

POPULATION VIABILITY ANALYSES OF *CHAMAECRISTA KEYENSIS*: EFFECTS OF FIRE SEASON AND FREQUENCY

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Abstract. Conservation of species of concern in fire-dependent ecosystems requires restoring the historical fire regime that has shaped the species' life history. The historical fire regime of the endangered pine rockland ecosystem is controversial. In this study, we attempted to infer the historical fire regime of this ecosystem by studying the effects of contrasting experimental fire regimes on *Chamaecrista keyensis*, a narrowly endemic species of the pine rocklands of the Lower Florida Keys, USA. We constructed multiple matrix population models for *C. keyensis* using demographic data from replicated wet- and dry-season burns, 1–30 years since fire, and seed bank dynamics derived from extensive field seed bank experiments. We then carried out deterministic analyses and stochastic simulations. Recently burned sites (1–2 years postfire) had the highest finite population growth rates of all sites. Differences in finite population growth rate between winter and summer fires were more pronounced during the year of burn than in subsequent years. Stochastic simulations show that dry-season (winter) burns generated lower extinction risks and population decline probabilities than a wet-season (summer) fire regime. Fire return intervals of 5–7 years generated the lowest extinction and population decline probabilities for both seasons. *C. keyensis* may have evolved under a fire regime that consisted of both anthropogenic dry-season fires along with lightning-caused wet-season fires. If phenology is also a key to fire responses in other pine rockland species, a diverse fire regime including a wide range of fire seasons may be critical to maintaining the diversity of the pine rockland ecosystem.

Key words: *Chamaecrista keyensis*; conservation biology; endemic species; Fabaceae; fire ecology; historical fire regime; Lower Florida Keys, USA; matrix models; pine rockland; stochastic population modeling.

INTRODUCTION

Fire has been widely recognized as an important ecological process influencing the population dynamics of plants and animals (Bond and van Wilgen 1996, Whelan 1996). The best conservation management strategy for plant populations adapted to fire-prone habitats is presumably the one that coincides with the historical fire regimes under which the plant species has evolved (Leach and Givnish 1996, Hiers et al. 2000). In some cases, however, it is difficult to identify these historical fires (Snyder et al. 1990). Studying demographic responses of the endemic species to contrasting experimental fire regimes may provide the scientific basis for choosing fire management regimes (Streng et al. 1993, Brewer and Platt 1994a, b, Spier and Snyder 1998, Hoffmann 1999, Caswell and Kaye 2001, Quintana-Ascencio et al. 2003).

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Many fire-related studies measure a limited array of plant population features, such as postfire mortality, fecundity, or recruitment (Whelan 1996). However, only long-term demographic monitoring of replicated populations that have been subjected to experimental fire treatments can generate reliable information on the effects of alternative fire regimes on population dynamics (Streng et al. 1993, Whelan 1996). Such data may be summarized in population matrices and analyzed by population matrix modeling. Population matrix modeling offers analytical tools to identify life history stages affecting population growth and to compare alternative management strategies (Menges 1990, 2000, Schemske et al. 1994, Kaye and Pyke 2003, Menges and Quintana-Ascencio 2003). However, analytical results from matrix models may not be realistic and natural variance in population growth rates may be masked if matrices are built using averaged demographic parameters (Menges 2000, Menges and Quintana-Ascencio 2003). In contrast, the use of multiple, site/year-specific matrices, though laborious and time consuming, can reveal strong patterns in finite rates of increase, relationships of demography with environmental gradients, and natural variation in finite rates of increase and elasticities (Oostermeijer et al. 1996,

Menges and Dolan 1998, Satterthwaite et al. 2002, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004).

Another outstanding challenge to the credibility of demographic modeling lies in seed bank dynamics. Seed banks are recognized to have important demographic and genetic functions, such as reducing extinction risk (Kalisz and McPeck 1992) and buffering the local extinction of genotypes (Silvertown and Lovett Doust 1993). However, since dynamics of seeds in the soil are difficult to study, they have usually been ignored in plant demographic studies (reviewed in Menges [2000]). One way to alleviate this problem is to employ experimental seed banks, but this approach has rarely been used (Menges 2000).

In fire-dependent habitats, some critical environmental and demographic characteristics change cyclically instead of randomly, with disturbance frequency determining the cycle length. The impact of periodic disturbance and of subsequent recovery on population dynamics can be explicitly modeled by organizing matrices based on demographic data corresponding to fire regimes composed of different fire frequency, season, and intensity (Menges 2000). Such a disturbance-explicit, stochastic modeling approach is a powerful tool for comparing contrasting disturbance management regimes (Menges 2000), e.g., in fire-dependent communities (e.g., Menges and Dolan 1998, Hoffmann 1999, Caswell and Kaye 2001, Kaye et al. 2001, Satterthwaite et al. 2002, Quintana-Ascencio et al. 2003).

Florida pine rockland is a fire-dependent ecosystem. Beneath the canopy of *Pinus elliottii* var. *densa*, fire-sensitive hardwoods increase in density and cover over time since fire (Snyder et al. 1990), reducing herb diversity (Robertson 1955, Snyder et al. 1990). Long-term fire exclusion converts pine rockland into hardwood hammock (Alexander 1967). Currently, pine rocklands are fragmented by urban or agriculture developments. Active prescribed fires are necessary to maintain this fire-dependent ecosystem because natural ignitions may no longer support the fire extent and intensity of a continuous forest. Nevertheless, the pre-European fire regime is uncertain, especially the seasonal timing of burning (Snyder et al. 1990). Convective thunderstorms are common during the summer/wet season (May to October), and lightning-caused fires occur mostly during that time (Duever et al. 1994). Lightning was probably a major source of ignition in southern Florida before European settlement. However, native Americans have been present in this region for thousands of years (Carr and Berialt 1984, Gleason and Stone 1994), and they may have used fire extensively at times other than the wet season (Snyder 1991, Spier and Snyder 1998). Thus, anthropogenic fires may also have constituted a selective force, especially for short-lived plants, in south Florida ecosystems. Systematic demographic evaluation of different fire regimes on pine rockland endemic plants is rare (but see

Spier and Snyder [1998], Negron-Ortiz and Gorchov [2000]), and none have been conducted in the Florida Keys, USA.

