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Population Growth, Structure, and Seed Dispersal in the Understory herb *Cynoglossum virginianum*: a Population and Patch Dynamics Model

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Abstract **We use a combined model of forest canopy dynamics and patch-specific demography to examine the response of a forest understory herb, *Cynoglossum virginianum*, to changes in rates of forest disturbance, rates of long distance seed dispersal, and patterns of seed dormancy. The matrix modelling approach followed that of Horvitz and Schemske (1986), in which empirically-determined demographic parameters of a population experiencing open canopy conditions are modified depending upon demographic decay functions describing plant demography in a series of patch-types undergoing succession toward fully closed canopy. In our analysis, demographic transition elements were estimated from 14 years of long-term census data on three subpopulations at the Smithsonian Environmental Research Center, Anne Arundel County, Maryland. One of the three subpopulations was subjected to full canopy exposure in the second year of data collection, while the other two subpopulations remained in full understory conditions for the entire census period. Our results suggest small negative effects of a doubling of the rate of canopy disturbance (defined as the rate at which new treefall gaps appear in closed canopy) and only small positive effects of long distance dispersal on population growth rate, which predicts little selection for long distance dispersal. However, our analyses predict positive benefits of enhanced seed dormancy in this species, particularly if dormancy is higher in new gaps relative to understory conditions. These results are primarily a product of enhanced reproductive output in the years immediately following gap opening which is counterbalanced by increased seedling mortality in those years and a near complete suppression of reproductive output in later years (closing gaps). The suppression of reproduction in closing gaps may be a manifestation of a delayed effect of high costs of reproduction imposed in prior years. We discuss our results in terms of observed patterns of seed dispersal and in terms of the overall potential influence of forest gap dynamics on the demography of understory herbs similar to *C. virginianum*, in which demographic responses to changes in canopy conditions differ in strength and direction among life history stages.**

***Key words: Cynoglossum virginianum*, matrix models, tree gaps, woodland herb.**

Spatial and temporal environmental variation is a major factor influencing the demography of populations, and thus the evolution of dispersal (Gadgil, 1971). For stage-structured plants, dispersal is primarily restricted to the seed stage, and different stages may vary independently in their responses to environmental variation. The consequences of environmental variation for stage-structured plant populations depend upon stage- and patch-specific demographic parameters as well as the spatial and temporal dynamics of the habitat.

In this paper, we utilize a matrix population modelling approach developed by Horvitz and Schemske (1986) to examine the effects of forest dynamics and variation in modes and rates of dispersal on mean population fitness in *Cynoglossum virginianum*, an epizoochorous understory herb. Examination of responses of population growth rate to changes in specific life-history parameters may provide insight into the potential for selection to act upon that particular character (Caswell, 1989), as population growth rate is a measure of the mean fitness of a population (Fisher, 1930). Following Horvitz and Schemske's model, we use a projection matrix approach to combine patch-specific plant demographies with patch dynamics to determine the effect on population growth and structure of: 1) Changes in forest disturbance rate, defined as the probability of new treefall gap formation, 2) Changes in the rate of long-distance seed dispersal, defined as the proportion of seeds dispersed out of patches, and 3) Changes in patterns of seed dormancy.

Methods

1. *Species Description and Study Site*

Cynoglossum (Wild Comfrey) is a long-lived non-clonal

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spring flowering perennial of deciduous forests of eastern North America. Asexual plants form a basal rosette of between 1 and 7 basal leaves; reproductive plants also produce cauline leaves that decrease in size acropetally on the single inflorescence. Seeds (mericarps) mature by August. While seeds appear to be adapted for animal dispersal, most fall to the ground still attached to inflorescence (D.F. Whigham and J. O'Neill, pers. obs.).

We have studied three populations of *Cynoglossum* that occur in an approximately 125 year old deciduous forest on the property of the Smithsonian Environmental Research Center (SERC). SERC is located (38°51'N, 76°32'W) approximately 45 miles east of Washington (DC) on the Inner Coastal Plain of Maryland. Additional life history information and characteristics of the forest are described in Whigham et al. (1993).

2. *Methods*

Individuals in three populations that were marked in 1978 were censused annually for the following: 1. Number of rosette leaves on asexual plants, 2. Number of rosette and cauline leaves on flowering individuals, 3. Number of flowers, 4. Number of mature seeds. New seedlings were marked each year and the number of leaves recorded. Additional methodological details are given in Whigham et al. (1993).

Matrix Model Construction

1. *Treefall Gap Dynamics*

We used a modification of the combined model of forest dynamics and patch-specific population dynamics described by Horvitz and Schemske (1986). Forest canopy dynamics were modelled as a linear Markovian process of forest succession (Fig. 1) following disturbance caused by treefall gaps (Appendix 1), represented by the transition matrix **P**, whose entries p_{ij} represent the probabilities that type-j patches become type-i patches in one year's time. The probability that a patch becomes a new treefall gap, p_{1j}, depends upon the number of years since the last treefall occurred in that patch. Beginning at a low probability for newly formed gaps (0.0001), p_{ij} increases to an asymptotic value k (Fig. 2). These assumptions lead to an $j \times j$ matrix of the form represented in Table 1. The column eigenvector, **f***, associated with the dominant eigenvalue (λ) of the **P** matrix is proportional to the stable patch-type distribution.

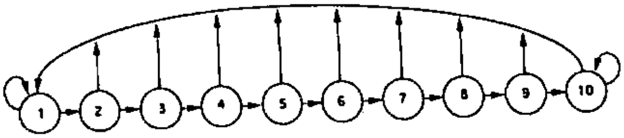

Fig. 1. Diagram of the linear Markovian patch dynamics model employed in this study. Circles represent patch-types beginning with newly-formed gaps (1) and ending with full understory patches (10). Arrows represent transitions among the various patch-types across one year's time.

