The rare and newly described Gabilan manzanita (*Arctostaphylos gavilanensis*) in its habitat at the headwaters of Pescadero Creek in the Gabilan Mountains of Monterey County. All photographs by the author.

DIVERSITY AND EVOLUTION OF *ARCTOSTAPHYLOS* AND *CEANOTHUS*

by V. Thomas Parker

Few genera evoke an image of chaparral more than *Arctostaphylos* (manzanitas), *Ceanothus* (California lilacs) or *Adenostoma* (chamise). *Adenostoma* contains only two species, one of which is quite common and widespread. This scarcity of species contrasts to the large number of endemic and widespread species characterizing the other two genera. *Arctostaphylos* and *Ceanothus* both have a center of diversity in California, especially along the central coast. In California, *Arctostaphylos* and *Ceanothus* together are represented by more than 150 taxa!

These are large numbers for woody plants in such a small spatial area. Many of these species are quite rare and can be found on CNPS rare plant lists. Why are so many of these plants difficult to distinguish from one another, and how did California end up with so many of them? Be careful asking those kinds of questions. I've been working with Mike Vasey of San Francisco State Univeristy, on *Arctostaphylos* for nearly the past 20 years, and more recently with Jon Keeley of the U.S. Geological Survey, trying to understand the evolution of these plants. What a wonderful group.

Arctostaphylos evolved at least as far back as the Miocene, 15 million years ago, which corresponded to a time of global warming, while *Ceanothus* is thought to be an even older genus. Yet relatively few taxa are found in the fossil floras for most of their history. Only during the last 1.5 million years have large numbers of new fossil types rapidly appeared. Currently we have some 95 species and subspecies of *Arctostaphylos* within the political boundaries of California, and 104 of the world's 105 species and subspecies have some or all of their distribution within the California Floristic

Province that includes parts of Oregon and Baja California, Mexico. *Ceanothus* is not much different with about 75% of the 76 known species or varieties found in the California Floristic Province. Not only do these two genera have a lot of species, they also are peculiarly Californian.

The increase in the diversity of species in these two genera started about 1.5 million years ago, and is thought to have been a response to changes in the physical structure of California's geography, and a significant shift in climates. Tectonic changes were one important aspect, as the whole region was folded, faulted, elevated, and dissected at about the time the burst of diversity began. Such changes opened up new soil types, depths, and levels of development, produced windward slopes and rain shadows, and variously created a diversity of ecological opportunities that selected for new species. Our summer-dry Mediterranean climate developed and spread during the same general time period. Lack of summer rain forced the extinction of numerous plant groups that were unable to adapt and subsequently were eliminated from the region. However, their loss provided yet more opportunities for chaparral species like manzanitas to spread into new areas.

PECULIAR RELATIONSHIP TO FIRE: DIFFERENT LIFE HISTORIES

The abundance of taxa in *Arctostaphylos* and *Ceanothus* result not only from California's marked topography, edaphic (soil) diversity, and the shift to a drier climatic, but also from wildfire, a process that arises more frequently under those conditions. The species richness reflects more than the physical environmental diversity and dry climate; it also reflects a mutual interrelationship between fire and plant life history characteristics.

Arctostaphylos and *Ceanothus,* along with *Adenostoma,* have strongly persistent seed banks that are fire stimulated. Seeds that are not consumed by animals are slowly incorporated into the soil, where they remain until a wildfire occurs. Other woody shrub genera in California either lack these types of seed banks, or only a small fraction of their seeds may remain dormant. Persistent seed banks compress the recruitment process, the germination of seeds and the establishment of new individuals, to a single year after each fire, regardless of the interval between fires. This is an important process we will come back to later.

Additionally, a characteristic that distinguishes *Arctostaphylos* and *Ceanothus* from all other shrub genera in chaparral is that they contain species with different life histories. One group of species has burls or root crowns with dormant buds that permit resprouting of the plants after wildfire. These individuals usually survive a large number of fires, and indeed, unless shaded out by larger plants, may persist indefinitely.

