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# Population viability analysis and fire return intervals for an endemic Florida scrub mint

Eric S. Menges<sup>a,\*</sup>, Pedro F. Quintana Ascencio<sup>b</sup>, Carl W. Weekley<sup>a</sup>, Orou G. Gaoue<sup>c</sup>

<sup>a</sup>Archbold Biological Station, P.O. Box 2057, Lake Placid, FL 33862, USA

<sup>b</sup>Department of Biology, University of Central Florida, Orlando, FL 32816-2368, USA

<sup>c</sup>Department of Botany, University of Hawaii at Manoa, Honolulu, HI 96822, USA

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## ABSTRACT

We use population viability analysis of an endangered Florida scrub mint, *Dicerandra frutescens*, to specify the optimal fire return intervals for its long-term persistence and for its specific habitat. We derived 83 population projection matrices from 13 years of demographic data from eight populations, 59 matrices from scrub populations and 24 from firelane or yard edges. Seed dormancy and germination transitions were inferred based on experimental data and verified by comparing modeled vs. observed population trajectories. Finite rates of increase in scrub sites were highest shortly after fire and declined steeply through 10 years postfire. The break-even value of  $\lambda = 1$  was passed quickly, in about six years, suggesting that populations >6 years postfire were already facing decline. The decline is probably related to the rapid growth of competing shrubs in the habitat of *D. frutescens*. In long-unburned sites, finite rates of increase were nearly always <1 and declined the most in the long-unburned site with no foot trails or treefall gaps. Finite rates of increase in firelane populations also declined with years since fire or last disking. The yard edge population showed  $\lambda$  values both >1 and <1, with no temporal trend. Stochastic simulations in scrub sites suggested an optimal regular fire return interval of about 6–12 years. Regular fires at this interval were more favorable than stochastic fire regimes, but stochasticity reduced extinction percentages at longer fire return intervals. Stochastic fire return intervals implied a wider optimal fire return interval of 6–21 years. We suggest that prescribed fire in Florida scrub on yellow sand has occurred (and needs to occur) more frequently than previously recommended.

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## 1. Introduction

Population viability is strongly affected by spatial and temporal variation in the environment. Ecological disturbances such as fire, flooding, and wind drive demographic variation in many species (Pickett and White, 1985; Menges and Quintana-Ascencio, 2003). Many species are sensitive to fire regime, requiring fire at certain intervals or of certain intensi-

ties (e.g., Gross et al., 1998; Brewer, 2001; Kaye et al., 2001; Russell-Smith et al., 2002; Lloret et al., 2003; Menges and Quintana-Ascencio, 2004). Long-term demographic data collection combined with demographic modeling can be used to assess the effects of various burning treatments (Oostermeijer, 2003).

Demographic modeling has been used to examine population viability under different fire regimes (e.g., Bradstock and

\* Corresponding author. Tel.: +1 863 465 2571; fax: +1 863 699 1927.

E-mail address: [emenges@archbold-station.org](mailto:emenges@archbold-station.org) (E.S. Menges).

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O'Connell, 1988; Burgman and Lamont, 1992; Canales et al., 1994; Gross et al., 1998; Menges and Dolan, 1998; Pfab and Witkowski, 2000). These models have been used to predict extinction risk and population growth rate varying with fire frequency, and to estimate optimal fire return intervals (e.g., Manders, 1987, on *Widdringtonia cedarbergensis*; Canales et al., 1994, on *Andropogon brevifolius*; Enright et al., 1998a,b, for *Banksia* species; Gross et al., 1998, for *Hudsonia montana*; McCarthy et al., 2001 on *Banksia ornata*). A particularly thorough fire/population viability analysis (PVA) using both deterministic and stochastic modeling, and both matrix and element selection, found that fire was beneficial to an endangered prairie perennial, *Lomatium bradshawii*, with critical annual fire probabilities of 0.4–0.9 (Kaye et al., 2001; Caswell and Kaye, 2001).

However, most of these approaches have been based on only a few years of demographic data and/or a few fires. PVAs can only be reliable when the underlying data are unbiased and extensive enough to represent the dynamics of the population studied (Coulson et al., 2001). With respect to fire, this will be particularly true when fire effects include subtle or opposing impacts on different vital rates or species. For example, for *Banksia cuneata* in southwestern Australia, the fire frequency that maximizes population size (15–25 year fire return interval) does not minimize extinction risk because entire postfire seedling cohorts may fail during drought years (Burgman and Lamont, 1992).

A relatively infrequently studied aspect of fire regime is the effect of regular vs. stochastic fire return intervals on population viability. Land managers often spend considerable time and energy trying to enforce regular fire return intervals, but if stochastic fire regimes provide similar benefits they could provide added flexibility. However, for populations specialized for a narrow range of fire frequencies, stochastic fire regimes may include a greater proportion of intervals that are either too long or too short to sustain viable populations. Stochastic fire regimes may also affect other aspects of demography. For example, stochastic fire return intervals may allow a greater proportion of very old individuals to persist in the landscape, relative to unvarying fire return intervals (McCarthy and Burgman, 1995). If older (and hence larger) individuals are particularly fecund, as is often true in plants (e.g., Herrera, 2004), then stochasticity could have positive effects on population responses to disturbance. Stochasticity in fire return intervals may also affect life history traits. To predict the intermediate level of serotiny in *Banksia attenuata*, variation in fire return intervals had to be included in models (Enright et al., 1998a).

Many fire-driven PVAs have evaluated the effect of regular fire intervals, but stochastic fire distributions are the norm in most natural ecosystems (McCarthy and Burgman, 1995). Model simulations considering the variation around average optimal fire return intervals will provide more realistic management recommendations. In addition, variable fire return intervals can promote species diversity because they allow species with conflicting optimal fire return intervals to coexist (Hoffmann, 1999). In contrast, human-imposed management with regular prescribed fires may allow only a subset of species to thrive.

The evolution of life history traits may be shaped by recurrent events such as fire (e.g., Schwilk and Ackerly, 2001). In

turn, species specialized for certain ecosystems can serve as indicators of disturbance regime for their vegetation type (McCarthy et al., 1999; Bond et al., 2004). Life history traits such as postfire recovery, fire-stimulated germination, and fire-stimulated flowering suggest evolution of traits in response to fire (Christensen, 1985). Specific links of species' traits to particular components of a fire regime, such as fire return interval, are more elusive. Population viability analysis is well suited to identifying the "best" fire return interval as it does better in predicting relative (rather than absolute) outcomes (Menges, 2000; Morris and Doak, 2002; Lindenmayer et al., 2003; McCarthy et al., 2003).

Because land managers can manipulate some disturbances, such as fire, managing disturbances to maintain population viability is a distinct possibility. An "optimal fire return interval" can be derived for a species from PVA models that incorporate environmental stochasticity and responses of populations to disturbance events and post-disturbance changes in the ecosystem. An accumulation of such optimal fire return intervals for multiple species could lead to an assessment of the range of fire return intervals appropriate for maintaining a mix of species in an ecosystem (as in analyses of life history traits; Gill and McCarthy, 1998; Russell-Smith et al., 2002; Bradstock and Kenny, 2003; Lloret et al., 2003). Because many narrowly endemic species are habitat specialists (e.g., Cowling and Holmes, 1992; McCoy and Mushinsky, 1992; Fiedler, 1995), they may provide more fine-tuned information on fire return intervals for specific ecosystems (e.g., Liu et al., 2005) than dominant species that occur in a wider variety of ecological situations.

In Florida scrub, a shrubland found on xeric sands (Menges, 1999), several endemic species show enhanced population viability in relation to fire, according to PVA modeling using both deterministic and stochastic matrix selection approaches. For example, *Eriogonum longifolium* var. *gnaphaliifolium*, while benefiting from frequent and complete fires, can tolerate a range of fire return intervals (Satterthwaite et al., 2002). This flexibility is consistent with the wide range of natural fire return intervals in its sandhill and scrub habitats (Menges, 1999). Two plants endemic to Florida rosemary (*Ceratiola ericoides*) scrub, an ecosystem characterized by fire return intervals of greater than 10 years (Myers, 1990; Menges, 1999), benefit from periodic fires. *Hypericum cumulicola* requires return times less than 50 years for long-term persistence of most populations (Quintana-Ascencio et al., 2003), while the co-occurring *Eryngium cuneifolium* has the lowest extinction risks for fires occurring at least every 15 years (Menges and Quintana-Ascencio, 2004). These studies suggest that previous recommendations to burn rosemary scrub every 15–100 years (Menges, 1999) need to be adjusted downward.

