

Evaluating stability in *Ziziphus celata*, a highly endangered clonal shrub endemic to Lake Wales Ridge, central Florida

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ABSTRACT: Florida ziziphus *Ziziphus celata* is a self-incompatible clonal shrub comprising fewer than a dozen remnant, uniclonal populations in south-central Florida, USA. We model the population viability of this highly endangered species based on 9 yr of data from 2 populations. The matrix projection model is based on hypothetically independent 'plants' defined as clumps of ramets within a 25 cm radius. Seedling recruitment is unknown in the uniclonal study populations and is not modeled. The populations modeled here have stable demographics characterized by high survival and stasis, but variable levels of new plant production (clonal recruitment). Population growth rates suggest protracted long-term declines in population size, but predicted extinction rates over 50 yr are as high as 20% in one population. Changes in new plant production and survival had greater effects on population growth rates than did changes in growth rates of individual plants. Augmenting clonal plant production and protecting survival of new 'plants' are short-term management goals. The establishment of sexually reproducing populations through the translocation of cross-compatible genotypes is a long-term necessity for the persistence of Florida ziziphus populations.

KEY WORDS: Population viability analysis · Florida ziziphus · Clonal reproduction · Endangered species · Rare plant conservation

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INTRODUCTION

Population viability analysis (PVA) is a powerful tool for assessing the sustainability (or extinction risk) of plant populations (Menges 2000a, Morris & Doak 2002, Reed et al. 2002). Stage-based matrix models incorporating the various sources of stochasticity (environmental, demographic, genetic) have been increasingly used in recent years to aid conservationists in identifying demographic threats to the persistence of rare plant populations (e.g. Liu et al. 2005, Smith et al. 2005, Maschinski et al. 2006, Meyer et al. 2006).

Most PVAs for plants have not considered those with clonal growth (Menges 2000b). Clonal species constitute a special challenge for PVAs because of the difficulty of distinguishing genets (genetically distinct individuals) from ramets (modular units of a genet which may be physiologically independent) in the field

(Menges 2000b). In some species, where clonal growth can be directly tied to clearly defined individuals with aboveground clonal connections, a PVA can proceed with the addition of a 'new clonal ramet' life history stage (e.g. Eriksson 1988, Weppler et al. 2006). In some cases, both ramets and genets can be distinguished, and modeling can be carried out at both ramet and genet levels, which may differ in their predictions (Eriksson 1994, Damman & Cain 1998, Colling & Matthies 2006). In populations with high genetic variation, genotyping can be combined with demographic modeling to provide demographic analyses (Kynci et al. 2006). However, because genets cannot always be easily identified, most clonal plant PVAs use ramet level data.

Ramet population viability varies among sites (Boeken & Canham 1995), among years (Huenneke & Marks 1987), between the clone periphery and its cen-

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ter (e.g. Wikberg & Svensson 2006), and with harvesting levels (Nault & Gagnon 1993). Even in species without known sexual reproduction, ramet-based PVAs can compare various scenarios of decline (Schwartz et al. 2000). Here, we generate a PVA for a clonal species in which most 'populations' consist of a single genet. We evaluate the role of clonal reproduction in the long-term population dynamics of Florida ziziphus *Ziziphus celata*, a federally endangered shrub endemic to the Lake Wales Ridge of central-peninsular Florida (USFWS 1999).

Our goals in the present study are to develop stage-based models of the ramet dynamics of Florida ziziphus and to use these models as the basis for a population viability analysis. Modeling the dynamics of Florida ziziphus' uniclonal populations will contribute to its recovery in 2 ways: (1) the critical life history stages of the long-lived plants that constitute these 'populations' will be identified, and (2) it allows us to infer the fate of these remnant populations given the current absence of sexual reproduction.

