Two contrasting vegetation alliances with chamise (*Adenostoma fasciculatum*) and whiteleaf manzanita (*Arctostaphylos viscida*). Chamise will both resprout from the base and germinate from seeds while this manzanita only germinates from seeds following fires. Photograph by T. Keeler-Wolf.

INTERPRETING FIRE AND LIFE HISTORY INFORMATION IN *THE MANUAL OF CALIFORNIA VEGETATION*

by Todd Keeler-Wolf, Julie M. Evens, and John O. Sawyer

Fire is a pervasive force impacting the composition and structure of vegetation throughout most of California. As discussed throughout this issue of *Fremontia,* fire has shaped our state's flora and is one of the major natural processes regularly affecting our ability to coexist with nature. Here we consider changes in *The Manual of California Vegetation* (MCV2) as they relate to fire.

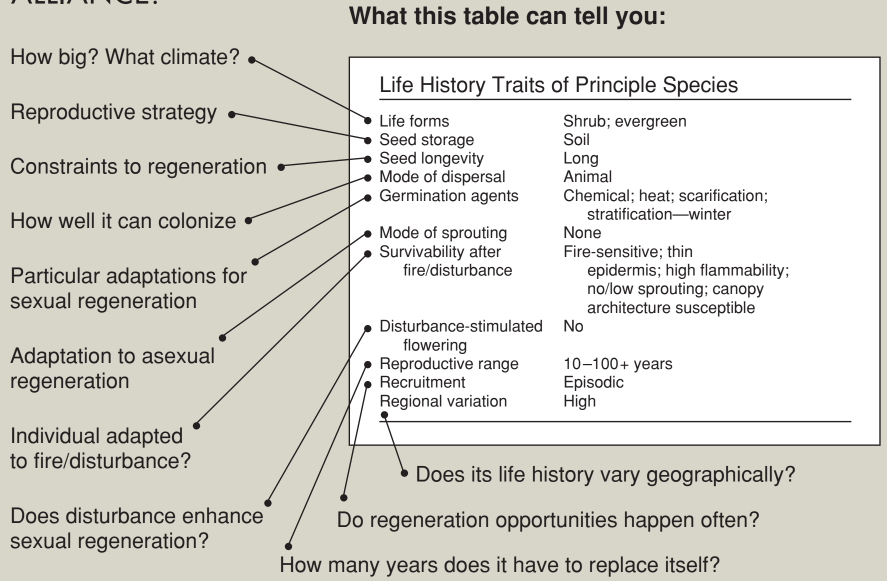

FIGURE 1. LIFE HISTORY FOR THE *ARCTOSTAPHYLOS VISCIDA* ALLIANCE.

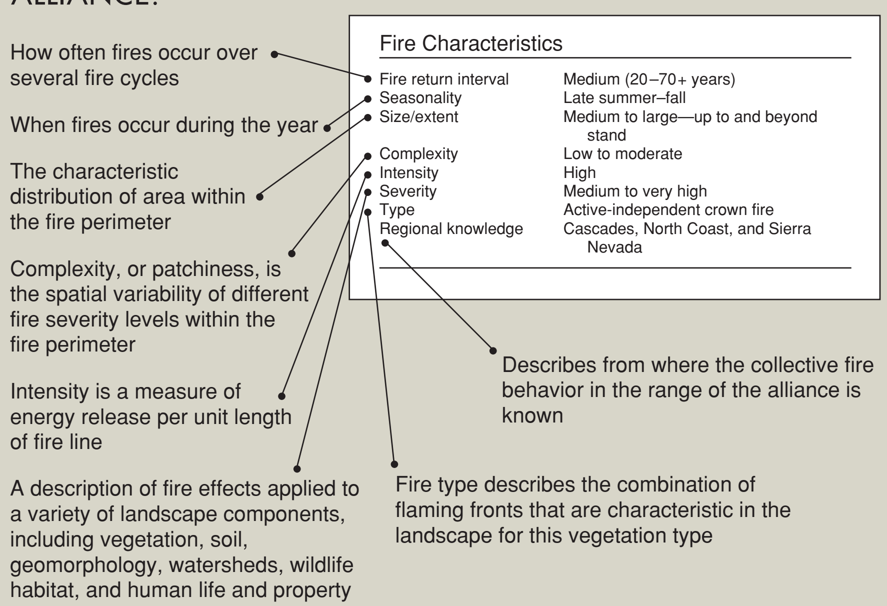

FIGURE 2. FIRE REGIME FOR THE *ARCTOSTAPHYLOS VISCIDA* ALLIANCE.