A second, larger group of species in these genera is killed by fire. Their populations are completely dependent on the germination and establishment of new individuals arising from the soil seed banks. They have been termed "obligate seeders" as a consequence. This life history style may seem risky, and it is, but the benefits appear to be rapid and successful growth in chaparral and the ability to adapt to changing conditions. Almost 40 years ago, Phil Wells, at the University of Kansas, pointed out that not only do *Ceanothus* and *Arctostaphylos* have a peculiarly large number of taxa compared to other chaparral genera, but that diversity is concentrated in those taxa killed by fire, the obligate seeders. Researchers ever since have accepted that this life history style contributes to more rapid rates of speciation. Other plants associated with chaparral may also display an obligate seeding lifestyle, as for example the closed-cone species in *Pinus* and *Cupressus*. Other Mediterranean-climate regions show similar patterns, with a few genera developing obligate seeding life histories and becoming more species rich compared to other groups.

The characteristic rich red-brown smooth bark on the twisted branches of the common manzanita (*Arctostaphylos manzanita*) in a Sonoma County woodland edge.

RECENT HISTORY

The high diversity of these two genera emphasize the importance of the origin of a summer-dry Mediterranean-climate, the incredible topographic, edaphic, and climatic diversification of

California, and the development of both sprouting and obligate seeding life histories in the context of frequent fire. Of course, there is even more to the story of this rapid radiation of species. Glacial periods have also occurred during the last two million years or more, and have significantly impacted the distribution of plants. Glacial advances and retreats force the shifting of plant distributions. The last glacial period finally retreated a little over 10,000 years ago. During the time since the last ice age, climates have not been stable, with a particularly dry and warm period occurring from about 4,000-8,000 years ago. Chaparral expanded north into the Columbia River Basin, followed by a retreat back into California when the climates moderated again.

These climatic fluctuations stimulated migration of populations adapted to narrow climatic conditions and brought into contact populations that formerly were geographically quite separate. During such times of rapid change, not only are populations rapidly advancing to follow climatic shifts, but they also leave behind relict populations—remnants of formerly widespread species that persist in relatively isolated areas. Hybridization becomes possible between formerly separated populations as their migrants and relicts overlap, and new genetic recombinants may have a better set of adaptations to shifting local conditions than their progenitors. This is especially possible for the obligate seeders of *Arctostaphylos* and *Ceanothus*. Hybridization appears to be quite easy among a number of the species in these genera; geographic separation is the current primary reproductive barrier. The advantage to obligate seeders is that fire eliminates all the adults and permits selection among those new, and genetically diverse, seedlings arising from the seed bank. If there were new recombinants with better adaptations, models indicate that it would take only a little over 20 fire cycles for a completely new species of hybrid origin to take over a habitat. Importantly, the original adults, killed by the wildfire, are not around to genetically swamp out these new recombinants. That is presumably a principal reason obligate seeding genera are so species rich worldwide.

Consider the San Francisco Bay Area as an example. The Bay Area was a forested river valley during the last glacial period. As glaciers retreated, climates rapidly shifted to moderate conditions, followed by a rapid shift to much drier and warmer conditions that lasted until around 4,000 years ago, then changed to conditions similar to those of today. Species of *Arctostaphylos* and *Ceanothus* were especially favored during that dry and warm period as forests and woodlands retreated to wetter sites and fires swept the tree communities. Today relict stands of forest, woodland, and savanna within broad tracts of chaparral attest to the spread of chaparral.

Currently, the region from San Francisco Bay to Monterey contains 42 species or subspecies of *Arctostaphylos*, 32 of which are narrow endemics to sites that were probably forested only 10,000 to 20,000 years ago. Almost all the narrow endemics are obligate seeders. *Ceanothus* exhibits a similar pattern in the same region, although it is not as species rich. These narrow endemic species, the rare species, are important to consider. Influential botanist, geneticist, and evolutionary biologist, G. Ledyard Stebbins, and others, have estimated that the maximum age for many of these narrowly endemic species is only 10,000 to 20,000 years. Hybridization and recombination under intense ecological selection could account for this rapid radiation; in fact, these are just about the only set of processes that could account for that speed of adaptation. Having such a recent origin, one can imagine that many of these species may have only slightly changed in morphology from their predecessors, making them difficult to identify.

