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ORIGINAL ARTICLE

Biennial cycling caused by demographic delays in a fire-adapted annual plant

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Abstract We explored models explaining population cycling in the annual *Warea carteri*. We modeled the life cycle of *W. carteri* and compared projected trajectories to independently observed trajectories (up to 16 years) of plants in 74 patches in three populations. We built matrix models with an annual time step for two populations, including four stages, (recently produced seeds, seeds in the seed bank, seedlings, and adults) and five vital rates, summarized in seven transitions. Fluctuations of both observed and modeled populations were evaluated using power spectra, autocorrelation, amplitude, and damping. Observed populations had two point cycling. Observed amplitude was higher in frequently burned populations, reached its maximum 1 year after fire, and then dampened. Asymptotic transition and vital rate elasticities showed that seedling survival was the most important factor for long-term population growth, but transient elasticities showed that recruitment from the seed bank was important during the first years post-fire. Deterministic modeling and elasticity analyses indicated that delayed germination (for 1 year) may explain biennial population cycling. Stochastic models created similar cycling with slower damping than deterministic models, but still had lower amplitudes (especially 1–3 years post-fire) than observed populations. The biennial cycle in *W. carteri* is likely caused by the delay in seed germination, which creates two overlapping cohorts of plants, much like a strict biennial. Fire initiates the cycle by killing aboveground individuals and promoting seedling recruitment in the first post-fire year.

Keywords Florida · Lake Wales Ridge · Matrix modeling · Population fluctuations · Transient dynamics

Introduction

Populations that fluctuate in size at more or less regular intervals are of great interest to biologists because understanding cycling can provide insights into population regulation and persistence. Examples include population fluctuations of Canadian hares (Krebs 1996), British grouse (Hudson et al. 1992; Moss et al. 1996), voles and lemmings (Stenseth 1999), and forest insects such as the European larch bud moth (Anderson and May 1980). Delayed density-dependent variation, consumer–resource interactions, and environmental fluctuations are frequently invoked as possible causes of population cycling in vertebrates and insects (Anderson and May 1980; Ginzburg and Inchausti 1997; Inchausti and Ginzburg 1998; reviewed in Kendall et al. 1999).

Whether plant populations experience population cycles is more controversial (Rees and Crawley 1989). Silvertown (1991) suggested that, because of long generation times, cycles may be unlikely in perennial plants, and that only longer-term studies in annual plants are

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likely to detect cycling empirically. Four proposed examples of plant population cycles involve annual species. Thrall et al. (1989) suggested that a particular functional form for density-dependent seed set in *Abutilon theophrasti* could lead to persistent oscillations, but cautioned that seed dormancy could dampen oscillations. Two-year cycles in *Erophila verna* were attributed to overcompensating density dependence (Symonides et al. 1986). However, Rees and Crawley (1991) argued that neither of these two examples satisfactorily demonstrated population cycles. Analysis of a 16-year field experiment with time-series and modeling attributed population cycling to delayed density dependence in the annual *Descurania sophia* (Gonzalez-Andujar et al. 2006). Delayed parental density effects also explained population cycles in the annual *Cardamine pensylvanica* (Crone 1997). Spatially explicit modeling of a hypothetical, non-clonal perennial has also revealed population cycling possibly caused by competition-controlled mortality and recruitment (Bauer et al. 2002).

In addition to these mechanisms, demographic delays may be another parsimonious explanation for population cycling. Although demographic delays have been described in biennials, no previous study has explored the utility of demographic delays in explaining population fluctuations in plants with other life histories. In strict biennials, the consistent delay in flowering until the second year initiates population cycles (Kelly 1985a, b, 1989a, b, c; De Jong et al. 1987; Hart 1997; Petrü 2005; Pardini et al. 2009). Demographic delay can co-occur with density dependent effects to determine cycling (Pardini et al. 2009). Population cycles in annual plants may also be caused by a consistent demographic delay that, when coupled with a disturbance that triggers germination from dormant seeds, synchronizes fluctuations across a population (see Lande et al. 2006).

Here, we test the demographic delay hypothesis using a fluctuating, fire-responsive annual species *Warea carteri* Small (Carter's mustard; Brassicaceae). This species is characterized by large fluctuations in aboveground population size, including the appearance and disappearance of populations from particular sites (Menges and Gordon 1996). Our goals were to characterize population cycles in *Warea carteri* from observed data and then to examine whether different types of models could reproduce the main cycle characteristics: autocorrelation, amplitude, and damping. We used data on seed germination, seedling survival, and fecundity, collected independently of density counts, to build a matrix projection model. We then considered population cycle characteristics with deterministic as well as stochastic models with different levels of variation in vital rates and transitions, with and without the synchronizing effect of fire.

Materials and methods

Study species and sites

Warea carteri is a narrowly endemic annual plant found on the Lake Wales Ridge in Lake, Polk, and Highlands Counties, central Florida, with historical records from the Atlantic Coastal Ridge. It occurs primarily on xeric yellow sands supporting sandhill or oak–hickory scrub, and on gray sands supporting scrubby flatwoods (Menges et al. 2007). Plants are usually single-stemmed, branched herbs up to 1 m tall. *W. carteri* produces white flowers in spherical inflorescences in the fall, and siliques mature in late fall, dehiscing to release small, gravity-dispersed seeds. Seeds can remain dormant in the soil for several years. Seedling recruitment occurs from June to April (i.e., recruitment begins prior to fruiting of the previous year's cohort), so cohorts overlap. Seedlings often remain as rosettes throughout the dry fall–spring season, typically producing flowering stalks in summer.

Warea carteri is self-compatible, and spontaneous self-fertilization (autogamy) frequently occurs (Evans et al. 2000). Floral morphology indicates a generalist insect pollination syndrome; flowers are visited by bees, flies, and wasps (Menges et al. 1998). Nonetheless, greater fruit and seed set under hand pollination than in open-pollinated controls indicated that *W. carteri* is pollinator-limited (Evans et al. 2000). Aboveground populations experience dramatic booms 1 year after fire, followed by equally dramatic crashes in the second post-fire year (Menges and Gordon 1996). Small fluctuating populations may persist in mechanically disturbed sites such as firelanes or trails.