A major reason for preparing a second edition was to provide more useful descriptions of the state's natural vegetation so that we can better preserve it. Principally, we thought to improve the book's utility by including life history and fire behavior characteristics for each of the more than 380 main California vegetation types, which are known formally as "alliances." The life history of the main distinguishing plant species (bolded in the first line of an alliance's description), coupled with a summary of the natural processes affecting it, explain the conditions that enable the alliance to exist. In a sense, it is akin to having a general "recipe" for sustaining each alliance listed in the book, although this "recipe" must be thought of as broadly defined and not subject to precise measurements.

In each full alliance description there are two separate tables with accompanying text—one for the life history traits of the distinguishing plant species and another for the associated fire regime for that alliance. The logic behind the two tables addresses the tendency of distinguishing plant species of an alliance to have specific abilities that are adapted to a set of specific environmental and ecological conditions. For example, a desert scrub type defined by creosote bush (*Larrea tridentata*) will respond very differently to fire than a chaparral type defined by chamise (*Adenostoma fasciculatum*), even though both shrubs are similar in size and have small evergreen leaves.

The conditions under which an alliance can persist depend, to a great degree, on adaptations of the distinguishing species (its longevity, germination requirements, general morphology, and other genetically controlled traits) **plus** the type, frequency, and intensity of the natural processes associated with that vegetation over time. If conditions change sufficiently beyond the distinguishing species' general range of tolerance, then the vegetation will also change as a reaction

Open stand of Creosote Bush (*Larrea tridentata*) Alliance with an understory including red brome (*Bromus madritensis* ssp. *rubens*) and Mediterranean grass (*Schismus* spp.). Recent invasion by non-native grasses increase the risk of this vegetation burning. Photograph by T. Keeler-Wolf.

to the new processes. Taken more broadly, by comparing characteristics of multiple vegetation types within a large parcel of land or watershed, we can begin to understand how its diversity has changed, or has not, under current conditions. In addition, we can better understand how to conserve its diversity by grasping the role of fire and other natural processes at the landscape level.

HOW WE PRESENT THE INFORMATION

With help from members of the U.S. Forest Service's Joint Fire Sciences Program, we held a series of five regional workshops around the state between 2000 and 2003. At these meetings, we collectively considered the longevity, germination requirements, general morphology, and other genetically controlled traits for each distinguishing plant species and the type, frequency, and intensity of fire or other natural processes associated with a set of alliances in that region. We used this information, together with literature surveys and detailed interviews with other fire ecologists, in developing the two tables for each alliance. All told, over 50 professional ecologists, land managers, and other scientists contributed to the information in these tables, in addition to information derived from scores of publications.

The categories in the Life History Table (Figure 1) summarize essential traits for distinguishing species that define an alliance. These traits comprise the "code" or the basic set of advantages and constraints of plants that allow them to interact with their current environment. Some of these traits are evolutionarily conservative and unvarying, while others are more pliable and may vary throughout the range of the species. This last notion is captured in the category "regional variation."

The concept behind the Fire Regime Table (Figure 2) is to describe the fire characteristics for each alliance with respect to temporal (fire return, seasonality), spatial (fire size, complexity), and magnitude (fire intensity, severity, type) attributes using the currently authoritative book on California fire ecology (Sugihara et al. 2006). The resulting fire regime information describes fire conditions favorable to the plant species that define the alliance.

It is important to note that wildfires can burn across whole landscapes. Fires are often impartial to biologically defined boundaries; one fire often impacts several adjacent stands of many other alliances in the burned areas. However, the biological and physical characteristics of each stand of vegetation can *also* affect how the fire burns; in some cases a fire may burn only portions of a single stand or lots of stands of many alliances. Fire is also not a completely regular and predictable event, and it may occur at different times of the year, and at different frequencies, affected by seasonal weather, topography, geography, yearly variances in plant productivity, and human influences.