The subject of this paper, *Dicerandra frutescens*, occurs in neither sandhill nor rosemary scrub. Its preferred Florida scrub habitat occurs on xeric yellow sands (Menges, 1992) and includes oak-hickory scrub (sensu Menges, 1999; southern ridge sandhill hickory phase sensu Abrahamson et al., 1984), and sand pine scrub oak phase (sensu Abrahamson et al., 1984). These scrub systems recover from fire with vigorous resprouting of the dominant shrubs (especially *Quercus myrtifolia*) and gaps are much less abundant than in other scrub habitats (Menges, personal observation). The fire return

interval for this type of scrub is “not known” (Menges, 1999) or specified widely for broad vegetation types (e.g., Myers, 1990, 15–100 for “scrub”) or not specified (e.g., Abrahamson et al., 1984). Since *D. frutescens* is one of the few plants restricted to this type of scrub, its demography can provide a clue to the historical fire return intervals of Florida scrub on yellow sands.

*D. frutescens* also occurs in habitats disturbed by humans, such as mown or occasionally disked edges of roads and firelanes, and (in at least one case) edges of a suburban yard. We studied the demography of *D. frutescens* in all its various and contrasting habitats to provide insights into its life history and to gather information on potential management alternatives to fire. We use long-term demographic data and population modeling to analyze the demography and viability of *D. frutescens* populations, in particular, to:

1. determine the optimal fire return interval for *D. frutescens* under regular burning;
2. contrast the effects of regular and random fire return intervals on the risk of extinction and population decline;
3. estimate modal fire return intervals of *D. frutescens*' preferred scrub habitat.

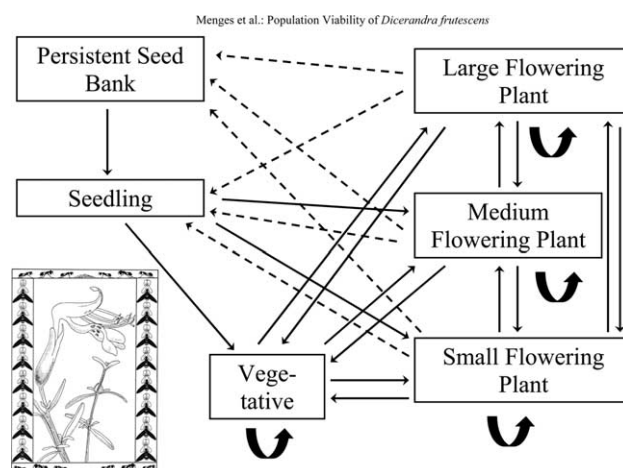
## 2. Methods

### 2.1. Study species

*Dicerandra frutescens* is endemic to central Florida's Lake Wales Ridge, one of several dozen plants endemic to this biodiversity hotspot (Christman and Judd, 1990; Dobson et al., 1997), with a large population protected and managed at Archbold Biological Station. These studies occurred in Highlands County, identified as the top-ranked county for endemic plants in the southeastern United States, in part because it harbors two species of *Dicerandra*, the highest ranked genus of rare southeastern endemic plants (Estill and Cruzan, 2001). *D. frutescens* is a low-growing suffrutescent mint occurring in yellow sand supporting Florida scrub, mainly in gaps, recently burned scrub, and along old disturbances such as trails and roads (Menges, 1992; Menges et al., 1999). Fire kills all plants (Menges, 1992). Although populations appear robust after fires, the species also persists in some long-unburned areas. *D. frutescens* populations include flowering and vegetative plants of various sizes, as well as seedlings and seeds dormant at the time of the annual census (September) (Fig. 1). Seedlings come (in part) from seeds germinating in the winter immediately following flowering and fruit production, and have survived the spring and summer through September. In addition, seeds that survive may lie dormant in the soil and germinate in subsequent years.

### 2.2. Field sites

We collected demographic data on *D. frutescens* from 1988 to 2000 in seven populations at Archbold Biological Station and from one nearby yard-edge population (Table 1). Long-term censuses were developed for five populations in two natural vegetation types: two in oak-dominated sand pine scrub,



**Fig. 1 – Life cycle of *Dicerandra frutescens*. Each box is a life history stage used in modeling. Solid arrows indicate survival/growth/stasis/regression transitions. Dotted arrows indicate fecundity transitions. The drawings showing *D. frutescens* and its bee-fly pollinator (on the vertical frames) were done by Kevina Vulinec and Mark Deyrup, respectively (Deyrup and Vulinec, 1996). (The ants play no known role in *D. frutescens* biology.)**

and three in oak-hickory scrub (see Abrahamson et al., 1984 and Menges, 1999, for more information on vegetation), along the edge of two firelanes (one along a formerly disked firelane that became a narrower sand road and a second formerly disked firelane that was allowed to partly revegetate, and was subsequently burned) and in a population on the edge of a suburban yard that was occasionally watered. Four of these populations have been burned during the course of the study (Table 1).

### 2.3. Demographic data collection

Demographic data were collected from 6 to 84 m<sup>2</sup> quadrats at each study site with the goal of sampling >50 established plants per population per year. We placed quadrats randomly or along long pre-determined belt transects 1 or 2 m wide. In low-density populations, we added subjectively placed quadrats in areas where groups of plants grew. Within each quadrat, each plant was mapped with X and Y coordinates to the nearest cm. Plants were marked with colored plastic swizzle sticks (when seedlings) and metal tags (when adults). Survival and recruitment were recorded monthly from September 1988 to September 1992 and quarterly thereafter to the present (we analyze data through 2000). We recorded size measurements (basal diameter, number of branch tips) and an index of fecundity (number of reproductive branch tips) on each individual plant in September annually. In most years, we also collected detailed fecundity data (as numbers of fruits and nutlets from subsamples) from most populations.

### 2.4. Determining a size measure

To determine which size measure would be the best predictor of survival, we performed a logistic regression of survival by

**Table 1 – Study populations (Pop) of *Dicerandra frutescens*, habitat type, number of plants in dataset (N), first year of study, area of plots, history of fire and other management, and number of matrices (total, 0–10 years after fire [Burn], and in long-unburned [LU] scrub)**

Pop	Habitat <sup>a</sup>	N	First year	Area studied (m <sup>2</sup> )	Burn years	Number of matrices <sup>b</sup>			
						Total	Burn scrub	LU scrub	Non-scrub
0	FL edge	1040	1988	39	1996	7 <sup>c</sup>	0	0	7
11	FL edge	281	1988	17	1990 <sup>d</sup>	8	0	0	8
2	SPS	980	1988	84	None	12	0	12	0
4	SPS	646	1988	37	1998	12	3	9	0
10	OHS	269	1988	12	1984, 1996	12	12	0	0
12	OHS	482	1988	13	1990	13 <sup>e</sup>	11	2	0
19	OHS	310	1990	30	None	10	0	10	0
24	Yard edge	850	1991	6	None	9	0	0	9
Sum	–	4858	–	238	–	83	26	33	24

a Habitats include firelane edge (FL); sand pine scrub (SPS); and oak-hickory scrub (OHS).

b Not all matrices have associated  $\lambda$  values because some have only seeds, seedlings, or vegetative plants (see Table 5).

c This site was disked through ca. 1983 and was studied as a post-disking sequence from 1988 to 1995. Although this population was burned in 1996, we do not use matrices after this event since the effects of burning and the prior diskings may be confounded.

d Partial burn.

e Two matrices in 1989–1990, one burned in 1990, and one unburned.

each of three size metrics, basal diameter, number of branch tips and number of flowering branch tips, using natural log-transformed data. The number of branch tips was the best predictor of survival in simple logistic regressions, and this variable was also most often entered in multiple logistic regressions (Table 2). The equations were successful in predicting the survival of individual plants 74–84% of the time, depending on year. The number of branch tips also proved superior to basal diameter in predicting a fecundity parameter, the number of flowering branch tips, in each year from 1990 to 2000 (analyses not shown). Based on these analyses, we concluded that the number of branch tips was the best size measurement to use in choosing size cut-offs for stage classes of flowering *D. frutescens* plants.

