

THE ROLES OF SOIL TYPE AND SHADE INTOLERANCE IN LIMITING  
THE DISTRIBUTION OF THE EDAPHIC ENDEMIC *CHORIZANTHE*  
*PUNGENS* VAR. *HARTWEGIANA* (POLYGONACEAE)

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ABSTRACT

Understanding the ecological factors that cause narrow geographic range and habitat specificity is essential for the conservation of rare species of edaphic endemic plants. Here we investigated the relative roles of soil and light in limiting the distribution of *Chorizanthe pungens* Benth. var. *hartwegiana* Rev. & Hardham (Polygonaceae), an annual plant endemic to open patches of low nutrient soils in the sandhills habitat of the Santa Cruz Mountains, Central Coastal California. Seedlings were grown in a controlled pot experiment under three light conditions and five soil treatments. The growth, survival, and reproduction of individual plants were compared.

Plants were least successful when grown on their native low nutrient soil, suggesting that soil type is not a limiting factor in the taxon's distribution. However, when grown under high shade, survivorship, growth, and reproduction of individuals were low. This suggests that shade intolerance is the major cause of this taxon's restriction to open, sandy areas. Thus management to preserve this federally endangered species should include artificial or natural disturbances to prevent populations from being extirpated due to encroachment of taller, shade-producing species.

The geographic distributions of plant species are determined by many factors. While history, geographic barriers, and isolation all influence the distribution of species, the ultimate determinant of where a taxon can be found is its inherited tolerance to environmental factors (Kruckeberg and Rabinowitz 1985). Climatic, biotic, and edaphic characteristics of a given environment determine the constraints or opportunities an individual plant faces, depending on its genetically determined physiologic capabilities (Mason 1946; Baskin and Baskin 1988). The question of what limits plant distributions is important both to biogeography and in assessing the threats to populations of rare species.

Among the most striking of geographic factors affecting plant distribution are unique edaphic conditions, including unusual bedrock outcrops (e.g., serpentinite), nutrient poor soils, and varying water regimes (e.g., vernal pools). Areas with these unusual conditions, which are considered inhospitable to the growth and reproduction of most plant species, are often inhabited by unique assemblages of specialized, morphologically distinct plant taxa. Due to their narrow habitat specificities and small geographic ranges, these endemic taxa are often among the rarest of plants (Rabinowitz 1981). Fur-

thermore, small population sizes, limited geographic distributions, and generally poor competitive abilities render edaphic endemic plants highly vulnerable to extinction due to stochastic events, habitat degradation, and invasion by weedy species (Harper 1981; Kruckeberg and Rabinowitz 1985; Janzen 1986; Falk 1991; Schemske et al. 1994). Here we report the results of an experiment designed to determine the relative roles of soil and light in limiting the distribution of a rare taxon endemic to the Zayante soils of Central Coastal California.

Recent studies on edaphic endemic plants have attempted to determine the specific factors that allow them to inhabit their typically harsh habitats, as well as the factors that confine them to those habitats (Latham 1983; Baskin and Baskin 1988; Buchele et al. 1989; Snyder et al. 1994). Three general hypotheses have been advanced to explain the habitat restriction of edaphic endemic plants. First, edaphic endemics may have specific chemical, physical, or biological requirements that are met only on a particular substratum (Walker 1954). Second, edaphic endemics may tolerate, though not require, the inimical conditions where they typically occur, while they are excluded from more hospitable habitat due to competitive interactions with other species. In particular, these often diminutive species may be limited to open communities where they are unshaded by taller, more competitive species that thrive in adjacent habitats (Baskin and Baskin 1988; Collins et al. 1989; Ware and Pinion 1990). Finally, edaphic endemics may be highly susceptible to soil pathogens found in nutrient-rich soils, and thus limited to low productivity areas in

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which their exposure to pathogens is decreased (Tadros 1957; Latham 1983). In addition to these three ecological factors (soil requirements, shade intolerance, and susceptibility to soil pathogens) low genetic diversity has been suggested as the root cause of the poor competitive abilities hypothesized for edaphic endemics (Stebbins 1942).

Little evidence supports the hypothesis that edaphic endemics are restricted to their habitats due to specific chemical, physical, or biological requirements. Most edaphic endemic plants can be cultivated more successfully in soils which do not contain the unique edaphic material in which they normally grow (Walker 1954; Kruckeberg 1954; Hart 1980; Ware and Pinion 1990). In studies of edaphic endemic plants, many species were found to have relatively high levels of genetic variation, suggesting that a lack of genetic diversity is also unlikely to be a common factor restricting many edaphic endemic plants to edaphically inhospitable and sparsely vegetated areas (Baskin and Baskin 1988; Collins et al. 1989; Menges 1992).