In this study we conducted a population viability analysis of *Chamaecrista keyensis*, a narrowly endemic understory herb of the Florida Keys pine rockland, by constructing fire-season and time-since-fire specific matrices, incorporating different scenarios of seed bank dynamics derived from extensive field seed bank experiments. We calculated the finite population growth rates (λ) and also carried out stochastic simulations to evaluate effects of alternative fire regimes, with contrasting fire return intervals and seasons of fire, on extinction risk and population decline probabilities.

MATERIAL AND METHODS

Study system

Study species.—*Chamaecrista keyensis* (Pennell) Britton & Rose is a pine rockland understory sub-shrub. It has one to several branched herbaceous or woody stems arising from a contorted rootstock. Each stem dies back every year and can sometimes resprout after being top-killed by fire or herbivory (Liu and Menges 2005). Plants flower and fruit mainly during the summer (May–August). The yellow flowers are buzz-pollinated by bees, plants are self-compatible, and fruit set is pollinator-dependent (Liu and Koptur 2003). One to 10 seeds may be found in a mature seedpod, with no obvious dispersal mechanism except for limited projecting force provided by the twist-opened seed pod.

Chamaecrista keyensis only occurs in the Lower Florida Keys, USA (Irwin and Barneby 1982). This narrowly endemic herb is currently listed as endangered by the State of Florida and recommended for listing by the U.S. Fish and Wildlife Service (Florida Natural Areas Inventory 2002, *available online*).⁵ A recent survey (Ross and Ruiz 1996) found it only on Big Pine Key, an island with the largest fragment of pine rockland in the Lower Keys. Habitat destruction is an obvious reason for the disappearance and decline of this species. Invasion and shading from heavy shrubs due to inadequate fire frequency may be responsible for the disappearance of *C. keyensis* from islands where the pine rocklands are protected as part of the National Key Deer Refuge.

Study area.—Florida pine rocklands occur on outcroppings of limestone in extreme southern Florida. The canopy of pine rockland is monotypic, composed of south Florida slash pine (*Pinus elliottii* var. *densa*). In contrast, a diverse shrub and herb layer is present in pine rocklands due to the relatively open canopy (Snyder et al. 1990).

Big Pine Key, with the largest pine rockland fragments in the Lower Keys, is an important habitat for the federally endangered Key deer, *Odocoileus virginianus clavium* Barbour and Allen (Dickson 1955, Al-

⁵ (<http://www.fnai.org>)

TABLE 1. Summary of *Chamaecrista keyensis* census regime at each experimental plot in the Lower Florida Keys, USA.

Block	Fire treatment	Plot name	Pineland type	Time since fire (yr) [†]	Density (no./m ²) [‡]	No. census plots [§]	Census start year	Burn date
Orchid	control	OC	open	8	2.90	60	1998	NA
	summer	OS	open	8	3.10	60	1998	August 1998
	winter	OW	open	8	2.30	60	1998	December 1998
Poisonwood	control	PC	shrubby	12	0.51	100	1998	NA
	summer	PS	shrubby	12	0.15	100	1998	August 1998
	winter	PW	shrubby	12	0.32	90	1998	December 1998
Iris	control	IC	open	8	0.86	95	1999	NA
	summer	IS	open	8	1.03	95	1999	July 1999
	winter	IW	open	13	0.27	105	1999	December 2000
Dogwood	control	DC	shrubby	30	0.25	105	1999	NA
	summer	DS	shrubby	30	0.47	105	1999	June 1999
	winter [¶]	DW	shrubby	30	0.96	85	1999	NA

[†] Time since fire at the first census.

[‡] Density is based on counts in stratified random plots only.

[§] In the Orchid block, only three-quarters of the herb plots were used because of the high density of *C. keyensis*. For all other blocks, additional nonrandom plots are included.

^{||} Winter burn in this block was delayed one year.

[¶] Winter burn in this block was canceled.

exander and Dickson 1972). No record is available on fire history before European arrival in the Florida Keys. European settlers used fire from about 1840 to 1950, but fire was suppressed thereafter until 1977, when the National Key Deer Refuge established a limited prescribed burning program (Bergh and Wisby 1996). Prescribed burns have been conducted in the Refuge mainly for fuel reduction and to promote new plant growth for Key Deer consumption. Since 1985, most burns have been in late summer when fuel was wet enough for safe burning (Bergh and Wisby 1996). The current pinelands on Big Pine Key are a mosaic of open and shrubby forests, which reflect variation in burning frequency. Open pinelands have better developed herb layers than shrubby pinelands.

Field methods

Experimental design.—This study took advantage of the experimental design of a four-year study (1998–2001) on Big Pine Key to develop ecological criteria for prescribed fire in pine rockland (M. Ross, S. Koptur, and J. Snyder, *unpublished manuscript*). For each type of pineland (open or shrubby) a block was randomly chosen each of two years (1998 and 1999) for a total of four blocks (Orchid, Poisonwood, Iris, and Dogwood). Each of these four blocks was divided into three experimental burn units: summer burn, winter burn, and control unburned; one macroplot (1 ha) was embedded in each experimental burn unit of 2–10 ha. Prescribed fires of wet (May–October) and dry (November–April) seasons were replicated within and between years (Table 1). However, the winter burn in Dogwood could not be carried out, and the winter burn in Iris was delayed one year for logistical reasons (Table 1).

Within each macroplot, 20 subplots (4 m in diameter) were stratified and randomly located for shrub sampling

for the fire and vegetation project, and four 1-m² herb plots were located at cardinal directions 2.5 m from the center of each shrub plot. The *C. keyensis* census was carried out in the herb plots. While only three-quarters of the herb plots were sampled in Orchid block due to high *C. keyensis* density, in the other three blocks additional census plots were located nonrandomly to include additional *C. keyensis* individuals (Table 1).

