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ASSOCIATION BETWEEN FIRE RETURN INTERVAL AND POPULATION DYNAMICS IN FOUR CALIFORNIA POPULATIONS OF TECATE CYPRESS (*CUPRESSUS FORBESII*)

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ABSTRACT—The Tecate cypress (*Cupressus forbesii*) is a tree species associated with chaparral ecosystems in southern California and northern Baja California, Mexico. It is fire-adapted, its regeneration triggered by the opening of serotinous cones when adult trees are burned. Surveys made in the 1980s by others suggested that some Tecate cypress populations were declining, and some authors suggested that increased fire frequency in southern California was a major factor for this decline. We asked whether current population trends were still negative for Tecate cypress 20 years later, and whether population growth was associated with fire return interval length. Based on demographic, survival, and growth-rate data, we calculated the rate of population increase (λ) for the 4 known California populations of Tecate cypress (Coal Canyon-Sierra Peak in Orange County and Guatay Mountain, Otay Mountain, and Tecate Peak in San Diego County). The rate of population increase was positively associated with fire return interval length, which varied among populations. A 40-year or longer fire return interval corresponded to $\lambda > 1$, suggesting the population trend is positive, while a fire return interval shorter than 40 years corresponded to $\lambda < 1$, suggesting that populations burning more often than once every 40 years are declining.

RESUMEN—El ciprés Tecate (*Cupressus forbesii*) es una especie de árbol asociado con el ecosistema chaparral del sur de California y Baja California Norte, México. Está adaptado al fuego, su regeneración se inicia con la apertura de los conos serotoninos cuando los árboles adultos son quemados. Investigaciones en los años 1980 sugirieron que algunas poblaciones de ciprés Tecate estaban declinando, y algunos investigadores sugirieron que el incremento en la frecuencia de fuegos en el sur de California fue una causa importante de este decline. Nosotros preguntamos si las tendencias poblacionales actuales todavía eran negativas para el ciprés Tecate 20 años más tarde, y si el crecimiento de la población estuvo relacionado con la frecuencia de los incendios. Basados en datos de demografía, supervivencia y tasa de crecimiento, calculamos la tasa de crecimiento de la población (λ) de las cuatro poblaciones conocidas de ciprés Tecate en California (Coal Canyon-Sierra Peak en el condado de Orange y Guatay Mountain, Otay Mountain, y Tecate Peak en el condado de San Diego). La tasa de incremento de la población estuvo relacionada positivamente con el lapso de tiempo entre fuegos, la cual varió entre poblaciones. Un intervalo de 40 años o más de regreso de fuego correspondió a $\lambda > 1$, sugiriendo que la tendencia poblacional es positiva, mientras que un intervalo de menos de 40 años en el retorno del fuego correspondió a $\lambda < 1$, sugiriendo que poblaciones que se queman más frecuentemente que una vez cada 40 años están disminuyendo.

The Tecate cypress (*Cupressus forbesii*) is one of 10 species of closed-cone cypresses found in California (Vogl et al., 1988). It is associated with chaparral vegetation and occurs in several populations between 250 and 1,500 m elevation in southern California and northern Baja California (Fig. 1) (Little, 1975; Dunn, 1986; Min-

nich, 1987; Minnich and Vizcaíno, 1998; Minnich and Everett, 2001). Although its conservation status is a matter of debate among biologists and it is not listed as threatened or endangered by either the federal or state government in the United States, Tecate cypress is classified as “seriously endangered” in Cali-

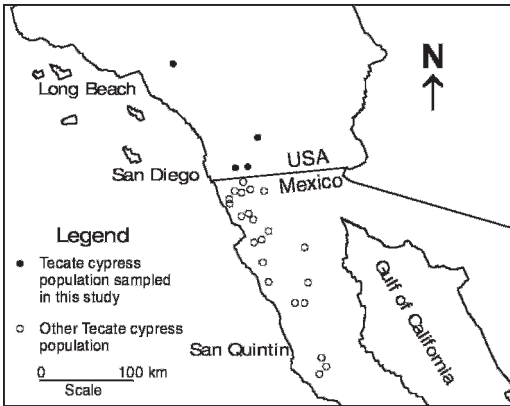


FIG. 1—Locations of Tecate cypress (*Cupressus forbesii*) populations in southern California and northern Baja California (adapted from Minnich, 1987; Minnich and Vizcaíno, 1998; Minnich and Everett, 2001). Locations are approximate.

