuela. Boletin de la Sociedad Venezolana de Ciencias Naturales 27: 70-103.

GRIGULIS, K., A. W. SHEPPARD, J. E. ASH and R. H. GROVES 2001. The comparative demography of the pasture weed Echium plantagineum between its native and invaded ranges. Journal of Applied Ecology 38: 281-290.

HARRISON, P. J. 1973. Hyptis. Turnoff 4: 28-29.

HOLMES, J. E. 1969. Noxious weeds. Turnoff 4: 28-29.

LAL, R. 1987. Tropical ecology and physical edaphology. Willey & Sons, New York.

MANLY, B. F. J. 1991. Randomization and Monte Carlo Methods in Biology. Chapman & Hall, New York.

MARKS, M. K. and A. C. NWACHKU. 1985. Seed-bank characteristics in a group of tropical weeds. Weed Research 26: 151-157.

MEDINA, E. and J. F. SILVA. 1990. Savannas of Northern South-America - A Steady-State Regulated by Water-Fire Interactions on a Background of Low Nutrient Availability. Journal of Biogeography 17(4-5): 403-413.

MERTENS, S. K., F. VAN DER BOSCH and J. A. P. HEESTERBEEK. 2002. Weed populations and crop rotations: exploring dynamics of a structured periodic system. Ecological Applications 12:1125-1141.

MOHLER, C. L., J. C. FRISCH and C. E. MCCULLOCH. 2006. Vertical movement of weed seed surrogates by tillage implements and natural processes. Soil and Tillage Research 86: 110-122.

MONASTERIO, M. and G. SARMIENTO. 1976. Phenological strategies of plant species in the tropical savanna and the semi-deciduous forest in the Venezuelan Llanos. Journal of Biogeography 3: 325-356.

PANDEY, V. N., and N.K. DUBEY. 1994. Antifungal potential of leaves and essential oils from higher plants. Soil Biology and Biochemistry 26: 1417-1421.

RAO, E., D.S. KUMARY, and A. SATYANARAYANA. 1987. Allelopathic potential of Hyptis suaveolens Poit. on seed germination of weeds and crops. Indian Botanical Reports 6: 77-78.

ROJAS, A., L. HERNANDEZ, R. PEREDA-MIRANDA, and R. MATA. 1992. Screening for antimicrobial activity of crude drug extracts and pure natural products from mexican medicinal plants. Journal of Ethnopharmacology 35: 275-283.

ROSS, M. A. and C. A. LEMBI. 1985. Applied weed science. Burgess Pub. Co., Minneapolis.

SARMIENTO, G. 1984. The Ecology of Neotropical Savannas. Harvard Univ. Press, Cambridge.

SARMIENTO, G. 1992. Adaptive strategies of perennial grasses in South American savannas. Journal of Vegetation Science 3: 325-336.

SCHWARZKOPF, T. 1992. Estudio demografico de Hyptis suaveolens Poit., una maleza de las sabanas. Universidad de Los Andes, Tesis de Maestría, Merida.

SEBERT-CUVILLIER, E., F. PACCAUT, O. CHABRERIE, P. ENDELS, O. GOUBET and G. DECOCQ. 2007. Local population dynamics of an invasive tree species with a complex life-history cycle: A stochastic model. Ecological Modelling 201: 127-143.

SILVA, J. F. and M. ATAROFF. 1985. Phenology, seed crop and germination of coexisting grass species from a tropical savanna in Western Venezuela. Acta Oecologica 20: 41-51.

SINGH, G., R.K. UPADHYAY, and G.P. RAO. 1992. Fungotoxic activity of the volatile oil of Hyptis suaveolens. Fitoterapia 63: 462-465.

SMITH, L., R. P. FRECKLETON, L.G. FIRBANK and, A.R. WATKINSON. 1999. The population dynamics of Anisantha sterilis in winter wheat: comparative demography and role of management. Journal of Applied Ecology 36: 455-471.

THRALL, P. H., S. W. PACALA, and J. A. SILANDER Jr. 1989. Oscillatory dynamics in populations of an annual weed species Abutilon teophrastii. Journal of Ecology 77: 1135-1149.

VAN DER PIJL, L. 1972. Principles of dispersal in higher plants, Springer Verlag.

VARESCHI, V. 1962. La quema como factor ecologico en los Llanos. Boletin de la Sociedad Venezolana de Ciencias Naturales 101: 9-31.

WERNER, P. A. and H. CASWELL. 1977. Population

Growth Rates and Age Versus Stage-Distribution Models for Teasel (Dipsacus Sylvestris Huds.) Ecology 8:1103-1111.

WULFF, R. D. 1973. Intrapopulational variation in the germination of seeds of Hyptis suaveolens. Ecology 54: 646-649.

WULFF, R. D. 1987. Effects of irradiance, temperature, and water status on growth and photosynthetic capacity of Hyptis suaveolens. Canadian Journal of Botany 65: 2501-2506.

WULFF, R. D. and E. MEDINA. 1971. Germination of seeds in Hyptis suaveolens Poit. Plant and Cell Physiology 12: 567-579.

Recibido 28 de abril de 2009; revisado 11 de junio de 2009; aceptado 26 de junio de 2009