MATERIALS AND METHODS

Study species. Florida ziziphus *Ziziphus celata* Judd & D. Hall (Rhamnaceae) is a narrowly endemic and critically endangered shrub (USFWS 1999, Ward et al. 2003, Turner et al. 2006). At the time of its description in 1984 from a 36 yr old herbarium specimen, Florida ziziphus was thought to be extinct (Judd & Hall 1984). However, between 1988 (DeLaney et al. 1989) and 2002, 9 remnant populations were discovered along a 45 km stretch of the Lake Wales Ridge in south-central peninsular Florida. All populations occur on yellow sands that historically supported longleaf pine/wiregrass *Pinus palustris*/*Aristida stricta* var. *beyrichiana* sandhills, although 6 populations now occupy grazed pastures subject to frequent mowing. Of the 9 populations, 8 are uniclonal (Godt et al. 1997, Weekley et al. 2002) and, because Florida ziziphus is self-incompatible (Weekley & Race 2001), most populations are sterile.

Extant populations have apparently persisted for several decades through clonal growth. Populations vary in size from a few dozen to several hundred ramets and comprise more or less discrete clumps of ramets which may function as eco-physiologically independent entities ('plants'). Only one small uniclonal population is publicly protected. While the recovery of Florida ziziphus requires the creation of sexually viable populations through the translocation of genetically diverse and cross-compatible genotypes (USFWS 1999, Weekley et al. 2002), management of existing uniclonal populations is a critical intermediate task.

Selection of study populations. We have conducted demographic research in all known Florida ziziphus populations since 1997. However, small sample sizes and disturbances to marked plants limit the number of cases in the dataset. For example, mowing and damage by cattle have resulted in tags being displaced from marked plants, thereby reducing sample sizes for those populations. For this study, we chose 2 populations for analysis based on many censuses and larger samples sizes. One population (PO3) occurs in a remnant sandhill site and one (PO4) in a pasture. The PO3 population occupies a 250 m² site characterized by plants typical of Florida sandhill (e.g. longleaf pine, wiregrass, and several sandhill endemics), but surrounded by exotic vegetation. In contrast, the PO4 population occupies a 625 m² site converted to pasture several decades ago. The PO3 and PO4 datasets include 63 and 263 records of individual histories, respectively. During the study period, the number of live plants in the PO3 population ranged from 17 to 28. At PO4 the number of live plants ranged from 29 to 143.

Data collection. We censused the 2 study populations annually, beginning in January 1997. We defined a 'plant' as a group of ramets within a 25 cm radius of one another; this rule was based on observations of groups of stems that appeared physiologically independent. While this definition was arbitrary, some way of classifying individuals at a scale between the population and the individual stem was necessary. In some cases, stems grew too closely together to access or census individually. Using this rule, we defined new 'plants' (clonal recruits) as new stems (i.e. root shoots) occurring >25 cm from the base of an existing plant or new stems occurring within 25 cm of a plant that had previously died back (i.e. resprouts of a pre-existing plant). We marked each plant with a numbered aluminum tag, and, in January/February of each year (the time of peak flowering), recorded its height, maximum crown diameter, number of stems, flowering stage (vegetative or reproductive), and number of flowers. Data collected from 1997 to 2005 were included in this study, resulting in 8 annual projection matrices for each population.

Model structure and analysis. We defined a 3-stage life history for Florida ziziphus: new plants (clonal recruits), vegetative plants, and reproductive plants. Because we have never observed seedling recruitment in *in situ* Florida ziziphus populations, we did not model this or fecundity. To identify the best model structure, we used logistic regression to model survival (Table 1) as a function of each of the following variables: height, number of stems, number of flowers (estimated in 5 log-10 categories), a binary variable indicating whether the individual was a new ramet in

Table 1. Multiple regression predicting annual survival from size and stage variables. Survival was regressed against height, number of stems, number of flowers, whether the plant first appeared in the current year (new), and stage (combining age and flowering). The intercepts and coefficients for each variable are shown with the standard error associated with that estimate and associated p-values