We studied *Warea carteri* at three sites in central Florida. At Archbold Biological Station and the adjacent Lake Placid Scrub (part of the Lake Wales Ridge Wildlife and Environmental Area; considered as one site for these analyses: ABS/LPS), patches of *W. carteri* occurred in scrubby flatwoods (especially if recently burned) and along disturbed roadsides. Fire return intervals at ABS/LPS varied from frequent (2–5 years) to infrequent (20–59 years) in areas supporting this species. At Lake Wales Ridge State Forest (RSF), populations of *W. carteri* grew mainly along narrow trails in oak–hickory scrub. Only two patches at RSF were burned during our study. At Tiger Creek Preserve (TCP), *W. carteri* occurred in longleaf pine–wiregrass (*Pinus palustris–Aristida stricta* var. *beyrichiana*) sandhills or in adjacent scrubby flatwoods. Fire has been frequently (3–6-year intervals) applied to TCP in recent years.

Field data collection

Estimating vital rates

We conducted field experiments and observations that provided the parameters for modeling. Our seed experiment included seeds buried in 314 mesh bags divided among seven treatments that varied in burial depth (surface or 1–2 cm deep), litter versus sand cover, shading, and movement of seeds among depths. For this paper, we pool germination data from all treatments. Mesh bags were retrieved at 1, 8, 13, 19, and 25 months. Approximately 95–99% of the seeds were viable when tested in January 1998 (immediately after installing the experiment), decreasing to 85% viable seeds in February 1998 (1 month later). No field germination had occurred by this time, nor after 8 months (August 1998). Germination was high in February 1999 (13 months post-sowing); and continued with fewer germinants in August 1999 (19 months) and February 2000 (25 months). For input into models, we grouped each August's germination rate with the next February's rate since we considered both within the same June–April germination season. By the end of the experiment, we found very few recognizable seeds in the mesh bags; these had low subsequent survival, indicating that the seed bank decays to near zero after a few years.

We used data from censuses for naturally recruiting seedlings in permanent 0.25-m^2 plots monitored monthly (1999–2002) year-round at RSF ($n = 50$ plots) and at ABS/LPS ($n = 10$ plots), recording survival, plant height, and the presence of reproductive structures (Weekley et al. 2007). Most seedlings appeared in September through December. Nearly all (99%) seedlings that survived through the next germination season reached reproductive stage. Within years, we totaled number of seedlings across monthly cohorts and calculated the median value for each population across years and sites (ABS/LPS and RSF) to estimate the seedling-to-adult transition.

A common problem with seedling demographic data is a disparity between observations from seed germination experiments and what can be observed in periodic seedling cohorts in fixed quadrats. In the former context, germinants are typically counted in particularly accessible conditions such as petri dishes, plant pots, or mesh bags (in our case), facilitating accurate counts; in the latter context, seeds in the field may germinate but never emerge or may be overlooked in field censuses. We considered our germination-derived parameter estimates too optimistic, generating more seedlings than observed during monthly seedling censuses. To account for this source of mortality, we estimated the number of seedlings that may have germinated and died during the prior month, before they could be observed. We fitted a survivorship curve (logarithmic model) to our monthly seedling data and then extrapolated the likely number of seedlings that would have initiated the cohort. The difference between the extrapolated estimate and the number of seedlings actually observed was attributed to lost (i.e., dead) seedlings. These constituted an additional mortality term (51.2% of the seedlings) that was incorporated into estimates of seedling survival.

Our fecundity data consisted of counts of fruits per plant (mean 19.89 ± 2.53 SE) and seeds per fruit (9.00 ± 0.59) based on annual collections made in native scrub (excluding plants in roadsides) at ABS/LPS in November 1994–1996 ($n = 101$ plants; 116 fruits). These data were pooled across years as mean fecundity and multiplied by seed viability of seeds sown just after harvesting in the study sites (0.87 at RSF and 0.85 at ABS/LPS).

Population dynamics

We quantified population size annually for all known *Warea carteri* patches at each site (ABS/LPS, RSF, and TCP) during fall at peak flowering time, usually in early October. Locations of all *W. carteri* patches were mapped with a Trimble global positioning system with sub-meter accuracy (GPS) and stored in an ArcView Geographic Information System database. Each fall, we visited all previously known locations, and traveled all roads, many trails, and across recently burned sites in search of new patches. Patches were defined as spatially contiguous groups of plants separated by 50 m or more, or occurring in different management units. For each patch, we counted all flowering plants.

Data on flowering plant numbers in *W. carteri* typically included large fluctuations with many years with zeroes or very small population sizes. To increase the number of patches that could be analyzed, we grouped neighboring small patches ($n < 9$ plants for 5 or more years) with identical fire histories. Only patches with at least 5 years of data were included, because shorter time periods were not useful for characterizing cycles. We made no assumptions about the population size of a patch prior to our visit (i.e., we did not assume zero plants in this case). These rules created a dataset of 74 patches with 5–16 years of population size data.

Characterizing cycle period, amplitude and damping

We characterized both observed population cycles and those emerging from modeling by estimating autocorrelations, amplitudes, and damping. Data on time trends of flowering plant numbers from the three sites validated our models because count data used to characterize population cycling were independent of data for seed germination, seedling survival, and fecundity that underlay the matrix projection models.

We used two methods to identify the characteristic period of the population cycles. For each patch, we conducted an autocorrelation analysis (Chatfield 1984) of year-to-year differences in the natural logarithm of population size +1. We considered autocorrelation periods of 1, 2, 3, and 4 years. There is usually little point in calculating the autocorrelation statistic r_k for cycle periods (k) greater than about $n/4$ (n being the number of years in the dataset; Chatfield 1984). In addition, we implemented a MATLAB program by Reuman et al. (2006) to calculate consistent estimates of power spectra (i.e., the spectral density function of a stationary time-series; Parzen 1956; Brillinger 1981).

We calculated amplitude as the difference between the maximal and minimal natural logarithm-transformed population counts within a cycle (Ginzburg and Inchausti 1997). We averaged amplitudes of annual cycles across burned patches within populations. We graphed amplitudes with respect to time-since-fire to evaluate damping.