Census.—We carried out annual censuses in the summer (flowering season) just before each wet season burn and annually postfire for up to three years. We recorded annual plant fates (new plant, new seedling, surviving, died, dormant), and stage (seedling, vegetative, or flowering) from 1998 to 2001 along with the size and reproductive information for each year. Three size variables, the number of stems, the longest stem length (in centimeters) and the total stem length (in centimeters), were recorded every census year except for 2001. In 2001, only number of stems and the longest stem length were recorded.

In addition, we recorded total number of mature fruits at the end of the fruiting season. This is possible because fruit stalks persist even after dehiscence. Only plants producing mature fruits were considered reproductive. We counted numbers of seeds per fruit from fruits randomly sampled outside experimental plots (Appendix A: Tables A1 and A2). We also marked seedlings at all sites quarterly from 1999 to 2001 in order to determine naturally occurring seedling survival rate to the first census (see *Fertility and seed bank matrix elements*). A total of 416 seedlings were marked inside or outside the regular census plots.

Seed bank and seedling survival experiments.—To characterize the seed bank dynamics of *C. keyensis*, we employed a three-fold approach: (1) a seed bank experiment with bagged seeds, (2) a seed bank experiment

with sown seeds, and (3) an experiment on seed mortality due to a fire event.

1. *Bagged-seed bank experiment.*—Ten seed bank experiment plots were established via a stratified random selection process in experimental plots at Dogwood and Iris blocks. Freshly collected, visually sound seeds from outside the experimental plots were used. Seed bags (10×10 cm) made of fine-mesh nylon window screen material, with 20 seeds per bag, were placed at the soil surface around the plot center. We set out three bags into each of the 10 seed bank plots in July 1999 in IC, IS, DC, and DS (see Table 1 for abbreviations). One bag was retrieved after one year (2000), and the other two after two years (2001). Retrieved seeds were examined under a dissecting scope. Visually intact seeds were nicked and placed in petri dishes with moist filter paper for viability test. Only seeds producing radicles were considered viable. We categorized the retrieved seeds as (1) germinated in the field, (2) viable, (3) dead, or (4) missing.

We repeated the experiment in the same plots in early August 2000 using freshly produced seeds, with only one bag in each plot. In addition, a single seed bag was set out at the center of each of seven randomly selected shrub plots in each experimental unit (OC, OS, OW, PC, PS, and PW) in the Orchid and Poisonwood blocks (which burned in 1998). The second batch of seed bags was retrieved in summer 2001 (after one year in the field). Estimates from 1- and 2-yr-old seed bags were used to calculate the seed bank elements of the matrices (Appendix A: Table A3). Seeds that were not retrieved (either in the form of intact seeds or seed coats from germinated seeds) were either omitted from the calculations of seed bank elements (pessimistic scenario) or assumed to have germinated (optimistic scenario).

2. *Sown-seed bank and seedling survival experiment.*—Ten 0.25×0.25 m² field seed germination plots were established near the bagged-seed bank experiment plots in DC, DS, IC, and IS. Twenty seeds were spread onto the soil surface in each of these plots in early August 2000, when most seeds produced that year were dispersing from parent plants. These plots were monitored for seedling emergence and survival every two weeks for the first two months and monitored monthly thereafter for one year (through August 2001). New seedlings at each survey were marked with color- and shape-coded toothpicks. An area of the same size (0.25×0.25 m²) next to the seed germination plot was used as a control plot for monitoring background (naturally occurring) seedlings. Annual percentage of seed germination was derived from this and the previous experiments (Appendix A: Table A4). We used these two sets of estimates as separate scenarios for calculation of *C. keyensis* fertilities in the site/year/fire history-specific matrices (see *Fertility and seed bank matrix elements*). Similarly, we derived seedling survival rates from this experiment and from the regular census of the same experimental plots (Appendix A: Table A5).

They were also used as two contrasting scenarios for calculation of fertilities (see *Fertility and seed bank matrix elements*).

3. *Seed mortality due to fire.*—In the Iris summer-burn plot (IS) one day before the burn in July 1999, 10 plots (0.25×0.25 m²) were established near the bagged-seed experimental plots and 30 seeds were spread onto the soil surface of each plot. The top litter/soil layer at each plot was retrieved immediately after the fire event using a hand-held vacuum cleaner. *Chamaecrista keyensis* seeds were picked out from the mixture of seeds, litter, and soil. The retrieved seeds were counted and then planted in potting soil for a germinability test for two months. The remaining litter was spread onto trays with potting soil to detect overlooked *C. keyensis* seeds. The percentage of seeds surviving the fire was used to adjust the fertility elements of the burned year. This experiment was not repeated due to delay or cancellation of subsequent prescribed fires. Unrecovered, missing seeds were assumed dead. Under this assumption, a mean of 18% of seeds survived the fire. This estimate was used for fertility and seed bank elements calculations (see *Fertility and seed bank matrix elements* and Appendix A: Table A2).

Matrix model building

Size classification using Moloney algorithm.—We used total stem length (estimated in 2001) to define plant size (Appendix B). One underlying assumption of matrix population models is that individuals in the same class have similar behavior in growth, fecundity, and mortality. In reality, the assumption is usually violated to various degrees (termed distribution error) that depend on the class size. If one has small class intervals, the number of individuals in each class will be small and so will the distribution error. However, the small number of individuals will introduce large sampling error. The situation is reversed for large classes. We used the Moloney algorithm (1986) to define plant size class based on growth behavior, to minimize the sum of sampling and distribution errors, using a Pascal program developed by P. F. Quintana-Ascencio (Appendix B). We generated three cutoff points for total stem length, 15, 37, and 79 cm, and thus four possible size classes: 1–15, 16–37, 38–79, >79 cm (Appendix B).