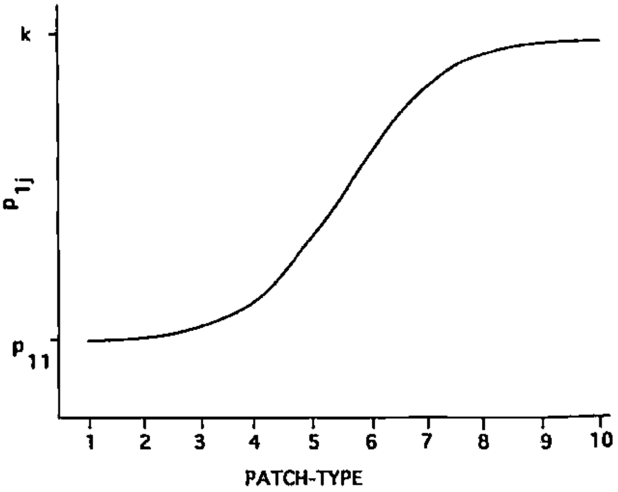

Fig. 2. Diagrammatic representation of the probability of new treefall gap formation (p_{1j}) as a function of patch-type.

2. *Patch-specific Population Dynamics*

To model plant population dynamics within a particular patch type, we assumed a stage-classified matrix model (Caswell, 1989). This type of model can be represented by a life cycle diagram in which arrows represent transitions among stages over one year's time. The life history diagram represented in Fig. 3 is based upon our demographic field studies of *C. virginianum* at SERC. The model contains eight life history stages:

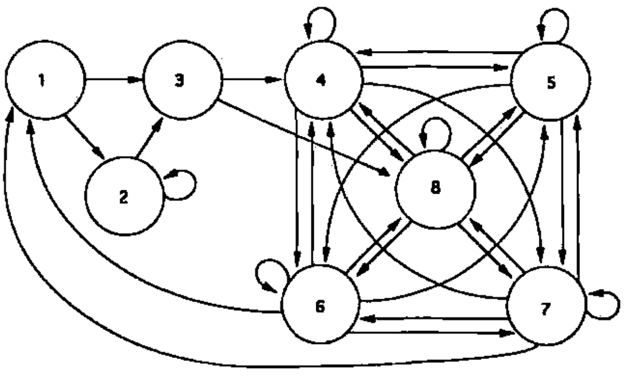

Fig. 3. Life cycle diagram for *Cynoglossum virginianum* at SERC, Maryland. Circles represent life-history stages: 1 = seeds, 2 = dormant seeds, 3 = seedlings, 4 = small non-reproductives, 5 = large non-reproductives, 6 = small reproductives, 7 = large reproductives, 8 = dormant plants. Arrows represent transitions or reproductive contributions of any particular stage to another stage over one year's time.

Table 1. Patch type transition matrix (P) under two rates of canopy disturbance (k).

Probability of new gap formation in closed canopy (k)=0.0086									
0.000100	0.000704	0.003466	0.007194	0.008384	0.008571	0.008596	0.008599	0.008600	0.008600
0.999900	0	0	0	0	0	0	0	0	0
0	0.999296	0	0	0	0	0	0	0	0
0	0	0.996534	0	0	0	0	0	0	0
0	0	0	0.992806	0	0	0	0	0	0
0	0	0	0	0.991616	0	0	0	0	0
0	0	0	0	0	0.991429	0	0	0	0
0	0	0	0	0	0	0.991404	0	0	0
0	0	0	0	0	0	0	0.991401	0	0
0	0	0	0	0	0	0	0	0.991400	0.991400
Probability of new gap formation in closed canopy (k)=0.0172									
0.000100	0.000842	0.005363	0.013752	0.016724	0.017145	0.017194	0.017199	0.017200	0.017200
0.999900	0	0	0	0	0	0	0	0	0
0	0.999158	0	0	0	0	0	0	0	0
0	0	0.994637	0	0	0	0	0	0	0
0	0	0	0.986248	0	0	0	0	0	0
0	0	0	0	0.983276	0	0	0	0	0
0	0	0	0	0	0.982855	0	0	0	0
0	0	0	0	0	0	0.982806	0	0	0
0	0	0	0	0	0	0	0.982801	0	0
0	0	0	0	0	0	0	0	0.982800	0.982800

seeds, dormant seeds, seedlings, small and large juveniles, small and large adults, and dormant plants. Within one year's time: 1) Seeds (stage 1) can either germinate, die, or become dormant seeds, 2) Dormant seeds (stage 2) may either die, remain dormant, or become seedlings, 3) Seedlings (stage 3) either die or become juveniles or go dormant, 4) Juveniles (stages 4 and 5) may die, go dormant, remain juveniles of the same or a different size, or move to one of the adult classes, 5) Adults (stages 6 and 7) may die, go dormant, remain adults of the same or a different size, or regress to one of the juvenile stages, and 6) Dormant plants (stage 8) may remain dormant or move to one of the juvenile or adult stages. Plants contribute to the seed class through reproduction by adults (stages 6 and 7), a process represented by arrows leading from later stages to the seed stage. Size classes of juveniles and adults were determined using Moloney's (1986) algorithm for multiple censuses and multiple subpopulations. We were able to distinguish two size classes, which we termed small (1 to 4 leaves) and large (5 leaves and larger).

The matrix representation (M) of this life history is shown in Table 2. The elements of M, m_{ab}, represent transitions from stage b to stage a in one year's time. Such a stage classified matrix is known as a Lefkovitch (1965) stage-projection model (Caswell, 1989), and is analogous to a Leslie (1945) age-classified model. In the present model, only stages 6 and 7 (small and large reproductives) actually reproduce; however, other stages contribute to seed production via the product of their transitions to stages 6 and 7 (m_{6b}, m_{7b}) and the stage-specific fertilities of those size classes (z_6, z_7) (Appendix 1). The initial numerical equivalent that represents population dynamics in a new treefall gap, is called 'PATCH-1' type demography, and was obtained by boot-strap resampling ($n=100$ resamples) of the data for subpopulation 3 (new gap conditions) for the first six years following the 1980 treefall (Table 3).

The mathematical properties of the matrix M correspond to basic demographic properties of the population (Caswell, 1989). The long-term dynamics of the

Table 2. Generalized form of the population demographic matrix (M) corresponding to the life-history diagram of *C. virginianum* represented in Fig. 3.