However, we cannot determine exact fire return intervals (e.g., how frequently fire affects a particular stand of vegetation) for each alliance for two main reasons. We often do not have enough data on plant responses to fire to arrive at precise fire return intervals. More importantly, natural processes such as fire influence the character of the vegetation depending on the time between events (whether a relatively short or long interval), and the pattern of the events (whether a mild understory surface or an intense crown fire). These two variables, in turn, affect the composition and structure of the resulting vegetation. So, we assign general terms (e.g., short, medium, long) in the tables. These are often

LEFT: Fires significantly reduce the shrub cover, and species such as the matchweed (*Gutierrezia* spp.) and non-native grasses that thrive following disturbances dominate for many years afterwards before creosote can recover. • BELOW: Bigpod ceanothus (*Ceanothus megacarpus*) occurs in a patchwork with other chaparral in the Santa Monica Mountains in Ventura County, where fire and other disturbance modify the nature of stands. Photographs by J. Evens.

supplemented by a range of years for the shorter and the longer averages of time between fires, when this information is known from observations. The fire types listed (defined in Appendix 2 of MCV2) also may vary depending on the character of the vegetation and its geographic location.

It is important to note that the statements on fire return intervals should not be taken out of context, particularly since they may be used to make decisions about land management. For example, when interpreting these parenthetical ranges in a fire return interval, one should not strictly select an upper or lower value or the calculated mean between the extremes. We present these ranges as broad guides, not as stringent and literal rules. A good case in point can be illustrated by chaparral stands containing species with different adaptive strategies, such as white leaf manzanita (*Arctostaphylos viscida*), an obligate seeding shrub, and birch leaf mountain mahogany (*Cercocarpus montanus*), a resprouting shrub. Keeley et al. (2005) have found that stands of these species are tolerant of long fire-free periods, and even 100+ year-old stands show no perceptible reduction in their ability to recover following fire.

With the standardized attributes presented in the life history and fire regime tables, users may apply the information in the book to a given patch or stand of vegetation to help answer a series of questions. For example, are the factors that influence its effective reproduction, recruitment, and regeneration being met in this stand, so there is a high likelihood of the vegetation's persistence (Figure 1)? Such questions are relative to the recent history of the particular stand. Since fire history is a principal influential natural process that impacts the viability of vegetation stands in California, the fire regime table (Figure 2) is also helpful in answering these questions.

FIGURE 3. THE LIFE HISTORY AND FIRE REGIME TABLES OF *LARREA TRIDENTATA–AMBROSIA DUMOSA* ALLIANCE.

Life History Traits of Principle Species

	Larrea tridentata	*Ambrosia dumosa*
Life forms	Shrub; drought deciduous	Shrub; drought deciduous; clonal
Seed storage	Soil	Soil
Seed longevity	Medium	Medium
Mode of dispersal	Animal; gravity wind	Animal; tumbling
Germination agents	Chemical; heat	None
Mode of sprouting	Underground structures	Underground structures
Survivability after fire/disturbance	Fire-sensitive; no/low sprouter	Fire-sensitive; no/low sprouter

Fire Characteristics

Fire return interval	Truncated long
Seasonality	Spring–summer–fall
Size/extent	Small to moderate
Complexity	Low
Intensity	High
Severity	Moderate
Type	Passive-active crown fire

Note: Additional information in these tables can be found in the MCV2

For example, the life form (tree, shrub, herbaceous plant) and the particular genetic traits of the species (e.g., seed storage, mode of sprouting, and survivability after fire) clearly influence the species' perseverance under certain fire characteristics. Fire type, the interval between fires, fire intensity, and the other characteristics synthesized in each fire regime table expresses the physical, temporal, and spatial effects of fire on the vegetation of each alliance. Taken together, these tables can be used to interpret the ecological status of any stand of vegetation and understand how it has been impacted by fire.