Identifying seedlings vs. vegetative plants.—During annual censuses, if a newly encountered plant had cotyledons, it was easy to know that it was a seedling. But for those plants without cotyledons, it was difficult to judge if they were seedlings (less than one year old) or small vegetative plants (at least one year old). Therefore, we used size data of known seedlings (individuals marked with a toothpick when first seen with cotyledons at times other than regular annual census) and of known non-seedling individuals to derive the best size cutoff point to distinguish seedlings from vegetative plants (Appendix C: Fig. C1). Such a cutoff size si-

multaneously maximized the probabilities of identifying seedlings and non-seedlings correctly. The optimal size cutoff was 15 cm of total stem length. New plants smaller than 15 cm total length have a 78% probability of being true seedlings, while plants greater than 15 cm have an 81% probability of being non-seedlings (Appendix C: Fig. C1).

Define size-stage classes.—We cross-tabulated the four size classes based on Moloney (1986) analysis with the plant stage categories of seedling, vegetative, and reproductive. The number of reproductive plants that are in the 1–15 cm size class is consistently low (total < 20) across sites in all four census years. We decided to pool 1–15 cm and 15–37 cm reproductive plants into one category. Similarly, sample sizes of vegetative plants >79 cm were consistently low, therefore we pooled the vegetative size classes of 37–79 cm and >79 cm. As a result, we defined seven aboveground size and stage classes as follows: (1) seedlings, total length ≤ 15 cm, for new plants only; (2) small vegetative, total length ≤ 15 cm, for plants >1 yr old; (3) medium vegetative, 15 cm < total length ≤ 37 cm; (4) large vegetative, total length > 37 cm; (5) small reproductive, total length ≤ 37 cm; (6) medium reproductive, 37 cm < total length ≤ 79 cm; and (7) large reproductive, total length > 79 cm. Some sample sizes in the small reproductive class were still small after pooling (Appendix C: Table C1). ANOVA tests suggested that the small vs. medium classes differed significantly in growth during all censuses and differed in fruit production in 1999, so separate small and medium classes were retained.

Non-fertility matrix elements.—Non-fertility elements are elements other than the number of seeds and seedlings produced by plants in each stage. They are the annual transition probabilities among aboveground plant stages for each site. We generated 30 site/year/fire history-specific matrices. However, 25 of 210 matrix columns had fewer than five individuals (bold columns in Appendix D), which may produce unacceptable sampling errors. Such stages were pooled with the same stage of the most similar matrix (in terms of time since fire, fire season, and block) to obtain transition probabilities (Appendix D: Table D1). In total, 11.9% (150/1260) of the total non-fertility matrix elements were based on pooled data.

Fertility and seed bank matrix elements.—Fertility elements are transitions to seedlings from reproducing plants or from the seed bank, as well as transitions to the seed bank. These transitions are products of several components: fecundity, yearly percentage of seed germination, percentage of seed dormancy, and seedling survival to the first census of that plant (Appendix A: Fig. A1). We generated eight scenarios of fertility and seed bank matrix elements based on data from various seed bank-related experiments (Appendix A: Table A6).

Scenario selection based on model verification

To select among the eight fertility scenarios, we projected population trajectories for two or three consecutive years (depending on plots) by multiplying the initial observed population vector of each plot with the plot/year-specific matrix of each scenario. These projected population structures were then compared against observed site/year-specific population structure using chi-square tests. A nonsignificant result indicated that the predicted population structure was not significantly different from that of the observed. Scenario 3 (based on sown-seed experiment and assuming missing seeds germinated in the bagged-seed experiment) had the most correct projections and was selected as the base scenario for further deterministic and stochastic analyses (Appendix A: Table A7).

Deterministic modeling analyses

Lambda (λ) is the finite population growth rate, and elasticity is the relative contribution of a particular transition to the finite population growth rate (Caswell 2000). We used MATLAB (MathWorks 1997) to obtain the dominant eigenvalues (λ) and elasticity matrices for each of the 30 site- and year-specific transition matrices of the base scenario. Linear regressions were carried out between ln-transformed λ (excluding the burn year) and time since fire (continuous variable).

We summarized the elasticity matrices in the following two ways: (1) combined the elasticity elements into growth/progression (elements below the diagonal line, including transitions from nonreproductive to reproductive stages), survival/stasis (elements on and above the diagonal line, except for transitions from adult plants to seed bank and seedling), and fecundity (the transitions to seed bank and seedling from adult plants) (Silvertown et al. 1996) and (2) summarized the elasticity matrices based on initial plant stages.

Stochastic simulation

We used the stochastic simulation program DISPROJH (P. F. Quintana-Ascencio and E. S. Menges, *unpublished program*) written in MATLAB (Mathworks 1997) to model population decline or extinction probabilities with fire regimes incorporating fire season (fixed or mixed) and fire frequency (fixed or probabilistic). Three fire season scenarios were used: wet-season fires only, dry-season fires only, and mixed wet- and dry-season fires with equal probability. Fire return interval was simulated in two ways: fixed intervals of 2, 3, 4, 5, 6, 7, 8, 10, 15, 20, and 30 years and logistic probabilistic intervals with mean fire return interval of 3, 4, 5, 6, 7, 8, 10, 20, and 30 years (Appendix E). Logistic probabilistic functions were used for simulating fire probability because it is a reasonable model for biomass accumulation after fire (Sah et al. 2003). To incorporate spatial and temporal variation of demographic parameters for a given fire history, we grouped

TABLE 2. Matrix organization and interpolation functions for stochastic simulation of extinction risks and population decline probabilities of *Chamaecrista keyensis* on Big Pine Key.

Phase	Time since fire (yr)	No. time steps	No. matrices†	Interpolation function
I	0–1	1	4 (s), 3 (w)	NA
II	1–2	1	4 (s), 2 (w)	NA
III	2–3	1	2 (s), 2 (w)	NA
IV	3–8	5	0	exponential decay from phase III to V
V	8–12	3	5	NA
VI	12–15	3	4	NA
VII	15–30	15	0	linear decay from phase VI to VIII
VIII	>30	2	4	NA

† Separate sets of matrices were available for summer- and winter-season burning regimes (s and w, respectively) from phase I to III. The same sets of matrices were used for both fire seasons from phase V to VIII.

the replicated fire treatment/year-specific transition matrices into different phases based on fire season and time since fire (Table 2). We then used an algorithm to choose among the matrices from phases that corresponded to the last simulated fire season and time since fire. Each matrix in the same phase has equal opportunity of being drawn if the phase has more than one matrix. For phases with no matrix, an interpolation probability function was used to draw the matrix from either the previous or later phase (Table 2).