fornia by the California Native Plant Society (California Native Plant Society, 2005) and as “rare, subject to special protection” in Mexico (Secretaría de Medio Ambiente y Recursos Naturales, 2001; Ezcurra, pers. comm.). Because many cypress populations are located in Baja California (Minnich and Vizcaíno, 1998; Minnich, pers. comm.), the “seriously endangered” classification might not reflect the status of Tecate cypress across its entire range. Tecate cypress stands are prime habitat for many animal species, including rare species, such as the San Diego horned lizard (*Phrynosoma coronatum blainvillii*) and the Thorne’s hairstreak butterfly (*Mitoura thornei*) (Spenger, 1985; Klein, pers. comm.).

The Tecate cypress is a fire-dependent “obligate seeder” species that can only establish after fire disturbance (Little, 1975; Zedler, 1977, 1981, 1995; Dunn, 1986; Vogl et al., 1988). Adult trees bear serotinous cones that open only in the heat of the wildfire that typically kills the stand of adult trees. The seeds released by cones following a wildfire have a much greater chance of germinating on the nutrient-rich ash layer covering the ground after the fire has consumed the surrounding chaparral vegetation. The small seedlings have a greater chance of surviving in the burnt areas without competition from chaparral shrubs for light and soil moisture. As with many other fire-dependent obligate seeder tree species, Tecate cypress is sensitive to fire

return interval (henceforth referred to as fire interval) because the latter influences seed-bank size, confronting cypress populations with what Ne’eman et al. (1999) and Zedler (1995) referred to as a potential “immaturity risk” if the fire interval is too short or a “senescence risk” if the fire interval is too long.

While fire has been recognized as a natural component of chaparral ecosystems in California and Baja California (Zedler, 1981, 1995; Hanes, 1988; Keeley and Swift, 1995), there is little agreement on what constitutes an average chaparral fire interval (Zedler, 1995; Keeley and Fotheringham, 2001a, 2001b; Minnich, 2001). Average fire intervals proposed for southern California chaparral range from 10 to 40 years (Vogl, 1977; Wright and Bailey, 1982; Hanes, 1988; Zedler, 1995). Wells et al. (2004) studied historical fire records and found that most chaparral stands in San Diego County were between 30 and 50 years old, suggesting a slightly longer mean fire interval.

Dunn (1986) calculated a cypress reestablishment index and suggested a minimum fire interval of 35 to 40 years for Tecate cypress. However, Zedler (1995) argued that a typical fire interval in Tecate cypress stands is probably longer than 35 to 40 years, because cone production per tree increases up to at least 90 years of age, precluding any senescence risk until cypress stands reach that age. A possible difference in fire interval adaptation between chaparral shrubs and Tecate cypress raises an interesting ecological conundrum, because the fire regime of a Tecate cypress-dominated phase of chaparral is likely influenced by the fire regime of the adjacent, non-cypress phase (Zedler, 1995). While other environmental factors influence Tecate cypress-dominated chaparral structure and dynamics (Vogl et al., 1988), fire interval is a critical factor (Zedler, 1977, 1995; Dunn, 1986; Franklin et al., 2001) and Zedler (1977) suggested that more studies of the population-level responses of individual chaparral species to different management strategies (including fire management) would advance our understanding of chaparral ecosystems.

The purposes of this study was 1) to assess the current status of the 4 known populations of Tecate cypress in southern California and compare our findings to the observations by Dunn (1986) that 2 of these populations were declining 20 years ago and 2) to determine if

Tecate cypress population dynamics are associated with fire interval length. We parameterized matrix models from demographic and growth data we collected in southern California populations that have been subjected to different fire intervals, and we compared their modeled rates of population increase. Based on the findings of Dunn (1986) and Zedler (1977, 1995), we hypothesized that Tecate cypress populations subjected to relatively long fire intervals should exhibit a higher rate of population increase than populations subjected to relatively short fire intervals.