Overall post-glacial distributions of a number of narrow endemics suggest that their origins are based on two different paths of evolution. One origin is relict populations that have been left behind as populations moved north after the retreat of glaciers, and subsequently have been ecologically selected to local conditions. *Arctostaphylos columbiana* may fit this model, widespread to the north with morphologically similar narrow endemics to the south, such as Marin manzanita (*A. virgata*), found only in the foggy areas of Marin County, and *A. montereyensis* found at Fort Ord and nearby areas of Montery County.

The second potential origin is from hybridization between more rapidly migrating species moving north as they encounter lagging or relict populations of other species. Hybridization under these circumstances might result in recombination and the development of a new species. *Arctostaphylos canescens* seems to provide a number of examples as a potential parent to species of possible hybrid origin. For example, *A. luciana* near San Luis Obispo, *A. auriculata* on Mt. Diablo, *A. glutinosa* in the southern Santa Cruz Mountains, and *A. malloryi* on volcanics north of the Bay Area all seem to share an unusually large number of features with *A. canescens*. At the same time, other characters indicate the influence of other evolutionary lineages, such as the arrowhead-shaped auriculate leaves found in *A. auriculata*, *A. luciana*, and *A. glutinosa*. Similarly, the widespread big berry manzanita (*A. glauca*) also appears to be a potential parent in the origin of a number of taxa, such as *A. gabilanensis* and *A. refugioensis*.

Arctostaphylos also seems to have a process of species origin lacking in other chaparral species. Two old lineages appear to exist in manzanitas, but reproductive isolation between these lineages is not complete. However, hybridization appears limited which suggests some fertility barriers. Unlike *Ceanothus* or other chaparral shrubs, *Arctostaphylos* has species at both a diploid level (2 sets of chromosomes) and a tetraploid level (4 sets of chromosomes). Research on a number of these tetraploids, which make up almost a third of the taxa, indicate they are of hybrid origin arising from crosses of species from the two lineages. Polyploidy is a common process in plants that permits regaining complete fertility from combinations that may be partially infertile. Most of these tetraploids contain a large number of subspecies, like *A. tomentosa*, *A. crustacea*, *A. glandulosa*, and *A. manzanita*. Adaptive hybridization may be the source of the diverse and difficult to identify tetraploids and their many subspecies.

A very old specimen of Montara manzanita (*Arctostaphylos montaraensis*) growing on Montara Mountain in San Mateo County with huckleberry (*Vaccinium ovatum*) and bracken fern (*Pteridium aquilinum* var. *pubescens*).

CONCLUSIONS

At this point, the diversity of *Ceanothus* and *Arctostaphylos* and their central role in California chaparral lies in how their life histories interact with California's multiple topographic, edaphic, and climate gradients. Their dormant seed banks and wildfire create conditions for rapid change. Glacial epochs, migrations, and hybridization have kept the process of adaptation and speciation ongoing. Recent research using molecular genetic techniques indicates that for both *Arctostaphylos* and *Ceanothus* there are two old and distinct lineages. However, when it comes to the current species, the genetic levels explored so far indicate little differentiation exists. Future work will eventually tease out these patterns of history and give us a richer understanding of the extent and multitude of evolutionary pathways that these plants have wandered.

REFERENCES

Axelrod, D.I. 1981. Holocene climatic changes in relation to vegetation disjunction and speciation. *American Naturalist* 117:847–870.

Boykin, L.M., M.C. Vasey, V.T. Parker and R. Patterson. 2005. Two lineages of *Arctostaphylos* (Ericaceae) identified using the Internal Transcribed Spacer (ITS) region of the nuclear genome. *Madroño* 52:139–147.

Fross, D. and D. Wilken. 2006. *Ceanothus*. Timber Press, Portland, OR.

Keeley, J.E. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68:434–443.

Nobs, M.A. 1963. Experimental studies on species relationships in Ceanothus. *Carnegie Institution of Washington Publication* 623. Washington, D.C.