Population	Variable	Intercept	Coefficient	p
PO3	Height	1.70 ± 0.34	0.00	0.996
	No. of stems	1.83 ± 0.27	0.01 ± 0.08	0.885
	No. of flowers	1.47 ± 0.24	0.22 ± 0.12	0.071
	New	1.80 ± 1.22	-0.86 ± 0.49	0.08
	Stage	0.99 ± 0.38	0.58 ± 0.28	0.037
PO4	Height	2.33 ± 0.26	0.003 ± 0.003	0.369
	No. of stems	2.22 ± 0.25	0.24 ± 0.122	0.044
	No. of flowers	2.38 ± 0.16	0.08 ± 0.09	0.356
	New	2.54 ± 0.16	-0.37 ± 0.31	0.218
	Stage	2.19 ± 0.25	0.25 ± 0.20	0.205

that year (age); and, since we observed that new plants do not appear to flower, a separate categorical variable with 3 levels: (1) plants that flowered, (2) new plants, and (3) plants > 1 yr that did not flower (stage). Maximum crown diameter correlated strongly with height (Pearson's correlation coefficient: $r^2 = 0.903$ [PO3], 0.861 [PO4]), and therefore we did not include it in this analysis.

We chose to base our vital rates on the categorical variable incorporating both age and flowering (stage) because this variable produced sizable differences in survival, and minimized the number of stages that would be required to parameterize matrix models. Stage had a marginally significant relationship with survival ($p = 0.037$) in PO3, but was non-significant ($p = 0.205$) in PO4. The number of stems also had a marginally significant relationship with survival in PO4 ($p = 0.044$); however, there was much less support for this relationship in PO3 ($p = 0.885$). Survival most likely depends on many plant characteristics, including the ones we have listed here. Our use of matrices with a small number of stages, however, is consistent with recommendations for slow-growing species with limited data (Ramula & Lehtila 2005).

Using annual demographic census data from each of our 2 study populations, we constructed projection matrices summarizing stage-specific transitions for the following 3 stages: new plants (subscript 1), vegetative plants (subscript 2) and flowering plants (subscript 3):

$$\mathbf{n}_{t+1} = \begin{bmatrix} 0 & pr & pr \\ s_1(g_{12}) & s_2(1-g_{23}) & s_3(1-g_{33}) \\ 0 & s_2(g_{23}) & s_3(g_{33}) \end{bmatrix} \cdot \mathbf{n}_t \quad (1)$$

Survival and growth probabilities were calculated separately and then combined to generate matrix transitions. We calculated survival (s_j) for each stage i as

the percentage of individuals present in one year that was present in the following year. An individual that was missed in a given year (i.e. tag not found) was included in these calculations as surviving if it was found alive in subsequent years. We calculated growth transition rates as the percentage of surviving individuals that transitioned from stage i to stage j (g_{ij}). Since older plants could not transition into the new plant stage, the matrices had at most 2 possible outcomes for individuals in each stage: growth (g_{23}) or stasis (g_{22}) for vegetative plants, stasis (g_{33}) or regression (g_{32}) for flowering plants, and growth (g_{12}) for new plants. We calculated g_{12} , g_{22} , and g_{32} as $(1-g_{j3})$. We estimated the rate of new plant production (pr) from the ratio of new plants in the current year to all vegetative and reproductive plants in the previous year within each population.

Small sample sizes necessitated some pooling of data across years. We decided *a priori* that if sample sizes were <6 for any given stage (as in Menges & Quintana-Ascencio 2004) we would use pooled data to parameterize the model. In order to maintain population differences, overall survival and growth probabilities were calculated for each population by pooling data across years. Instead of replacing transitions with the pooled value entirely, however, we simulated the fates of the additional plants needed to complete a sample size of 6 by a binomial random draw where the probability of surviving was the pooled population survival rate. The overall probability of survival in that year was then calculated using the summed observed and simulated fates. Similarly, if fewer than 6 plants survived to calculate the probability of growth to the next stage, pooled probabilities were used to predict the missing fates. We took this approach to maintain any trends in survival that were present in the original samples. These substitutions were necessary in 7 out of 72 matrix elements for PO4 data and 16 out of 72 for PO3.