Although previous work has implicated light competition as a common limitation of edaphic endemics, the relative importance of competition for light and the influence of various soil factors, including competition for nutrients and the limiting effects of soil pathogens, has not been thoroughly evaluated for any single species. In this study, we chose to examine the composite effects of soil types in combination with varying shading levels on a highly restricted edaphic endemic. To compare the effects of different limiting factors and to understand the importance of interaction among these factors, we grew individuals of the federally endangered edaphic endemic, *Chorizanthe pungens* Benth. var. *hartwegiana* Rev. & Hardham (Polygonaceae) (the Ben Lomond Spineflower) in a controlled growth experiment in which we varied shade levels and soil types. By measuring growth, survivorship, and reproduction of this rare annual plant, we were able to evaluate the combined importance of shading and soil factors in limiting performance of this highly restricted species, thus providing a functional understanding of its distributional limits.

We chose a controlled growth experiment as a complementary approach to a previous study examining the demographic performance of *C. pungens* var. *hartwegiana* through a reciprocal transplant experiment in the field (J. Kluse and D. Doak personal communication). Experimental manipulation of environmental conditions allowed us to examine the specific effects of soil and shade while controlling for other factors. We note at the onset that we did not attempt to control or measure individual aspects of soils. Instead, given that each soil type is very distinct, our goal was to evaluate the multiple effects of soil characteristics in their entirety.

#### METHODS AND MATERIALS

*The study species.* *Chorizanthe pungens* var. *hartwegiana* is a diminutive annual plant found on many of the 'islands' of sandhills soils of the Santa Cruz Mountains, including the Bonny Doon Ecological Reserve, located at 37°03'N latitude, 122°08'W longitude. The taxon is further restricted to open, sandy, and frequently disturbed areas of this soil type. Due to its limited population size, narrow geographic range, and habitat degradation, *C. pungens* var. *hartwegiana* was listed as federally endangered in February of 1994 (Federal Register 1994). Though not noted as a separate species in The Jepson Manual, both the United States Fish and Wildlife Service and the California Native Plant Society recognize *C. pungens* var. *hartwegiana* as distinct.

The population biology of *C. pungens* var. *hartwegiana* previously has not been described in a peer-reviewed publication. Although little is known about the phenology of this rare plant, the basic seasonal pattern is similar to that of other winter-spring annuals. Seeds germinate in late fall after the first substantial rain in this region. The plants mature through the wet winter, then bolt and produce branches, flower in April and May, and die soon after seed production in June.

To date, researchers have considered habitat destruction to be the predominant threat to the taxon's existence (Morgan and Marangio 1987). Sand quarrying has already greatly reduced population numbers, and at least half of the sandhills habitat currently occupied by *C. pungens* var. *hartwegiana* is on property owned by sand and gravel companies with plans to expand mining operations. Residential development on smaller parcels also has eliminated populations and fragmented the remaining habitat (Federal Register 1994). The reduction in habitat area and the resulting decrease in population size greatly increases the likelihood of extinction due to environmental and demographic stochasticity (Falk 1991). Changes in the disturbance regimes (e.g., fire suppression) appear to be further reducing populations of *C. pungens* var. *hartwegiana* by allowing for the encroachment of larger, more competitive species such as *Arctostaphylos silvicola* Jepson & Wiesel. (personal observation).

*The study site.* The vegetation of the Santa Cruz Mountains of the Central California Coast is comprised of two main plant communities: Redwood Forest and Hardwood Forest-Oak Woodland (Barbour and Major 1977). Interspersed within these two vegetation types are small islands of deep, coarse sand derived from the highly erodible Zayante soil series, which were formed from weathered marine sediment of Santa Margarita sandstone (Soil Conservation Survey 1980). Over fifty separate islands, comprising approximately 8000 acres, of sandhills habitat have been mapped in the Santa Cruz Mountains (Marangio 1985). Managed by the

California Department of Fish and Game, the Bonny Doon Ecological Reserve (BDER) contains approximately 120 acres of sandhills habitat set aside for preservation and ecological research.

The well-drained, low nutrient soil of the sandhills habitats supports the sandhills plant communities—unique assemblages of species found primarily or exclusively on these soils (Marangio 1985). Analogous to the distinct communities found on serpentinite soil, the sandhills flora consists of many diminutive annuals and shrub species, several of which are state or federally listed (Morgan and Marangio 1987).