Parker, V.T. and V.R. Kelly. 1989. Seed banks in California chaparral and other mediterranean climate shrublands. In *Ecology of Soil Seed Banks*. M.A. Leck, V.T. Parker and R.L. Simpson, eds. Academic Press, New York, NY.

Parker, V.T., M.C. Vasey and J.E. Keeley. In press. *Arctostaphylos*. The Jepson Manual of Higher Plants of California. 2nd Edition. University of California Press, Berkeley.

Raven, P.H. and D.I. Axelrod. 1978. Origin and relationships of the California flora. *UC Publications in Botany* 72. University of California Press, Berkeley.

Stebbins, G L. and J. Major. 1965. Endemism and speciation in the California flora. *Ecological Monographs* 35:1–35.

Wells, P.V. 1969. The relation between mode of reproduction and extent of speciation in the woody genera of the California chaparral. *Evolution* 23: 264–267.

V. Thomas Parker, Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132. parker@sfsu.edu

Zonation of chaparral, in response to freezing, along Malibu Canyon Road from the ocean near Malibu to inland Tapia Park. Shrubs with bright red leaves are laurel sumac (LS, *Malosma laurina*), which our data have shown undergo leaf death at -6°C and nearly 100% embolism of their stem xylem (Pratt et al. 2005; Davis et al. 2005; Davis et al. 2007). There are less red leaves high on the slopes in the background, which suggests temperatures were above -6°C on higher slopes. All photographs by the author.

CHAPARRAL ZONATION IN THE SANTA MONICA MOUNTAINS: THE INFLUENCE OF FREEZING TEMPERATURES

by Stephen D. Davis, Anjel M. Helms, Marcus S. Heffner, Anthony R. Shaver, Amory C. Deroulet, Nicole L. Stasiak, Spencer M. Vaughn, Caleb B. Leake, Han D. Lee, and Eli T. Sayegh

A principal objective in plant ecology is to explain the distribution of species and vegetation patterning. In the case of the chaparral shrub community in the Transverse Mountain Ranges of Southern California, previous explanations of chaparral zonation have focused on differential water resources, exposure to solar radiation, and edaphic factors (Davis et al. 1999). Here we examine an alternate possibility, gradients in freezing temperatures.

The Pacific Ocean near Malibu, California, ameliorates fluctuations between minimum temperatures at night and maximum temperatures during the day. Minimum temperatures rarely dip below 0°C on cold winter nights. In contrast, just 5 kilometers inland, deep canyons reduce the ocean's ameliorating influence, reduce insolation, and increase cold air drainage, enhanced by radiative heat loss from plants to cold skies on calm, clear nights. These factors can lead to a steep 12°C gradient in minimum temperature over a short distance of 5 kilometers (Figure 1, page 13). This gradient in temperature is accompanied by a dramatic shift in chaparral species composition, with coastal greenbark ceanothus (*Ceanothus spinosus*), bigpod ceanothus (*C. megacarpus*), and laurel sumac (*Malosma laurina*) dominating the Malibu landscape while inland wedgeleaf ceanothus (*C. cuneatus*), hoaryleaf ceanothus (*C. crassifolius*) and sugar bush (*Rhus ovata*) dominate the landscape near Tapia Park (Figure 1).

The primary zonation (1° Zonation) is from the ocean inland (0°C to -12°C) but superimposed on this pattern is a secondary zonation (2° Zonation) from hilltop to valley floor. The latter results from cold air drainage and thermal inversion (Langan et al. 1997; Ewers et al. 2003). Perhaps readers have felt the chill of entering a valley floor on early morning hikes in the Santa Monica Mountains. This thermal inversion of temperature (colder at low elevations) is five- to ten-fold steeper, and in the reverse direction, to the standard elapse rate calculated for decreasing temperature with elevation in high mountains (drop in 5°C for every 1,000 meter increase in elevation).