To account for correlations among the demographic rates, we used a matrix selection approach to simulate population growth in the 2 Florida ziziphus populations. The initial population distribution was based on 2006 population sizes for PO3 and PO4. We selected matrices with an equal probability for each year ($p = 0.125$ for each population-year combination). We then used 1000, 50 yr simulations to calculate a stochastic growth rate r_s :

$$r_s = \frac{\sum_{j=1}^{1000} \log\left(\frac{N_{i,50}}{N_0}\right)}{50 \times 1000} \quad (2)$$

where $N_{i,50}$ refers to the number of plants at $t = 50$ for simulation $i = 1, 2, \dots, 1000$ and N_0 is the initial population size. In addition, we calculated deterministic (asymptotic) population growth rates (r) by simulating a single population–year matrix:

$$r = \log\left(\frac{N_{t+1}}{N_t}\right) \text{ for large } t \quad (3)$$

We calculated the deterministic sensitivities and elasticities from the population matrices to test how robust our model was to error and variation in the data (see Morris & Doak 2002 for a discussion of the following). A sensitivity S for a matrix element a_{ij} is the partial derivative of the finite rate of increase λ ($\lambda \approx e^r$) with respect to that transition (see Eq. 4), while an elasticity E is the proportional rate of change in λ with respect to a proportional change in the transition a_{ij} (Eq. 5):

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \quad (4)$$

$$E_{ij} = \frac{a_{ij}}{\lambda} \times \frac{\partial \lambda}{\partial a_{ij}} \quad (5)$$

where a_{ij} is the i^{th} , j^{th} element and λ is the dominant eigenvalue of the transition matrix in (Eq. 1). Since individual vital rates, such as g_{23} and g_{33} , may appear in multiple transitions in a matrix (see Eq. 1), we also calculated sensitivity to the vital rates x (see Eq. 6). For consistency in scale, we multiplied the sensitivities by $1/e^r$, according to the chain rule (see Eq. 7).

$$S_x = \frac{\partial \lambda}{\partial a_{ij}} \times \frac{\partial a_{ij}}{\partial x} \quad (6)$$

$$S_x = \frac{\partial \lambda}{\partial x} = \frac{\partial}{\partial x}(e^r) = e^r \frac{\partial r}{\partial x} \quad (7)$$

We conducted these analyses for both population average matrices and each population–year matrix separately.

Next, we used a life table response experiment (Caswell 1989) to calculate the contribution of the observed vital rates to the amount of variation observed in the growth rates in each population–year. The contribution of a vital rate is different from the sensitivity to that vital rate in that sensitivities represent the theoretical response of the population growth rate, while the contributions show how observed differences in vital rates have affected population growth rates. Thus, contributions C_x identify which vital rates x were responsible for the observed variation in population growth rates (Caswell 1989):

$$C_x = \frac{\partial r}{\partial x} \times (x_{\text{obs}} - \bar{x}) \quad (8)$$

where x_{obs} is the rate observed in a given population–year and \bar{x} is the mean rate in that population.

Here, we have calculated the percent contribution relative the total contribution of all vital rates in each population–year matrix.

RESULTS

Florida ziziphus is a shrub with high annual survival and stasis, modest advances between stages, and highly variable new plant production (clonal recruitment) (Table 2). In most years, stage-specific survival was $>80\%$ and often 100% . The probability of transitioning from a vegetative plant to a flowering plant, however, was low ($<30\%$), although most flowering plants continued to flower in consecutive years. Production of new plants was extremely variable between populations and among years, with a coefficient of variation ($CV = 100 \times SD/\text{mean}$) of 119% in PO3 and 153% in PO4. In 1999, PO4 was comprised of 19 individuals, but produced 50 new plants in 2000 ($pr = 2.32$). This unusually high value for new plant production is greater than 2 standard deviations from the mean for PO4, and may be an outlier.

Most population growth rates (r) produced from individual population–year matrices (Table 3) were close to zero; they varied from -0.32 at PO4 in 1997 to 0.75 at PO4 in 1999 (Fig. 1). Stochastic simulations of population growth based on matrix selection produced stochastic growth rates ($r_s \pm SD$) of -0.01 ± 0.02 in PO3 and 0.15 ± 0.04 in PO4. In these simulations, 88.0% of PO3 populations declined in the 50 yr compared to 0.1% from PO4. Removing the 1999 matrix from PO4 simulations increased the probability of decline to 22.9% . In either scenario in PO4 (with or without possible outlier), none of the simulated populations reached