We used the Moloney algorithm (Moloney, 1986), based on branch tip number, to delimit size classes for *D. frutescens* reproductive plants, following the approach detailed in Menges and Quintana-Ascencio (2004). Sample sizes for vegetative

plants were smaller, so this life history stage was not subdivided by size. Reproductive class cutoffs were determined using demographic data classified by population or by time-since-fire. While the first cutoff (12 branch tips) was consistent between data classified by population or by time-since-fire, the second cutoff was not (35 vs. 27 branch tips, respectively). We decided on the cutoff obtained with data classified by time-since-fire because it provided better sample-size distribution of plants among classes. Using this procedure, we identified three reproductive stages based on size: small ( $\leq 11$  branches), medium (12–27 branches), and large ( $\geq 28$  branches) (Fig. 1).

## 2.5. Form of each projection matrix

Each projection matrix for *D. frutescens* has six rows and six columns, each representing a stage (seed bank, seedling, vegetative, small flowering, medium flowering, and large flowering; see also Fig. 1). Seed bank transitions include remaining

**Table 2 – Significant predictors of annual survival in individual and multiple logistic regressions in *Dicerandra frutescens***

Year	N	P for Pearson's r			Variables in multiple logistic regression	Percent correct
		Ln basal diameter (BD)	Ln number of branch tips (BT)	Ln number of flowering branch tips (FBT)		
1988–89	348	<0.001	<0.001	NA	BT (+)	76.1
1989–90 <sup>a</sup>	219	0.018	<0.001	NA	BT (+)	75.2
1990–91	222	0.809	0.127	0.788	None	–
1991–92	206	0.404	0.006	0.002	FBT (+)	83.0
1992–93	208	0.132	0.263	0.463	None	–
1993–94	183	0.788	0.011	0.033	BT (+), FBT (+)	79.2
1994–95	118	0.536	0.028	0.656	BT (+)	83.1
1995–96 <sup>a</sup>	99	0.852	0.022	0.612	BT (+)	73.7
1996–97	103	0.126	0.030	0.056	BT (+)	79.4
1997–98 <sup>a</sup>	81	0.258	0.028	0.253	BT (–)	84.0
1998–99	110	0.546	0.004	0.186	BT (+)	82.7
1999–2000	111	0.152	0.484	0.582	None	–

Positive and negative signs refer to direction of effect of variable(s) in multiple logistic regression. Percent correct refers to percent of plants classified correctly by multiple logistic regression.

a Burned populations were not included.

in the seed bank or germinating and surviving to become a seedling. Seedlings may become vegetative or move to one of the flowering plant classes. Vegetative plants may remain vegetative or move to one of the flowering plant classes. Flowering plants may remain flowering in the same or a different class or regress to a vegetative state. Flowering plants also contribute seeds to the seed bank and produce seedlings (the top two rows of the matrix). Impossible transitions include seed production by non-flowering plants, regression to seedling status, and germination to a non-seedling stage. Projection matrices are available in digital form (see Appendix A).

## 2.6. Survival and growth terms in *D. frutescens* matrices

Survival and growth were directly ascertained by fates of plants of the various stages from one year to the next, kept separate by population. We used the population and year-specific data if there were five or more observations for a stage. In total, more than 3/4 of survival/growth transitions were represented by data specific to the population and year. If a stage had fewer than five observations, we pooled data for that stage to reduce the effect of estimates based on extremely low sample sizes. Data were pooled for individuals within the same habitat type, same or near time-since-fire or (for population 0) time-since-disking, until the sample threshold of five observations was reached. In the eight matrices where no plants transitioned into the large category, we used pooled data to “connect” loops within a matrix. We substituted pooled data for all transitions from medium flowering plants in these cases. When all large flowering plants survived as large flowering plants (four matrices), we used a value of 0.999 instead of 1 for the large flowering plant to large flowering plant transition. If we had used the value of 1, it would have dominated the eigenvalue for that matrix.

## 2.7. Determination of fertility parameters for modeling

### 2.7.1. Seed production (fecundity)

Fertility (seedling production) in *D. frutescens* is a function of seed production (fecundity), seed germination, and survival of seeds in the seed bank. Since this species has a persistent seed bank (Finer and Menges, unpublished data), germination percentages must be specified in the year following seed production (a direct transition from flowering plants to seedlings) and in subsequent years from the soil seed bank.

*D. frutescens* seeds are enclosed in nutlets (one seed per nutlet), with up to four nutlets per fruit (schizocarp). Fruits (and, earlier in development, flowers) are borne on distinct, erect branch tips. The number of flowering branch tips is the starting point for estimating seed production. Each year, from 1990 to 2000, we counted flowering branch tips on each reproductive plant during fall demographic monitoring. (For 1988 and 1989, flowering branch tips were predicted from total branch tips on flowering plants, using population-specific regressions from 1991.)

Fecundity subsampling was accomplished by collecting ~30 flowering branch tips from multiple plants outside the demographic quadrats in each population with sufficient flowering material. We counted the number of fruits (schizocarps) on each flowering branch tip and the number of nutlets

per fruit (or in some years, from a subsample). Schizocarps have a sheath of hairs inside the top surfaces that tend to prevent nutlets from falling out. We included only schizocarps with sheaths of hair and in mature condition when counting nutlets per schizocarp. Nutlets were then examined individually under a 10× dissecting microscope for signs of damage, fungal attack, or parasitism. Only intact nutlets that did not collapse under light pressure were counted as intact.

To estimate nutlet production, we used mean numbers of fruits per flowering branch tip and mean number of nutlets per fruit for individual populations and years if the number of individuals in a given flowering class is greater than 5; otherwise, we pooled data (same rules as survival and growth pooling) to produce estimates. Nutlet production was calculated as the product of number of flowering branch tips, number of schizocarps per flowering branch tip, and number of nutlets per schizocarp.

### 2.7.2. First year seed germination

We conducted a number of germination trials in the lab (in Petri dishes), on a veranda (an outdoor, covered porch, in native soil in greenhouse flats), and in the field between 1989 and 1999. The experiments used nutlets from seven individual populations (Table 3) and lasted 1–2 years. In some experiments, we tested the effects of various factors on germination percentages, including wet heat, dry heat, litter removal, sun vs. shade, transplant site, and exclusion of ants. Due to low germination rates in most experiments, we do not have enough data to assess the effect of these treatments on germination percentages. We used germination percentages without respect to treatment for individual populations (Table 3) and as a species-wide weighted mean of 0.0137.

### 2.7.3. Subsequent seed behavior

Nutlets ungerminated after one year may include viable nutlets with persistent seed dormancy. We had insufficient data to directly calculate seed bank survival and germination from the seed bank. Based on observations of high seedling recruitment densities postfire, we hypothesized that germination would be highest immediately postfire. Consequently, we considered postfire germination as a separate parameter taking on higher values. To estimate seed bank and germination parameters, we assessed alternative scenarios evaluating the degree of agreement between observed (demography plot data) and modeled population trajectories using a range of values for three parameters: seed survival (0.1–1), ≤3 years postfire germination from the seed bank (0.1–1), and >3 years postfire seedling germination from the seed bank (0.001–0.01). One thousand models including the combinations of 10 values of each of the three parameters (increasing step by the lowest unit) were evaluated for sites burned. One hundred models including only the two unburned parameters were evaluated for unburned sites.

