

Distribution of plant life history types in California chaparral: the role of topographically-determined drought severity

Meentemeyer, Ross K.^{1*} & Moody, Aaron²

¹Department of Geography, Sonoma State University, Rohnert Park, CA 94928-3609, USA;

²Department of Geography, University of North Carolina, Chapel Hill, NC 275993220, USA;

Fax +19199621537; E-mail aaronm@email.unc.edu;

*Corresponding author; Fax +17076643920; E-mail meenteme@sonoma.edu

Abstract. Spatial patterns of shrub life history and *Ceanothus* distribution are examined in relation to topographically-mediated differences in drought severity within 3 watersheds on the coastal and inland flank of the Santa Ynez Mountains, California. Spatially distributed fields of drought severity are simulated for the studied watersheds using high-resolution digital terrain data and daily climate data in combination with a process-based hydro-ecological model (RHESSys). Field samples of species composition are spatially integrated with the distributed drought data for analysis of ecological relationships. Patterns of seedling recruitment type correspond to topographic variability in drought severity in ways that are consistent with concepts presented in the literature. Species that depend on fire for recruitment are increasingly represented with increasing drought severity, the converse also applies. Sites that experience moderate drought severity permit co-dominance of species from both recruitment modes. Residual analysis suggests that some of the unexplained variability is related to substrate. Analyses also indicate that the distribution of 5 *Ceanothus* shrubs reflect differences in drought severity in ways that are consistent with their resistance to water stress-induced xylem dysfunction. Species from the subgenus *Cerastes* sort in accordance with moisture availability and have unique spatial distributions. Results are evaluated and discussed with respect to studies on plant morphology, resource use and seedling establishment patterns.

Keywords: *Ceanothus*; Digital terrain model; RHESSys; Soil water limitation; Topography.

Abbreviations: DEM = Digital Elevation Model; FOV = Field of View; MT-CLIM = Mountain Microclimate Simulator; RHESSys = Regional Hydro-Ecological Simulation System.

Nomenclature: Hickman (1993).

Introduction

Recurrent summer drought is a critical factor influencing patterns of plant resource use, productivity and seedling establishment in California chaparral and other mediterranean-type ecosystems (Miller 1981; Mooney 1989; Rundel 1995). The effects of drought may be particularly important in governing regeneration patterns in chaparral after fire because recently germinated seedlings with shallow root systems must endure 4 to 6 months of water stress during their first growth year (Kummerow et al. 1985; Frazer & Davis 1988; Thomas & Davis 1989). Under such conditions, seedling mortality will vary considerably between shrub species, depending on their drought tolerance and life-history strategies for reproduction (Keeley & Zedler 1978; Frazer & Davis 1988). While much data has been synthesized on the interrelationships between plant composition, physiology and life history in chaparral shrubs (e.g. Keeley 1986, 1998; Davis et al. 1998), little work has focused on whether spatial variability in soil-water availability during summer drought governs the actual spatial distribution of shrub composition in chaparral.

This study examines the degree to which topographically-regulated differences in drought severity are expressed in spatial patterns of chaparral shrub composition and evaluates whether these patterns correspond to accepted principles and ecophysiological data presented in the literature on chaparral shrub physiology. Spatially distributed fields of drought severity are simulated across 3 small watersheds in the Santa Ynez Mountains, California using high resolution (10 m) digital terrain data and daily climate data in combination with a process-based hydro-ecological model (RHESSys; Band et al. 1993). Field sampled species composition data are spatially integrated with the drought data for analysis of ecological relationships.

Patterns of life history mode are first examined in relation to topographic variation in drought severity. These patterns are based on aggregated canopy cover

percentage for all shrub and tree species within each life history mode. Keeley (1998) defines 2 life-history modes of seedling recruitment in California chaparral: *disturbance-dependent* species that limit recruitment to post-fire environments and *disturbance-free* species that recruit most effectively in the long-term absence of fire. Disturbance-dependent species establish seedlings from long-lived, fire-resistant seeds that are stored in the soil (Parker & Kelly 1989) until germination is cued by fire-related heat shock or chemical signals (Keeley 1987). Most shrubs that utilize this recruitment strategy, commonly called 'obligate seeders', cannot regenerate vegetatively from root crowns or lignotubers (Wells 1969). A few disturbance-dependent species, such as *Adenostoma fasciculatum* and *Ceanothus spinosus*, are referred to as 'facultative seeders' because they can establish seedlings from refractory seeds, as well as sprout vegetatively following fire. Disturbance-free shrubs (e.g. *Heteromeles arbutifolia*, *Quercus berberidifolia*, *Cercocarpus betuloides*), commonly called 'obligate resprouters', resprout aggressively after fire, but rarely establish seedlings the first year after fire. Population expansion is primarily accomplished by establishing seedlings from animal dispersed, non-refractory seeds germinating beneath mature canopies with relatively moist soils, low light and ample leaf litter (Keeley 1992a, b).