Three distinct types of sandhills vegetation are found on the BDER: maritime coast range ponderosa pine forest, the endemic *Arctostaphylos silvicola* (manzanita) mixed chaparral, and sparse assemblages of low-growing herbaceous species populating the open, sandy areas. *Chorizanthe pungens* var. *hartwegiana* occur almost exclusively in this last community type.

The soils of the BDER are comprised mainly of the Zayante coarse sands derived from weathered marine sediment of Santa Margarita sandstone. However, the soil within each of the three plant communities is distinct in color, content, and humus level. In open areas of the reserve, the sands have remained relatively free of organic addition. However, in the manzanita and ponderosa pine areas, organic matter from the overstory has created sandy loams. The redwood soil is composed of slightly acidic loams with high levels of organic matter characteristic of the Lompico-Felton complex. Similarly, the oak soil is composed of sandy loams of the Ben Lomond-Felton complex with a subsoil of clay loams (Soil Conservation Survey 1980). The upper layers of both soils are rich with decaying redwood and oak duff, respectively.

*Experimental design.* To determine the relative effects of edaphic factors and light levels on *C. pungens* var. *hartwegiana*, we conducted a controlled growth experiment at the University of California, Santa Cruz Arboretum. For this experiment, the plants were grown in five soil types. We chose to test performance in the three most predominant soils of the sandhills habitat (pure sand, manzanita, and pine) as well as the two most widespread soils bordering the BDER (oak and redwood forest). On 22 January 1994, we collected approximately 57 liters of each soil type from three sites within a single 10 × 10 m area, homogenizing it before use. The redwood soil was collected in a grove 3 km from the reserve's northern border and the oak soil from an oak woodland 5 km east of the reserve. The sand, pine, and manzanita soils were collected within the reserve. To collect all soils, we cleared away any leaves, duff, or herbaceous ground cover and then removed the top 10 cm of soil.

On 25 January 1994 we collected *C. pungens* var. *hartwegiana* seedlings from the open, sandy

areas of the BDER by removing blocks of sand containing 10 to 30 seedlings each. The plants were transported in plastic bags and transplanted into standard 4 liter (15.2 cm rim diameter) pots within 4 h after removal from the reserve.

We planted 5 seedlings in each of 12 pots of each soil type for a total of 300 individuals. Five seedlings were planted in a circle within each pot such that each individual was 6 cm from the nearest neighbor and 3 cm from the edge of the pot. Plants for each pot were taken from several of the collected blocks of sand in order to mix the seedling sources. Extra plants were planted in separate pots for later use as replacements.

The pots were placed in two protective wire cages in an unshaded field at the University of California at Santa Cruz Arboretum. On 1 February 1994, shade treatments were established by suspending neutral shade cloth 30 cm above the top of the pots. Two different densities of shade cloth were used to create the low and high shade treatments. Each cage contained one block of each of the three shade treatments (high, low, and no shade) and two pots of each soil type were placed under each shade treatment. Both the placement of the pots within each shade treatment and the placement of the shade treatments within each cage were randomized. Each plant was assigned a number so that we could record and track the fate of each of the 300 plants individually (20 plants per treatment combination).

In order to prevent water from being a limiting factor in growth, plants were kept moist by watering with tap water whenever any one pot showed significant drying.

In a second transplant on 3 February 1994, one week after initial transplanting, we replaced any seedlings which were dead or dying. Five days following the second transplant initial size measurements of all 300 seedlings were taken. For each plant, we recorded the length of the longest leaf, a measure shown to have a strong positive correlation with total aboveground biomass in this taxon (Kluse 1994). Intermediate measurements were taken on 12 February, 13 March, and 11 April 1994. We recorded deaths and observations of plants infected by an unidentified rust common among *C. pungens* var. *hartwegiana* at the BDER.

Plants in our experiment flowered between 21 April (78 days after transplant) and 12 June (118 days after transplant). As each plant flowered, we recorded a final measurement of longest leaf length and then harvested it by cutting the plant at ground level, taking care not to disturb the other plants in the pot. Plants were dried to a constant mass then weighed to obtain final aboveground biomass.

Since the closed cages in our experiment prevented natural pollinator visitation, we could not measure seed production directly. However, *Chorizanthe* spp. are known to produce a single, one-seeded flower within each involucre (Hickman

1993). Thus, we counted the number of involucre produced by each individual and used this as our measure of reproductive output.

In order to compare the light levels under our shade treatments with those in the field, we measured photosynthetically active radiation (400–700 nm) using an LAI-2000 Plant Canopy Analyzer. Photon flux measurements above and below each canopy type were considered in our experiment. These values were compared to percent transmittance measurements in our three shade treatments.