Matrix models have inherent limitations (Condit et al., 1998; Easterling et al., 2000). For example, the models assume that a population has a stable age distribution over time and that reproduction occurs regularly. Despite these limitations, matrix models have proved useful in population ecology to investigate the trend of plant and animal populations following disturbances, management, or a combination of both (Crouse et al., 1987; Caswell, 2001). Warton and Wardle (2003) used a matrix model to project the population trend of *Acacia suaveolens*, a perennial shrub of Australia following fire, and Keeley and Swift (1995) used matrix models to project population dynamics of obligate seeder shrub species of the genus *Ceanothus* that regenerate following fires in southern California chaparral. Van Mantgem and Stephenson (2005) found that short-term (ca. 10-year) population projections from matrix models agreed well with actual population dynamics for several coniferous species in California, including *Pinus ponderosa* and *P. jeffreyi*, 2 species that regenerate in pulses following favorable climatic (Savage et al., 1996) and fire (Minnich et al., 2000; Ehle and Baker, 2003) events.

METHODS—We sampled the 4 known populations of Tecate cypress in southern California – Coal Canyon (north face of Sierra Peak) in Orange County and Guatay Mountain, Otay Mountain, and Tecate Peak in San Diego County – from December 2003 through June 2004. At each population, we collected vegetation data in a plot (20 × 30 m) located within a stand randomly chosen from several stands identifiable in the landscape. Within that stand, we randomly selected a starting point and a bearing constrained within a 90° window to insure that the plot would fit within the selected stand. The 20-m × 30-m plot was then subdivided into 24 quadrats (5 × 5 m).

In each plot, we measured the diameter (10 cm above ground) of all live or recently (1 to 2 years prior to sampling) burned Tecate cypresses ≥5 cm diameter

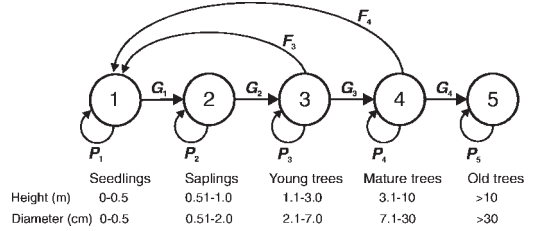


FIG. 2—Life cycle graph for the Tecate cypress (*Cupressus forbesii*). G_i is the yearly probability of surviving and growing to the next stage, P_i is the yearly probability of surviving and remaining in the same stage, and F_i is the number of seedlings produced per tree per year in each fertile stage.

and randomly selected a subsample of these trees to collect tree cores with an increment borer. We visually estimated the cone crop of each cored tree and collected cone samples to measure the number of seeds per cone and estimate seed crop as a function of tree size. All Tecate cypress seedlings, saplings, and young trees <5 cm in diameter were recorded and measured in 3 randomly chosen 5-m × 5-m quadrats (with blocking) within each 20-m × 30-m plot. In plots containing saplings, we collected stem cross-sections from saplings <5 cm in diameter to complement tree cores for determining size-age relationship.

We dried and mounted all Tecate cypress tree cores on wood bases and measured tree ring width with a Velmex (Bloomfield, New York) tree ring measuring system and a stereomicroscope. We checked the accuracy of our tree core dating using skeleton plots (Stokes and Smiley, 1996) to cross-date all cores collected from each population. The software Measure JX (VoorTech Consulting, Holderness, New Hampshire) was then used to collect digital ring width data for estimating the age of each cored tree and its growth rate as a function of diameter.

The demographic and growth data, our observations about the life history of Tecate cypress, and life history data from Dunn (1986) and Zedler (1977) were used to construct a life cycle graph (Fig. 2) and build matrix population models for Tecate cypress. Given the relatively short life span of Tecate cypress (the oldest tree we recorded from cores was 52 years old), we used 5 stages for its life cycle graph, with seed production declining to 0 in stage 5.

The life cycle graph (Fig. 2) was used as a guide to build a Lefkovich matrix A for each of the 4 modeled populations as

$$A = \begin{bmatrix} P_1 & 0 & F_3 & F_4 & 0 \\ G_1 & P_2 & 0 & 0 & 0 \\ 0 & G_2 & P_3 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 \\ 0 & 0 & 0 & G_4 & P_5 \end{bmatrix}$$

where G_i is the yearly probability of surviving and growing to the next stage, P_i is the yearly probability of surviving and remaining in the same stage, and F_i is the

number of seedlings produced per tree per year in each fertile stage (see below). We set our projection time interval for matrix A equal to one year. We then used the matrix to project population growth for each of the 4 modeled populations for 10 time intervals (10 years) using the linear equation: $n(t+1) = An(t)$, where $n(t)$ is a vector of stage abundance at time t and $n(t+1)$ is the projected vector of stage abundance at time $t+1$.