It is also important to remember that many stands in California have persisted for thousands of years without regular influence by fire. Only relatively recently has fire become frequent in some areas with the introduction of nonnative weedy plants along with human-instigated fires. For example, increased fire frequencies have altered much of the vegetation in California's warm deserts. A classic example involves a widespread alliance, the *Larrea tridentata–Ambrosia dumosa* Alliance. A quick look at the life history and fire regime tables for this alliance will tell you how troublesome frequent fire can be (Figure 3).

The fire characteristics found in Figure 3 are from page 567 in the *Manual*. Both *Ambrosia dumosa* and *Larrea tridentata* exhibit limited sprouting ability after fire, and *L. tridentata* has resinous foliage that is highly flammable (Vasek 1979, 1983, Marshall 1995b). Low-intensity fires can cause up to 100% mortality in both *L. tridentata* and *A. dumosa*, but some shrubs can survive if crowns are only partially consumed. Mortality rates are probably related to rainfall conditions during the immediate post-fire years, and both species may colonize successfully by seed from offsite sources in high rainfall years following a fire (Brooks and Minnich 2006). However, *A. dumosa* can colonize more rapidly after fire and may dominate alone for a number of years before both *L. tridentata* and *A. dumosa* regain similar pre-fire dominance.

ANOTHER EXAMPLE

Big pod ceanothus (*Ceanothus megacarpus*) is a classic obligate seeding chaparral shrub of southern California. It typically dies after the normally intense fires of the region. Yet as with *Arctostaphylos viscida* (Figure 1), seeds of the ceanothus are stored in the soil. Seedlings germinate within a few years after fire under natural fire regimes, and grow quickly to replace previously burned stands, sometimes preceded by short-lived stands of disturbance followers like deer weed (*Lotus scoparius*).

Large acreages of big pod ceanothus (pp. 452-543 in MCV2) have covered the Santa Ynez, Santa Monica, and other coastal mountains in the past, yet stands are less extensive today, even in areas that still are covered with natural vegetation. Why? A likely reason is that human-initiated fires are occurring more frequently than *C. megacarpus* stands can build up the necessary banks of soil-stored seeds for stands to regenerate. As with other chaparral shrubs, larger ceanothus plants can produce many seeds. While ceanothus may start producing some seeds from small young shrubs, if fires occur when the shrubs are relatively young, fewer seeds are likely to be stored in the soil. If fires occur every few years, just after young ceanothus are first producing seeds, it may only take a few successive close-interval fires to deplete the seed bank.

By properly interpreting the MCV2, readers will notice that while this ceanothus' fire return interval is estimated to average between 25 and 55 years, the plant is reproductively viable from 10 to 100+ years. Thus, a fluctuating fire return interval between the youngest reproductive age (about 10 yrs.) and oldest age (100+ yrs.) is reasonable. Repeat fires at the short end of the reported range (ex., between 10 and 25 yrs.) are much less likely to ensure stand regeneration than longer intervals (> 25 yrs.). Thus, understanding the natural history of diagnostic vegetation species and the effects of unnatural fire regimes on native vegetation is extremely important to long-term ecosystem viability.

SUMMARY AND CONCLUSIONS

We include the new tables and text in the *Manual* as guides for conservationists, natural historians, and land managers, so that mosaics of natural vegetation can be interpreted and information can be used appropriately within an ecological context. This information, in many cases, has been summarized for the first time in our book, and was assembled from a wide variety of sources including published and peer-reviewed literature and interviews with knowledgeable experts. Fire ecology is a rapidly expanding field and much new information is coming to light even since the publication of the MCV2.

Sometimes older assertions in the literature are in direct conflict with recent findings. For example, chemicals that accumulate in the soil from chamise chaparral (*Adenostoma fasciculatum* Alliance) do not appear to negatively impact the community of plants as once thought. Furthermore, these chemicals do not cause stand stagnation, but rather can increase after fire (Keeley et al. 1985, Halsey 2004, and summarized in McMurray 1990). As research of life history and fire regime characteristics continues to expand, our tables and descriptions must be updated. We seek any information that will improve our descriptions, and are planning to produce an online version of the *Manual* so it can be updated periodically.

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