To test for significant soil or shade effects on growth, we performed a 2-way analysis of variance (ANOVA) on longest leaf length measurements recorded throughout the experiment. Similarly, we used 2-way ANOVA to test for soil and shade effects on the reproduction and final biomass of *C. pungens* var. *hartwegiana* using (number of involucre)<sup>2</sup> and ln (final mass) as dependent variables (transformations to achieve normality). Due to the significant effect of initial seedling size on final biomass ( $P = 0.02$ ), we performed all subsequent analyses of final biomass as ANCOVAs, using initial leaf length measurements as a covariate. Pairwise post-hoc comparisons (Tukey-Kramer) were then conducted to determine significant differences between means of final biomass and reproduction in the various shade and soil treatments. Finally, we used G-tests to test for treatment effects on survivorship to final harvest.

## RESULTS

**Light measurements.** Percent light transmittance values for sand, manzanita, pine, redwood, and oak habitats were 99.5%, 26.2%, 59.4%, 1.6%, and 3.2% respectively ( $SD = 1.2, 16.4, 30.2, 0.4,$  and  $1.8$ , respectively). The no shade treatment allowed complete light transmittance, the low shade 38.6% transmittance, and the high shade 19.7% ( $SD = 2.4$  and  $0.5$ , respectively).

**Morphological observations.** Throughout the growth period, substantial variation in plant morphology and time to flowering among the different treatments was observed. Plants in full sun grew prostrate with no basal stem and showed much secondary branching. Their leaves were short, wide, had crinkled edges and turned deep orange to red with age. Low shade plants also were prostrate, yet had fleshier, smoother (lacking crinkled edges) leaves which did not redden with age. Low shade plants showed less secondary branching. The high shade conditions produced etiolated plants with highly elongated basal stems. These plants lacked the three-branched pattern typical of the species' natural growth pattern. Their leaves were elongated, thin, fleshy, and very light in color.

Although there was overlap among flowering times in all treatments, plants that received more sunlight flowered earlier. Plants grown in full sun flowered first, as early as 21 April, 78 days after

initial transplantation. The low shade plants began to flower a week later. However, most of the high shade plants did not flower until the last week of harvest.

**Survivorship.** Shading level had a significant effect on the survival ( $G = 30.6, 2 \text{ df}, P < 0.005$ ) with 48% of the plants surviving under full sun, 55% under low shade, and 20% under high shade conditions (Fig. 1a). In contrast, soil type did not significantly affect survival ( $G = 6.6, 4 \text{ df}, P = 0.127$ ), but certain treatment combinations of soil and shade yielded incongruent results. For example, plants in oak soil under high shade conditions had the lowest survivorship (10%), while those in oak soil in low shade had one of the highest survival rates overall (65%; Fig. 1c). While this pattern suggests a possible interaction between soil and shade treatments, there was no significant interaction effect ( $G = 11, 8 \text{ df}, P = 0.202$ ). In addition, high mortality of plants in oak soil under high shade resulted in a small sample size (i.e., two plants) for this treatment, thus caution must be taken in interpreting these data.

**Reproduction.** Shade had a highly significant effect on the number of flowers produced ( $P < 0.001$ ; Fig. 2a). The low shade plants averaged significantly higher flower output than both high shade and no shade plants ( $P = 0.001$  and  $P = 0.049$ , respectively). While plants grown under no shade produced a greater average number of flowers than the high shade plants, this result was not significant.

There was no significant effect of soil on flower output ( $P = 0.109$ ; Fig. 2b) when the interaction effect between soil and shade is included in the analysis. However, when the interaction effect, which was not significant, was removed from the model, there was a significant effect of soil on flower output ( $P = 0.012$ ). Plants in oak soil produced dramatically more flowers than those in any other treatments while plants in sand produced the fewest flowers; however pairwise comparisons showed no significant difference between flower output in any of the soil types.

In all five soil types, low shade plants generated the greatest number of flowers, high shade plants the fewest, and no shade plants an intermediate number (Fig. 2c), paralleling the result that shade and soil did not significantly interact in their effects on reproduction.

**Final biomass.** Analysis of the ln(mass) by ANCOVA, using initial leaf length of transplanted seedlings as a covariate, showed that final mass was affected by shade treatment ( $P = 0.036$ , Fig. 3a). Plants in the low shade accumulated the greatest mass while no shade plants reached moderate masses and plants in the high shade had the lowest masses. However, the only significant difference by pairwise comparison was between the low shade and the high shade ( $P = 0.027$ ).