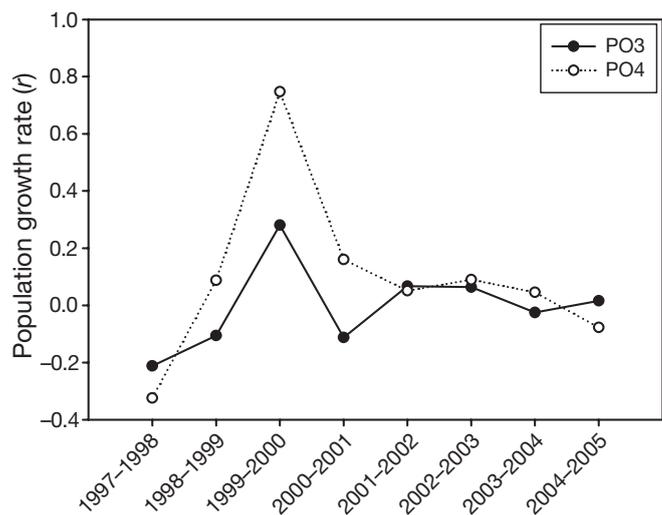


Fig. 1. Population growth rates from populations PO3 and PO4 between 1997 and 2005

Table 2. Summary of model parameters across 8 yr. Growth transitions g_{12} (New-Veg), g_{22} (Veg-Veg), and g_{32} (Rep-Veg) are calculated as $(1-g_{i3})$. All new plants that survive become vegetative plants ($g_{12} = 1 - g_{13} = 1$). For details of survival (s) and growth stages (g_1, g_2, g_3) see 'Model structure and analysis'. Rep: reproductive; Veg: vegetative

Parameter	Median (range)	PO3		Median (range)	PO4		
		Mean	CV (%)		Mean	CV (%)	
Survival	New plants (s_1)	0.67 (0.33–1.00)	0.68	31	0.84 (0.37–1.00)	0.79	25
	Vegetative plants (s_2)	0.87 (0.47–1.00)	0.85	20	0.93 (0.29–1.00)	0.83	29
	Reproductive plants (s_3)	0.90 (0.80–1.00)	0.90	10	0.90 (0.75–1.00)	0.90	11
Growth transitions	New-Rep (g_{13})	0	0	–	0	0	–
	Veg-Rep (g_{23})	0.34 (0.14–0.53)	0.33	48	0.15 (0.09–0.67)	0.22	89
	Rep-Rep (g_{33})	0.90 (0.40–1.00)	0.82	29	0.90 (0.83–1.00)	0.91	8
New plant production (pr)	0.10 (0.04–0.60)	0.15	119	0.16 (0–2.32)	0.49	159	

Table 3. Transition matrices for 2 Florida ziziphus populations: 1997 to 2005

PO3			PO4		
1997–1998			1997–1998		
0	0.0385	0.0385	0	0	0
0.667	0.4	0	0.833	0.4447	0.125
0	0.0667	0.8182	0	0.222	0.625
1998–1999			1998–1999		
0	0.1176	0.1176	0	0.8846	0.8846
0.5	0.7143	0.1	0.667	0.0951	0
0	0.1429	0.7	0	0.1906	0.8333
1999–2000			1999–2000		
0	0.6	0.6	0	2.3158	2.3158
1	0.4286	0	1	0.833	0
0	0.4286	0.875	0	0.167	0.8333
2000–2001			2000–2001		
0	0.0588	0.0588	0	0.2321	0.2321
0.625	0.6939	0.55	0.9545	0.8286	0.05
0	0.1391	0.3667	0	0.1429	0.95
2001–2002			2001–2002		
0	0.1364	0.1364	0	0.1771	0.1771
0.667	0.4118	0	0.7692	0.8143	0.0833
0	0.4706	1	0	0.0857	0.875
2002–2003			2002–2003		
0	0.0833	0.0833	0	0.14	0.14
0.833	0.6	0.1538	0.8824	0.8676	0.1724
0	0.4	0.8462	0	0.1029	0.8276
2003–2004			2003–2004		
0	0.16	0.16	0	0.0877	0.0877
0.833	0.5	0.0667	0.8462	0.8734	0.1563
0	0.4	0.7333	0	0.0886	0.8438
2004–2005			2004–2005		
0	0.045	0.045	0	0.113	0.113
0.333	0.7143	0.5	0.375	0.76	0.0938
0	0.2857	0.5	0	0.1467	0.75

extinction, whereas 20.1% of the PO3 simulations had no individuals remaining after 50 yr.