Tree fertility was estimated from either direct measurement of seedling yield per tree in recently burned populations or from counts of cones per tree and of seeds per cone in the unburned populations that did not contain seedlings. Because seed predation is typically high in other closed-cone species of the genus *Cupressus* (70 to 90% in *C. sempervirens*) and germination rates are typically low (below 50% and as low as 7.5% for seeds from 7-year-old cones in *C. arizonica*) (De Magstris et al., 2001; Battisti et al., 2003), we assumed a conservative 10% overall seed survival and germination rate for Tecate cypress when estimating fertility from cone counts. When we estimated fertility from counts of 2-year-old seedlings produced per seed tree (as in Coal Canyon), we used these counts uncorrected as a fertility rate (already discounted for seed predation and germination rates). When we estimated fertility from counts of <1-year-old seedlings per seed tree (as on Otay Mountain), we assumed a density-dependent seedling mortality rate of 60% from time 0 to year 2 based on the study by Dunn (1986). In all cases, each per capita stage fertility rate (from seedling counts or from cone production) was converted to a yearly per capita fertility rate equivalent by dividing it by the population-specific age of the oldest tree (live or recently killed for recently burned populations) recorded in the corresponding population, which was our best estimate of fire interval for that population.

Tecate cypress survivorship data from Dunn (1986) were used to calculate stage survival probabilities [$P(\text{surv})$] as follows: baseline $P(\text{surv})$ of seedling (stage 1) at time $t_0 = 100\%$. $P(\text{surv})$ from seedling to stage 2 = 40%. $P(\text{surv})$ from seedling to stage 3 = 20%. $P(\text{surv})$ from seedling to stage 4 = 13%. $P(\text{surv})$ from seedling to stage 5 = 8%. We then used these data to calculate s_i , the probability of transition [$P(\text{transition})$] from one stage to the next as: $P(\text{transition from 1 to 2}) = 0.40$; $P(\text{transition from 2 to 3}) = 0.50$; $P(\text{transition from 3 to 4}) = 0.65$; $P(\text{transition from 4 to 5}) = 0.62$ and $P(\text{transition from 5 to } >5) = 0$. In other words, stage 5 is final and all trees graduating from stage 5 die.

We calculated the rate of population increase (λ) as follows, assuming a post-breeding census model. We estimated each stage duration T_i as the number of years a cypress tree would typically spend in a given stage through a regression analysis of tree age with tree diameter and height. Assuming that σ_i (the survival probability of an individual in stage i per time interval) is constant for trees of different sizes within a given stage i (Caswell, 2001), and therefore, that $\sigma_i^{T_i} = s_i$, we calculated $\sigma_i = s_i^{(1/T_i)}$. P_i (the probability of surviving and staying in stage i) and G_i (the probability of surviving and growing from stage i to stage $i+1$) were calculated as per Caswell (2001):

$$G_i = \sigma_i \times \gamma_i$$

$$P_i = \sigma_i \times (1 - \gamma_i)$$

We estimated $\gamma_i = \frac{(\frac{\sigma_i}{\lambda})^{T_i} - (\frac{\sigma_i}{\lambda})^{T_i - 1}}{(\frac{\sigma_i}{\lambda})^{T_i - 1}}$ by using the

iterative calculation of λ suggested by Caswell (2001), where λ is the dominant eigenvalue of A and also the rate of increase of the modeled population. Stage 3 and stage 4 fertilities were calculated as $F_i = P_i m_i + G_i m_{i+1}$, where m_i is the estimated fertility (number of seedlings produced per tree of stage i per year, estimated from cone crops or seedling counts as explained above). We assumed that $F_i = 0$ for juvenile trees in stages 1 and 2 and for old trees in stage 5.