Final biomass also was strongly affected by soil

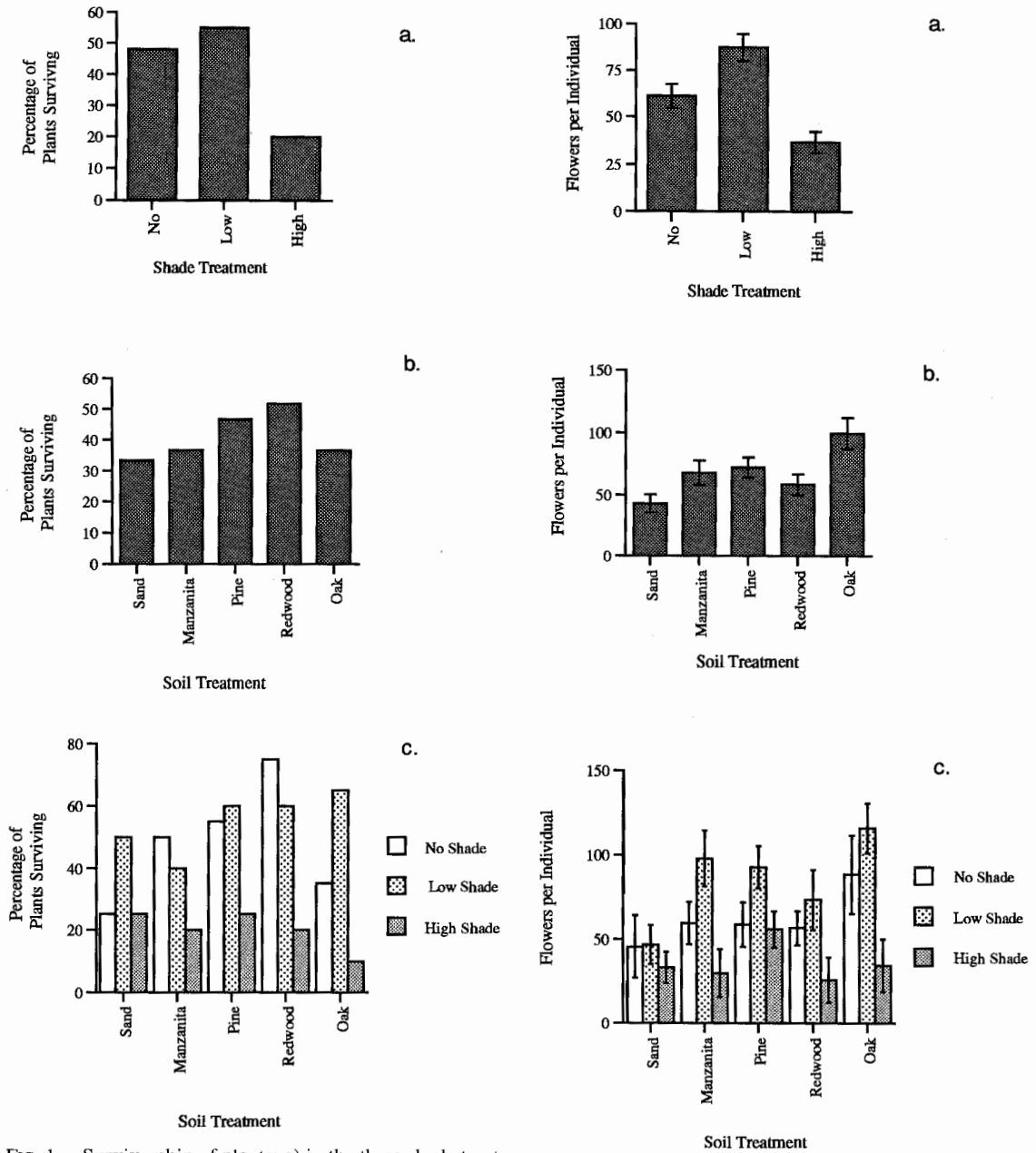


FIG. 1. Survivorship of plants: a) in the three shade treatments; b) in the five soil treatments; c) grown in the 15 different soil and shade treatment combinations. All values plotted are the percentages of *C. pungens* var. *hartwegiana* in each treatment which survived until harvest.