Survival and new plant production (clonal recruitment) had strong effects on population growth rates, while changing growth probabilities had little effect on

the population growth rate (Table 4). Sensitivities were very similar for both the survival and new plant production parameters. Although the sensitivity of these parameters varied among the annual matrices, these results were consistent between the 2 populations.

In contrast, new plant production had a much larger contribution to observed growth rates than did any of the survival rates. The median value for the contribution of new plant production to differences in the observed growth rates across all population-years was 50% compared to 19% for vegetative survival and ~11% for new and reproductive plant survival, while advances in flowering stage made contributions less than 5% (Fig. 2).

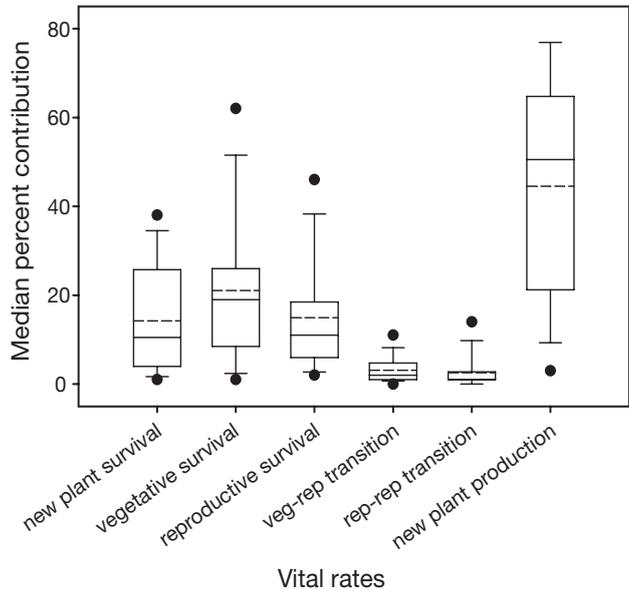


Fig. 2. Contribution of each parameter to differences between the observed and predicted population growth rate. Boxplots show medians as solid bar within the box, means as dashed bar. Upper and lower horizontal bars are 75th and 25th percentiles, respectively; upper and lower whiskers are 90th and 10th percentiles, respectively. Filled circles are extreme outliers. Veg: vegetative; rep: reproductive

Table 4. Sensitivity and elasticity to parameters across 8 yr. Ranges in parentheses

Parameter	PO3		PO4		
	Sensitivity	Elasticity	Sensitivity	Elasticity	
Survival	New plants (s_1)	0.49 (0.42–0.65)	0.25	0.47 (0.42–0.61)	0.27
	Vegetative plants (s_2)	0.37 (0.29–0.54)	0.24	0.36 (0.26–0.65)	0.22
	Reproductive plants (s_3)	0.38 (0.23–0.46)	0.26	0.38 (0.14–0.44)	0.25
Growth transitions	New–Rep (g_{13})	0	0	0	0
	Veg–Rep (g_{23})	0.01 (–0.02–0.07)	0.0	0.02 (–0.03–0.08)	0.01
	Rep–Rep (g_{33})	0.01 (–0.02–0.05)	0.0	0.02 (–0.03–0.06)	0.01
New plant production		0.37 (0.21–0.48)	0.25	0.40 (0.27–0.51)	0.27

DISCUSSION

Our initial modeling paints a picture of Florida ziziphus populations as stable, but with some chance of extinction, and with variable rates of new plant production via clonal recruitment. Increasing new plant production could increase population sizes. Our field observations suggest that new plant production sometimes increases in response to disturbances that expose the roots of larger plants. Sensitivity analysis did not indicate that new plant production had a greater influence on population growth than survival. However, because it may not be possible to increase survival in Florida ziziphus above current high levels, increasing new plant production and promoting sexual reproduction appear to be the most promising avenues of promoting population increases. In these circumstances, sensitivity or elasticity results cannot be blindly interpreted as management recommendations, as analytical sensitivity analyses do not take into account the full range of possible variation (Silvertown et al. 1996, Wisdom et al. 2000).