Every simulation began with a stage vector representing the summation of initially sampled populations of four blocks (2153 seeds, 493 seedlings, 131 small vegetative plants, 490 medium vegetative plants, 361 large vegetative plants, 94 small reproducing plants, 175 medium reproducing plants, and 202 large reproducing plants). Number of seeds was inferred from ratios of aboveground plants to seeds in stable stage distributions. This vector was multiplied by a randomly drawn matrix from the burn-year matrix pool of either a wet- or dry-season fire, depending on which fire season was being simulated, then by a randomly drawn one-year postfire matrix, then by a two-year postfire matrix, and so on. This process continued until the next burn; the cycle repeated starting with the burn-year matrix. In mixed season fire regime, a 50% probability was given for fire to be burned either during summer or winter. Each run lasted for 100 simulated years, with

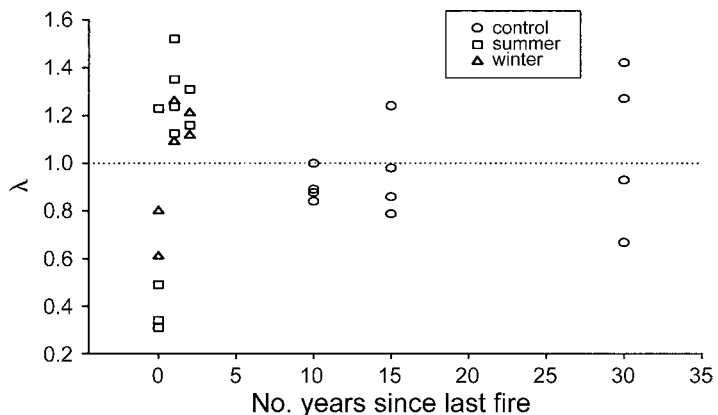
500 replicate runs for each simulation. A run was terminated and counted as extinction if the simulated population dropped below the quasi-extinction threshold of 10 plants, including seeds. We counted a run as a decline if the final population size was smaller than the initial population size. We present extinction and decline probabilities without confidence intervals because we are primarily interested in the relative rankings of extinction risk under different fire management regimes rather than a precise quantitative estimate.

RESULTS

Lambda, elasticity, and sensitivity analysis

The finite population growth rates (λ) were <1 during the burn year and were higher following winter burns than summer burns, except for the summer fire in Dogwood (Fig. 1). However, λ values in both types of burns were considerably >1 during the first and second year after fire. The mean λ of control plots 10 years since fire (with lighter vegetation cover) was 0.923 with relatively small variance (standard deviation = 0.075), while the means λ of plots unburned for 15 and 30 years (with heavier vegetation cover) were 0.968 and 1.07, but with increasing variance (standard deviations, 0.194 and 0.306, respectively) (Fig. 1). There was a weak negative relationship between $\ln(\lambda)$ and time since fire when λ values of the burn year were excluded ($R^2 = 0.125$, $P = 0.097$).

FIG. 1. Finite population growth rates (λ) of populations of *Chamaecrista keyensis* as a function of time since fire and season of burn in the Lower Florida Keys. Control plots were not burned during this study. Zero on the x-axis indicates the burn year.



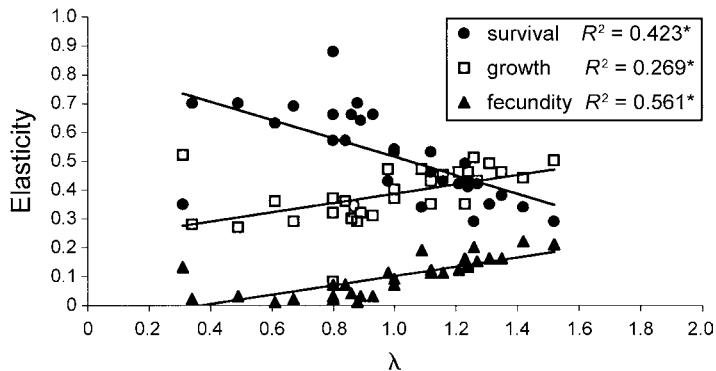


FIG. 2. Elasticities of survival (stasis), growth (progression), and fecundity of *Chaemaecrista keyensis* populations on Big Pine Key as a function of the finite population growth rate (λ).

* $P < 0.05$.

Elasticities of fecundity and progression increased with λ ($R^2 = 0.561$, $P < 0.001$ and $R^2 = 0.269$, $P = 0.003$, respectively; Fig. 2), but survival elasticities decreased with λ ($R^2 = 0.423$, $P < 0.001$).

Elasticities of seedlings increased with λ ($R^2 = 0.5614$, $P < 0.001$) (Fig. 3a), but elasticities of medium and small vegetative stages decreased ($R^2 = 0.2046$, $P = 0.012$ and $R^2 = 0.1732$, $P = 0.022$, respectively) (Fig. 3b). The relationships between elasticities of seed bank, large vegetative, small, medium, and large reproductive stages and λ were not significant (Fig. 3a–c).

Stochastic simulation

Under all regular fire return intervals, quasi-extinction probabilities were smaller if burns were in the winter than in the summer (Fig. 4a). Extinction probabilities were intermediate when mixed seasons of fires were used. The lowest extinction probability occurred when sites were burned every six years for a summer fire regime and every 3–6 years for a winter fire regime or burning every four or ten years using mixed seasons of fires (Fig. 4a). Under probabilistic fire return intervals, a winter burning fire regime (4–8-year fire intervals) again generated smaller extinction probabilities than the summer burning regime (7-year fire intervals) (Fig. 4b). When using both seasons of fires, a mean fire return interval of six years produced the lowest extinction probability (Fig. 4b).