Modeling

Describing the life cycle

We characterized the life cycle of *Warea carteri* based on data derived independently of the plant counts used to describe population cycling. We parameterized our model based on the field seed germination experiment, data on seedling demography (Weekley et al. 2007), and fecundity estimates based on data collected at ABS/LPS (1994–1996). Our model consisted of four stages and seven transitions (Fig. 1). We used matrix projection modeling based on a life cycle with an annual time step centered at peak flowering in October (September through November among years; referred to as “fall”). Seed production also occurred in the fall (November). Seedling recruitment occurred from June through the following April, but most seedlings (84%) emerged from September through December.

Based on our seed germination experiment, seeds produced in October germinated 18–24 months later. This pattern is consistent with the appearance of seedlings in October and earlier, while another generation of seeds is still maturing on parental plants. Therefore, in the fall of one season there are two distinct cohorts of plants aboveground: flowering plants and new seedlings. There are also seeds in a persistent seed bank. Based on our germination experiment, older seeds did not survive as well as younger ones, so we model the seed bank in two age classes. Thus, there are four life-history stages during any one annual cycle: flowering adults, seedlings, first year seed bank, and older seed bank. There is no direct step from adults to adults; that is, all germination is delayed for a year or more. We used five vital rates [fecundity (f), seed survival (s_1), seed dormancy (d_1, d_2, d_3), germination (g_1, g_2, g_3), and seedling survival (z_1, z_2); Table 2]; the subscripts for dormancy and germination refer to freshly produced seeds, seeds in the first year seed bank, and seeds in the second year seed bank; the subscripts for seedling survival refer to before seedling detection and after seedling detection. From these five vital rates, we built seven transitions between censuses (Fig. 1): (1) flowering adult to seedling (FSD); (2) flowering adult to seed bank (FSB); (3) survival of viable/dormant seeds in the first-year seed bank (SBK_1); (4) survival of viable/dormant seeds in the older seed bank (>1 year; SBK_2); (5) seedling recruitment and early survival from the first year seed bank (SDS_1); (6) seedling recruitment and early survival from the older seed bank (SDS_2); and (7) seed/seedling survival (up to a year depending on when they germinate) to the next October, when they can become adults and flower (SUR; Tables 1, 2).

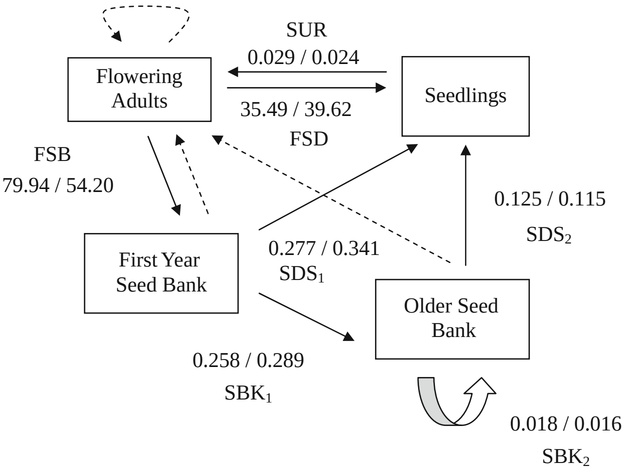


Fig. 1 Life cycle of *Warea carteri* showing mean annual transitions for Archbold Biological Station/Lake Placid Scrub (ABS/LPS) and Lake Wales Ridge State Forest (RSF), separated by slashes. *Discontinuous lines* show theoretical transitions of individuals without delayed dormancy. For abbreviations, see text

Deterministic modeling and transient dynamics

We used MATLAB to calculate the dominant eigenvalues [λ (lambda), the deterministic population growth rates], subordinate eigenvalues, the ratios of dominant to the second subordinate eigenvalue (λ_1/λ_2; measuring damping ratios), transient elasticities for matrix transitions with reference to seedling numbers (Caswell 2007) and

Table 1 General population matrix model for *Warea carteri*

	Older seed bank	1st year seed bank	Seedlings	Flowering adults
Older seed bank	SBK_2	SBK_1	–	–
1st year seed bank	–	–	–	FSB
Seedlings	$SDS_2 \times (1 - D)$	$SDS_1 \times (1 - D)$	–	$FSD \times (1 - D)$
Flowering adults	$SDS_2 \times (D) \times SUR$	$SDS_1 \times (D) \times SUR$	SUR	$FSD \times (D) \times SUR$

There are seven transitions: flowering adult to seedling (FSD); flowering adult to persistent seed bank (FSB); survival of viable/dormant seeds in the first-year seed bank (SBK_1); survival of viable/dormant seeds in the older seed bank (>1 year; SBK_2); seedling recruitment and early survival from the first year seed bank (SDS_1); seedling recruitment and early survival from the older seed bank (SDS_2); and seedling survival (up to a year depending on when they germinate) to the next October, when they can become adults and flower (SUR)

– Structural zeroes (impossible transitions), *D* the proportion of seeds that germinate without dormancy; the value of *D* is equal to 0 for the data-based matrices, based on our germination experiments

Table 2 *Warea carteri* vital rates (and asymptotic vital rate elasticity) and matrix transitions (and asymptotic transition elasticity) for Archbold Biological Station/Lake Placid Scrub and Lake Wales Ridge State Forest matrix models