Observed population trajectories were obtained by plotting the number of total individuals recorded (during annual demographic censuses) within a population and across 6–12 years, depending on available matrices. We calculated a likelihood ratio ( $G$ ) to evaluate the goodness of fit between observed and modeled population trajectories

$$G = 2 \sum f_i \ln(f_i/f_i).$$

**Table 3 – Experiments producing estimates of first-year germination percentages ( $G_1$ ) for *Dicerandra frutescens*, by population (Pop), 1989–1999**

Pop	Location	Year Coll.	Expt. Ended	Conditions (+control)	Nutlets/Replic.	Total nutlets	Number of germination	Proportion germinated	Pop. mean
0	Lab	1989	2/90	Petri dish	20	160	0	0.0	0.0006
0	Field	1989	3/91	Sun/shade litter/bare	28	672	0	0.0	
0	Veranda	1991	11/93	Heat	50	1200	2	0.0017	
2	Lab	1989	2/90	Petri dish	20	80	12	0.1500	0.1417
2	Veranda	1991	11/93	Heat	50	150	20	0.1333	
4	Field/lab	1998	3/00	Canopy/litter burn	20	80	9	0.1125	0.1125
10	Lab	1989	2/90	Petri dish	20	160	2	0.0125	0.0125
11	Lab	1989	2/90	Petri dish	20	160	0	0.0	0.0017
12	Lab	1989	2/90	Petri dish	20	160	1	0.0062	0.0062
24	Veranda	1991	11/93	Heat	50	1200	9	0.0075	0.0075

The overall weighted mean first-year proportional germination was 0.0137. Population means were used in fertility calculations, except in the cases of population 11 (set to minimum non-zero value) and population 19 (assigned value of nearby, similar population 12).

In this equation,  $f_i$  is the modeled density value and  $f_o$  is the observed density value in each year. This formula can be seen as the sum of the independent contributions of departures from expectation weighted by the value of the particular density (Sokal and Rohlf, 1995). An absolute lower value indicates a better fit between observed and modeled trajectories. We used these values and the difference between observed and modeled final density as criteria for model selection (Table 4).

#### 2.7.4. Seedling mortality through september

Survival through germination is an estimate through the prime germination period, from December to February. However, many seedlings die between germination and the annual census in September. Realized fertility needs to be discounted by mortality during this period. We performed this calculation for specific years and populations, where sufficient data existed. For other situations, we substituted means based on time-since-fire and habitat, in a similar manner as adjustments for survival, growth, and fecundity data.

#### 2.7.5. Resulting values for annual reproduction

The steps outlined above lead to estimates of fecundity (number of nutlets produced by flowering plants of each of the three size classes) and fertility (number of seedlings surviving to the next census by parental flowering size class and number of nutlets contributed to the seed bank still alive at the next census).

#### 2.8. Simulation protocol

We used stochastic simulations on scrub sites to evaluate the effect of fire on demography. Stochastic simulations were conducted using MATLAB (Mathworks, 1996). Finite rates of increase and elasticities were calculated directly for each matrix except those matrices 0, 1, or 2 years after fire, which lacked some of the life history stages, and reducible matrices (lacking paths to one or more life history stages; Caswell, 2001). Stochastic simulations utilized the MATLAB program DISTPROJ. Each simulation was run for 75 years, with initial

**Table 4 – Parameters for the best models per population (Pop) under each germination scenario (averages within population or global)**

Pop	sb	fg	fgb	Final number (observed)	Final number (predicted)	Likelihood ratio	Scenario
4	0.4	0.004	0.4	51	54	–65	Global
4	0.7	0.001	0.1	51	259	–3038	Within
10	0.1	0.001	0.1	40	40	–919	Global
10	0.1	0.001	0.1	40	35	–578	Within
2	0.6	0.007	0	42	43	–101	Global
2	0.1	0.001	0	56	233	–4204	Within
0	0.1	0.001	0	56	426	–11239	Global
0	0.1	0.002	0	56	55	29	Within
19	0.2	0.001	0	24	25	–7	Global
19	0.1	0.002	0	24	24	–10	Within
24	0.1	0.009	0	38	38	–314	Global
24	0.5	0.002	0	38	39	–301	Within
11	0.1	0.002	0	21	32	77	–
12	0.1	0.001	0.1	19	52	487	–

Abbreviations for parameters are: sb, seed survival; fg, >3 years postfire seed bank germination; fgb, <3 years postfire seed bank germination. Parameters used in the simulations were those with the lower Likelihood Ratio Parameters for populations 11 and 12 were derived from populations 0 and 10 respectively, based on similar habitats.

population sizes corresponding to small, medium, and large populations of *D. frutescens*. Each simulation was started at the time of a complete fire, with the corresponding stage structure: plants only in the seed bank. Seed bank sizes were 10,000, 100,000 or 1,000,000 seeds for small, medium, and large populations, respectively. Simulations lasted 75 years, with regular fires at one of the following frequencies: every 3, 6, 9, 12, 15, 18, 21, 24, 27, or 30 years, or unburned. We also simulated random fire intervals at these median intervals using logistic functions  $1/(1 + \beta_1 \times \exp[\beta_2 \times \text{year}])$  to generate probabilities of burning each simulation year. The dependent variables in stochastic simulations were the probability (in 3000 runs) of (quasi-) extinction for populations dropping below thresholds of 1, 10, 100, or 1000 individuals at any time during the simulation.

### 3. Results

#### 3.1. Population and time-since-fire effects on finite rates of increase

We derived 83 projection matrices to summarize population viability of *D. frutescens*. These included 17 full matrices representing populations from 2 to 10 years postfire and 33 from long-unburned populations (Table 5). Full matrices contained data on all life history stages. We included populations burned within that year and, one or two year postfire to simulate population dynamics. However, since they represent transient conditions and only part of the life cycle, they were not used to calculate equilibrium parameters such as finite rates of increase.

We calculated finite rates of increase ( $\lambda$ ) for 46 scrub matrices and 19 matrices from firelanes and yard edges (Table 5). We only calculated  $\lambda$  for irreducible matrices (matrices with at least one nonzero transition probability connecting each stage; Caswell, 2001) >2 years postfire. Lambdas ranged between 0.39 and 1.61, with 50% of  $\lambda$ s between 0.77 and 1.04. The mean  $\lambda$  was 0.91 and the median value was 0.87.

Lambdas of scrub populations declined steadily from 3 to 10 years postfire, being generally above one within 5 years of fire and generally below one from 6 to 10 years postfire (Fig. 2(a)). Unburned scrub populations usually had finite rates of increase below one (mainly 0.7–0.95), with no temporal trend for two of three populations (Fig. 2(b)). Population 19 shows an evident decline in finite rates of increase through 1998 (Fig. 2(b)). Firelane populations showed lambdas mainly <1, with declining rates 5–11 years post-disking (population 0, Fig. 2(c)) and 3–7 years postfire (population 11, Fig. 2(c)). The suburban yard edge population had  $\lambda$  values both above and below one, with no temporal trend (Fig. 2(d)).

#### 3.2. Extinction risk as a function of fire regime

Fire is necessary for the persistence of *D. frutescens* populations. With no fire, initial populations of 10,000, 100,000 and 1,000,000 nutlets always became extinct within 75 years. Under a fire regime with fires occurring at regular intervals, the optimal fire return interval was about 6–12 years; this fire return interval produced the lowest extinction risks for all

quasi-extinction thresholds (Fig. 3). Shorter and longer intervals produced greater risks, with an interval of 3–18 years allowing a >50% chance of persistence if starting with a population size of 1,000,000 seeds after an initial fire. Smaller initial population sizes predicted higher extinction risks but similar relative patterns of extinction risks with fire return interval.

Stochastic fire regimes produced roughly similar patterns of extinction probability as did regular fire return intervals (Fig. 4). However, the optimal fire return interval (about 6–21 years) was wider due to the flatter response of quasi-extinction risk to stochastic fire return intervals. Intervals longer than 21 years produced only slowly increasing extinction probabilities. When compared to a regular fire regime, stochastic fire return intervals near the optimum produced slightly higher extinction risks than regular fire return intervals (Figs. 3 and 4). However, away from the optimum, the extinction risks were actually lower (right side of Figs. 3 and 4).