FIG. 2. Mean number of flowers per plant: a) in the three shade treatments; b) in the five soil treatments; c) in the 15 different soil and shade combinations. All values plotted are the mean number of flowers produced by each plant  $\pm$  one standard error. Sample sizes ranged from two to fifteen among the different treatment combinations.

type ( $P = 0.004$ , Fig. 3b). Plants grown in the non-sandhill soils had the greatest final biomass with the biomass for plants grown in pine and manzanita soils intermediate, and plants in sand soil remaining, on average, very small. Both pine and redwood soils yielded plants with significantly higher biomass than sand soil ( $P = 0.008$  and  $P = 0.015$ , respectively). Although plants grown in oak soil at-

tained the highest average mass, pairwise comparisons showed no significant differences in biomass between oak and the other soil treatments. This is most likely due to the low sample size which resulted from high mortality in oak soil.

There was no significant interaction effect be-

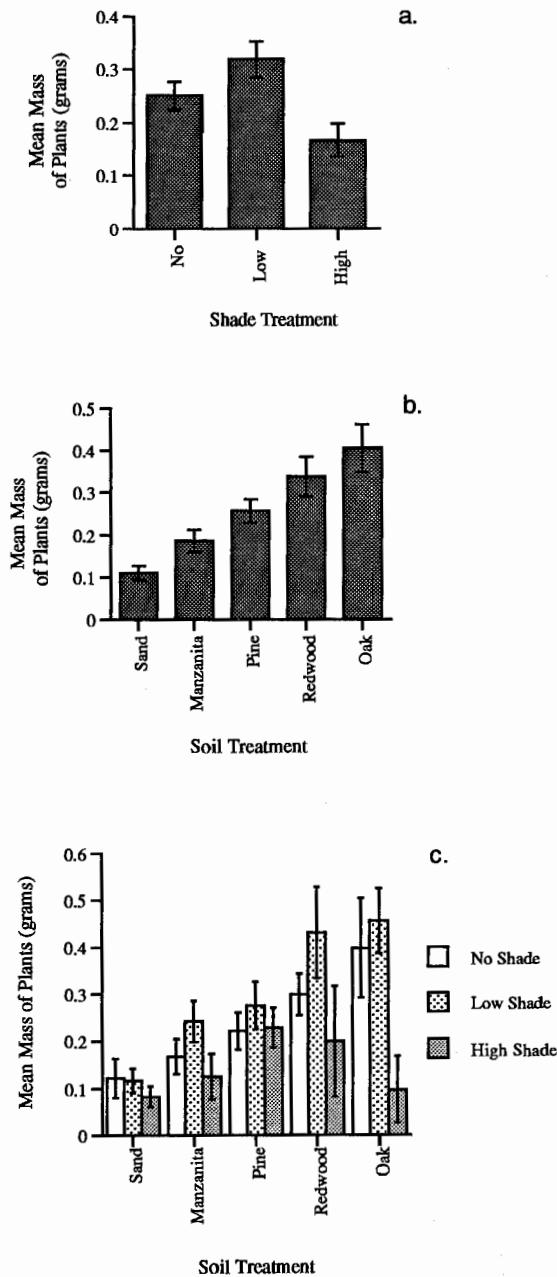


FIG. 3. Mean final aboveground biomass of *C. pungens* var. *hartwegiana*: a) in the three shade treatments; b) in the five soil treatments; c) in the 15 different soil and shade treatment combinations. Values plotted are the mean dry weights of plants  $\pm$  one standard error. Sample sizes ranged from two to fifteen among the different treatment combinations.

tween soil and shade treatments on biomass. However, when grown under low shade, plants in oak soil averaged the largest biomass; yet, when grown under high shade, plants in oak soil had the second to smallest final biomass (Fig. 3c).

Table 1 shows the percentage of the variance (measured as percentage of total sum of squares from a two way ANOVA) in the longest leaf length explained by the variables soil, shade, and the interaction of soil and shade at each of the three intermediate measurements times in our study. By the eleventh day of the experiment, the interaction effect between soil and shade treatment accounted for the greatest amount of variance not due to error (16%). Although they accounted for a small amount of variance, the separate effects of shade (7.8%) and soil (5.5%) were statistically significant. By the forty-fifth day of the experiment, the amount of variance caused by the interaction effect had decreased to 10%, while the influence of both shade (8.7%) and soil (7.6%) had increased. This trend continued until the final measurement 113 days after transplanting, when the effect of soil became the most prominent cause of variance (18.8%), and shade had increased slightly, to 8.9%, leaving the interaction effect to account for only 2% of the variance.

#### DISCUSSION

*Ecological implications.* Our results implicate shade as a primary factor in limiting the distribution of *C. pungens* var. *hartwegiana*. Soil treatment also had significant effects on performance but, because atypical soils were most conducive to growth, survival, and reproduction, soil per se cannot be viewed as a limiting factor in the distribution of *C. pungens* var. *hartwegiana*. Instead, results showing that high shade levels correlated with relatively low survivorship, reproduction, and final biomass implicate shade intolerance as the primary cause of the species' restriction to open sandy areas.