This temperature inversion may be counter-intuitive, but over microclimate scales (hill-valley effects) and in the Santa Monica Mountains where a contiguous elevation gradient is lacking, thermal inversions dominate and impact species distribution somewhat paradoxically. For example, it has been established that greenbark ceanothus typically grows in moist, shaded ravines but bigpod ceanothus is restricted to drier, more exposed microsites. Thus why does greenbark ceanothus not extend its distribution into moist valley bottoms near Tapia Park (photograph, page 14)? Apparently low temperature (winter freezes) prevents their establishment and survival at these relatively moist sites. Why does hoaryleaf ceanothus which typically thrives at the high elevation, snowbelt region of the San Gabriel Mountains, occupy the low valleys in the Santa Monica Mountains (Fig. 2A)? This is probably because of cold air drainage in the Santa Monica Mountains.

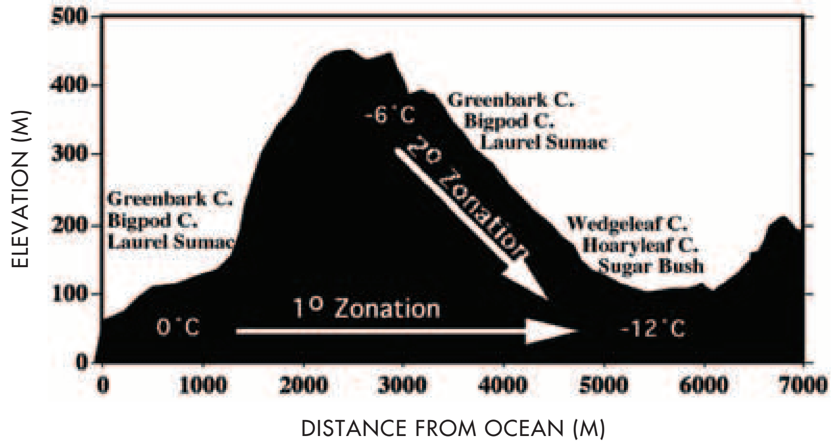


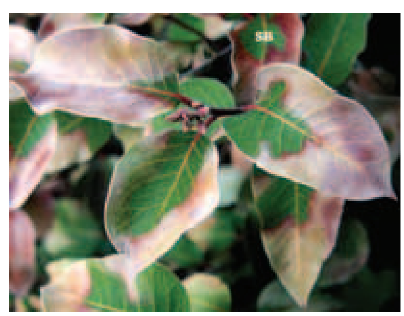
Figure 1. Profile of the change in dominant shrub species of chaparral along a South to North (left to right) transect from the coastal bluffs near Malibu to inland regions near Tapia Park in the Santa Monica Mountains. The transect roughly follows Malibu Canyon Road and the hillsides along this road allow visualization of a vegetation response to this 12°C temperature gradient between the ocean and Tapia Park, approximately 5 km inland (see photograph on page 12).

Consistent with this interpretation, our measurement of freeze-tolerance among species has shown that leaves of coastal species are much more susceptible to freeze damage than inland species. Whether one used a vital stain, variable fluorescence, electrolyte leakage into a bathing solution, or simply the color change of leaf pigment with freezing injury, the lethal temperature for 50% cell death was -6°C for laurel sumac and -10°C for greenbark and bigpod ceanothus. In contrast, the leaves of inland species were more tolerant of freezing with 50% cell death of -16°C for sugar bush and -18°C for hoaryleaf ceanothus (Boorse et al. 1998). We have not measured 50% cell death for wedgeleaf ceanothus but field observations suggest it is below -10°C (bottom photograph, page 15).

This year (2006-2007) has been the driest in recorded history for the Santa Monica Mountains (seasonal total of 87 mm, normal is 380 mm), but also one of the coldest winters on record (minimum temperatures of -12°C at Tapia Park on January 14, 2007). Furthermore, the summer drought of 2006 extended into the winter months causing a "perfect storm" in terms of plant survival in response to environmental stress. That is, plants were severely dehydrated when they also experienced a hard freeze, a combination that is catastrophic to the water transport system of some species and a serious threat to chaparral shrubs that must maintain year-round water supplies for persistence of evergreen leaves (Langan et al. 1997; Ewers et al. 2003; Pratt et al. 2005; Davis et al. 2007).