Vital rates	Transitions											V. rate elasticity
	FSB	SBK_1	SBK_2	FSD	SDS_1	SDS_2	SUR	Autocorrelation				
	$f \times s_1^2 \times d_1$	$s_1^2 \times d_2$	$s_1 \times d_3$	$f \times s_1 \times z_1 \times g_1$	$s_1 \times z_1 \times g_2$	$z_1 \times g_3$	$z_1 \times z_2$	First lag		Second lag		
ABS/LPS												
Fecundity (*f*)	151.40			151.40				−0.113	0.21	0.144	0.179	0.4198
Seed survival (s_1)	0.962	0.962	0.962	0.962	0.962			−0.163	0.02	0.104	0.029	0.7278
Dormant (d_1)	0.571							−0.165	0.01	0.110	0.007	0.1476
Dormant (d_2)		0.279						−0.166	0.01	0.110	0.003	0.0126
Dormant (d_3)			0.019					−0.165	0.002	0.110	0.001	0.0002
Germination (g_1)				0.476				−0.165	0.007	0.112	0.025	0.2722
Germination (g_2)					0.563			−0.165	0.001	0.110	0.005	0.1349
Germination (g_3)						0.244		−0.168	0.03	0.109	0.032	0.0126
Seedling survival (z_1)				0.512	0.512	0.512	0.512	−0.173	0.14	0.109	0.085	0.8396
Seedling survival (z_2)							0.057	−0.172	0.04	0.109	0.038	0.4198
Transition value	79.94	0.258	0.018	35.49	0.277	0.125	0.029	**−0.165**		**0.110**		
Transition elasticity	0.1475	0.0126	0.0002	0.2723	0.1349	0.0126	0.4198					
RSF												
Fecundity (*f*)	155.05			155.05				−0.108	0.17	0.101	0.145	0.4299
Seed survival (s_1)	0.958	0.958	0.958	0.958	0.958			−0.129	0.01	0.066	0.028	0.7001
Dormant (d_1)	0.381							−0.131	0.003	0.072	0.004	0.1300
Dormant (d_2)		0.315						−0.131	0.003	0.072	0.001	0.0101
Dormant (d_3)			0.017					−0.131	0.002	0.072	0.001	0.0001
Germination (g_1)				0.521				−0.131	0.004	0.072	0.019	0.2999
Germination (g_2)					0.696			−0.131	0.001	0.072	0.003	0.1199
Germination (g_3)						0.224		−0.132	0.013	0.072	0.025	0.0101
Seedling survival (z_1)				0.512	0.512	0.512	0.512	−0.143	0.096	0.068	0.07	0.8598
Seedling survival (z_2)							0.047	−0.134	0.012	0.073	0.03	0.4299
Transition value	54.20	0.289	0.016	39.62	0.341	0.115	0.024	**−0.131**		**0.072**		
Transition elasticity	0.1300	0.0101	0.0001	0.3000	0.1198	0.0101	0.4299					

The table also presents the mean autocorrelation (first and second lag; and their SD) of 1000 stochastic models with variation in each vital rate (SD = 10% of the mean vital rate) starting after a fire. The autocorrelation of the models without variation is in bold in the row of the transitions. The equations in the third row indicate how the vital rates were used to build the transitions asymptotic elasticities for matrix transitions and vital rates, and periods of oscillation (Caswell 2001). Complex second subordinate eigenvalues with a real and an imaginary part generate oscillations in the stage distribution during the transient phase (Fox and Gurevitch 2000). The period of these oscillations is given by Caswell (2001):

$$P_i = \frac{2\pi}{\tan^{-1}\left(\frac{\Im(\lambda_i)}{\Re(\lambda_i)}\right)}$$

where $\Im(\lambda_i)$ and $\Re(\lambda_i)$ are the imaginary and the real parts of λ_i. The longest-lasting of the oscillatory components is linked with λ_2 (Caswell 2001). Elasticities measure the proportional change in λ resulting from a proportional change of a matrix transition when all the other components are kept constant (de Kroon et al. 1986). Larger damping ratios indicate more rapid convergence of a population to stable growth (Caswell 2001). We explored how hypothetical changes in the proportion of seeds with demographic delay by dormancy affected λ and matrix transition elasticities. We then combined this analysis with a consideration of how variation in seedling production and dormancy affected λ and transient oscillations.

Stochastic modeling and fire

We conducted stochastic modeling based on one matrix for each of two sites (ABS/LPS and RSF). Stochastic variations in vital rates provoke perturbations and transient dynamics in the population structure that may be conducive to cycling behavior. We simulated variation in the five vital rates. We generated beta distributions to simulate variation in the vital rates between zero and one (Morris and Doak 2002). For fecundities which have values with no upper bound, we used a lognormal distribution to generate variation (observed fecundity values for many plant species are lognormally distributed; Lovett-Doust and Lovett-Doust 1990; Morris and Doak 2002). We simulated assuming a 10% coefficient of variation for each vital rate to compare among them.

We chose fecundity (*f*), the vital rate that had the largest positive autocorrelation for the second lag (as evidence of cycling) among our simulations (Table 2), and used its observed estimates of variation to evaluate the combined effect of this variation with a single fire. We examined population cycling properties of a simulated population started at stable stage distribution (0.1089, 0.5241, 0.3588, 0.0083 for ABS/LPS) burned after 5 years, and censused during the 6 years post-fire. In these time-since-fire-neutral model runs, mean model parameters did not change due to fire; rather, our simulation merely allowed fire to kill all individuals except those in the seed bank. We compared these simulated population cycling properties (periodicity, amplitude, and damping) to those of data from observed populations. We only used the data for ABS/LPS populations for the comparison between simulated and observed trajectories, since it is the only site that had simultaneously population counts and detailed demographic data.

Results

Observed population dynamics

Forty-four percent (33 of 74) of populations showed fluctuations in the number of flowering plants (see Fig. 2 for an example showing all populations in TCP). Autocorrelation analyses showed that negative correlations were pronounced for lags of 1 year, while positive autocorrelations were pronounced for lags of 2 years (Table 3). Few lags of other lengths ever yielded significant autocorrelations for any population. There were a few negative autocorrelations for 3-year lags and a few positive autocorrelations for 4-year lags. Consistent estimates of the power spectrum analysis confirmed that a 2-year cycle dominated observed population fluctuations at all three sites (Table 3).

Across all years, populations differed significantly in amplitude ($F_{2/71} = 6.37$, $P = 0.003$); cycle amplitudes were greatest for the frequently burned TCP population (mean 2.26, 38 patches, $n_{\mathrm{obs}} = 431$) and lower for the less-frequently burned populations (ABS/LPS: mean 1.59, 21 patches; $n_{\mathrm{obs}} = 229$; RSF: mean 1.33, 11 patches; $n_{\mathrm{obs}} = 82$). Amplitudes were greatest shortly after fire, particularly for TCP. We found damping amplitudes with time-since-fire for both ABS/LPS and TCP.