0	0	0	m_{14}	m_{15}	m_{16}	m_{17}	m_{18}
m_{21}	m_{22}	0	0	0	0	0	0
m_{31}	m_{32}	0	0	0	0	0	0
0	0	m_{43}	m_{44}	m_{45}	m_{46}	m_{47}	m_{48}
0	0	0	m_{54}	m_{55}	m_{56}	m_{57}	m_{58}
0	0	0	m_{64}	m_{65}	m_{66}	m_{67}	m_{68}
0	0	0	m_{74}	m_{75}	m_{76}	m_{77}	m_{78}
0	0	m_{83}	m_{84}	m_{85}	m_{86}	m_{87}	m_{88}

Table 3. Seedling-to-seed ratios and mean reproductive rate (*R*) for three *C. virginianum* subpopulations at SERC. Understory conditions prevailed for the entire census period (1979 to 1992) for subpopulations 1 and 2, while subpopulation 3 became exposed by a treefall gap in the winter of 1980 (end of year 1). For each subpopulation, *R* (multiplicative growth rate) was calculated as the mean of N_{t+1}/N_t across the indicated census periods. Germination (Germ) estimates represent overall seedling-to-seed ratios for the indicated census period.

Population	Interval	Seeds	Seedlings	Germ	*R*
1	First 6 years	145	34	0.2345	0.942
	Second 7 years	150	53	0.3533	1.037
	Overall	295	87	0.2949	0.993
2	First 6 years	205	44	0.2146	0.910
	Second 7 years	132	49	0.3712	1.057
	Overall	337	93	0.2759	0.989
3	First 6 years	360	95	0.2639	1.685
	Second 7 years	22	6	0.2727	0.776
	Overall	382	101	0.2643	1.195
	Grand total	**1014**	**281**	**0.2771**	**1.059**

matrix are governed by its dominant eigenvalue, λ, which provides a measure of asymptotic multiplicative population growth rate. The column eigenvector, **w**, is proportional to the stable stage distribution, while the elements of the row eigenvector, **v**, are proportional to stage-specific reproductive values. Elasticities, e_{ab}, which are equal to $(m_{ab}/\lambda) \times (d\lambda/dm_{ab})$ (de Kroon, et al., 1986), represent the relative effects of proportional changes in the elements of the matrix **M** with respect to their effects on λ.

3. *Changes with Forest Succession*

Although we have data available for demographies spanning 14 years of succession following gap formation in subpopulation 3, sample sizes within any particular year were insufficient to obtain reliable within-year transition matrices. Thus, we combined data for the first six years following gap formation (PATCH-1 = new gap conditions), and combined the data for the last seven censuses of subpopulation 3 into a second data set (PATCH-6 = closing gap conditions). Data for the first year of the data set for subpopulation 3 were combined with data from all years for subpopulations 1 and 2 to form the data set we considered representative of full understory conditions (PATCH-10 = full understory). For each of the three data sets, we resampled the data with replacement ($n = 100$ resamples) to obtain means and error estimates for the transition elements and stage-specific fertilities (Table 4). Because our estimates for transitions involving seeds and dormant seeds were indirect (Appendix 1), these values were initially held constant among matrices.

To create demographic matrices for the full range of patch-types ($n = 10$), we modelled linear change in each transition element from its value in PATCH-1 to its value in PATCH-6, and from its value in PATCH-6 to its value in PATCH-10. We thus arrived at transition matrices we considered representative of the first nine years following gap formation (PATCH-1 through -9) as well as all patches aged 10 years or older (PATCH-10). Row 1 of each new submatrix was created in the same fashion as row 1 the PATCH-1 matrix (Appendix 1).

4. *Overall Population Dynamics*

To characterize overall population dynamics, the model of forest dynamics was combined with the model of patch-specific population dynamics. The population at time *t* could then be characterized by a vector, **n**, with a dimension equal to the number of stage classes × the number of patch types; in our case, $8 \times 10 = 80$. All possible transitions among stages and among patch types were contained in a matrix **G**, comprised of one-hundred 8×8 submatrices, $\mathbf{SUB}_{ij}$. Each entry in **G**, g_{abij}, represents the probability that an individual in stage class *b* in patch type *j* contributes to or appears as an individual in stage class *a* in patch type *i* after one year's time.

A model representing static spatial heterogeneity without long-distance dispersal was first developed by ordering the ten patch-specific matrices along the diagonal of **G**, beginning with the PATCH-1 matrix in the upper left corner. To include successional processes, the 8×8 submatrices of **G** ($\mathbf{SUB}_{ij}$) were altered to form new submatrices ($\mathbf{SUBT}_{ij}$) determined by the successional dynamics of the forest and the timing of gap formation with respect to the annual census (Ap-

Table 4. Population demographic matrices (M) for *C. virginianum* considered representative of a) newly-formed gap conditions, b) closing gap conditions, and c) full understory conditions.

a) PATCH-1 (newly formed gap):

0	0	0	1.3060	5.9211	7.9723	5.4391	0
0.7710	0.2290	0	0	0	0	0	0
0.2290	0.0480	0	0	0	0	0	0
0	0	0.5032	0.4689	0.4176	0.3447	0.1641	0.8047
0	0	0	0.0965	0.1999	0.1283	0.5819	0.1953
0	0	0	0.0123	0.0804	0.2722	0.2540	0
0	0	0	0.0536	0.2159	0.1102	0	0
0	0	0.0864	0.0229	0.0364	0.1446	0	0

b) PATCH-6 (closing gap):

0	0	0	0	0.6327	1.5227	0	0
0.7710	0.2290	0	0	0	0	0	0
0.2290	0.0480	0	0	0	0	0	0
0	0	0.7190	0.7477	0.2502	0.6571	0.6690	0.6885
0	0	0	0.0238	0.6876	0.1932	0.3310	0
0	0	0	0	0	0	0	0
0	0	0	0	0.0622	0.1497	0	0
0	0	0	0	0	0	0	0.3115

c) PATCH-10 (full understory):

0	0	0	0.1464	1.4138	1.5227	1.4668	0.2370
0.7710	0.2290	0	0	0	0	0	0
0.2290	0.0480	0	0	0	0	0	0
0	0	0.6252	0.6785	0.2985	0.6571	0.2589	0.6614
0	0	0	0.1261	0.5100	0.1932	0.5574	0.1122
0	0	0	0.0038	0.0082	0	0	0
0	0	0	0.0112	0.1321	0.1497	0.1442	0.0233
0	0	0.0457	0.0252	0.0126	0	0	0.2031

pendix 1). The patch dynamics transition parameters, p_{ij} (Table 1) determine the probabilities that patch types will change before the next census. We assumed that most tree falls at SERC occur during times of high wind in the springtime (March and April, just before the annual census). As such, we post-multiplied the SUB_{ij} matrices by the p_{ij}'s to obtain the new submatrices, SUBT_{ij}. The resulting matrix represented overall population dynamics including successional changes and patch-specific demography.