Disturbance-dependent recruitment relies on the abundance of light and nutrients in the post-fire environment (Wells 1969), but seedlings must withstand considerable water stress. Many disturbance-dependent species have physiological adaptations to offset drought stress such as sclerophyllous leaves with stomata that can continue carbon uptake at low water potentials (Miller & Poole 1979; Parsons et al. 1981; Schlesinger et al. 1982; Davis 1989). Disturbance-free shrubs, on the other hand, tend to have poorer stomatal control and productivity declines considerably with water stress (Poole et al. 1981; Mooney 1989). These relatively drought-sensitive shrubs generally avoid water stress by developing deep root systems that access underground moisture reserves during summer drought (Hellmers et al. 1955; Poole et al. 1981). Although this strategy increases the chances of survival for adult shrubs during drought, it does not help seedlings escape water stress (Kummerow et al. 1985; Frazer & Davis 1988). Based on these principles, Keeley (1986) hypothesized that patterns in regeneration mode correspond to differences in moisture availability (Fig. 1).

We test the hypothesis that the disturbance-dependent mode will be increasingly represented with increasing drought severity while the disturbance-free mode will be decreasingly represented with increasing drought severity. It is expected, however, that within recruit-

ment modes, significant variability will still exist due to differences in species' responses to drought stress. As such, we also examine the distribution of 5 disturbance-dependent shrub species within the genus *Ceanothus* in relation to topographically-mediated differences in drought severity. The analysis includes all the *Ceanothus* shrubs that occur in the study area, all of which have known physiological responses to water stress (Davis et al. 1999). The genus *Ceanothus* has experienced relatively recent speciation, with 2 subgenera having different mechanisms for regeneration and coping with drought stress (Wells 1969; Zedler 1995). The subgenus *Cerastes* does not resprout after fire and is better adapted to the relatively recent emergence of recurrent summer drought in southern California than the resprouting subgenus *Euceanothus* (Tables 1 and 2; Wells 1969; Axelrod 1989; Stine 1994; Zedler 1995). The physiological mechanism underlying differences in drought tolerance between *Ceanothus* species is believed to relate to the vulnerability of stem xylem to water stress-induced embolism (Kolb & Davis 1994; Jarbeau et al. 1995; Davis et al. 1998, 1999). Based on the differences in physiology and life history it is hypothesized that: (1) distribution of the 5 *Ceanothus* species reflect topographically-mediated differences in drought severity in ways that are consistent with their susceptibility to water stress-induced xylem dysfunction (Table 2) and (2) that subgenus *Cerastes* establishes in sites with greater drought severity than subgenus *Euceanothus*.

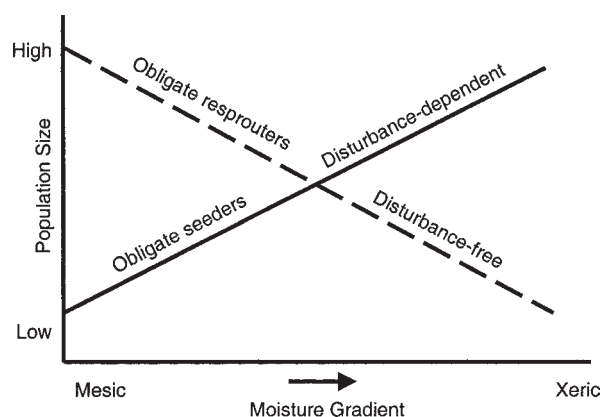


Fig. 1. Hypothesized abundance of species with disturbance-dependent (obligate and facultative seeders) and disturbance-free recruitment (obligate resprouters) modes in relation to soil moisture availability (based on Keeley 1986).

Table 1. Morphological and physiological characteristics of 2 *Ceanothus* subgenera (after Davis et al. 1999). ψ = water potential.

	Subgenera of <i>Ceanothus</i>		References
	<i>Cerastes</i>	<i>Euceanothus</i>	
Resprout after fire	No	Yes	Van Rensselaer & McMinn (1942); Wells (1969)
Maximum root depth(range, m)	Shallow 1.4 - 2.4	Deep 3.1 - 3.6	Hellmers et al. (1955); Thomas & Davis (1989)
Leaf specific mass(range, g m ⁻²)	High 280 - 317	Low 161 - 163	Cooper (1922); Barnes (1979)
Leaf thickness(range, μ m)	Thick 462 - 605	Thin 214 - 352	Cooper (1922); Barnes (1979)
Cuticle thickness(range, μ m)	Thick 3.3 - 7.0	Thin 1.1 - 2.2	Cooper (1922); Barnes (1979)
Stomatal crypts	Yes	No	Nobs (1963)
ψ at stomatal closure (range, MPa)	Low -4.5 - -5.5	High -2.0 - -3.0	Poole & Miller (1975); Miller & Poole (1979); Barnes (1979)

Study sites

The study sites are 2 small watersheds along the coastal flank of the Santa Ynez Mountains and one on the inland flank (Fig. 2). Located on the coastal side of the range Mission Canyon encompasses 8.2 km² and includes La Cumbre Peak (1215 m a.s.l.), the highest position along the Santa Ynez. The base and headwaters of Mission Canyon are located 6.6 and 9.4 km from the coast, respectively. Romero Canyon is a 7.1-km² watershed located 12 km east of Mission Canyon with a maximum elevation of 1067 m a.s.l. The base and headwaters of Romero Canyon are 4 and 6.5 km from the coast, respectively. The inland watershed, Devils Canyon (8.5 km²), is situated a few kilometers northeast of Mission Canyon with a generally north-facing position. Reduced exposure to the moist marine layer permits greater diurnal and seasonal variability in temperatures.