Although it may not be possible to greatly increase survival, our results also emphasize the importance of maintaining current survival rates. If survival decreases, population growth rates will plummet, even if the production of new plants increases. Many other studies of long-lived organisms have similarly emphasized the importance of maintaining survival rates (Silvertown et al. 1993, Pfister 1998, Crone 2001). Additional research to quantify the effects that different management activities have on Florida ziziphus plant survival could provide guidance, although small population sizes make manipulative experiments difficult.

This study represents the first attempt to model population dynamics in Florida ziziphus, and it provides some important insights for Florida ziziphus conservation. There are several caveats to our efforts, however. We modeled population dynamics based on ‘plants’ defined as clumps of stems (ramets) within a 25 cm radius because ramets appear clumped at this scale. However, without knowledge of clonal structure or

nutrient and water integration, we cannot unambiguously determine the level of physiological independence of plants at various distances from each other. Determining the relationships among neighboring stems or clumps by excavation is risky, since any manipulation to determine root structures could result in mortality.

There are 3 possibilities for dealing with this complication. The most conservative approach is to treat each uniclinal population as a single organism based on its shared genotype. This approach, however, is uninformative with respect to within-population dynamics and does not address field observations that individual clumps (i.e. ‘plants’) have independent fates. The second alternative is to treat each stem as a separate individual, regardless of the degree of clumping. This is logistically impossible due to high stem densities, overlapping canopies, and Florida ziziphus’ thorny geniculate habit. The third possibility, and the option we have chosen, is to pick a cut-off distance in accordance with our field observations to define an individual plant. Although this approach may cause some ‘individuals’ to be classified falsely with respect to physiological independence, it provides the most consistent explanation for generally observed spatial patterns.

Our second concern in interpreting these results is that it is unlikely in such a short-term study that the environmental variation observed over the study period is a realistic reflection of the actual range of variation (Coulson et al. 2001). Specifically, in a single year for population PO4, population growth rates were extremely high due to high new plant production (clonal recruitment). We assigned this year a 1 in 8 chance of occurring, but if the real rate of occurrence is higher or lower, that would have strong effects on our predictions. Likewise, if that condition reflected a certain level of disturbance (e.g. from cattle grazing), it would apply to grazed, but not ungrazed, populations. This sort of limitation is common in plant PVAs (Menges 2000a), and shorter term studies (e.g. <10 yr) may lead to less reliable predictions (McCarthy et al. 2003). For Florida ziziphus, the small number of plants

and populations and idiosyncratic site histories (e.g. damage to plants or tags by cattle) pose additional challenges.

Additional data from experimentally introduced populations may greatly increase the confidence with which we can model Florida ziziphus population dynamics. Four such populations have been initiated since 2002 (Weekley & Menges 2005). With more exact knowledge of individual histories and genetics, we will be able to delve more deeply into the relationships between existing plants and new ramets, one of the major gaps in our current modeling scheme. Integration of genetic and demographic approaches can provide more focused answers to conservation questions (Oostermeijer et al. 2003). If we are successful in establishing sexually viable populations, the addition of seedlings to the life cycle model may change the relative importance of other demographic rates, e.g. by increasing the importance of reproductive plant survival. All other things being equal, plants in larger and genetically diverse populations have higher fitness (Leimu et al. 2006). There are also many examples of vital rates increasing with heterozygosity (Westemeier et al. 1998).

As the new data on introduced Florida ziziphus populations become available and sample sizes increase, more detailed approaches, such as integral projection modeling (Ellner & Rees 2006) or individual-based modeling (Schwartz et al. 2000) may be more informative. Individual-based modeling approaches offer the possibility of including genetic variability in estimates of long-term viability (Morris & Doak 2002), which will provide important new insights given the genetic structure of Florida ziziphus.

Ultimately, recovery of Florida ziziphus requires the creation of genetically diverse and sexually reproductive populations (USFWS 1999). In the meantime, we have much to learn from the survival of this rare species, which has avoided extinction for decades with only a handful of individuals in degraded habitat. Modeling can help us understand how this species has persisted and what we can do to ensure that it will continue to survive into the future.

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