### 4. Discussion

#### 4.1. Fire and population viability

Several approaches suggest fairly frequent fire is desirable for *D. frutescens* population viability. Patterns of finite rates of increase trend downward from five years onward. Stochastic simulations using both regular and stochastic fire regimes predicted that a fire return intervals of 6–12 and 6–21 years, respectively, were optimal for minimizing extinction risk.

Even in this range, our model outputs emphasize that local extinctions will occur for *D. frutescens*. Indeed, such local extinctions are likely to have occurred, but we cannot study such populations after the fact. The surviving plants in long-unburned areas are often associated with local disturbances such as trails or treefall gaps. (Populations also occur along roadsides through long-unburned scrub, although these data were not used in these analyses.) Another possibility is that episodic seedling recruitment creates more persistent cohorts and forestalls local extinctions. High numbers of seedlings occurred in some years independently of fire. However, our models considered recruitment terms averaged among calendar years (although specific by time-since-fire). Sporadic recruitment in this perennial plant may result in greater persistence than continuous recruitment. A final possibility is that populations contain far more seeds than we have used in model runs, so that the absolute extinction probabilities predicted in our research would be shifted downward (with similar patterns). Direct sampling of the persistent seed bank by sifting suggests that this final possibility is not likely because seed banks were modest and were many times lower in long-unburned than in recently burned sites (Finer and Menges, unpublished data).

This is the fourth PVA of a Florida scrub species; all address the issue of fire management and population viability. For *E. longifolium* var. *gnaphalifolium*, frequent fires are favorable although not essential (Satterthwaite et al., 2002). Fires could probably occur every few years, as this species resprouts postfire and has very high survival in multiple burns (McConnell and Menges, 2002). *E. longifolium* var. *gnaphalifolium*

Table 5 – Summary of the 83 matrices constructed for *Dicerandra frutescens*

Matrix	Pop	Year	Time <sup>a</sup>	Habitat	$\lambda$	Matrix type
1	4	1997–98	tsf = 0	Scrub	–	All die
2	10	1995–96	tsf = 0	Scrub	–	All die
3	12	1989–90	tsf = 0	Scrub	–	All die
4	4	1998–99	tsf = 1	Scrub	–	Only seeds
5	10	1996–97	tsf = 1	Scrub	–	Only seeds
6	12	1990–91	tsf = 1	Scrub	–	Only seeds
7	4	1999–00	tsf = 2	Scrub	–	Seeds/seedlings
8	10	1997–98	tsf = 2	Scrub	–	Seeds/seedlings
9	12	1991–92	tsf = 2	Scrub	–	Seeds/seedlings
10	10	1998–99	tsf = 3	Scrub	1.6066	I
11	12	1992–93	tsf = 3	Scrub	1.3158	I
12	10	1988–89	tsf = 4	Scrub	1.0960	I
13	10	1999–00	tsf = 4	Scrub	1.3475	I
14	12	1993–94	tsf = 4	Scrub	1.3170	I
15	10	1989–90	tsf = 5	Scrub	1.0997	I
16	12	1994–95	tsf = 5	Scrub	0.5710	I
17	10	1990–91	tsf = 6	Scrub	0.4000	I
18	12	1995–96	tsf = 6	Scrub	1.0720	I
19	10	1991–92	tsf = 7	Scrub	0.9237	I
20	12	1996–97	tsf = 7	Scrub	1.0132	I
21	10	1992–93	tsf = 8	Scrub	0.7724	I
22	12	1997–98	tsf = 8	Scrub	0.8560	I
23	10	1993–94	tsf = 9	Scrub	0.7155	I
24	12	1998–99	tsf = 9	Scrub	0.8720	I
25	10	1994–95	tsf = 10	Scrub	0.6711	I
26	12	1999–00	tsf = 10	Scrub	–	Reducible
27	4	1988–89	tsf = lu	Scrub	0.6915	I
28	4	1989–90	tsf = lu	Scrub	0.7711	I
29	4	1990–91	tsf = lu	Scrub	0.8052	I
30	4	1991–92	tsf = lu	Scrub	0.8781	I
31	4	1992–93	tsf = lu	Scrub	0.8132	I
32	4	1993–94	tsf = lu	Scrub	0.6942	I
33	4	1994–95	tsf = lu	Scrub	0.6900	I
34	4	1995–96	tsf = lu	Scrub	0.7884	I
35	4	1996–97	tsf = lu	Scrub	0.9222	I
36	2	1988–89	tsf = lu	Scrub	0.6866	I
37	2	1989–90	tsf = lu	Scrub	1.0209	I
38	2	1990–91	tsf = lu	Scrub	1.0470	I
39	2	1991–92	tsf = lu	Scrub	0.8236	I
40	2	1992–93	tsf = lu	Scrub	0.8757	I
41	2	1993–94	tsf = lu	Scrub	0.8379	I
42	2	1994–95	tsf = lu	Scrub	0.9161	I
43	2	1995–96	tsf = lu	Scrub	0.7467	I
44	2	1996–97	tsf = lu	Scrub	0.7869	I
45	2	1997–98	tsf = lu	Scrub	0.9722	I
46	2	1998–99	tsf = lu	Scrub	0.9820	I
47	2	1999–00	tsf = lu	Scrub	1.0369	I
48	19	1990–91	tsf = lu	Scrub	0.9242	I
49	19	1991–92	tsf = lu	Scrub	0.9132	I
50	19	1992–93	tsf = lu	Scrub	1.0408	I
51	19	1993–94	tsf = lu	Scrub	0.7215	I
52	19	1994–95	tsf = lu	Scrub	0.7661	I
53	19	1995–96	tsf = lu	Scrub	–	Reducible
54	19	1996–97	tsf = lu	Scrub	0.7500	I
55	19	1997–98	tsf = lu	Scrub	0.3850	I
56	19	1998–99	tsf = lu	Scrub	0.6670	I
57	19	1999–00	tsf = lu	Scrub	0.7126	I
58	12	1988–89	tsf = lu	Scrub	–	Reducible
59	12	1989–90	tsf = lu	Scrub	–	Reducible
60	0	1988–89	tss = 5	Firelane	0.8568	
61	0	1989–90	tss = 6	Firelane	0.8307	I
62	0	1990–91	tss = 7	Firelane	0.7566	I
63	0	1991–92	tss = 8	Firelane	0.9898	I

(continued on next page)



Table 5 – (continued)

Matrix	Pop	Year	Time <sup>a</sup>	Habitat	$\lambda$	Matrix type
64	0	1992–93	t <sub>sa</sub> = 9	Firelane	0.8012	I
65	0	1993–94	t <sub>sa</sub> = 10	Firelane	–	Reducible
66	0	1994–95	t <sub>sa</sub> = 11	Firelane	0.6638	I
67	11	1989–90	t <sub>sf</sub> = 0	Burned firelane	–	All die
68	11	1990–91	t <sub>sf</sub> = 1	Burned firelane	–	Only Seeds
69	11	1991–92	t <sub>sf</sub> = 2	Burned firelane	–	Seeds/seedling
70	11	1992–93	t <sub>sf</sub> = 3	Burned firelane	1.2606	I
71	11	1993–94	t <sub>sf</sub> = 4	Burned firelane	1.1503	I
72	11	1994–95	t <sub>sf</sub> = 5	Burned firelane	1.0331	I
73	11	1995–96	t <sub>sf</sub> = 6	Burned firelane	0.9549	I
74	11	1996–97	t <sub>sf</sub> = 7	Burned firelane	1.0125	I
75	24	1991–92	–	Yard Edge	1.0402	I
76	24	1992–93	–	Yard Edge	–	Reducible
77	24	1993–94	–	Yard Edge	1.0456	I
78	24	1994–95	–	Yard Edge	1.2295	I
79	24	1995–96	–	Yard Edge	0.9499	I
80	24	1996–97	–	Yard Edge	1.1525	I
81	24	1997–98	–	Yard Edge	0.8521	I
82	24	1998–99	–	Yard Edge	1.2184	I
83	24	1999–00	–	Yard Edge	1.2573	I

Lambda was not calculated for time-since-fire (tsf) of 0, 1, or 2 years. I, irreducible matrix (contains a path among all nodes) vs. reducible matrix (one stage cannot contribute by any path to other stages) (Caswell, 2001).

a – For “Time”, tsf, time since fire; t<sub>sa</sub>, time since abandonment of disking; and LU, long-unburned.