The watersheds are characterized by mediterranean-type climate conditions, with variable rainfall from late fall to mid-spring and extended drought from late spring

to mid-fall. Soil water is extremely limited during summer, with a pronounced impact on plant productivity (Schlesinger et al. 1982) and survival of shrub seedlings (Frazer & Davis 1988). Summer fog frequently forms along the coastal watersheds when moist marine air is trapped between the mountains and the prevalent summertime temperature inversion. The altitude of the inversion fluctuates (Bailey 1966), but typically occurs around 400 m a.s.l. (Miller et al. 1977; pers. comm. J. Michaelsen). Little is known about the direct impact of summer fog on soil moisture and plant function in chaparral (but see Oberlander 1953; Miller 1979; Campbell 1980).

The 3 study watersheds are composed primarily of shale and sandstone substrates that was formed from river and marine sediments of the upper Eocene and Oligocene epochs (Page et al. 1951). The landscape is extremely dissected with steep slopes and deep canyons. The major streams drain away from the ridge with tributary streams often tracking shales that are more prone to weathering and erosion than the sandstones (Page et al. 1951).

Table 2. Location and physiological response to water stress for species of *Cerastes* and *Euceanothus* subgenera. Physiological data are taken from Davis et al. (1999). ψ = water potential.

	<i>Cerastes</i>			<i>Euceanothus</i>	
	<i>C. megacarpus</i>	<i>C. crassifolius</i>	<i>C. cuneatus</i>	<i>C. spinosus</i>	<i>C. oliganthus</i>
Location	South Flank	Both flanks	North flank	South flank	Both flanks
Elevation range (m a.s.l.)	317-996	671-1157	490-671	292-935	491-1157
Mean (m)	649	890	607	588	858
Minimum seasonal ψ (MPa)	- 8.4	- 6.0	- 7.3	- 6.2	- 4.3
ψ (MPa) @ 100% embolism	- 13.8	- 11.6	- 12.9	- 9.2	- 8.2
ψ (MPa) @ 50% embolism	- 11.0	- 7.3	- 9.5	- 7.2	- 6.2
Specific conductivity \leftrightarrow 10 ⁻⁷ (m ² MPa ⁻¹ s ⁻¹)	1.06	1.48	1.34	1.52	1.64

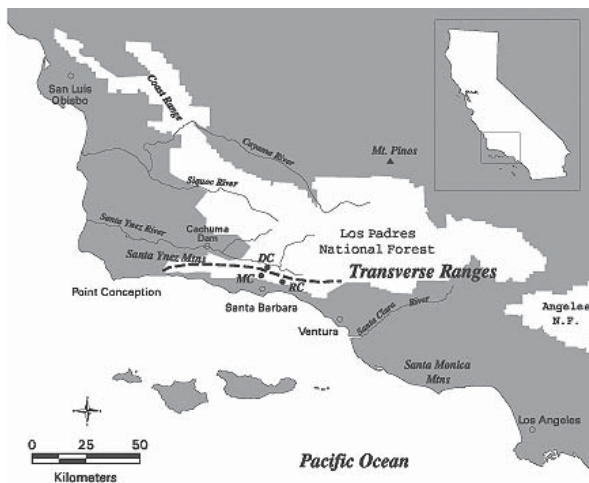


Fig. 2. The study region. Mission Canyon (MC) and Romero Canyon (RC) watersheds are located on the southern flank of the Santa Ynez Mountains, California. Devils Canyon (DC) is located on the northern flank. The dashed line represents the main ridge of the Santa Ynez Range.

Vegetation within the study sites is primarily drought-tolerant, evergreen sclerophyllous shrubs and trees known as chaparral (Keeley 2000). On the coastal side, xeric, rocky sites at low to mid-elevations often support herbaceous species and drought-deciduous subshrubs from the coastal sage scrub community (e.g. *Salvia mellifera*, *Artemisia californica*, *Eriogonum fasciculatum*) (Smith 1998). With increasing elevation, shrubs such as *Ceanothus megacarpus*, *C. spinosus* and *Adenostoma fasciculatum* start to dominate exposed, south-facing slopes (Schlesinger et al. 1982). Topographically sheltered slopes often support deep rooted, broad-leaved shrubs (e.g. *Heteromeles arbutifolia*, *Cercocarpus betuloides*) and trees (e.g. *Umbellularia californica*, *Quercus agrifolia*) with less drought adapted features (Campbell 1980). A higher elevation community is characterized by *Arctostaphylos* spp., *C. crassifolius* and shrub forms of *Quercus* spp. (Smith 1998). At the highest elevations small stands of conifers, such as *Pinus coulteri* and *Pseudotsuga macrocarpa*, are scattered with understorey shrubs.

Most species from the coastal watersheds also occur in the north-facing inland watershed, with the emergence of a few additional species (e.g. *C. cuneatus*) and absence of others (e.g. *C. megacarpus* and *Malosma laurina*). High elevation, sheltered slopes support a diversity of shrubs (e.g. *C. oliganthus*, *Garrya veatchii*, *Rhus ovata*, *Prunus ilicifolia*, *Heteromeles arbutifolia*, *Quercus* spp.) and occasional trees (e.g. *Arbutus menziesii*, *Lithocarpus densiflora*). Less sheltered slopes and ridges, across the entire elevation range, tend to be dominated by shrubs, such as *C. crassifolius*, *A. fasciculatum* and *Arctostaphylos* spp.