5. *Long-distance Seed Dispersal*

To model effects of long distance seed dispersal, we defined y as the proportion of seeds that move out of patch type j. We then assumed that the probability that a dispersed seed reaches patch type i depends only upon the relative frequency of patch types in the environment, f^*_i, where f^* is a vector representing the stable patch-type distribution. The overall population model with long-distance dispersal (D) was essentially identical to the model without dispersal (G), except that in every submatrix the element g_{31ij} (seed-to-seedling transitions) was reduced by the proportion of seeds dispersed out of the patch and increased by the fraction dispersed into the patch (Appendix 1).

6. *Increased Seed Dormancy*

Seed dormancy, which was included explicitly in our transition matrices in order to allow tracking of dormant seed frequencies, can be modified through changes in the seed-to-dormant seed or in the dormant seed-to-seedling transitions (m_{21} and m_{32}, respectively). Because our estimates of parameters involving seed germination and dormancy were indirect, we modelled variation in the seed-to-dormant seed transition (m_{21}) as a means of assessing potential effects on population growth. To do this, we linearly increased the transition from seeds-to-dormant seeds in each of the 10 patch-types starting with the PATCH-1 estimate and increasing to a level of twice that in the PATCH-10 matrix (dormancy higher in new gap conditions), a condition we termed "INC1". We also modelled the opposite pattern (seed dormancy higher in understory conditions) by increasing the seed-to-dormant seed transition linearly from its PATCH-10 value to a level of twice that in the PATCH-1 matrix, a condition we termed "INC2".

7. *Matrix Analysis and Modelled Parameters*

We used AT-MATLAB (The Mathworks, Inc., 1989) to construct the models and to obtain for each matrix: λ, w, v, and the matrix of elasticities (E). We modelled all combinations of variation in three different parameters: 1) Forest canopy disturbance (k), at the observed rate of 0.0086 and at a doubling of that rate (0.0172). 2) Long-distance seed dispersal (y), at values ranging from 0 to 1.0, and 3) Seed dormancy (m_{21}), at the observed rate and for the two patterns of increased seed dormancy (INC1 and INC2).

Results

1. *Forest Canopy Dynamics*

Based upon prior analyses (Cipollini et al., submitted), we have estimated that new treefall gaps in 1992 comprised 0.86% of the area in closed canopy in 1991. Based upon an estimated rate of radial gap closure (0.35 m per year), mean time to closure was 8.3 years, which yielded the nine gap stages used in this model. At $k=$ 0.0086, the stable patch-type distribution (f^*_i) was dominated by understory patches; i.e. over 92% of patches were understory (Fig. 4). The relative area in gaps of all ages (sum of f^*_1 through f^*_9) was 0.0744, which compared favorably with our empirical estimate of 0.0542 (Cipollini et al., submitted). When k was doubled to 0.0172, f^*_i was shifted accordingly, with an increased relative abundance of patches in the various stages of succession (Fig. 4).

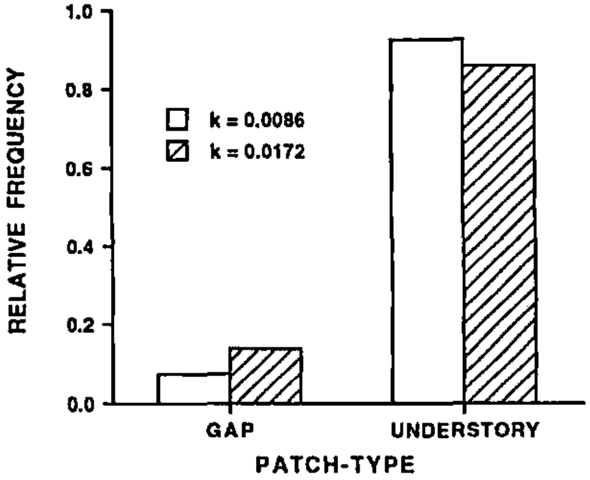

Fig. 4. Effect of rate of new gap formation in closed canopy (k) on the relative frequency of gaps (patch-types 1–9: GAP) and fully-closed understory (patch-type 10: UNDERSTORY).

2. *Patch-specific Demography*

Numerical estimates for PATCH-1, PATCH-6, and PATCH-10 demography are shown in Table 4. Relative to full understory conditions (PATCH-10 demography) notable differences in the other two transition matrices included: 1) An increase in reproductive output in new gap conditions (PATCH-1), which was associated with an increase in plants moving from juvenile to reproductive classes; 2) A near complete suppression of reproduction in closing gap conditions (PATCH-6); and 3) An increase in seedling mortality in new gap conditions (PATCH-1).

Eigenanalysis of the individual submatrices showed that population size should increase exponentially in patch-types 1 and 2, whereas it should decrease in all other patch-types (Fig. 5). As such, these results suggest that the demography of *C. virginianum* may be dependent upon rates and spatial patterning of treefall gap formation. Elasticity analyses indicate that the most influential transitions were seed-to-seedling, seedling-to-small juvenile, and the small juvenile self-loop (m_{31}, m_{43} and m_{44}, respectively) in new gaps, and the small and large juvenile self-loops (m_{44} and m_{55}, respectively) in both closing gaps and understory conditions (Table 5).