Finally, we computed 95% confidence intervals (95% CI) around λ using the delta method (Caswell, 2001) by first calculating the variance of λ as:

$$\text{Var}(\lambda) \sim \sum_{ij} \text{Var}(a_{ij})(\partial\lambda/\partial a_{ij})^2$$

where a_{ij} is any Lefkovich matrix element and $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to changes in a_{ij} . A 95% CI was computed as:

$$95\% \text{ CI} = \lambda \pm 1.96 \times \sqrt{\text{Var}(\lambda)}$$

We assumed that if $\lambda > 1$, the number of Tecate cypresses (N) in the modeled population is increasing, if $\lambda < 1$, N is decreasing, and if $\lambda = 1$, N is constant and the population trend is stable, with a level of uncertainty given by the confidence interval around λ . For the populations that did not burn within the past 5 years (Guatay Mountain and Tecate Peak), our matrix models assumed these populations burn and post-fire regeneration is triggered according to our fertility estimates (Table 1). We used linear regression in SPSS (SPSS, Inc., Chicago, Illinois) to analyze the relationship between λ and estimated fire interval length across the 4 populations.

RESULTS—The demography of Tecate cypress populations varied across the 4 sites, with some populations exhibiting uneven-aged structure (Table 1). Across all populations, tree height was a better predictor of tree age ($P = 0.002$, $R^2 = 0.47$, $df = 18$) than tree diameter ($P > 0.1$, $R^2 = 0.01$, $df = 18$). None of the trees we measured across the 4 populations were older than 52 years, but young trees (ca. 5 cm in diameter) already produced an average of 40 cones (approximately 3,600 seeds) per tree. Mature trees (ca. 10 cm in diameter) produced an average of 200 cones (approximately 18,000 seeds) per tree. The only population that did not burn in more than 50 years (Guatay Mountain) did not contain any seedlings, saplings, or young trees.

Three of the populations (Otay Mountain, Tecate Peak, and Guatay Mountain) seemed to

TABLE 1—Demographic data, fertility estimates, and rate of population increase (λ) of 4 Tecate cypress (*Cupressus forbesii*) populations in southern California. Number of trees in parentheses refer to recently (1 to 2 years before sampling) burned and dead trees.

	Population			
	Coal Canyon-Sierra Peak	Guatay Mountain	Otay Mountain	Tecate Peak
Locality	117°39'58"W 33°50'48"N	116°43'40"W 32°51'00"N	116°52'00"W 32°34'30"N	116°40'00"W 32°34'00"N
Year of last stand-replacement fire on records	2002	?	2003	1975
Number of seedlings ≤ 0.5 m height (mean/m ²)	3	0	19	0
Number of saplings 0.51 to 1.0 m height or <2 cm diameter (mean/m ²)	0	0	0	1
Number of young trees 2.1 to 7 cm diameter (mean/ha)	(8,400)	0	(17)	6,600
Number of mature trees 7.1 to 30 cm diameter (mean/ha)	(267)	67	(100)	50
Number of old trees >30 cm diameter (mean/ha)	0	8	(33)	0
Diameter of trees 5 to 10 cm diameter (cm) mean (SD)	6.0 (1.3)	—	7.3 (2.8)	6.5 (0.3)
Height of trees 5 to 10 cm diameter (m) mean (SD)	3.5 (0.8)	—	3.0 (1.4)	5.3 (0.4)
Age of trees ca. 5 cm diameter (years) mean (SD)	—	—	31 (7.8)	—
Diameter of trees >10 cm diameter (cm) mean (SD)	—	21.9 (6.0)	20.8 (9.7)	10.2 (1.1)
Height of trees >10 cm diameter (m) mean (SD)	—	5.5 (1.8)	6.2 (2.9)	4.6 (2.9)
Age of oldest tree sampled – live or recently killed (years)	38	52	43	46
Number of cones per tree ca. 5 cm diameter mean (SD)	33 (25)	—	60 (–)	40 (42)
Number of cones per tree ca. 10 cm diameter mean (SD)	—	400 (430)	150 (71)	75 (28)
Average number of seeds per cone (SD)	89 (22.3)	103 (26.2)	89 (22.3)	75 (18.5)
Estimated number seeds per tree ca. 5 cm diameter	2,937	—	5,340	3,000
Estimated number seeds per tree ca. 10 cm diameter	—	41,200	13,350	5,625
Rate of population increase λ (95% C.I.)	0.96 (0.88, 1.04)	1.17 (1.01, 1.33)	1.08 (0.98, 1.18)	1.06 (0.98, 1.14)

be stable or potentially increasing ($\lambda > 1$), while the Coal Canyon/Sierra Peak population seemed to be declining ($\lambda < 1$). Our λ estimates have site-specific levels of uncertainty given by population-specific confidence intervals (Table 1). The rate of population increase (λ) was positively associated with estimated fire interval length across the 4 populations ($P = 0.050$; $R^2 = 0.90$, $df = 3$) (Fig. 3). A fire interval shorter than 40

years, such as in Coal Canyon/Sierra Peak, was associated with a negative population trend, while greater than 40-year fire intervals were associated with positive population trends.