Methods

Field sampling

Closed-canopy chaparral develops a heavy thicket of understorey biomass on steep, and often loose terrain. These conditions impede field access and prevent collection of numerous vegetation samples. Moreover, many studies have required the use of small plots (e.g. 100 m²) with inter- and intra-plot variability that may respond to processes operating at a finer scale than our focus. To reduce the cost of data collection and obtain many, well-distributed samples, shrub composition was sampled at a hierarchy of spatial units using a high-powered telescope from remote viewing locations in the field. This method has been used in Moody & Meentemeyer (2001) and evaluated for assessing landscape-scale patterns of shrub composition in Meentemeyer & Moody (2000). In chaparral, the closed, single-layer canopy typically precludes understorey plants (Christensen & Muller 1975), thus limiting underestimation of plants beneath the canopy.

The sampling strategy was organized around a spatial unit referred to as a *patch*, a stand of vegetation composed of homogeneous shrubs, and total cover. Candidate patches, defined in the field, were distributed to represent the range of elevations, aspects and slope positions within the 3 watersheds. Patch boundaries were delineated where transitions occurred either in shrub composition or in the relative abundance of dominant species. The following criteria, although not strictly quantified, were used as guidelines to help maintain consistent patch identification. Patches composed of a single species with > 60% relative cover were considered dominant species patches. In these cases, a patch boundary was mapped if a change in the dominant species occurred or if there was a transition to a mixed shrub composition. Patch boundaries were also identified within a continuum of mixed species composition where the cover of any shrub or tree species changed by 20% or more. Finally, boundaries were mapped where absolute cover changed by 20% or more. A minimum patch size of 0.25 ha was used to filter out fine scale floristic variability and to avoid sampling within the range of patch sizes in which species richness is dependent upon area (Greig-Smith 1983). A maximum size threshold was not set. Patches ranged in size from 0.25 ha to 7.9 ha.

A candidate patch was only chosen for sampling if it could be reliably mapped on the high resolution terrain model and it fulfilled the following criteria. First, patches had to be viewable at an angle greater than 45° between the line of sight and the terrain, where 90° is a perpendicular view angle. Second, patches were required to be

within 300 m of the remote viewing location and more than 10 m from a dirt road or trail. Analyses of Meentemeyer & Moody (2000) indicate that the internal floristic and environmental variability of patches is low and stable across the sample of patches.

Within each patch, several *sites* were randomly located from a regular array of grid points distributed at 20-m intervals. A zoom telescope (15× to 45×) was used to sample the cover percentage of shrub and tree species for each site from a remote viewing location. Composition for a site was determined by aggregating species composition within 3 to 4 telescope fields of view (FOV) that are clustered around the site. This process was repeated for each site within a patch. FOVs were constrained to approximately 100 m². Locating and sizing FOVs was accomplished by navigating on a high resolution terrain model overlaid with a 20 m grid in conjunction with clinometer and compass measurements.

For each FOV the following data were collected; (1) species present; (2) percentage cover of each species; (3) percentage cover of exposed bedrock and (4) total canopy cover. These data were aggregated from the FOV to the site level, and site-level data were aggregated to provide shrub composition for each patch. The patches were mapped onto the digital elevation model used to derive landscape-level variability in drought severity. A total of 296 patches were used for this study after removing samples from riparian zones and high elevation conifer woodland and 37 chaparral and coastal sage scrub species were catalogued. From these samples, within-patch measures of canopy cover percentage were derived for each seedling recruitment mode (disturbance-dependent and disturbance-free).

Species identification was based on leaf and bark colour; shrub form and stature; leaf shape, size and orientation and bud, flower and new growth characteristics. The accuracy of species identification was tested for a set of 15 FOV by comparing *in situ* identification with concurrent remote identification. All shrub species that were included in the *in situ* list were also included in the remote interpreter's list. A 90% accuracy of individual plant identification was achieved (Meentemeyer & Moody 2000).

Deriving topographic variability in drought severity

The Regional Hydro-Ecological Simulation System (RHESSys; Band et al. 1993) was used to model spatially distributed fields of plant water stress within the studied watersheds. RHESSys is a GIS-based modelling framework that unites 3 separate physically-based models with a landscape stratification approach in order to simulate water, carbon and nutrient fluxes across watersheds at a daily time step over multi-year intervals (Fig. 3). The

first model, MT-CLIM (Mountain Microclimate Simulator; Running et al. 1987), utilizes a digital elevation model (DEM) and daily climate-station data to spatially extrapolate solar radiation, minimum and maximum air temperature and precipitation across a watershed. Using the output from MT-CLIM, a plant canopy process model (BIOME-BGC, Running & Coughlan 1988; Running & Hunt 1993) is linked with a spatially distributed hydrologic model, adapted from Wigmosta et al. (1994), to derive saturated subsurface throughflow and overland flow. RHESSys has been applied in studies on forest productivity dynamics (Mackay & Band 1997), climate change effects (Band et al. 1996), nitrogen leaching (Creed et al. 1996), land cover change (Baron et al. 1998) and forest harvesting (Tague 2000). In this application of RHESSys, we extracted spatially distributed fields of daily leaf water potential (MPa) over the drought period 1986-90. These data were used to derive a drought stress index described below.