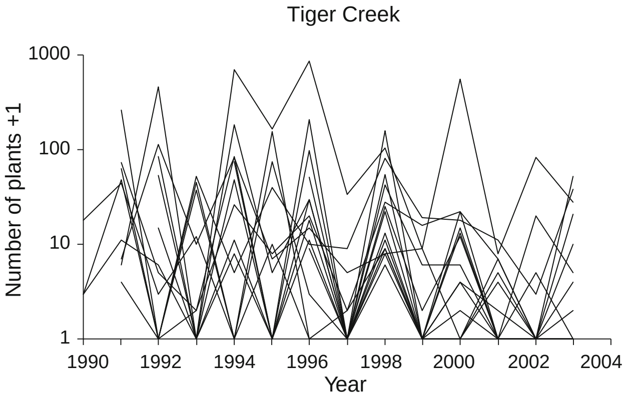


Fig. 2 Trajectories of all 15 populations at Tiger Creek Preserve (TCP) that showed significant ($P < 0.05$) negative autocorrelations for a 1-year time lag and significant ($P < 0.05$) positive correlations for a 2-year time lag

Table 3 Percent of patches with significant ($P < 0.1$) autocorrelations at 1, 2 or more years, by population, and average consistent estimate of power spectra (CEPS)

Site	No. patches (number of patches burned)	% with negative lags		% with positive lags		CEPS
		1 year	3 years	2 years	4 years	
ABS/LPS	21 (17)	66.7	0	57.1	0	2.0
RSF	11 (2)	45.4	0	18.2	9.1	1.9
TCP	42 (42)	64.3	4.8	45.2	4.8	2.4

The percentages do not sum to 100% since there were populations that did not have both types of autocorrelation

Deterministic modeling and transient dynamics

Under the equilibrium conditions implied by model matrices alone (no stochasticity or fire effects), λ values indicated growing populations (λ for ABS/LPS = 1.26; λ for RSF = 1.17). For ABS/LPS and RSF, the 2nd eigenvalues were imaginary numbers ($-0.557 + 0.287i$ and $-0.520 + 0.084i$, respectively). These sub-dominant eigenvalues suggest transient cycling population behavior, but their value relative to the dominant eigenvalue suggests fast damping (Caswell 2001). Transient dynamics include fluctuations with a near 2-year cycle (transient oscillation period = 2.36 for ABS/LPS, and 2.11 for RSF), with damping ratios 2.01 for ABS/LPS and 2.22 for RSF. Population trajectories moved to stable rates of change (to within 1%) in about 6–9 years, over a wide range of starting stage distributions.

Among transitions, seedling to adult survival (SUR) had the highest asymptotic transition elasticity in both populations, followed by recruitment of seedlings from recently produced seeds (FSD; Table 2). For vital rates, seedling survival (z_1) had the highest asymptotic elasticity followed by seed survival (s_1) (Table 2).

During the simulated first years post-fire, transient sensitivities with reference to number of seedlings were highest for germination from the seed bank. As the population approached the stable stage distribution, seedling survival and fecundity, in the form of both seeds and seedlings, became more important (Fig. 3).

The asymptotic transition elasticities changed with the hypothetical increase in the proportion of individuals without first-year seed dormancy (without demographic delay; Fig. 4). The fecundity to seeds (FSB), the direct transition of seedlings to adults (FSD(D)SUR and SDS$_1$(D)SUR; both hypothetical transitions; see Table 1) increased. On the other hand, the elasticities of germination of dormant seeds [SDS$_{1–2}$($1 - D$)] and the survival of their seedlings (SUR) decreased. Between populations, the most important differences were the slightly more pronounced decline for RSF (compared to ABS/LPS) in elasticities of recruitment from the seed bank and from recently produced seeds with a relaxation of demographic delay.

Hypothetical decreases in seed dormancy altered λ and the occurrence of cycling (Fig. 5). Lambda (λ) increased with the proportion of individuals without seed dormancy (D) in ABS/LPS and RSF (plots not shown). Evidence of oscillations (second eigenvalue, an imaginary number) was common for both populations when 80% or more of the population had seed dormancy (note dots with <0.2 proportion without dormancy in Fig. 5). Populations with 80% non-dormant individuals showed some oscillations.

Stochastic modeling and fire

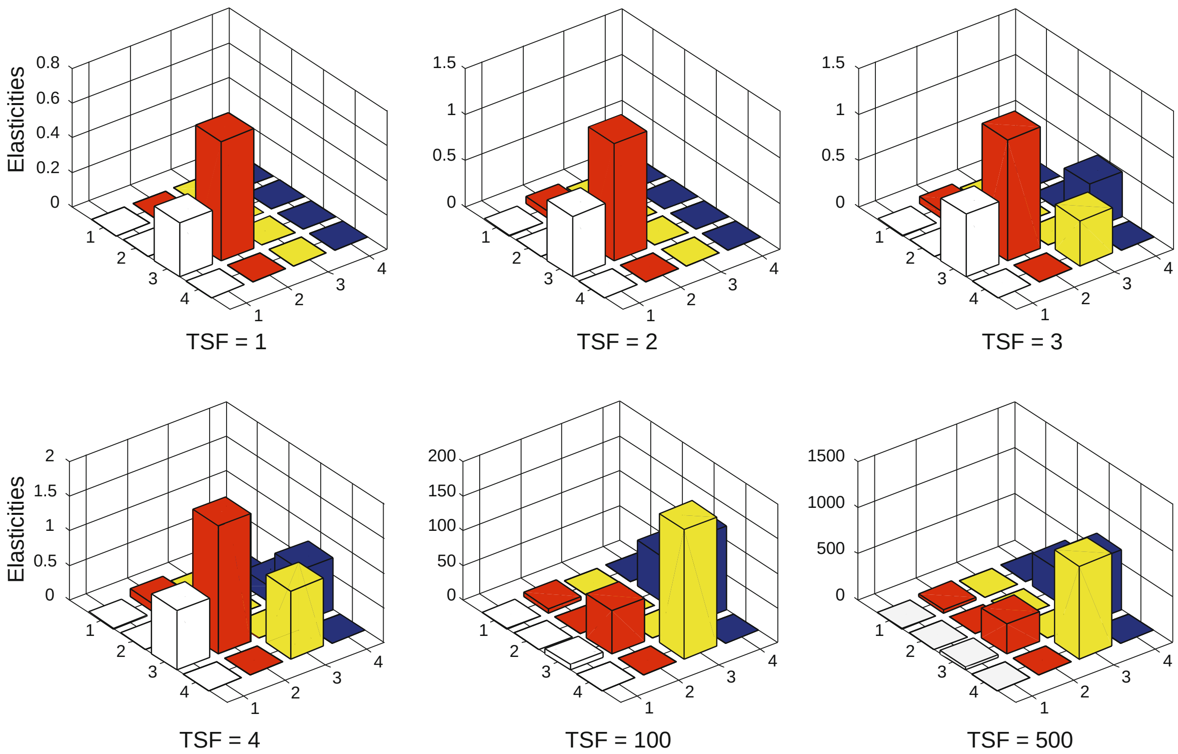
Stochastic variation in some of the vital rates produced more pronounced cycling behavior than deterministic simulations. We defined a 2-year cycle occurring during a stochastic simulation as a significant negative autocorrelation at the 1-year lag and a significant positive autocorrelation at the 2-year lag (autocorrelation $P < 0.1$). We found variable proportions of simulations with evidence of cycling behavior depending on population. In scenarios with fire, variation in germination from the seed bank (g_1) and fecundity (f) produced the highest proportion of 2-year cycle simulations.