DISCUSSION—Our study suggests that the observations by Dunn (1986) that some of the southern California Tecate cypress populations (Coal Canyon/Sierra Peak and Tecate Peak)

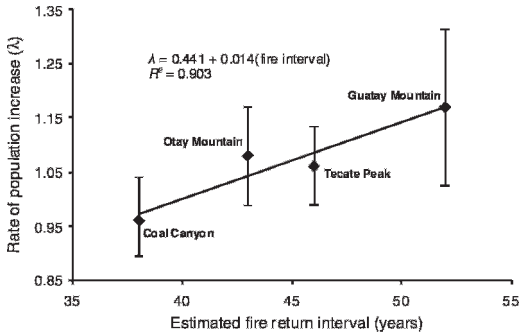


FIG. 3.—Association between population fire-return interval and rate of population increase (λ) for Tecate cypress (*Cupressus forbesii*) estimated from Lefkovich matrix models for 4 sampled sites. Bars represent 95% CI around λ estimates.

were declining 20 years ago is still true today for one of the 4 populations. Our results suggested that the Coal Canyon/Sierra Peak population was declining for the same reason described by Dunn (1986), namely that the current fire interval (38 years) is too short. However, our results also suggested that the Tecate Peak population, which Dunn (1986) described as most endangered among the 4 southern California populations, was stable even under a simulated burn scenario. If Tecate Peak burned, its complex fire history would generate fire intervals of 29 and 46 years in different parts of the Tecate cypress population (at the time of our study), and the estimated cypress seed bank should provide sufficient regeneration to maintain or increase that population.

The positive association of λ with fire interval length supports the suggestion by Zedler (1977, 1995) that longer fire intervals increase the likelihood that a population of Tecate cypress will regenerate and grow over time. Longer fire intervals allow cypress populations to produce larger seed banks stored in cones (Zedler, 1995), which can trigger greater post-fire regeneration and result in higher rates of population increase. These dynamics differ from the post-fire regeneration of another *Cupressus* species in the Santa Lucia Mountains of California. Ne'eman et al. (1999) found that post-fire *Cupressus sargentii* seedling density was negatively correlated with stand age, indicating that senescence risk is higher than for *C. forbesii* and, thus, longer fire intervals might not translate into higher rates of

population increase for *C. sargentii*. This difference is likely the result of higher growth rates of *C. sargentii* under less droughty conditions (Ne'eman et al., 1999).

The discrepancy between the relatively long (>40 year) fire intervals necessary for the maintenance of Tecate cypress populations and the shorter (<40 year) fire interval typically reported for non-cypress (i.e., chamise, red shank, or manzanita) chaparral (Vogl, 1977; Hanes, 1988; Zedler, 1995) is noteworthy. It suggests that, although both vegetation types are continuous in southern California, landscape heterogeneity creates environmental conditions that generate dissimilar fire intervals within that landscape. The steep north-facing slopes and rocky outcrops on which several of the Tecate cypress populations grow today (Hanes, 1988) might produce the complex mosaics of fire events observed on Tecate Peak and Otay Mountain (Zedler, 1981; Hanes, 1988), including areas where cypress groves escape some of the surrounding chaparral fire events (Hanes, 1988). These habitats are likely to sustain lower fire frequencies and, thus, might function as refugia for the Tecate cypress, which occurred more widely during glacial times, when the climate of southern California was cooler (Vogl et al., 1988) and fires might have been less frequent.

Although biologists disagree on the nature and importance of fire regime differences between California and Baja California chaparral ecosystems (Minnich and Chou, 1997; Gutsell et al., 2001; Keeley and Fotheringham, 2001a, 2001b; Minnich, 2001; Minnich, pers. comm.), fire suppression policies and land-use practices might have influenced the structure and dynamics of Tecate cypress populations differently on each side of the border (Minnich and Vizcaíno, 1998). Comparing the structure and dynamics of Tecate cypress populations in California and Baja California would help determine if and how the different fire regimes on either side of the USA-Mexico border are ecologically significant.

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