Daily climate data from Cachuma Dam (34.58° N, 119.98° W) and Santa Barbara (34.43° N, 119.83° W) were used (via MT-CLIM) to extrapolate daily precipitation and minimum/maximum air temperature across the coastal and inland watersheds, respectively. Elevation lapse rates were derived for each variable from mesoscale fields (850m grid resolution) of mean monthly air temperature and annual precipitation, provided by J. Michaelsen (unpubl.). For each variable, resulting mean lapse rates were calculated across the 3 watersheds, yielding an air temperature lapse rate of -3.9 °C/1000m and a precipitation lapse rate of 285

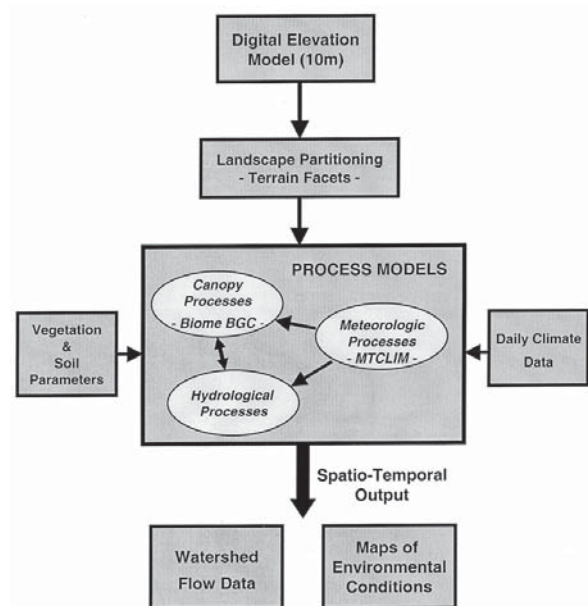


Fig. 3. Overview of RHESSys, the Regional Hydro-ecological Simulation System (Band et al. 1993; Tague et al. 1998).

mm/1000m (Meentemeyer & Moody 2000). Air temperature lapse rates for the coastal side watersheds were modified over the dry season (May-Oct) to account for the frequent temperature inversions that form from sea level to elevations of ca. 300-450 m a.s.l. (pers. comm. J. Michaelsen; Miller et al. 1977). Air temperatures were extrapolated across the watersheds such that maximum air temperatures below 400 m increase with elevation at a rate of 15 °C/1000m (Miller et al. 1977), but then decrease with elevation at the derived rate of 3.9 °C/1000m above 400 m. The precipitation lapse rate was used for all watersheds over the entire year.

RHESSys can be run by specifying vegetation (e.g. leaf area index) and soil (e.g. hydraulic conductivity) characteristics that are allowed to vary spatially. In this study, the model was parameterized using uniform soil characteristics because soil data are not available at a sufficient resolution for modelling topographic variations in soil water. Uniform vegetation is also assumed for simplification. Vegetation parameters, such as leaf conductance and rooting depth, were specified based on species-level characteristics from physiological studies in Miller (1981). The model was calibrated for a sub-catchment of Mission Canyon by iteratively varying saturated hydraulic conductivity and its decay with soil depth until monthly transpiration rates corresponded with observations in Miller (1981) ± 0.2 mm.

The years 1986-1987 to 1989-1990 had unusually low precipitation. Records from the Santa Barbara Botanical Gardens (244 m a.s.l.) at the base of the Mission Canyon watershed show that precipitation was only 12.71 cm per year over these drought years, whereas the climatological mean (1961-1991) at this station was 22.91 cm. The potential drought stress index was calculated, using the leaf water potential output from RHESSys, by summing the number of days over the 4 year drought period, when leaf water potential dropped below -5 MPa. Since uniform vegetation parameters had to be used, the -5 MPa threshold was selected based on the mean water potential at which stomatal closure occurs among several common shrubs (*Adenostoma fasciculatum*, *Arctostaphylos glauca*, *Artemisia californica*, *Quercus berberidifolia*, *Rhus ovata*, *Ceanothus greggii*) (Miller 1981). Although *C. greggii* does not occur in the Santa Ynez Mountains, it was included in order to represent a *Ceanothus* species. Fig. 4 illustrates the spatial distribution of drought severity (days) across the Mission Canyon watershed. A more detailed description of our application of RHESSys in vegetation modelling is described in Meentemeyer et al. (2001).

Analysis

Life history

Polynomial regression was used to test the hypothesis that the disturbance-dependent recruitment mode is increasingly represented (canopy cover %) with increasing drought severity and disturbance-free recruitment is decreasingly represented with drought severity. Substrate characteristics were not accounted for in the RHESSys-derived estimates. However, substrate may explain some of the variability not accounted for by the combined effects of rainfall, temperature and solar radiation on drought severity. Using Student's *t*-tests, residuals from the polynomial regression models were examined in relation to field samples of substrate rockiness (rocky versus not rocky) to determine if either mode is over- or under-estimated at rocky sites.



Fig. 4. Spatial distribution of drought severity (days of water stress 1987-1990) in Mission Canyon as derived by RHESSys. Disturbance-free species dominate mesic shaded slopes (A), ephemeral drainages (B), and moderately sheltered, high elevation slopes (C). Disturbance-dependent species dominate exposed slopes at low to mid-elevations (D) and ridges (E). Mixed stands form on exposed high elevation slopes (F).