Stable population distributions were dominated by seeds and dormant seeds in new gap conditions, whereas distributions were dominated almost exclusively by small and large juveniles in closing gap conditions (Table 5). Stable population distributions in full understory conditions were intermediate with respect to new gap and closing gap conditions, being dominated by small juveniles, seeds and dormant seeds. Reproductive values of the various stage classes also

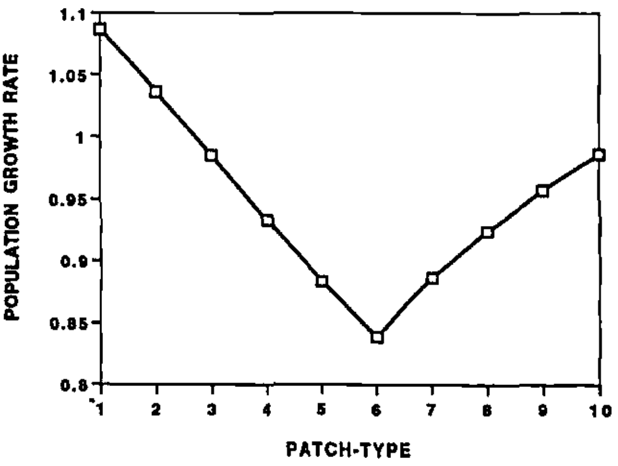

Fig. 5. Patch-specific population growth rate (λ) for each of 10 patch-types (PATCHES-1 to -10). Results were obtained from eigenanalysis of the individual submatrices, without patch dynamics or seed dispersal.

Table 5. Results of eigenanalysis of population demographic matrices corresponding to PATCH-1, PATCH-6, and PATCH-10 type demographies.

Submatrix=PATCH-1 (newly-formed gap): $\lambda=1.0858$

E=

0	0	0	0.0549	0.0507	0.0219	0.0220	0
0.0237	0.0063	0	0	0	0	0	0
0.1258	0.0237	0	0	0	0	0	0
0	0	0.1245	0.1415	0.0257	0.0068	0.0048	0.0247
0	0	0	0.0689	0.0291	0.0060	0.0401	0.0142
0	0	0	0.0102	0.0135	0.0147	0.0202	0
0	0	0	0.0446	0.0366	0.0060	0	0
0	0	0.0249	0.0081	0.0026	0.0033	0	0

Stable population distribution (w):

0.3805	*0.3460*	*0.0964*	*0.1176*	*0.0240*	*0.0077*	*0.0113*	*0.0120*

Stable reproductive values (v):

0.2098	0.0469	0.8378	1.5077	3.5671	4.1262	4.1516	1.7573

Submatrix=PATCH-6 (closing gap): $\lambda=0.8390$

E=

0	0	0	0	0.0226	0	0	0
0.0047	0.0018	0	0	0	0	0	0
0.0179	0.0047	0	0	0	0	0	0
0	0	0.0226	0.4823	0.0303	0	0.0060	0
0	0	0	0.0589	0.3192	0	0.0114	0
0	0	0	0	0	0	0	0
0	0	0	0	0.0174	0	0	0
0	0	0	0	0	0	0	0

Stable population distribution (w):

0.0908	0.1082	0.0310	0.6407	0.1204	<0.0001	0.0089	<0.0001

Stable reproductive values (v):

0.1652	0.0359	0.4842	0.5649	2.1625	1.4733	1.3039	0.7376

Submatrix=PATCH-10 (full understory): $\lambda=0.9864$

E=

0	0	0	0.0131	0.0463	0.0009	0.0096	0.0011
0.0125	0.0038	0	0	0	0	0	0
0.0585	0.0125	0	0	0	0	0	0
0	0	0.0653	0.3128	0.0503	0.0021	0.0087	0.0156
0	0	0	0.1027	0.1516	0.0011	0.0332	0.0047
0	0	0	0.0028	0.0022	0	0	0
0	0	0	0.0094	0.0404	0.0009	0.0088	0.0010
0	*0*	*0.0058*	*0.0141*	*0.0026*	*0*	*0*	*0.0058*

Stable population distribution (w):

0.2403	0.2446	0.0677	0.2990	0.1092	0.0021	0.0219	0.0155

Stable reproductive values (v):

0.1400	0.0315	0.4969	0.7202	1.2716	1.1432	1.3067	0.8715

shifted with patch-type, being highest for the two adult classes in new gap conditions and highest for large juveniles and small adults in closing gap conditions (Table 5). As with stable distributions, stable reproductive values for full understory were somewhat intermediate with respect to the two other matrices, with reproductive values highest for the large juvenile and large adult size classes.

3. *Population Dynamics Coupled with Forest Canopy Dynamics*

A. *Influence of doubling the rate of canopy gap formation (k)*

Under all conditions of seed dispersal rates, doubling the rate of canopy gap formation had small negative effect on overall population growth rate (Fig. 6). These results were a manifestation of an increased proportion of the landscape occupied by patches in later successional stages (closing gap conditions), where reproductive output is substantially decreased. For instance, for $y=0.2$, a doubling of k from 0.0086 to 0.0172 nearly doubled the proportion of each stage class within gaps, based upon the stable stage × patch-type distribution (results not shown). These results also suggest that, under current conditions at SERC, population growth rate is slightly lower than the level necessary for maintenance of population size.