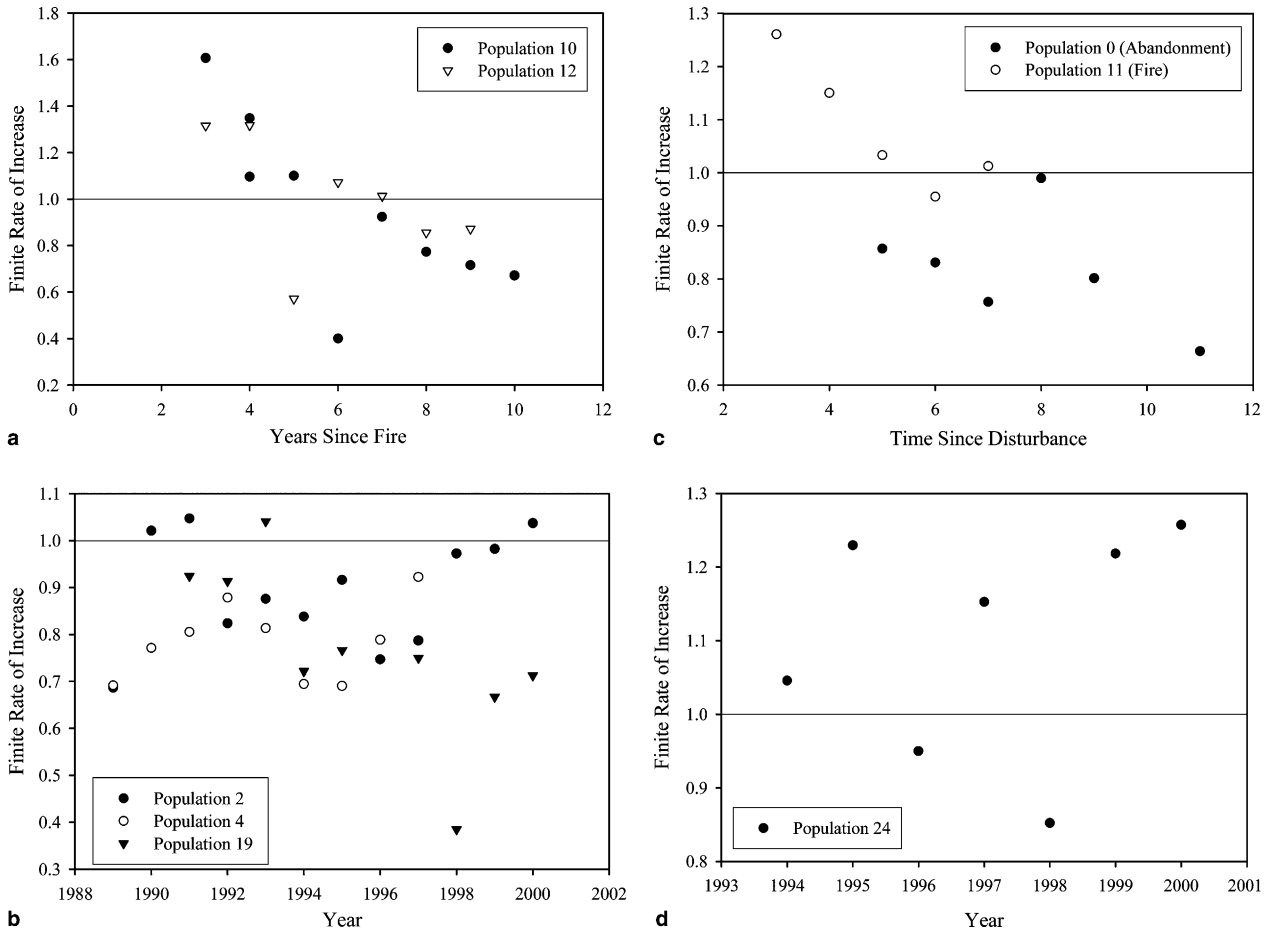
occurs in both frequently burned sandhill and less frequently burned scrub, and so cannot be used as a guide to fire return intervals in scrub alone.

The other two scrub species with PVA analyses, *E. cuneifolium* and *H. cumulicola*, have several similarities to *D. frutescens*. All three species are short-lived perennials with annual mortality rates greater than 20%, are killed by fire, and possess a persistent seed bank (Quintana-Ascencio et al., 2003; Menges and Quintana-Ascencio, 2004; Menges, unpublished data). We can compare these three species' sensitivity to post-fire habitat changes by evaluating the point at which finite rates of increase shift from >1 to <1. This break-even point in *D. frutescens* (six years) is slightly less than that found for *E. cuneifolium* (eight years) and much less than *H. cumulicola* (17 years), suggesting that initial *D. frutescens* declines in demographic rates after fire are relatively rapid. Due to dominance by resprouting shrubs, the oak-hickory scrub habitat of *D. frutescens* closes more rapidly than the rosemary scrub habitat of the other two species. *D. frutescens* occurs in small gaps (Menges et al., 1999) that close rapidly with taller shrubs. In contrast, the rosemary scrub habitat of *E. cuneifolium* and *H. cumulicola* remains relatively open for decades (Hawkes and Menges, 1996). In rosemary scrub, the percent of area in gaps declines with time-since-fire with an inverse relationship (Menges and Hawkes, 1998) that matches the pattern of decline in finite rate of increase for *E. cuneifolium* and *H. cumulicola*. This is indirect evidence that gap closure may be driving much of the demographic decline seen in these species. Because *D. frutescens* occurrence is higher in open, litter-free microhabitats (Menges, 1992; Menges et al., 1999), gap closure by overhanging shrubs and accumulation of litter in gaps may be key factors in driving the demographic decline in *D. frutescens*.

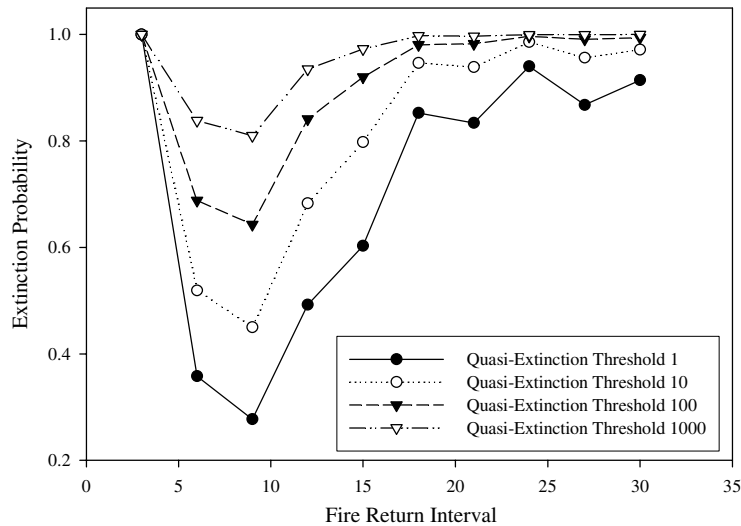
Nonetheless, *D. frutescens* may be more persistent in long-unburned scrub than *E. cuneifolium* and *H. cumulicola* in rosemary scrub. *D. frutescens* populations still occur on sites that have not burned for 72 years, a population persistence unknown for *E. cuneifolium*. Long-unburned *D. frutescens* sites have dense shrub growth and litter accumulation. In these sites, *D. frutescens* is restricted to gaps and areas with less litter cover and depth (Menges et al., 1999). Foot-trails and canopy gaps due to high sand pine mortality may be helping *D. frutescens* hold on in these areas. In long-unburned sites, population growth rates are negative ( $\lambda < 1$ ), suggesting continued population decline. The decline appears to be accelerating in population 19, judging by a continuing negative trend in  $\lambda$  during the study, suggesting a deteriorating environment for *D. frutescens*. This population is the only one of the three long-unburned sites that is not dissected by foot trails and does not have a senescing sand pine canopy. Local disturbances from foot traffic and treefalls may account for the relatively steady (rather than accelerating) decline of the other two long-unburned *D. frutescens* populations.