Typically plants under field conditions rehydrate overnight as stomata close, atmospheric humidity increases, and temperature declines. This allows sufficient time for the root system and plant tissues to return to approximate equilibrium

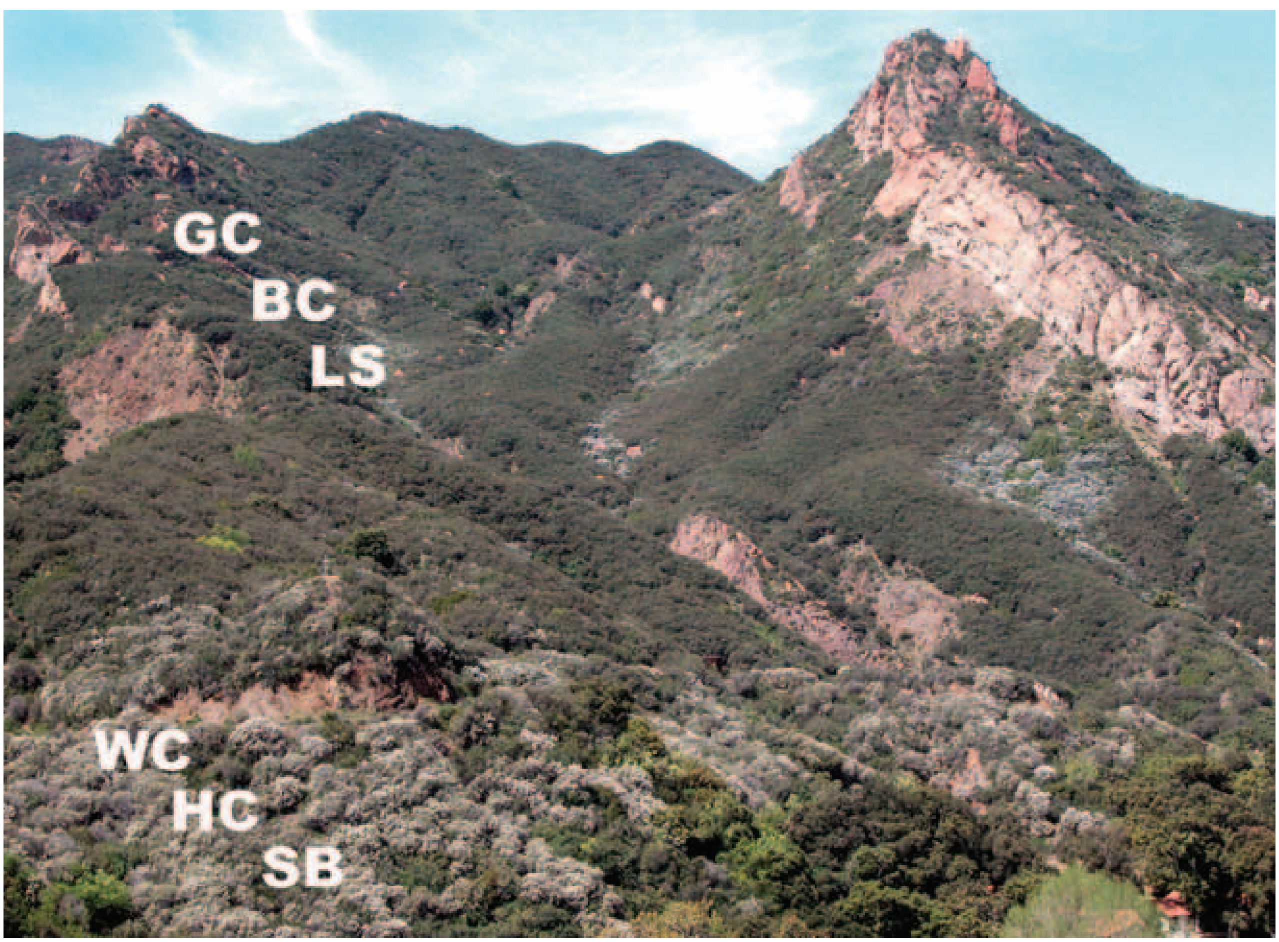
Close-up of leaf dieback on sugar bush (SB, *Rhus ovata*). The pattern of browning suggests that portions of the leaf closest to the water supply in midveins remain green longer than margins, presumably due to freeze-caused embolism.