The relative importance of the shade regime, soil treatment, and their interaction upon individual performance varied throughout the growing season. We note here that while the initial sample size was 100 plants for each shade treatment and 60 plants for each soil type, only 20 plants comprise each soil/shade treatment combination. Therefore, caution should be used when considering results of interaction tests. The interaction between soil and shade diminished during the course of the study. Conversely, the variation in plant size accounted for by both the shade and soil treatments increased throughout the experiment, with the soil effect more than tripling by the last measurement (Table 1). However, changes in the percentage of the variance explained by the soil, shade, and interaction effect may be an artifact of the change in plant growth form that occurred throughout the experiment. From the time that the plants bolted, additional growth in the form of increased branch length, and subsequently flowers, was observed, while leaf length remained constant.

Our results show that the distribution of *C. pungens* var. *hartwegiana* is not restricted by soil char-



TABLE 1. PERCENTAGE OF VARIANCE IN SIZE OF THE PLANTS EXPLAINED BY SOIL, SHADE, AND THEIR INTERACTION EFFECT AT THREE TIME INTERVALS DURING THE EXPERIMENT. Variance is measurement of the percentage of the total sum of squares accounted for by each independent variable in a two-way ANOVA on the longest leaf length, a measure of plant size. Both of the main effects and the interaction effect were significant at each sampling date ( $p < 0.05$ ).

Source of variance	Time elapsed since transplant (percent)		
	Day 11 (3/13/94)	Day 45 (4/21/94)	Day 113 (5/20/94)
Soil	5.5	7.6	18.8
Shade	7.8	8.7	8.9
Soil by Shade	16.2	10.1	2.6
Interaction Error	70.5	73.7	69.7

acteristics. In fact, all of our measures of performance were highest for individuals grown in the four soils where *C. pungens* var. *hartwegiana* does not naturally occur. The higher mass and flower number of plants in the manzanita, oak, pine, and redwood soils is perhaps due to the comparatively higher organic contents and greater water retention capacities of these soils relative to the sand soil. Many previous studies have used the addition of specific nutrients to controlled soil conditions to test the performance of edaphic endemics (Kruckeberg 1954; Baskin and Baskin 1988). However, we chose to use actual soils from the habitat adjacent to the naturally occurring populations in order to infer plant performance in these habitats. The success of *C. pungens* var. *hartwegiana* in the four test soils does not support the hypothesis that chemical, physical, or biological requirements of this taxon are met only on the sandy soil.

Although the soils with higher organic content, which have an inherently greater water holding capacity, significantly increased final biomass (Fig. 3b), growth in these soils did not result in strong or consistent increases in reproduction over the plants grown in the sand soil (Fig. 2b). Instead, only shade level had a significant effect on flower number through its effect on plant morphology. Plants grown in low shade and no shade treatments had multiple branches, and this translated into more inflorescences. *Chorizanthe pungens* var. *hartwegiana* growing naturally at the Bonny Doon Ecological Reserve were morphologically similar to those in the no shade treatment (personal observation).

Plants grown under the low shade treatment did consistently better in all three measurements of performance (biomass, survivorship, and reproduction) than plants grown in the no shade control treatment, which closely resembled natural light conditions. Low shade probably decreased water loss from evaporation and evapotranspiration while the corresponding decrease in light did not significantly reduce plant performance. In contrast, plants in the high shade showed drastically reduced success compared with individuals in the full sun treatments as high shade conditions caused etiolation, poor survival (Fig. 1a), low flower output (Fig. 2a), and small biomass (Fig. 3a).

These results support our hypothesis that *C. pungens* var. *hartwegiana* is shade intolerant. Increased growth, survival and fecundity of plants in the manzanita, oak, pine, and redwood soils, indicates that they are restricted from these areas because they are unable to compete for light with robust, common species that naturally occur on these soils. This helps to explain the distribution of *C. pungens* var. *hartwegiana* in the sandhills communities of the Bonny Doon Ecological Reserve, where the taxon is restricted to otherwise unvegetated, pure sand soils.

**Management implications.** The combination of habitat specificity and narrow geographic range of *C. pungens* var. *hartwegiana* renders the species vulnerable to extinction from both habitat degradation and the encroachment of other more competitive species. Habitat destruction by sand quarrying and residential development have been considered the major threats to the persistence of populations. Our results indicate additional threats to species' survival even within protected areas. In particular, shade intolerance increases vulnerability to extinction due to chaparral community succession and the encroachment of alien species. The taxon's inability to compete for light could explain its restriction to monospecific stands or open areas where it grows in association with other diminutive annual plants such as *Navarretia hamata* E. Greene.