We compared the output from the model (based on ABS/LPS) including fire and producing the largest proportion of 2-year cycle simulations (with variation in fecundity) to observed data from burned patches (81% of the patches at ABS/LPS) to assess its ability to reproduce observed amplitudes and damping post-fire. These models mimicked the general pattern of observed amplitudes with time-since-fire (Fig. 6; notice the overlap of 95% confidence limits of simulated and observed data; $n_{\text{model}} = 1000$ simulations, $n_{\text{obs}} = 9–15$ burned populations per time-since-fire). However, mean simulated amplitudes were outside of the CI of observed amplitudes at 1, 2 and 3 years post-fire (Fig. 6).

Discussion

Warea carteri populations oscillate with a distinct 2-year period, as confirmed with autocorrelation and power

a Archbold Biological Station/ Lake Placid Scrub



b RSF

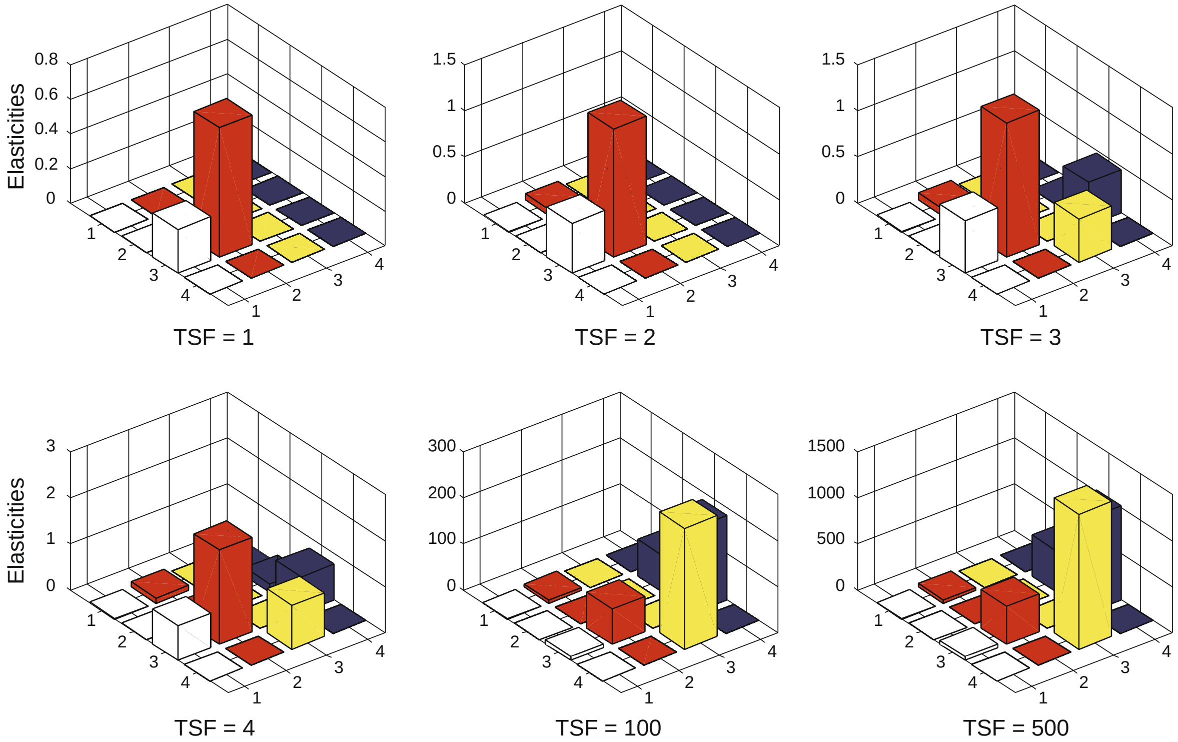


Fig. 3 Transient elasticities with reference to number of seedlings by time-since-fire for *Warea carteri* matrix models in **a** Archbold Biological Station/Lake Placid Scrub and **b** Lake Wales Ridge State Forest. Stages are (*1*) older seed bank, (*2*) first year seed bank, (*3*) seedlings, and (*4*) flowering adults. The populations started with only seeds in the seed bank (simulating the effects of a fire)