with stored soil moisture in the bulk-rooting zone. Thus plant water status measured just before sunrise represents the most hydrated state of chaparral shrubs during their 24-hour cycle, and also coincides with the lowest 24-hour temperature (Langan et al. 1997). The predawn water status of plants generates modest negative pressures in the water pipes of stems (xylem vessels), ranging between -2 to -4 atmospheres (atm) of pressure (-30 to -60 pounds per square inch of pressure or psi) during the cool, rainy winters of our Mediterranean-type climate. To place these values in perspective, automobile tires are fully inflated at +2 atm of pressure and crop plants such as corn and beans lose turgor (cell pressure) and visibly wilt around -15 atm. Surprisingly, at the time of severe winter freeze on January 14, 2007, predawn water status for our chaparral shrubs at Tapia Park ranged between -36 atm for greenbark ceanothus (*Ceanothus spinosus*) to -56 atm for hoaryleaf ceanothus (*Ceanothus crassifolius*). These values are two to four times drier than the wilting point of crop plants. This was particularly worrisome to us because previous data in our laboratory have demonstrated that low water status at the time of a freezing event could cause catastrophic xylem dysfunction leading to leaf drop and shoot death (Ewers et al. 2003). This is precisely what happened at the cold edge (ecotone) of our 1° and 2° Zonations shown in Figure 1 on page 13 (see photographs on pages 13 and 15 for examples of injuries due to freezing).

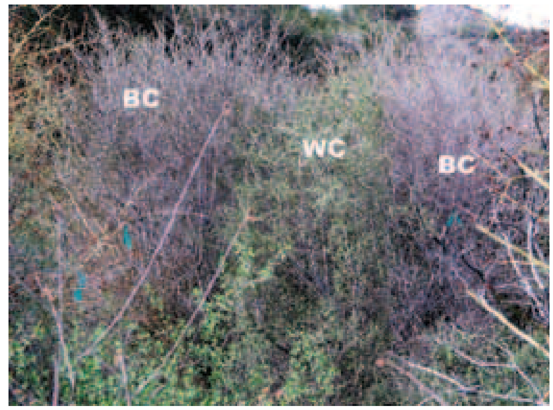
The mechanism by which water stress interacts with freezing to increase embolism formation in chaparral species is well understood (Langan et al. 1997; Davis et al. 1999b; Davis et al. 2007). When water turns to ice, any gases dissolved in the water come out of solution because of decreasing gas solubility in ice. Thus bubbles appear with ice formation. Perhaps readers have noticed how clear water often appears opaque after it is frozen into ice cubes in a freezer. The same occurs in the frozen water pipes of plant stems (xylem vessels). At the time of thaw, just after sunrise on cold winter nights, these ice bubbles in xylem

Inland 2° zonation of chaparral vegetation in the Santa Monica Mountains near Tapia Park as diagrammed in Figure 1 (page 13). Upper warmer slopes are occupied by coastal chaparral species greenbark ceanothus (GC, *Ceanothus spinosus*), bigpod ceanothus (BC, *Ceanothus megacarpus*), and laurel sumac (LS, *Malosma laurina*), whereas the lower and colder valley bottom is occupied by wedgeleaf ceanothus (WC, *Ceanothus cuneatus*), hoaryleaf ceanothus (HC, *Ceanothus crassifolius*), and sugar bush (SB, *Rhus ovata*).



conduits must redissolve into liquid water; otherwise small bubbles will coalesce to form large bubbles that occlude water transport (xylem embolism). Under hydrated conditions, -2 atm to -4 atm, gas bubbles readily dissolve at the time of thaw, but under unusually dry conditions, -36 atm to -56 atm, bubbles are pulled by the negative pressure of water stress to rapidly expand to form xylem embolism. Higher plants can only survive severe embolism in xylem conduits for one or two weeks. They must either reverse xylem embolism (highly unlikely if dry conditions persist, as in 2007) or grow new xylem tissue to replace nonfunctional conduits (also unlikely if dry conditions prevent positive turgor formation and cell expansion, as in 2007).