Ceanothus

Based on species presence, a Student's *t*-test was used to determine whether subgenus *Cerastes* establishes in sites with greater drought severity than subgenus *Euceanothus*. One-way ANOVA was used to test whether the 5 species are differentially distributed with respect to drought severity. Multiple comparisons were subsequently used to test hypothesized species-specific differences in the effect of drought severity. We used the Bonferroni multiple comparison procedure with a correction factor of α/k (0.05/10, where 10 = number of tests) to protect against falsely identifying differences where no differences exist. In this way we ensure a critical value of 0.05. To determine whether xylem resistance is manifested in species distribution, we calculated the correlation between shrub water potential at xylem embolism (Davis et al. 1999) (Table 2) and the median drought severity associated with each shrub species.

Results

Life-history patterns

Within the range of drought conditions considered, the disturbance-dependent mode exponentially increases in abundance with increasing drought severity (Fig. 5). Conversely, the disturbance-free mode exponentially decreases in abundance with increasing drought severity. *T*-tests indicate that the disturbance-dependent mode is under-estimated at rocky sites (mean residual = -10% cover; $P < 0.001$ whereas the disturbance-free mode is over-estimated (mean residual = 11% cover; $P < 0.001$).

Ceanothus

ANOVA indicates that the 5 disturbance-dependent *Ceanothus* species are differentially distributed along the drought severity gradient ($F = 62.8$; $P < 0.001$; Fig. 6). *C. megacarpus* tends to occupy sites with the greatest drought severity, followed by *C. cuneatus*, *C. spinosus*, *C. crassifolius* and *C. oliganthus* (Table 3). The multiple comparison tests of drought severity dif-

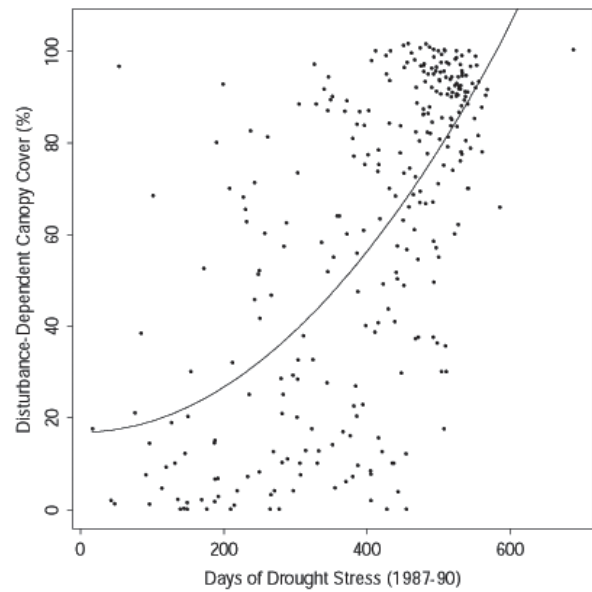


Fig. 5. Relationship between drought severity and canopy cover percentage of all shrub species with the disturbance-dependent recruitment mode. Data were fitted using polynomial regression: $y = 16.86 + 0.0002x^2$ ($r^2 = 0.45$; $P < 0.001$). Disturbance-dependent species in the study area include (classified based on Keeley 1991, 1998):

Adenostoma fasciculatum, *Arctostaphylos glandulosa*, *A. glauca*, *Ceanothus crassifolius*, *C. cuneatus*, *C. megacarpus*, *C. oliganthus*, *C. spinosus*, *Dendromecon rigida*, *Yucca whipplei*, *Artemisia californica*, *Erodium crassifolium*, *Eriogonum fasciculatum*, *Eriophyllum confertiflorum*, *Mimulus longiflorus*, *Ribes californicum*, *Salvia apiana*, *S. mellifera*.

Disturbance-free species include:

Arbutus menziesii, *Cercocarpus betuloides*, *Fraxinus dipetala*, *Garrya veatchii*, *Heteromeles arbutifolia*, *Lithocarpus densiflora*, *Malosma laurina*, *Prunus ilicifolia*, *Quercus agrifolia*, *Q. berberidifolia*, *Q. chrysolepis*, *Q. wislizenii*, *Rhamnus californica*, *R. ilicifolia*, *Rhus ovata*, *Toxicodendron diversilobum*, *Umbellularia californica*.

ferences between the sites occupied by each species are generally consistent with measures of water stress vulnerability (Table 2). However, *C. megacarpus* occurs at sites with statistically similar drought severity as *C. cuneatus* while *C. crassifolius* occurs at sites with similar drought severity as *C. spinosus* ($\alpha = 0.05$; Table 3). When the species are considered by subgenus, *T*-tests

Table 3. Summary of Bonferroni multiple comparison tests and drought conditions associated with *Ceanothus* shrub occurrences. Marks (<) indicate shrubs that occur at places with less drought days than the respective species in the previous column ($\alpha = 0.05$).