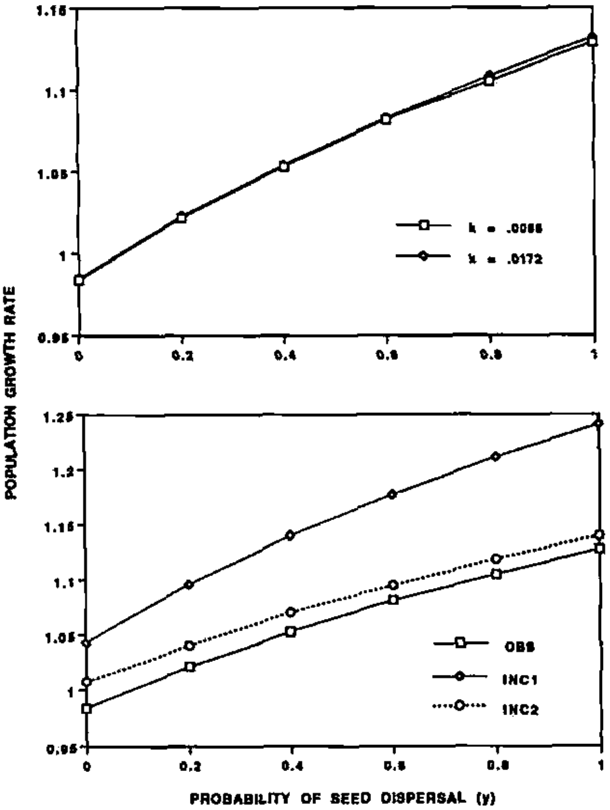

Fig. 6. Population growth rate (λ) as a function of long-distance seed dispersal (y) under two sets of conditions: Top) two levels of forest disturbance rate (k); Bottom) three conditions of assumed seed dormancy: OBS=observed dormancy pattern, INC1=dormancy higher in the understory relative to gaps, and INC2=dormancy higher in gaps relative to the understory.

B. *Influence of increasing the rate of long-distance seed dispersal (y)*

For both levels of forest disturbance, increasing the seed dispersal rate increased population growth rate (Fig. 6). The primary stage class influenced by increased long-distance seed dispersal were dormant seeds, whose presence was increased in understory conditions where survivorship was somewhat enhanced (Table 6).

C. *Influence of increased seed dormancy (INC1 and INC2 conditions)*

Under all conditions of forest disturbance rates (k) and long-distance seed dispersal rates (y), increases in the seed-to-dormant seed transition (m_{21}) increased population growth rate (Fig. 6). This positive effect of enhanced dormancy was particularly important when dormancy was made higher in new gap conditions (INC1). This effect was the result of an enhanced ability of seedlings, which are produced primarily by new gap adults, to survive in new gap conditions where seedling mortality is higher. This result was associated with a relative increase in seedlings appearing in the understory (Table 6).

Discussion

1. *Forest Canopy Dynamics*

Our estimate of the rate of treefall gap formation in closed canopy ($k=0.0086$) compares favorably with previous estimates for other mature forests, which generally range from about 1 to 2% per year (Hartshorn, 1978; Brokaw, 1982; Runkle, 1985; Runkle and Yetter, 1987). Additionally, our modelled estimate of the relative canopy area in gaps of all stages was close to our empirical estimate. Thus, it seems that the patch dynamics model we employed gives a reasonably accurate picture of treefall gap dynamics at SERC. Horvitz and Schemske (1986) indicated that the relative effect of assuming an increased number of patch-types is small when compared with increases in the rate of treefall gap formation (k). From the perspective of an understory herb, canopy conditions after nine years regrowth in an average-sized gap are probably very little different from conditions in full understory.

2. *Patch-specific Demography*

In their original formulation of the basic model that we employed, Horvitz and Schemske (1986) modelled demographic decays in a series of patch-types starting with the most favorable site (PATCH-1). As such, they assumed that demographic parameters decrease with succession for all life-history stages. Our model differs from their's primarily because different life history stages have different patterns of change such that

Table 6. Stable *stage* × patch-type distributions under two rates of long-distance seed dispersal (*y*) and two patterns of enhanced seed dormancy. GAP = summation of relative frequencies of individuals in patch-types 1 to 9, UND = relative frequency of individuals in patch-type 10, OBS = observed pattern of dormancy, INC1 = dormancy higher in gaps, and INC2 = dormancy higher in understory.

Stage Class	OBS		INC1		INC2	
	GAP	UND	GAP	UND	GAP	UND
I. Proportion of seeds leaving a patch (*y*) = 0						
Seeds	0.0284	0.2161	0.0246	0.1914	0.0213	0.1475
Dormant seeds	0.0304	0.2190	0.0490	0.1801	0.0344	0.4106
Seedlings	0.0084	0.0606	0.0107	0.1001	0.0109	0.0529
Small non-reproductive	0.0260	0.2697	0.0260	0.2872	0.0259	0.1973
Large non-reproductive	0.0050	0.0983	0.0043	0.0895	0.0041	0.0679
Small reproductive	0.0005	0.0019	0.0005	0.0017	0.0004	0.0013
Large reproductive	0.0013	0.0197	0.0011	0.0173	0.0010	0.0134
Dormant plants	0.0009	0.0138	0.0009	0.0153	0.0009	0.0102
II. Proportion of seeds leaving a patch (*y*) = 0.8						
Seeds	0.0229	0.1767	0.0178	0.1454	0.0198	0.1345
Dormant seeds	0.0213	0.1544	0.0292	0.1133	0.0274	0.3112
Seedlings	0.0127	0.1477	0.0141	0.2194	0.0161	0.1208
Small non-reproductive	0.0235	0.3146	0.0205	0.3295	0.0259	0.2464
Large non-reproductive	0.0038	0.0849	0.0029	0.0726	0.0036	0.0649
Small reproductive	0.0004	0.0017	0.0003	0.0015	0.0004	0.0013
Large reproductive	0.0010	0.0159	0.0008	0.0130	0.0009	0.0121
Dormant plants	0.0009	0.0174	0.0008	0.0190	0.0011	0.0137

growth, survivorship and reproductive parameters are not necessarily highest in new gaps or lowest in full understory. For instance, while reproductive outputs were highest for *C. virginianum* adults in early successional stages, seedling survivorship was lowest. Additionally, plants in closing gaps had the lowest reproductive outputs while seedling establishment was slightly enhanced under these conditions. These particular patterns may relate to the particular life history of *C. virginianum*, or to density-dependent effects; e.g. depressed seedling survivorship at high density in new gaps, depressed reproductive output of adults at high density in closing gaps. The suppression of reproductive output in closing gaps might also result from enhanced reproductive output in new gap conditions which may impose delayed reproductive costs as canopy closure progresses.