At the Bonny Doon Ecological Reserve, the distribution of *C. pungens* var. *hartwegiana* currently is limited to open, physically disturbed areas, such as trails and old roads, where chaparral species have not become established. Such open habitats are transitory and disappear in the absence of disturbance by fire, wind, or sand movement. Historically, the open areas of the sandhills were probably maintained by frequent fires (Potts 1993). However, fire suppression in the Santa Cruz Mountains may have allowed for the spread of chaparral species such as *Eriodictyon californicum* (Hook & Arn.) Torrey and *Arctostaphylos silvicola*, a sandhills specialist species, into formerly open, unshaded areas. Even in areas with partial shrub cover, *C. pungens* var. *hartwegiana* populations are generally sparse. We speculate that, in

the absence of fire or other physical disturbance, succession will result in widespread extirpation of *C. pungens* var. *hartwegiana*.

The invasion of alien weedy species poses a similar threat. These exotics not only create shade, but could also alter soil composition through nutrient addition (Vitousek 1990; Janzen 1986). Huenneke et al. (1990) found that increasing nutrient availability through fertilizing classically low-nutrient serpentinite soils resulted in increased biomass of the serpentinite endemic vegetation. By the second year, however, this addition of nutrients had allowed for the invasion and eventual dominance of non-native vegetation.

As native or exotic plants invade the pure sand areas of the sandhills, the deposition of nutrients can further facilitate the establishment of shade-producing species that were previously excluded due to low nutrient availability. The current invasion of smaller grasses (e.g., *Vulpia myuros* (L.) C. Gmelin) on the open sand areas of the Bonny Doon Ecological Reserve may not outcompete *C. pungens* var. *hartwegiana* for light; however, the cumulative alteration of the soil by this denser vegetation could facilitate the invasion of larger, shade-producing species such as *Genista monspessulana* (L.) L. Johnson. Encroachment by invasive species is especially threatening to the sandhills because of their small size and island-like geography. In particular, the large edge to area ratio of small habitat fragments increases their susceptibility to invasion by aggressive species in surrounding habitats (Schierenbeck 1995).

Given the shade intolerance of *C. pungens* var. *hartwegiana* and current threats of invasion, we suggest a management strategy aimed at the maintenance of unvegetated, open areas in the sandhills through controlled burning and intentional mechanical disturbance. Because little is known about the fire ecology of *C. pungens* var. *hartwegiana*, small scale field tests and seed viability analyses should be conducted prior to implementing controlled burn management. However, due to its close association with chaparral vegetation and the frequent fire history of the sandhills prior to suppression, it is likely that the taxon is fire tolerant.

Alternatively, a mechanical method of disturbance (e.g., bulldozing or hand clearing) could maintain open, unshaded areas required by *C. pungens* var. *hartwegiana*. Indeed, the largest populations of *C. pungens* var. *hartwegiana* currently at the Bonny Doon Ecological Reserve exist on old road cuts and human trails. However, disturbance is a double-edged sword, as it often allows for the invasion of weedy species (Parker et al. 1993; Schierenbeck 1995). Local invasive exotics such as *G. monspessulana*, and *V. myuros* are often found along the roads that border the reserve, apparently thriving because of disturbance. Future disturbance within the reserve could allow their spread into *C. pungens* var. *hartwegiana* habitat. To insure the vi-

ability of a disturbance-dependent plant, it is important to match the intensity and timing of novel disturbances with the natural disturbance regime to which the species is adapted (Pavlovik 1994). Therefore, we recommend further study on the responses of *C. pungens* var. *hartwegiana* to new disturbances prior to the widespread implementation of mechanical biomass removal or controlled burning.

In summary, the results of our study strongly suggest that a laissez faire approach to the conservation of the sandhills flora is not sufficient. Establishing reserves free of habitat conversion and destruction is the first step toward conservation of *C. pungens* var. *hartwegiana*. However, it is also essential to prevent the additional alterations in habitat caused by native chaparral succession in the absence of fire or alien species invasion from surrounding areas. Fortunately, the implementation of such management practices is feasible due to the small size of the sandhills habitats. Active conservation efforts aimed at controlling encroaching vegetation are likely to protect other similarly adapted endemics of the sandhills community in addition to preserving the remaining populations of *C. pungens* var. *hartwegiana*.

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