In conclusion, this episodic event of extreme drought at the time of a hard freeze has provided a unique opportunity for undergraduate students in my lab (co-authors on this paper) to test hypotheses concerning the interactions of drought- and freeze-caused dieback and to examine correspondence between species distribution patterns and susceptibility to freezing injury. This event is particularly significant in light of increasing evidence of impending climate change. There is wide agreement within the scientific community that such episodic events may regulate plant establishment and persistence in the landscape. Consequently, one of the main predictions of climate change models for Southern California is increasing episodic events such as droughts and wildfires. In 2007, the Malibu area (photograph, page 12) not only experienced a record freeze, but the driest year in recorded history, and three separate fire events: one on January 5, 2007, another on October 21, 2007, and a third on November 24, 2007. We hope that when post-fire, seasonal rains arrive this winter they will be gradual and gentle, and not add to the episodic list.



Top: At the cold ecotone between plant communities, greenbark ceanothus (GC) experienced catastrophic xylem failure (98.3% embolism of stem xylem causes blockage in water transport from roots to leaves) after the freezing event of January 14, 2007, and thus virtually all leaves turned brown and dropped. Because roots are below the soil surface they avoided embolism (24.0% embolism), allowing sustained water uptake for sprouting from basal burls. Stem photosynthesis (an advantage of having green bark) evidently kept the vascular cambium alive to support new leaf emergence. By June 2007 about 10% mortality had occurred, thus most individuals will survive, although stunted in growth and lacking fruit production during the 2007 growing season. Bottom: Also at the cold ecotone, freeze-sensitive bigpod ceanothus (BC, defoliated shrubs) can be found growing next to freeze-resistant wedgeleaf ceanothus (WC, live, green leaves). Bigpod ceanothus experienced 99.5% embolism of stem xylem whereas wedgeleaf ceanothus experienced only 82.4% embolism, evidently enough to produce flowers, fruits, and seeds and avoid foliar abscission (leaf drop). About 20% of the bigpod ceanothus died by June 2007 whereas none of the adjacent wedgeleaf ceanothus died.

REFERENCES

Boorse, G.C., F.W. Ewers and S.D. Davis. 1998. Response of chaparral shrubs to below-freezing temperatures: acclimation, ecotypes, seedlings vs. adults. *American Journal of Botany*. 85:1224–1230.

Davis, S.D., F.W. Ewers, J. Wood, J.J. Reeves and K.J. Kolb. 1999. Differential susceptibility to xylem cavitation among three pairs of *Ceanothus* species in the Transverse Mountain Ranges of Southern California. *Ecoscience* 6:180–186.

Davis, S.D., R.B. Pratt, F.W. Ewers and A.L. Jacobsen. 2007. Freezing tolerance impacts chaparral species distribution in the Santa Monica Mountains. In *Flora and Ecology of the Santa Monica Mountains*. D.A. Knapp ed. Southern California Botanists, Fullerton, CA.

Davis, S.D., J.S. Sperry and U.G. Hacke. 1999. The relationship between xylem conduit diameter and cavitation caused by freeze-thaw events. *American Journal of Botany*. 86:1367–1372.

Ewers, F.W., M.C. Lawson, T.J. Bowen and S.D. Davis. 2003. Freeze/thaw stress in *Ceanothus* of southern California chaparral. *Oecologia* (Berlin) 136:213–219.

Langan, S.J., F.W. Ewers and S.D. Davis. 1997. Differential susceptibility to xylem embolism caused by freezing and water stress in two species of chaparral shrubs. *Plant, Cell and Environment* 20:425–437.

Pratt, R.B., F.W. Ewers, M.C. Lawson, A.L. Jacobsen, M. Brediger and S.D. Davis. 2005. Mechanisms for tolerating freeze-thaw stress of two evergreen chaparral species: *Rhus ovata* and *Malosma laurina* (Anacardiaceae). *American Journal of Botany* 92:1102–1113.

Stephen Davis, Natural Science Division, Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263-4321, davis@pepperdine.edu