#### 4.2. Populations in disturbed habitats

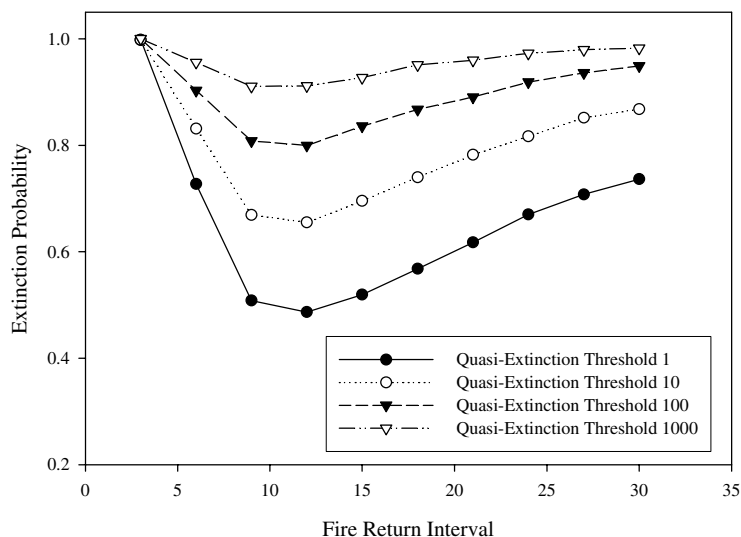
Firelane edges, yard edges, and other disturbed areas also provide habitats for *D. frutescens*. In firelane edges, declines in  $\lambda$  with time-since-fire or time-since-disking were dramatic and similar to postfire patterns in scrub. These habitats may only be temporarily favorable sites for *D. frutescens* in the absence of chronic disturbance. Garden edge habitats appeared somewhat more favorable (judging by the majority of  $\lambda > 1$ ), perhaps due to intermittent watering received during droughts. Based on preliminary evidence from *H. cumulicola* (Quintana-Ascencio and Weekley, unpublished data), we



**Fig. 2** – Finite rates of increase ( $\lambda$ ) for *Dicerandra frutescens* populations in individual years. Lambdas were not calculated for time-since-fire of 0, 1, or 2 years. (a) Populations in oak-hickory scrub (populations 10 and 12) as a function of time-since-fire. (b) Undisturbed and unburned populations (populations 2 and 19, population 4 before 1998 fire) as a function of calendar year. (c) Firelane populations as a function of time since abandonment of disking (population 0) and time since fire (population 11). (d) Suburban yard-edge population (population 24) as a function of calendar year.



**Fig. 3** – Extinction probability as a function of quasi-extinction threshold (different symbols for 1, 10, 100, and 1000) and regular fire return interval, for initial population size of 1,000,000 seeds.



**Fig. 4 – Extinction probability as a function of quasi-extinction threshold (different symbols for 1, 10, 100, and 1000) and stochastic fire return interval, for initial population size of 1,000,000 seeds.**

hypothesize that human-modified environments create conditions favoring more variation in demographic parameters (e.g., more variable  $\lambda$  values) and a shorter life span. Recently, we have added new roadside and firelane edge sites to our *D. frutescens* research to test this hypothesis.

#### 4.3. Optimal fire return intervals for Florida scrub on yellow sand

Because *D. frutescens* is a specialist for Florida scrub on yellow sand (oak-hickory scrub, some kinds of sand pine scrub), we can use the results of this PVA to infer optimal fire return intervals for these habitats [as in Liu et al. (2005)]. Optimal fire return intervals of 6–12 years would be of greatest benefit to *D. frutescens* and probably constitute the main part of the historic distributions of fire return times. While tiny populations of this species can persist for decades longer, this tail in fire return intervals will have to be “thin” (having low probability) for populations to persist through several fire cycles. For fire return intervals near an optimum, stochastically varying fire return intervals are disadvantageous to *D. frutescens*, likely because they include more frequent long intervals between fires. However, stochasticity produces lower extinction than deterministic fire regimes at longer fire return intervals and implies a longer optimal fire return interval of 6–21 years. While some variation in fire return intervals must certainly have occurred in the evolutionary history of this species, we believe that most fires in *Dicerandra* habitat would have re-occurred within about two decades.

Ecosystem management based on a single species, even a narrow specialist, is suspect. However, frequent fires in Florida scrub appear to pose little biodiversity risk. Most species of Florida scrub are capable of resprouting (Menges and Kohfeldt, 1995). Fires every 2–4 years, although they can increase herb abundances, do not seem effective at reducing the dominance of shrubs on yellow sands (Reinhart and Menges,

2004). Obligate seeders may be more susceptible to frequent fires, but in Florida scrub *D. frutescens* is typical of most obligate seeders in its rapid postfire recovery from a seedbank. On yellow sands, only sand pine (*Pinus clausa*) might appear disadvantaged by fire every 6–12 years. It was eliminated by two fires within six years on a scrub-invaded sandhill site (Reinhart and Menges, 2004). However, sand pine trees as young as five years old can produce cones (Cooper et al., 1959). Fires every decade or two are likely to reduce, but not eliminate, sand pines.

Therefore, we recommend that land managers wishing to manage Florida scrub on yellow sands need to shorten fire return intervals from the previous envelope of 15–100 years down to variation between 6–12 (occasionally to 21) years. This will certainly benefit populations of *D. frutescens* without reducing biodiversity. A modest amount of stochasticity will be tolerated by *D. frutescens* and will likely benefit species not as well adapted to frequent fire.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version at doi:10.1016/j.biocon.2005.08.002.