3. *Population Dynamics Coupled with Forest Canopy Dynamics*

Under all conditions, doubling the rate of canopy gap formation had small negative effects on population growth rate. These results were due to an increased proportion of the landscape occupied by patches in later successional stages (closing gap conditions), where demographic parameters were substantially decreased. Regardless of canopy disturbance level, overall population growth rates remained near 1.0, the level necessary to maintain population size. These levels, which ranged from 0.983 to 1.148 were close to the mean multiplicative growth rate (*R*) calculated from field census data for the understory subpopulations 1 and 2 (0.991), and were slightly lower than the mean *R* for the gap subpopulation 3 (1.195). These results demonstrate the need for integrative approaches such as matrix modelling to elucidate effects of canopy dynamics on understory plants. Based solely upon empirical estimates of *R*, one might have concluded that increased rates of canopy disturbance should increase overall population growth rate of this species.

Under all conditions, increased long-distance seed dispersal increased population growth rate. This benefit for long-distance dispersal resulted from the increased presence of seedlings and juveniles in understory conditions, where survivorship was somewhat enhanced. From these results, we predict selection pressure for long-distance dispersal in *C. virginianum*. This conclusion varies somewhat from field observations suggesting that, although potentially dispersed via epizoochory, most seeds germinate within a distance equal to the height of the flowering stalk (J. O'Neill, pers. obs.). Sporadic long-distance seed dispersal may play a larger role in gene flow and population genetic structure than it does in influencing population demography in this species.

Under all conditions of forest disturbance and long-distance seed dispersal, modelled increases in seed dormancy substantially increased population growth rate. This positive effect of enhanced dormancy was especially notable under conditions of enhanced dormancy in new gaps. Modelling increases in seed dormancy were the only modifications that resulted in population growth rates consistently above 1.0. Under conditions of enhanced dormancy in new gaps, lambda approximated the empirically-determined mean R (1.059 across all three subpopulations and years). Under those conditions, λ ranged from 1.043 to 1.241 depending upon the rate of long-distance seed dispersal. This effect was the result of an enhanced ability of seeds to survive in new gap conditions.

Overall, our modelling approach could be improved with better data on the relative performance of the various life history stages in all patch-types leading toward full canopy conditions. We know of no such data set for understory herbs such as *C. virginianum*, or for any other plant species. Such data are extremely difficult to obtain because of the constraints imposed by the sampling regimes necessary to obtain reliable transition element estimates. To conduct such an analysis, one must identify gaps of known ages and census individuals of all stages in these gaps over a sufficient number of years. Our data preclude stronger conclusions primarily because only one of our subpopulations was subjected to canopy exposure; changes in transitions that occurred in subpopulation 3 may not have resulted entirely from changes in canopy conditions. But because the data were taken from subpopulations that differed little in initial conditions, the assumption is not unreasonable that the reponses seen in subpopulation 3 were caused by the changes brought about by canopy opening and closure. Additionally, the small sample sizes made it impossible to obtain reliable within-year estimates of transition elements, thus we were forced to obtain estimates for initial (new gap) and later (closing gap) conditions based upon combined data across years. Because patch size and shape can also influence responses of understory plants (cf., Howe, 1990; Phillips and Shure, 1990; Dirzo, et al., 1992), one should obtain sufficient samples from treefall gaps of all ages and sizes, so as to allow more reliable transition element determination.

With these caveats, the salient result of this study is that the effects of canopy opening and closure may have differential non-linear effects upon different life-history stages. Demographic parameters may not simply decay over time at different rates and patterns, as in the model of Horvitz and Schemske (1986), but may show increases or decreases over the successional sequence, depending upon the particular responses to canopy conditions of particular life-history stages. Based upon our analysis, an increase in canopy disturbance should affect patterns of growth, mortality and reproduction in such a manner as to slightly decrease population growth in *C. virginianum*. This finding contrasts with conclusions for all conditions modelled by Horvitz and Schemske (1986) for the tropical understory herb *Calathea ovandensis* and with our results for the temperate-zone shrub *Lindera benzoin* obtained using similar modelling approaches (Cipollini et al., submitted). In these latter two analyses, growth, survivorship and reproduction were all made to decay with canopy closure; thus, increased canopy disturbance always increased population growth rate as the number of patches in gap stages increased. Based upon our results for *C. virginianum*, it is clear that field data concerning the effects of canopy opening and closure on all life history stages will be necessary for improved predictions concerning responses of understory plants to forest canopy dynamics.

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APPENDIX 1. The following details concerning the general model are summarized and modified from Horvitz and Schemske (1986).

1. Forest canopy dynamics

The linear Markovian process of forest succession following treefall gap formation is represented by the transition matrix **P** and the equation:

$$(1) \qquad \mathbf{f}_{t+1} = \mathbf{P} \times \mathbf{f}_t,$$

where **f** is a vector representing the patch-type distribution. The elements of **P**, p_{ij}, represent transition probabilities from type-j patches to type-i patches in one year's time. The probability that a particular patch becomes a new treefall gap, p_{1j}, is described by a logistic relationship between the probability of gap formation and the age of the gap:

$$(2) \qquad p_{1j} = k/\{1+(k/p_{11}-1)/e^{r(j-1)}\},$$

where r represents the rate of change of the probability of gap formation, k represents the probability of gap formation in closed canopy, and p_{11} represents the probability of new gap formation in new gaps. For any particular k, the value of r was approximated by trial and error while setting p_{11} at 0.0001 and $p_{1,10}$ at k. We used the lowest r yielding a p_{1n} equal to the empirically-derived k (to four decimal places). The column eigenvector, **f***, of the matrix P associated with its dominant eigenvalue ($\lambda = 1.0000$) is proportional to the equilibrium distribution of patch types and upon normalization such that its elements sum to 1, is termed the stable patch-type distribution.