Winter fires also produced lower probabilities of population decline for both deterministic (Fig. 4c) and probabilistic (Fig. 4d) simulations. Regular burning in the winter generated lower population decline probabilities than burning in the summer within the 3–8-year regular fire return interval (Fig. 4c). If fire occurred every 10–30 years, the probabilities of population decline were the same for either season of fires (above 0.99). Summer fires produced high population decline probabilities across all fire return intervals. A winter-burn fire regime with an interval of four years produced the lowest decline probability (0.63). Population decline probabilities rose when fire return interval was not regular (Fig. 4d).

DISCUSSION

Quantifying seed bank dynamics

In this study, matrix models that used data from the sown-seed germination experiment gave much more realistic projections than those based on bagged-seed experiments. The sown-seed estimates of percentage of germination were significantly lower than that of the bagged seed, possibly due to preemergence seedling mortality (Wagner and Spira 1994, Liu and Spira 2001) and predators. The differences may also be due to post-dispersal seed predation for sown seeds, although no known post-dispersal seed predator has been documented for *C. keyensis*. Other factors, such as higher moisture within bags or prevention of seed loss in bags, could also have affected the results. Overall, the sown-seed experiment might have given more accurate estimates of percentage of germination for calculation of fertility than bagged-seed experiments. However, the bagged-seed experiment provided estimates of percentage of seeds that remained viable to the second year, data that could not be obtained from the sown-seed experiment in which seeds could not be easily retrieved to account for seed mortality vs. dormancy. Therefore, a combination of these two experiments, though not usually done, is essential to quantify seed bank dynamics.

Although the sown seedlings were monitored more frequently than the natural seedlings (once every two weeks vs. every 2–4 months), these two samples gave similar estimates of seedling survival. Nevertheless, we may have missed some very short-lived seedlings in the natural seedling monitoring.

The experiment on seed mortality after fire demonstrated that the percentage of seeds surviving the direct impact of a fire was variable among plots, probably a reflection of patchy fires. Litter and soil could have provided protection to some seeds (Whelan 1996). In addition, seeds of *C. keyensis* have hard seed coats, which may help them survive a fire. Indeed, seeds of many *Acacia* spp., also legumes, in Australia survive fires at high rates (Auld 1996, Bell 1999; but see Radford et al. [2001]). The estimates of seeds surviving

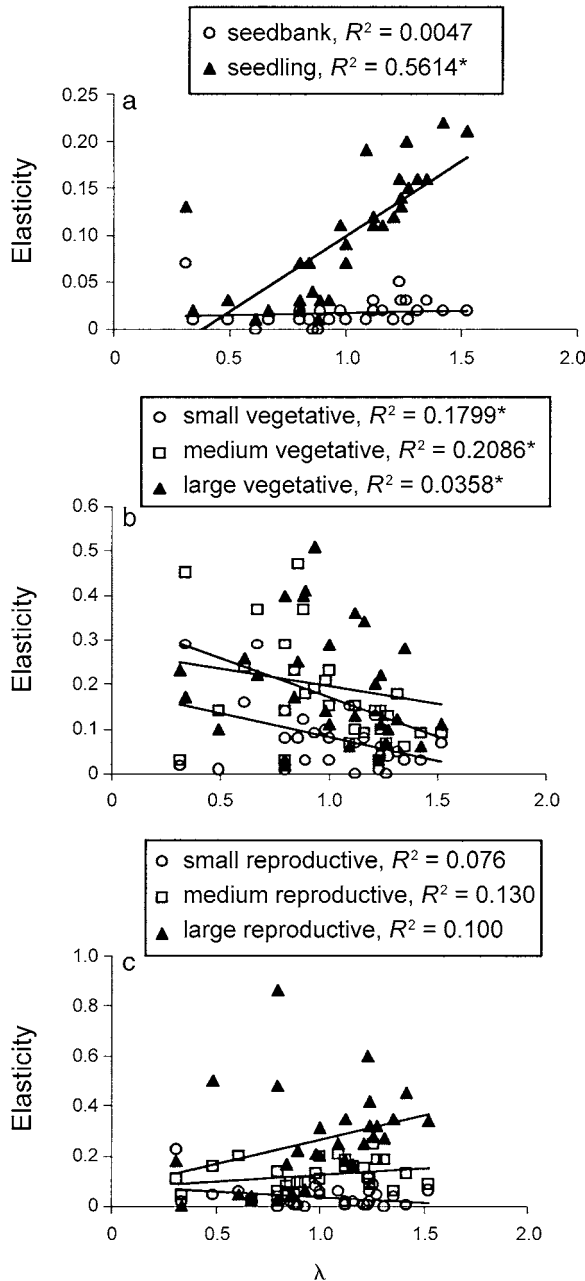


FIG. 3. Elasticities of different life history stages of *Chamaecrista keyensis* on Big Pine Key as a function of the finite population growth rate (λ): (a) seed bank and seedling; (b) vegetative stages; (c) reproductive stages.

* $P < 0.05$.

fire in this experiment may be conservative as seeds were spread only one day before the fire. Survival of seeds may be higher if seeds are spread early so that they have more time (or chances) to settle deeper in the litter or soil.

Fire effects on demography of *C. keyensis*

Pattern of the effects of fire season on finite population growth rates (λ) was not clear due to the limited

number of values for comparison. Nevertheless, winter burns seemed to result in greater finite population growth rates (λ) than summer burns during the burn year, except for the Dogwood summer burn. Dogwood summer burn occurred in early summer (June) and resulted in a very high λ during the burn year. However, differences in λ were small between the summer and winter burns during the two subsequent years postfire.

Time since fire has major effects on population growth of *C. keyensis*. The finite population growth rates (λ) were usually very low (<1) during the burn year, probably due to high mortality for plants of all stages (Liu and Menges 2005). At one and two years postfire, λ rapidly increased and reached the highest values observed, probably due to stimulated growth, reproduction, and recruitment shortly after fires (Liu and Menges 2005). Consequently, our data indicated a marginally significant negative relationship between λ and time since fire for sites more than one year postfire. Negative relationships between λ and time since fire were common among herbs of various fire-dependent habitats, such as *Eriogonum longifolium* var. *gnaphalifolium* (Satterthwaite et al. 2002), *Eryngium cuneifolium* (Menges and Quintana-Ascencio 2004), *Hudsonia montana* (Gross et al. 1998), *Hypericum cumulicola* (Quintana-Ascencio et al. 2003), *Lomatium bradshawii* (Kaye et al. 2001), *Silene regia* (Menges and Dolan 1998), and *Silene spaldingii* (Lesica 1999).