Species	Abbrev.	n	Number of drought days			Cm	Multiple comparison tests			
			Median	Mean	S ²		Ceu	Ccr	Cs	Co
<i>Ceanothus megacarpus</i>	Cm	135	500	515	5470	-	<	<	<	
<i>C. cuneatus</i>	Ccu	12	488	489	628	-	<	<	<	
<i>C. crassifolius</i>	Ccr	95	435	446	5171	-	<	<	<	
<i>C. spinosus</i>	Cs	103	447	452	16247	-	-	-	<	
<i>C. oliganthus</i>	Co	69	352	352	14750	-	-	-	-	

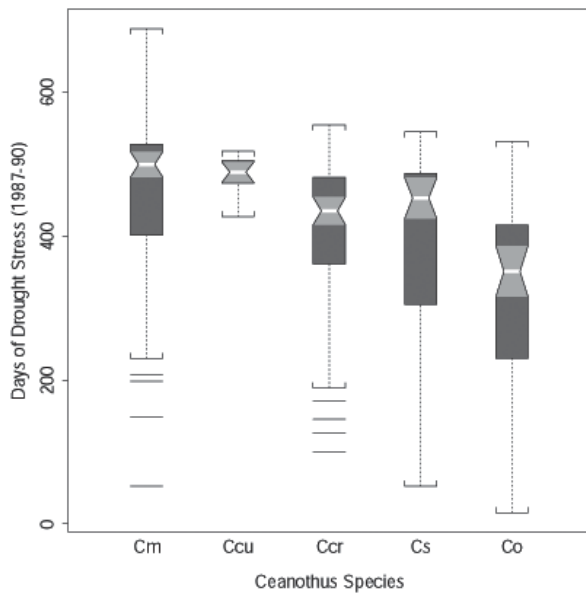


Fig. 6. Boxplots showing differences in drought severity at sites with established *Ceanothus* species. Cm, Ccu and Ccr belong to subgenus *Cerastes* and Cs and Co of subgenus *Euceanothus*. The upper and lower boundaries of each box represent the interquartile distance (IQD). The horizontal mid-line is the median value. The whiskers extend to $\pm 1.5 \times$ IQD. Outliers are illustrated as horizontal lines beyond the range of whiskers. If the notches of any two boxes do not overlap vertically, this suggests a significant difference at ca. 5% confidence interval. Species abbreviations as Table 3.

show that subgenus *Cerastes* is distributed at sites with significantly greater drought severity than *Euceanothus* ($P < 0.001$). Shrub water potential at 100% xylem embolism (Davis et al. 1999; Table 2) is correlated with the median drought severity associated with each species' distribution ($r = 0.88$; $P < 0.05$). That is, species with lower water potential at 100% xylem embolism occur at sites with greater drought severity.

Discussion

Life-history patterns

Spatial patterns of life history mode are related to the spatial distribution of potential drought severity. The results suggest with increasing drought severity, site suitability for disturbance-free recruitment decreases while the suitability for disturbance-dependent recruitment increases. Sites that experience moderate drought severity permit co-dominance of the 2 modes. These results are consistent with Keeley's (1986) hypothesis that spatial patterns of regeneration mode correspond to

variations in soil moisture (Fig. 1).

In this environment, landscape patterns of regeneration mode are primarily governed by topographically mediated soil water limitation. Disturbance-free species establish across the range of elevations but dominate (> 65% cover) on mesic shaded slopes, ephemeral drainages and some moderately exposed slopes at high elevations where rainfall is relatively high and temperatures are lower (Fig. 4: A, B, C). The median drought length is 282 days at sites dominated by disturbance-free species. These patterns are consistent with studies showing that most broad-leaved, disturbance-free shrubs (e.g. *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus* spp.) are sensitive to water stress at low leaf water potentials (Miller 1981; Jarbeau et al. 1995) require moist soils for seed germination (Keeley 1991) and are shade tolerant (e.g. photosynthesis of *H. arbutifolia* is saturated at less than 1/3 full sunlight) (Mooney et al. 1975).

In contrast, most disturbance-dependent shrubs are drought tolerant (Miller 1981; Kolb & Davis 1994; Davis et al. 1999), have seeds that can withstand hot, dry soil conditions (Keeley 1991) and are shade intolerant (Miller 1981; Mahall & Schlesinger 1982). We find that these ecophysiological factors are also expressed at the landscape scale. The disturbance-dependent mode, for example, dominates (> 65% cover) on hot, exposed slopes at low to mid-elevations and sharp ridges with little upslope contributing area (Fig. 4: D, E) (median drought length = 493 days). At sites with low drought severity (i.e. < 100 drought days) the disturbance-dependent mode is rare or absent.

The occurrence of mixed stands (both regeneration modes) at intermediate levels of drought severity (median = 414 days) suggests that compositional patterns of recruitment type vary along a continuum of topographic differences in soil water availability. Stands that are evenly mixed with both recruitment types tend to form on moderately sheltered slopes, particularly at high elevations (Fig. 4: F). Greater shrub-species richness also occurs in these environments due to species overlap at upper elevations where numerous species occur (e.g. *Quercus* spp.), but few species that are common at low elevations drop out (e.g. *Ceanothus megacarpus*; Moody & Meentemeyer 2001). Davis (1989) suggests that unequal rooting depth and differential water use in mixed stands contribute to the sharing of soil water resources and the maintenance of species diversity in chaparral systems.