## REFERENCES

- Abrahamson, W.G., Johnson, A.F., Layne, J.N., Peroni, P.A., 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Scientist* 47, 209–250.
- Bond, W.J., Dickinson, K.J.M., Mark, A.F., 2004. What limits the spread of fire-dependent vegetation? Evidence from geographic variation of serotiny in a New Zealand shrub. *Global Ecology and Biogeography* 13, 115–127.
- Bradstock, R.A., Kenny, B.J., 2003. An application of plant functional types to fire management in a conservation reserve in south-eastern Australia. *Journal of Vegetation Science* 14, 345–354.
- Bradstock, R.A., O'Connell, M.A., 1988. Demography of woody plants in relation to fire: *Banksia ericifolia* L.F. and *Petrophile pulchella* (Schr.) R.Br. *Australian Journal of Ecology* 13, 505–518.
- Brewer, J.S., 2001. A demographic analysis of fire-stimulated seedling establishment of *Sarracenia alata* (Sarraceniaceae). *American Journal of Botany* 88, 1250–1257.
- Burgman, M.A., Lamont, B.B., 1992. A stochastic model for the viability of *Banksia cuneata* populations: environmental, demographic, and genetic effects. *Journal of Applied Ecology* 29, 719–727.
- Canales, J., Trevisan, M.C., Silva, J.F., Caswell, H., 1994. A demographic study of an annual grass (*Andropogon brevifolius* Schwarz) in burnt and unburnt savanna. *Acta Oecologica* 15, 261–273.
- Caswell, H., 2001. *Matrix Models: Construction, Analysis and Interpretation*. Sinauer, Sunderland, MA.
- Caswell, H., Kaye, T.N., 2001. Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii*) in a dynamic fire regime. *Advances in Ecological Research* 32, 1–49.
- Christensen, N.L., 1985. Shrubland fire regimes and their evolutionary consequences. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL, pp. 85–100.
- Christman, S.P., Judd, W.S., 1990. Notes on plants endemic to Florida scrub. *Florida Scientist* 53, 52–73.
- Cooper, R.W., Schopmeyer, C.L., McGregor, W.H.D., 1959. Sand pine regeneration on the Ocala National Forest. US Forest Service Prod. Res. Rep. No. 30, Washington, DC (cited in Myers, 1990).
- Coulson, T., Mace, G.M., Hudson, E., Possingham, H., 2001. The use and abuse of population viability analysis. *Trends in Ecology and Evolution* 16, 219–221.
- Cowling, R.M., Holmes, P.M., 1992. Endemism and speciation in a lowland flora from the Cape Floristic region.
- Deyrup, M., Vulinec, K., 1996. *Florida Scrub Coloring Book*. Archbold Biological Station, Lake Placid, FL.
- Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. *Science* 275, 550–553.
- Enright, N.J., Marsula, R., Lamont, B.B., Wissel, C., 1998a. The ecological significance of canopy seed storage in fire-prone environments: a model for resprouting shrubs. *Journal of Ecology* 86, 960–973.
- Enright, N.J., Marsula, R., Lamont, B.B., Wissel, C., 1998b. The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *Journal of Ecology* 86, 946–959.
- Estill, J.C., Cruzan, M.B., 2001. Phytogeography of rare plant species endemic to the southeastern United States. *Castanea* 66, 3–23.
- Fiedler, P.L., 1995. Rarity in the California flora: new thoughts on old ideas. *Madrono* 42, 127–141.
- Gill, A.M., McCarthy, M.A., 1998. Intervals between prescribed fire in Australia: what intrinsic variation should apply? *Biological Conservation* 85, 161–169.
- Gross, K., Lockwood III, J.R., Frost, C.C., Morris, W.F., 1998. Modeling controlled burning and trampling reduction for conservation of *Hudsonia montana*. *Conservation Biology* 12, 1291–1301.
- Hawkes, C.V., Menges, E.S., 1996. The relationship between open space and fire for species in a xeric Florida shrubland. *Bulletin of the Torrey Botanical Club* 123, 81–92.
- Herrera, J., 2004. Lifetime fecundity and floral variation in *Tuberaria guttata* (Cistaceae): a Mediterranean annual. *Vegetatio* 172, 219–225.
- Hoffmann, W.A., 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80, 1354–1369.
- Kaye, T.N., Pendergrass, K.L., Finley, K., Kauffman, J.B., 2001. The effect of fire on the population viability of an endangered prairie plant. *Ecological Applications* 11, 1366–1380.
- Lindenmayer, D.B., Possingham, H.P., Lacy, R.C., McCarthy, M.C., Pope, M.L., 2003. How accurate are population models. Lessons from landscape-scale tests in a fragmented ecosystem. *Ecology Letters* 6, 41–47.
- Liu, H., Menges, E.S., Quintana-Ascencio, P.F., 2005. Population viability analyses of *Chamaecrista keyensis*: effects of fire season and frequency. *Ecological Applications* 15, 210–221.
- Lloret, F., Pausas, J.G., Vila, M., 2003. Responses of Mediterranean plant species to different fire frequencies in Garraf National Park (Catalonia, Spain): field observations and modeling predictions. *Plant Ecology* 167, 223–235.
- Manders, P.T., 1987. A transition matrix model of the population dynamics of the Clanwilliam cedar (*Widdringtonia cedarbergensis*) in natural stands subject to fire. *Forest Ecology and Management* 20, 171–186.
- Mathworks, Inc., 1996. *MATLAB version 5*. Natick, Massachusetts.
- McCarthy, M.A., Burgman, M.A., 1995. Coping with uncertainty in forest wildlife planning. *Forest Ecology and Management* 74, 23–36.
- McCarthy, M.A., Gill, M.A., Lindenmayer, D.B., 1999. Fire regimes in mountain ash forest: evidence from forest age structure, extinction models and wildlife habitat. *Forest Ecology and Management* 6, 193–203.
- McCarthy, M.A., Possingham, H.P., Gill, A.M., 2001. Using stochastic dynamic programming to determine optimal fire management for *Banksia ornata*. *Journal of Applied Ecology* 38, 585–592.
- McCarthy, M.A., Adelman, S.J., Possingham, H.P., 2003. Reliability of relative predictions in population viability analysis. *Conservation Biology* 17, 982–989.
- McConnell, K., Menges, E.S., 2002. The effects of fire and treatments that mimic fire on the Florida endemic scrub buckwheat (*Eriogonum longifolium* Nutt. var. *gnaphalifolium* Gand.). *Natural Areas Journal* 22, 194–201.
- McCoy, E.D., Mushinsky, H.R., 1992. Rarity of organisms in the sand pine scrub habitat of Florida. *Conservation Biology* 6, 537–548.
- Menges, E.S., 1992. Habitat preferences and response to disturbance for *Dicerandra frutescens*: a Lake Wales Ridge (Florida) endemic plant. *Bulletin of the Torrey Botanical Club* 119, 308–313.
- Menges, E.S., 1999. Ecology and conservation of Florida scrub. In: Anderson, R.C., Fralish, J.C., Baskin, J. (Eds.), *The Savanna, Barren, and Rock Outcrop Communities of North America*. Cambridge University Press, Cambridge, pp. 7–22.
- Menges, E.S., 2000. Applications of population viability analysis in plant conservation. *Ecological Bulletins* 48, 73–84.
- Menges, E.S., Dolan, R.W., 1998. Demographic viability of populations of *Silene regia* in midwestern prairies; relationships with fire management, genetic variation, geographic

- location, population size, and isolation. *Journal of Ecology* 86, 63–78.
- Menges, E.S., Hawkes, C.V., 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. *Ecological Applications* 8, 935–946.
- Menges, E.S., Kohfeldt, N.M., 1995. Life history strategies of Florida scrub plants in relation to fire. *Bulletin of the Torrey Botanical Club* 122, 282–297.
- Menges, E.S., Quintana-Ascencio, P.F., 2003. Modeling the effects of disturbance, spatial variation and environmental heterogeneity on population viability of plants. In: Brigham, C.A., Schwartz, M.W. (Eds.), *Population Viability in Plants*, Ecological Studies, vol. 165. Springer, Berlin, pp. 289–311.
- Menges, E.S., Quintana-Ascencio, P.F., 2004. Population viability with fire in *Eryngium cuneifolium*: deciphering a decade of demographic data. *Ecological Monographs* 74, 79–99.
- Menges, E.S., McIntyre, P.J., Finer, M.S., Goss, E., Yahr, R., 1999. Microhabitat of the narrow Florida scrub endemic *Dicerandra christmanii*, with comparisons to its congener *D. frutescens*. *Journal of the Torrey Botanical Club* 126, 24–31.
- Moloney, K.A., 1986. A generalized algorithm for determining category size. *Oecologia* 69, 176–180.
- Morris, W.F., Doak, D.F., 2002. *Quantitative Conservation Biology*. Sinauer Associates, Inc., Sunderland, MA.
- Myers, R.L., 1990. Scrub and high pine. In: Myers, R.L., Ewel, J.J. (Eds.), *Ecosystems of Florida*. University of Central Florida Press, Orlando, pp. 150–193.
- Oostermeijer, J.G.B., 2003. Threats to rare plant persistence. In: Brigham, C.A., Schwartz, M.W. (Eds.), *Population Viability in Plants*, Ecological Studies, vol. 165. Springer, Berlin, pp. 289–311.
- Pfab, M.F., Witkowski, E.T.F., 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. *Biological Conservation* 96, 262–270.
- Pickett, S.T.A., White, P.S., 1985. *The ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL.
- Quintana-Ascencio, P.F., Menges, E.S., Weekley, C.W., 2003. A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida rosemary scrub. *Conservation Biology* 17, 433–449.
- Reinhart, K.O., Menges, E.S., 2004. Effects of re-introducing fire to a central Florida sandhill community. *Applied Vegetation Science* 7, 141–150.
- Russell-Smith, J., Ryan, P.G., Cheal, D.C., 2002. Fire regimes and the conservation of sandstone heath in monsoonal northern Australia: frequency, interval, patchiness. *Biological Conservation* 104, 91–106.
- Satterthwaite, W.S., Quintana-Ascencio, P.F., Menges, E.S., 2002. Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. *Ecological Applications* 12, 1672–1687.
- Schwilk, D.W., Ackerly, D.D., 2001. Flammability and serotiny as strategies: correlated evolution in pines. *Oikos* 94, 326–336.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry*, third ed. Freeman, New York, NY.