This negative relationship may actually be more significant for *C. keyensis* if sampling bias could be avoided. In this study, we used nonrandom census plots >15 years postfire, established at locations where more than one individual of *Chamaecrista keyensis* occurred, in order to provide sufficient individuals for monitoring. Such a systematic sampling bias was difficult to avoid and is common among demographic studies of vegetation gap species (Menges and Quintana-Ascencio 2003, Quintana-Ascencio et al. 2003). In our simulation, extinction probability seemed to drop gradually at 15-year or longer fire return intervals. This is probably also an artifact due to the same sampling bias.

Composite elasticities changed significantly from the year of burn to one year postburn, and such changes were associated with corresponding changes in λ . As population growth rate increased, the importance of stasis decreased, but the importance of growth and fecundity increased. The relationships between λ and elasticities found in *C. keyensis* were consistent with several other herbaceous species (Oostermeijer et al. 1996, Silvertown et al. 1996, Menges and Dolan 1998). In addition, as λ increased, seedling progression (transition from seedling to other aboveground stages) became increasingly important. Therefore, improving seedling survival and growth is effective in increasing the population growth rates of *Chamaecrista keyensis* for stable or growing populations. On the other hand, elasticities of vegetative plants were high for declining populations, suggesting that stimulating progression

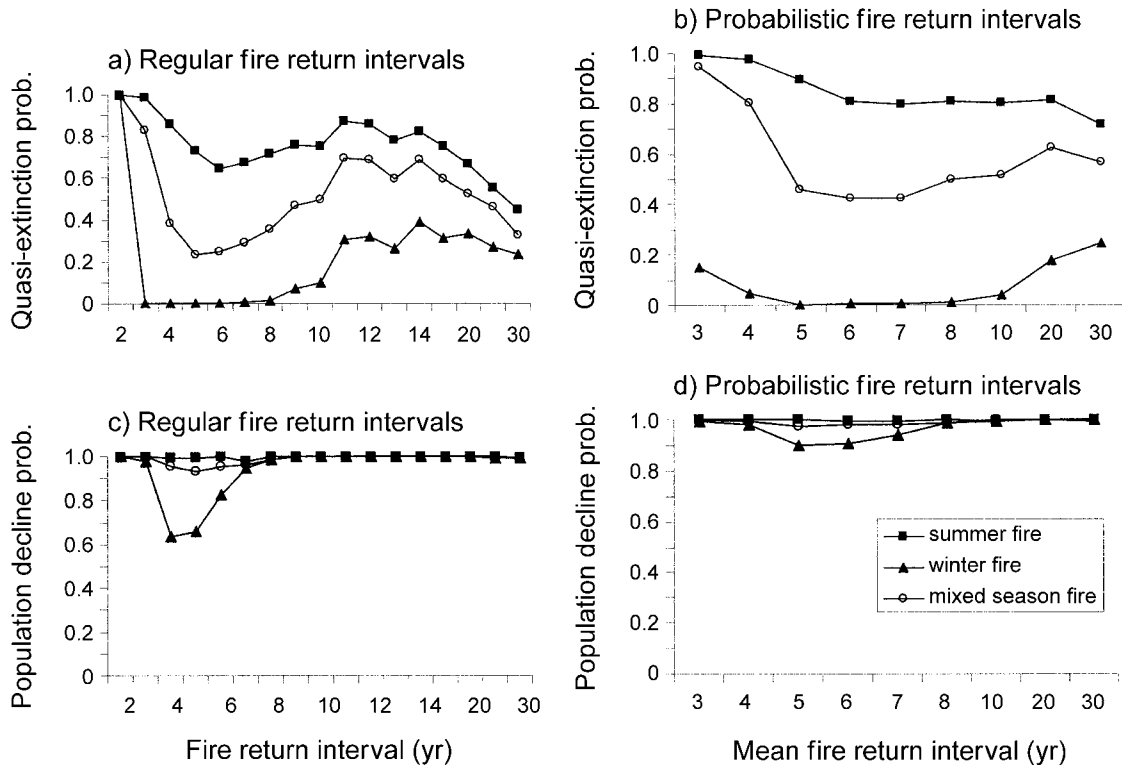


FIG. 4. (a, b) Quasi-extinction (threshold = 10) probability ("prob.") and (c, d) population decline probability over 100 years for *Chamaecrista keyensis* on Big Pine Key as functions of seasons of fire and fire return interval.

for vegetative plants, e.g., encouraging their transition to reproducing, may be effective for improving the status of a declining population. Fires of both seasons may stimulate reproduction (Liu and Menges 2005). Furthermore, elasticity of large flowering plants had consistently high values, indicating that keeping large plants flowering is effective in increasing population growth rate for all populations. Finally, elasticity of survival was greater during the year of burn than the subsequent year, suggesting that maximizing survival to fires is an effective way to minimize the reduction in finite population growth rate the year of burn. Early summer fires or dry-season fires may achieve this objective as they caused significantly lower mortality than late summer fires (Liu and Menges 2005).

Effects of fire return interval and fire season on extinction risk and population decline probability

Fire return intervals of 5–8 years are optimal to minimize extinction probability, while return intervals of 4–7 years minimize population decline probability of *C. keyensis*. Pine rockland fuel biomass recovers very quickly in the first few years after a fire and reaches asymptotic levels at around eight years postfire (Sah et al. 2003). Such a vegetation recovery pattern would sustain fires at frequencies of every 5–8 years. Although sensitive to closures of forest canopy as time since fire increases, *Chamaecrista keyensis* may persist

in open pineland gaps for up to 30 years. However, such persistence did not translate into low extinction probability for the population. Diminishing herb diversity, including *C. keyensis*, is evident in pine rockland patches that are more than 15 years postburn (Robertson 1955, Alexander and Dickson 1972, Carlson et al. 1993).