While it appears that recruitment strategy (and thus composition) is related to drought stress, considerable variability remains unexplained by the regression model of disturbance-dependent canopy cover on drought severity (Fig. 5). This variability is partially explained

by substrate characteristics, perhaps due to the influence of rockiness on seedling establishment (Keeley 1991; Zedler 1995). The finding that under estimation of the disturbance-dependent and over estimation of the disturbance-free mode occurs at rocky sites suggests that rocky soils hinder the establishment of disturbance-free species, but allow the establishment of certain disturbance-dependent species. Drought-sensitive, disturbance-free shrubs require well-developed, moist soils for seed germination (Keeley 1991) and maintenance of deep roots (Miller & Poole 1979). Conversely, disturbance-dependent shrubs readily establish on most substrates and plant function is not impeded by shallow soils (Miller 1981; Keeley 1986). In the Santa Ynez Mountains, disturbance-dependent shrubs, such as *Adenostoma fasciculatum* and *Arctostaphylos glauca* commonly occur at rocky sites (Meentemeyer et al. 2001; Schlesinger et al. 1982).

Another factor that may contribute to unexplained variability in the regression models is that each recruitment mode consists of a diversity of species with varying responses to drought and, in some cases, are not typical of their respective mode. For example, most disturbance-dependent shrubs, such as *Ceanothus megacarpus* and *C. crassifolius*, tend to increase in abundance at drier sites. However, the disturbance-dependent mode also includes some shrubs (e.g. *C. spinosus*, *C. oliganthus*) that decrease abundance at drier sites (Meentemeyer & Moody 2001). Fig. 5 illustrates distinct clustering of stands that are dominated by disturbance-dependent shrubs at sites with high potential drought stress. Many of these stands are dominated by *C. megacarpus* on hot, exposed slopes and ridges at low to mid-elevations in the 2 coastal watersheds. Disturbance-free shrubs, such as *Heteromeles arbutifolia*, *Prunus ilicifolia* and *Cercocarpus betuloides*, are often scattered in these stands, probably at rare micro-sites suitable for both seedling survival and establishment of deep roots (Keeley 2000).

It is often suggested that obligate seeding shrubs are better adapted to persistent summer drought than facultative seeders (Wells 1969; Zedler 1995; Keeley 1998; Davis et al. 1998, 1999). However, we found no significant differences in drought severity between sites dominated by the obligate seeding and facultative seeding modes (unpubl.). Facultative seeders, such as *Adenostoma fasciculatum* and *Arctostaphylos glandulosa*, often dominate on rocky ridges with high drought severity. Although facultative seeders are generally not as physiologically tolerant to water stress as obligate seeders (Davis et al. 1998), they have the advantage of utilizing 2 mechanisms for post-fire regeneration, one that facilitates population expansion (seedlings) and the other for maintaining an established

position (resprouts). This dual strategy, in combination with relatively high drought tolerance and relatively deep root systems, may help *A. fasciculatum* and *A. glandulosa* seedlings survive drought stress at sites with little soil and enable adults to tap into deeply stored water in the fissures and cavities of weathered bedrock.

Ceanothus distribution

As hypothesized, significant variability exists within recruitment modes due to differences in species' responses to drought stress. Relative to subgenus *Euceanothus*, species of subgenus *Cerastes* typically have shallower root systems, greater leaf mass, greater leaf and cuticle thickness, leaves with encrypted stomata, and are capable of carbon uptake at lower water potentials (Cooper 1922; Hellmers et al. 1955; Miller & Poole 1979; Thomas & Davis 1989) (Table 1). We also found that these physiological differences translate to landscape-scale spatial distribution of these subgenera, where *Cerastes* is distributed at sites with greater drought severity than *Euceanothus*.

Of the *Ceanothus* species considered, *C. megacarpus* has the greatest resistance to water stress-induced xylem dysfunction, followed by *C. cuneatus*, *C. crassifolius* and then the 2 *Euceanothus* shrubs, *C. spinosus* and *C. oliganthus* (Davis et al. 1999; Table 2). Within the studied watersheds, distribution of these species along topographically driven gradients in drought severity correspond to the drought tolerance data reported by Davis et al. (1999). The impact of plant vulnerability to xylem dysfunction has also been illustrated in other water-limited systems. Kolb & Sperry (1999), for example, find that three subspecies of *Artemisia tridentata* sort along a moisture gradient in accordance with their ability to resist water stress-caused xylem cavitation.

Given sufficient light and substrate, soil moisture limitation appears to be a critical factor governing landscape patterns of species distribution in chaparral. The significant correlation between shrub water potential at xylem embolism and the median drought severity associated with the distribution of each shrub illustrates the degree to which species-specific differences in drought tolerance are expressed in the spatial distribution of *Ceanothus* species. Although numerous samples were used, this result is based on only 5 species. As drought tolerance measures are estimated for additional species, it will be possible to determine whether our results extrapolate across larger taxonomic assemblages and broader geographic ranges. Development of empirical relationships between species distribution and drought severity, such as presented here, may also

provide a method for deriving indices of drought tolerance for species with unknown physiological responses to water stress.

Soil water is generally thought to be one of the most important limiting resources for chaparral shrubs, especially during extreme drought. The results of this study indicate that shrub composition patterns in chaparral are strongly related to topographic differences in drought severity. These results are evident at the species level, and also generalize to life history strategies for regeneration. The observed patterns complement current concepts regarding the interrelationships between chaparral regeneration, physiology and evolution (e.g. Keeley 1986, 1998; Davis et al. 1998) and suggest that the mechanisms for regeneration and drought resistance, known to govern the functioning of individual plants, also function at the landscape scale.

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