2. Plant population dynamics

Assuming 8 stage-classes, the linear dynamics of the system are represented by the matrix **M** and the equation:

$$(3) \qquad \mathbf{n}_{t+1} = \mathbf{M} \times \mathbf{n}_t,$$

where **n** is a vector representing the stage-class distribution. The elements of **M**, m_{ab}, are the probabilities that an individual in stage class b contributes to or moves to stage class a in one year's time. The first row of **M** is calculated by considering the probability that individuals in each stage class move to reproductive classes in one year's time. Let z_6 and z_7 represent the stage-specific fertilities of small and large females (stages 6 and 7, respectively). The first row (non-seed) entries of **M**, m_{1b}, are calculated as follows:

$$(4) \qquad m_{1b} = \{(m_{6b} \times z_6) + (m_{7b} \times z_7)\}$$

3. Transitions involving seeds

Generally, seed-to-seedling transitions are estimated from counts of seeds in one year coupled with counts of seedlings in the subsequent year. As a result of seed dormancy and our lack of data on seed longevity, we could not estimate directly transitions involving seeds and dormant seeds. Some census years had probabilities of seed germination that exceeded 1.0, when probability of germination was calculated as the number of seedlings per seed produced in the prior year (Table 3). We therefore assumed that a certain proportion of seeds remained dormant each year. From census data across all populations and all years, the seedling-to-seed ratio was 0.277, thus we assumed that the sum of m_{31} and m_{32} was 0.277. We then assumed that mortality of newly-produced seeds ($Mort_1$) was zero; i.e. newly-produced seeds either germinate or go dormant in one year's time. Because m_{31}, m_{32}, $Mort_1$, $Mort_2$ (overall dormant seed mortality) must sum to 1, we calculated dormant seed mortality:

$$(5) \qquad Mort_2 + m_{22} = 2 - 0.277 - 0 = 0.723.$$

Based upon our census data, a proportion of at least 0.192 seedlings germinated from dormant seeds. That is, a proportion of 0.192 of seedlings germinated from seeds that had to be > 1 yr old. These data were based on the numbers of seedlings appearing in subpopulations 1, 2 and 3 that exceeded the numbers of seeds produced in those subpopulations in the year prior to the census (seed dispersal in and out of subpopulations was assumed to be minimal and equal). In all three populations, germination of dormant seeds was completed within the course of four years. Assuming a constant germination rate of dormant seeds per year (no decay in germination until after the 4th year), the dormant seed-to-seedling transition was estimated:

$$(6) \qquad m_{32} = 0.192/4 = 0.048.$$

Assuming that m_{31} and m_{32} sum to 0.277, we estimated the seed-to-seedling transition:

$$(7) \qquad m_{31} = 0.277 - 0.048 = 0.229.$$

Because m_{21} and m_{31} must sum to 1, we estimated the seed-to-dormant seed transition:

$$(8) \qquad m_{21} = 1 - 0.229 = 0.771.$$

And finally, because m_{22}, $Mort_2$ and m_{32} must sum to 1, we estimated the dormant seed-to-dormant seed transition:

$$(9) \qquad m_{22} = 1 - 0.723 - 0.048 = 0.229.$$

4. Demographic changes with succession

To model demographic change for the full range of patch-types ($n = 10$), we modelled linear changes in

each transition element from PATCH-1 to PATCH-6, and from PATCH-6 to PATCH-10 matrices. Row 1 of each new submatrix was created in the same fashion as row 1 of the PATCH-1 matrix. Assume that z_{bj} is the stage-specific fertility of stage class b in patch j.
For $b = 2$ through 8:

$$(10) \qquad m_{1bj} = (m_{6bj} \times z_{6j}) + (m_{7bj} \times z_{7j})$$

5. Overall population dynamics

All possible transitions among stages and among patch types are contained in an 80×80 matrix **G**, such that:

$$(11) \qquad \mathbf{n}_{t+1} = \mathbf{G}_{ablj} \times \mathbf{n}_t,$$

where **n** represents the stage × patch-type distribution. The matrix **G** is comprised of one-hundred 8×8 submatrices, $\mathbf{SUB}_{ij}$. The elements of **G**, g_{abij}, represent the probability that an individual in stage class b in patch type j contributes to or appears as an individual in stage class a in patch type i after one year's time. The model representing spatial heterogeneity without successional change or migration was developed by ordering the ten 8×8 patch-specific population dynamics matrices along the diagonal of **G**, beginning with the PATCH-1 matrix in the upper left corner ($\mathbf{SUB}_{11}$=the PATCH-1 model, $\mathbf{SUB}_{22}$=the PATCH-2 model, ... $\mathbf{SUB}_{99}$=the *PATCH-9 model). Initially, other entries in* **G** *were* zeros.

To include successional processes, the one-hundred 8×8 submatrices ($\mathbf{SUB}_{ij}$) of **G** were altered using the following formula for calculating new $\mathbf{SUBT}_{ij}$ matrices:

$$(12) \qquad \mathbf{SUBT}_{ij} = \mathbf{SUB}_{ij} \times p_{ij}$$

The patch dynamics transition parameters, p_{ij} (Table 1) determine the probabilities that patch types will change before the next census, while the timing of gap formation determines if individuals in patch type j at time t undergo the demographic transitions of patch type j for most of the year or if they undergo the demographic transitions of patch type i for most of the year. Equation 12 uses the latter assumption.

6. Long distance seed dispersal

We defined y as the proportion of seeds that move out of patch type j, and assumed that the probability of a dispersed seed reaching patch-type i depends only upon the relative frequency of that patch-type in the environment, $\mathbf{f}^*_i$, where $\mathbf{f}^*$ is the stable patch-type distribution. The new matrix of overall population dynamics, **D**, is composed of one-hundred 8×8 submatrices, $\mathbf{SUBD}_{ij}$, defined in terms of the $\mathbf{SUBT}_{ij}$'s of the model without seed dispersal. $\mathbf{SUBD}_{ij} = \mathbf{SUBT}_{ij}$ in all entries except for d_{21ij} entries:

$$(13) \qquad d_{31ij} = g_{31ij} - (y \times g_{31ij}) + (y \times \mathbf{f}^*_i)$$

7. Seed dormancy

We linearly increased the m_{21} parameter in each of the 10 patch-types from the observed value for the PATCH-1 parameter to twice that level in the PATCH-*10 matrix (seed dormancy higher in new gap conditions*; INC1). We modelled the opposite pattern by increasing m_{21} linearly from its PATCH-10 value to twice that level in the PATCH-1 matrix (seed dormancy higher in understory conditions; INC2).