Optimal fire return intervals vary among species of the same and/or different ecosystems, depending on biology of the species of concern and postfire vegetation recovery (e.g., Menges and Dolan 1998, Caswell and Kaye 2001, McCarthy et al. 2001, Quintana-Ascencio et al. 2003, Menges and Quintana-Ascencio 2004). For example, populations of *Erygium cuneifolium*, a Florida scrub endemic herb, benefit the most from a fire return interval of <15 years (Menges and Quintana-Ascencio 2004), while *Hypericum cumulicola*, also a Florida scrub endemic, has a relatively wide optimum fire return interval of 15–50 years (Quintana-Ascencio et al. 2003). The effect of fire return interval on *C. keyensis* may not apply to other endemic species of the pine rocklands. More studies on other pine rockland species are needed to determine the variation in fire return interval that may help to ensure the diversity of this ecosystem.

Wet- and dry-season fires differed in extinction and population decline risks. A *Chamaecrista keyensis* population subject to summer burn only had the highest

extinction probability, especially with probabilistic fire return intervals (variable fire return intervals). Extinction probability would be reduced if the summer fire regime was mixed with winter fires or winter fires only were used. Only winter fire alone assures relatively low population decline probabilities. This was probably due to the differences in finite population growth rate between the summer- and winter-burn treatments during the year of burn. Summer fires, particularly late summer fires, caused greater plant mortality and lower seedling recruitment than winter fires (Liu and Menges 2005), resulting in lower finite population growth rates following the late summer-burn treatments.

Prescribed burns in the Lower Florida Keys have occurred mostly in the late summer season (August and September), when high fuel-moisture levels allow good control of fire behavior (Bergh and Wisby 1996). This timing of burning, as demonstrated in our study, may have negatively affected *C. keyensis*. In contrast, early summer-burn treatment resulted in the highest finite population growth rate due to outstanding positive response in *C. keyensis* vital rates (Liu and Menges 2005). Future fire management plans in the Lower Florida Keys should incorporate early summer and winter burning to ensure the health and continuing existence of *C. keyensis*.

Many studies have focused on the effects of fire season on plant populations in this and other fire-dependent ecosystems (Platt et al. 1988, Biondini et al. 1989, Robbins and Myers 1992, Brewer and Platt 1994a, b, Glitzenstein et al. 1995, Spier and Snyder 1998, Lesica 1999, Hiers et al. 2000). To our knowledge, however, this study is the first to assess the effect of fire season on population extinction risks using matrix modeling. By integrating all components of demographic vital rates, matrix modeling offered a comprehensive evaluation of the demographic consequences of fire season. Nevertheless, there were several limitations to this modeling. First, a low percentage (~12%) of the matrix elements were not site- or year-specific, which might reduce the natural demographic variation. Second, while the four years of census data captured crucial demographic transitions during and a few years after fires, it could not capture the whole range of temporal variation of demographic vital rates. Third, gaps in the chronosequence of time since fire for *C. keyensis* data have to be extrapolated based on certain assumptions. For example, the finite rates of population growth 4–7 years postfire were assumed to follow an exponential decay function between finite population growth rate of three years postfire and that of eight years postfire. Due to these limitations, we focused on comparative extinction risks and population decline probabilities, rather than believing in the absolute values, as cautioned by many authors (Burgman et al. 1993, Beisinger and Westphal 1998, Menges 2000, Reed et al. 2002, McCarthy et al. 2003, Menges and Quintana-Ascencio 2003).

Since this is the first known population viability analysis of a pine rockland plant, it is difficult to compare results from this study to others in the same system. Nevertheless, responses of *Chamaecrista keyensis* to fires of different seasons contrasted with those seen in *Jacquemontia curtisii*, another endemic herb of pine rocklands. Although not evaluated through population matrix modeling, some population vital rates (survival and reproduction) of *J. curtisii* responded positively to summer fire but not winter fire. Other vital rates (seedling recruitment) responded more positively to winter vs. summer fire (Spier and Snyder 1998), as did *Chamaecrista keyensis* (Liu and Menges 2005).

Although winter fires benefit population growth of *C. keyensis*, a fire regime including only winter fire is unlikely the historical fire regime under which the pine rockland ecosystem has evolved. Most lightning-ignited fires occur in the summer (Snyder 1991). In addition, a regime of exclusively winter fire may not be optimal for other endemic species of pine rockland (e.g., Spier and Snyder 1998). Nevertheless, our results suggested that fires at times other than the lightning season (summer) may have constituted a part of the historical fire regimes. According to our models, such a mixed-season fire regime can also sustain a low level of population extinction probability for *C. keyensis*. Phenology of *C. keyensis* is crucial in determining the effects of fire of different seasons (Liu 2003). Pine rockland plants differ widely in their seasons of growth and reproduction (S. Koptur, M. Ross, J. Snyder, C. Borg, and H. Liu, *unpublished data*). If phenology is also an important factor in determining how other species of pine rockland respond to fire, a fire regime with diverse fire seasons would be best for maintaining the plant diversity of pine rockland.

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APPENDIX A

Fecundity and fertility calculations for matrix building of *Chamaecrista keyensis* are available in ESA's Electronic Data Archive: *Ecological Archives* A015-005-A1.

APPENDIX B

A description of the methods used for choosing size variables and classes of *Chamaecrista keyensis* is available in ESA's Electronic Data Archive: *Ecological Archives* A015-005-A2.

APPENDIX C

A description of the methods used for identifying and pooling stages of *Chamaecrista keyensis* is available in ESA's Electronic Data Archive: *Ecological Archives* A015-005-A3.

APPENDIX D

Transition matrices of *Chamaecrista keyensis* are available in ESA's Electronic Data Archive: *Ecological Archives* A015-005-A4.

APPENDIX E

Cumulative fire occurrence probability curves of pine rockland on Big Pine Key, Florida, USA, are available in ESA's Electronic Data Archive: *Ecological Archives* A015-005-A5.