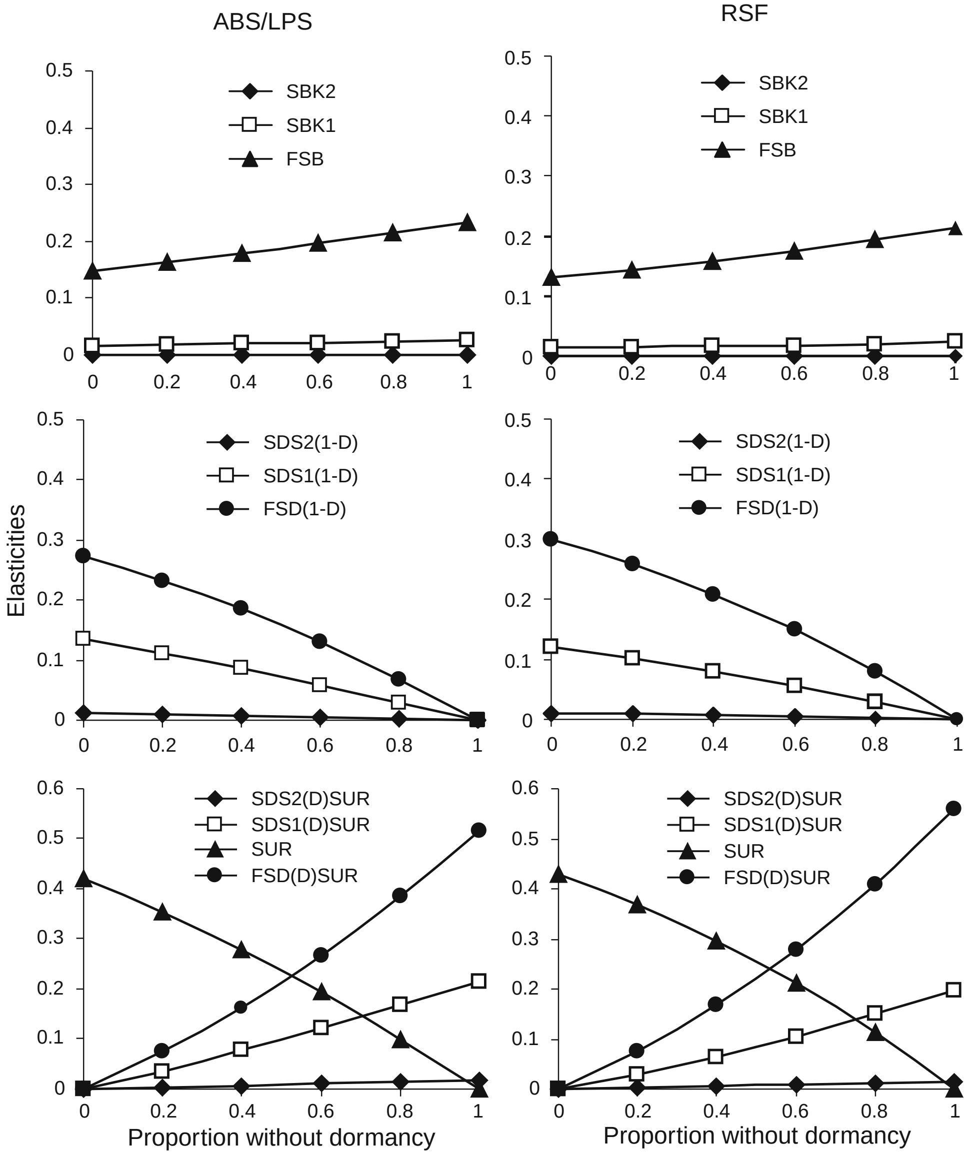


Fig. 4 Changes in asymptotic elasticities of matrix transitions for *Warea carteri* with hypothetical changes in the proportion of seeds without delayed dormancy, with other vital rates were kept constant, for Archbold Biological Station/Lake Placid Scrub (*ABS/LPS*) and Lake Wales Ridge State Forest (*RSF*). Abbreviations for transitions as in Table 1

spectra analyses. The cycle usually begins after fire and then damps over 6–9 years. We were able to reproduce these basic cycles with deterministic models, as long as the model included seed dormancy in at least 80% of plants, producing a demographic delay. Stochastic models were even more realistic in producing cycling and damping. Transitions that were key to cycling varied somewhat among populations, although germination and fecundity were most important.

Rapid population increases after fire may be a good strategy for this annual plant in an environment dominated by shrubs. *Warea carteri* depends on disturbances (mainly fire) to reduce competition with dominant shrubs. Its post-fire population dynamics are necessarily transient, as its future depends on the creation of a seed bank and subsequent disturbance. While the response to fire and the presence of seed dormancy are potentially adaptive, it is likely that the cycling associated with the demographic delay is a non-adaptive consequence of the transient nature of *W. carteri* population dynamics. Because fire removes any aboveground plants and encourages seedling recruitment, it initiates a large cohort. Because of demographic delay (i.e., delayed germination), the first post-burn cohort initiates the population's biennial cycling. Damping occurs because some seeds remain dormant for more than 1 year, germinating in the "off-year". As the "off-year" cohorts themselves begin to cycle, the overall population numbers appear damped.

Our analyses indicated that demographic delay is a reasonable cause of cycling in *Warea carteri*. This contrasts with previous studies that have demonstrated cycling due to density dependence (Symonides et al. 1986; Thrall

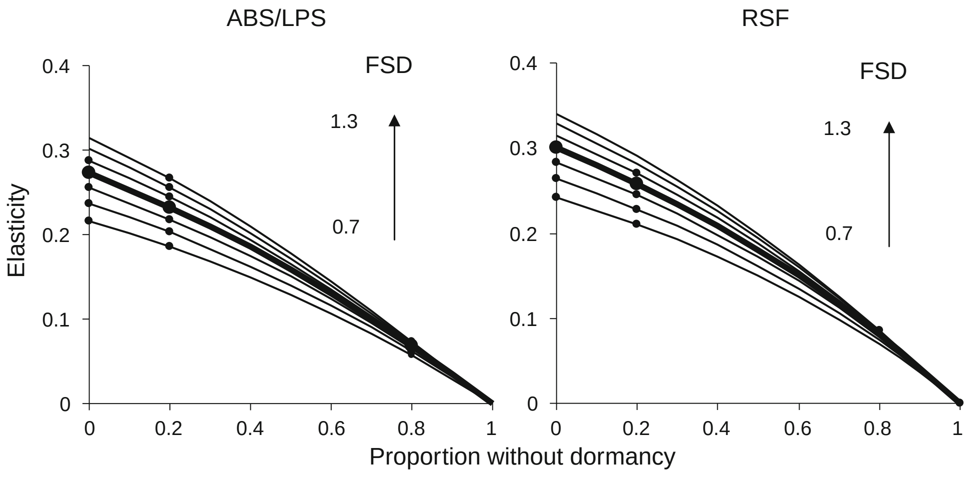


Fig. 5 Changes in the elasticities of flowering adult to seedling transition (from seeds with dormancy) with hypothetical changes in flowering adult to seedling transition (FSD; in 10% increments or decrements) and changes in the proportion of seeds without dormancy for Archbold Biological Station/Lake Placid Scrub (*ABS/LPS*) and Lake Wales Ridge State Forest (*RSF*). The *thick line* indicates the scenario with the original FSD value. *Points* with *dots* indicate populations with cycles (imaginary 2nd subdominant eigenvalues)

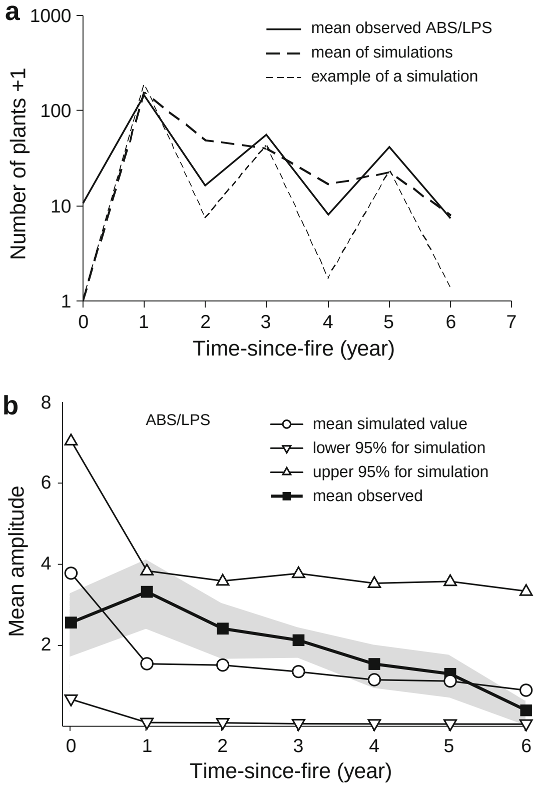


Fig. 6 **a** Observed mean post-fire trajectory for ABS/LPS populations, mean simulated trajectory and an example, **b** observed mean amplitudes for ABS/LPS (*thick line*; *gray areas* indicate 95% CI) in relation to time-since-fire and simulated mean amplitudes for the model with fire and variable fecundity (*f*). *Lines* with *triangles* indicate 95% CI of simulations, $n = 1000$

et al. 1989; Crone 1997; Gonzalez-Andujar et al. 2006). Our hypothesis, that cycling in annual plants may also be caused by demographic delays, emerges from comparisons of demographic model output with independent data on population fluctuations. Demographic delays are an additional explanation for population cycling in some annual species like *W. carteri* whose life cycle can generate overlapping cohorts.

Demographic delay is also an additional parsimonious explanation for cycling in strict biennials whose populations consist of two temporally separated sub-populations that flower in either odd or even years (Kelly 1985b). *Warea carteri* is classified as an annual because plants live about 1 year. However, the cycles of *W. carteri* have parallels with the cycles of strict biennials, e.g., the general mechanism of two cohorts that may cycle out of synchrony. In both cases, any mechanism that markedly increases or decreases the size of one sub-population can create biennial cycling. For example, in the strict biennial *Pedicularis sylvatica*, alternating years with many adults and then many seedlings have been observed across a range of management treatments (Petrü 2005). A delay of flowering until the second year creates biennial cycles in these plants. In facultative biennials that flower once but generally delay flowering for several years (Klinkhamer et al. 1987), such well-defined cycles do not occur (Caswell and Werner 1978; Klinkhamer et al. 1996).

While *W. carteri* can be considered as an annual, it combines some of the characteristics of extended annuals, winter annuals, and summer annuals. *Warea carteri*'s life cycle corresponds to that of "extended annuals" that display the "conventional" annual life history in favorable sites, but may take 2 years to complete their life cycles in less fertile sites (Kelly 1985b). Seeds produced in one fall flowering season germinated the following fall, creating an observed peak pulse of seedling emergence between

September and December (Weekley et al. 2007). Thus, germination of newly produced seeds was delayed by several months. Since seedling emergence of one cohort of *W. carteri* is concentrated in the fall while the previous cohort is still flowering and fruiting, there is a short period of time when two cohorts overlap. Because it recruits seedlings in the fall/early winter, *W. carteri* could be categorized as a winter annual (cf. Baskin and Baskin 1985). However, it also behaves like a summer annual because flowering is delayed until the fall following recruitment. This demographic delay is what creates the opportunity for cycling.

Observed and modeled population cycles in *Warea carteri* dampened with time. Damping occurs because some seeds remain dormant and create cohorts in "off-years" that reduce the amplitude of the cycle. Reduced cycle amplitude is a self-reinforcing phenomenon. Deterministic models produced oscillations, but the degree of damping was more rapid than in observed populations.

When stochastic variation in transitions was included, we obtained more realistic damping and larger-amplitude cycles. However, stochastic models still produced smaller amplitudes than those observed in observed populations, and somewhat more rapid damping. We suspect that this discrepancy occurs because fecundity, germination and seedling survival immediately post-fire may be higher than in subsequent years, but we did not have data to test this conjecture. If vital rates decrease between fires, e.g., lower germination due to poor seed quality, lower fecundity due to increased shading, or lower survival due to reduced nutrients (all potential trends post-fire), observed population sizes (relative to simulations that did not include these factors) could be altered.

Variation in recruitment was most effective at creating simulations with biennial periodicity. It is noteworthy that the life history component responsible for population size fluctuations (the delay in seed germination) is also the life history attribute whose variability produces the largest proportion of 2-year cycle simulations. Changes in the percent of a population with demographic delay also affected λ values and matrix element elasticities.

Fire plays a key role in initiating fluctuations of *Warea carteri* by synchronizing germination from dormant seeds in the seed bank. The post-fire seedling cohort constitutes a population boom, leading in turn to a bumper crop of seeds. Delayed germination of most seeds then continues the biennial cycle. By stimulating high germination in favorable conditions, fire is beneficial to *W. carteri* and should be used in its management. Cycling behavior creates periods of high population-level seed production and thus episodically higher contributions to the seed bank. The seed bank dampens fluctuations and provides a critical demographic and genetic reservoir for responses to the next disturbance event. Demographic responses to fire within Florida scrub are not restricted to *W. carteri*; high germination, growth, and flowering have been observed in many Florida scrub and sandhill perennials (Quintana-Ascencio et al. 2003; Menges and Quintana-Ascencio 2004; Menges et al. 2006), and positive responses to fire are common among rare plants across Florida ecosystems (Slapcinsky et al. 2010). Prescribed fire is the disturbance agent used to manage sandhill and scrub ecosystems that support *W. carteri* (Menges 1999), is cost-effective to implement (Provencher et al. 2001), and avoids potential problems with alternative management tactics (Menges and Gordon 2010).

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