

Biomass and Fuel Characteristics of Chaparral in Southern California

Jon C. Regelbrugge¹ and Susan G. Conard²

¹Pacific Southwest Research Station, USDA Forest Service, 4955 Canyon Crest Dr., Riverside, CA 92507 USA
tel. 909 680 1542; Fax 909 680 1501; e-mail: /s=j.regelbrugge/ou1=s27L05a@mhs-fswa.attmail.com

²Forest Fire and Atmospheric Science Research, USDA Forest Service, 201 14th St. SW, Washington, DC 20250, USA

Abstract. Accurate estimates of biomass components and fuel characteristics of southern California chaparral plant communities are important for planning prescribed fires, suppressing wildfires, and for understanding the ecological interactions between fire and chaparral community development and succession. We have sampled chaparral biomass and fuels on a variety of sites as part of our research into the fire ecology of chaparral. These sites have spanned a broad geographic range, as well as a range in age, species composition and productivity. Total aboveground biomass of chaparral stands greater than 15 years old can range from 10–40 Mg/ha (1 Mg/ha = 1000 kg/ha) for *Adenostoma fasciculatum*, with canopy heights of 1.5–2.5 m, to as much as 120 Mg/ha for several *Ceanothus* species with canopy height of up to 5.5 to 6 m. Within a stand, coefficients of variation of biomass among plots are commonly 25 to 30 percent, and community structure can vary dramatically in relation to topographic and edaphic gradients over short distances of 5 to 10 m. Foliage accounts for 3 to 25 percent of total biomass in *A. fasciculatum* and *Ceanothus*-dominated stands. The fraction of stand biomass that is considered to be fuel available for fire propagation, which includes foliage, live twigs less than 6 mm in diameter, and dead woody material, ranges from approximately 30 percent to 75 percent in mature chaparral stands. This available fuel fraction is probably related to climatic factors such as prolonged drought periods, as well as species composition, species morphology, and site productivity. Our ongoing work is focused on improving efficiency of biomass and fuels sampling, and relating biomass development through time to site and climatic factors.

Introduction

Periodically recurring, stand replacing fires are common in chaparral ecosystems in southern California, and land managers often use prescribed fire to achieve specific objectives as well. Site-specific information on fuel

characteristics is important for planning prescribed fires and suppressing wildfires. Knowledge of how chaparral biomass and fuels change over time, and how these changes are affected by climatic and site variability, is required to understand the ecological interactions between fire and chaparral community development and succession. Understanding these relationships will help us to effectively manage chaparral ecosystems to protect human life and property from wildfire and postfire flooding and sedimentation, while maintaining ecosystem quality, biodiversity, and productivity.

Various authors have reported on chaparral biomass and fuels, but our understanding of the issues listed above remains unsatisfactory. Several studies have reported only biomass components such as live wood and foliage, with no information on the distribution of this biomass among various fuel size class components (Specht 1969, Rundel and Parsons 1979, Schlesinger and Gill 1980, Gray 1982, Stohlgren et al. 1984). Fewer authors have presented detailed fuels information in addition to data on biomass components, (Riggan et al. 1988). Two limitations of these studies are that the results represent only a limited number of sites and species, and very little attempt has been made to relate differences in biomass or fuels among sites to geographic, topographic, or edaphic differences among sites. Rothermel and Philpot (1973) proposed a set of equations which describe age-dynamic fuel models that would allow estimation of biomass and fuels for different species compositions representative of a broad range of sites in the chaparral ecosystem. However, comparing these models to published data illustrates that the model for total biomass may not account for the wide variability of biomass among sites (Figure 1). Also, this dynamic fuel modeling system assumes a dramatic increase in dead fuel with increasing age, caused by widespread branch dieback (Rothermel and Philpot 1973). This assumption is questionable in light of other authors' data (e.g. Riggan et al. 1988), and particularly that of Paysen and Cohen (1990), who found no evidence that chamise

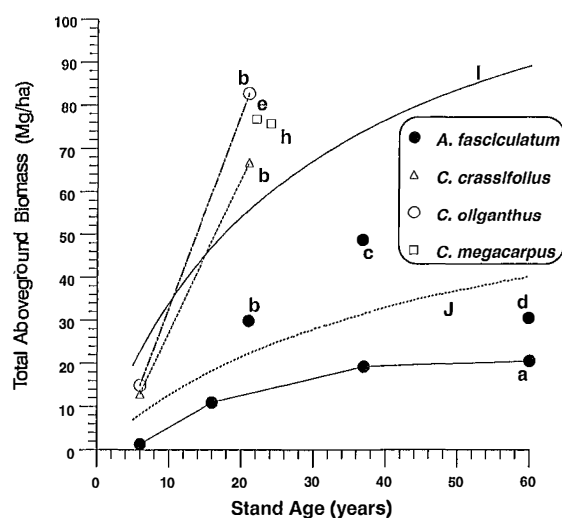


Figure 1. Biomass of various chaparral plant communities in relation to stand age. Different letters indicate different authors. a = Rundel and Parsons 1979; b = Riggan et al. 1988; c = Specht 1969; d = Stohlgren et al. 1984; e = Schlesinger and Gill 1980; h = Gray 1982; I, J = Rothermel and Philpot 1973, fuel models for mixed chaparral and chamise chaparral, respectively.

chaparral dead fuel fraction was reliably predicted by age. Paysen and Cohen (1990) found wide variation in dead fraction, irrespective of age, and hypothesized that temporal climatic variability, especially rainfall, may be a primary factor influencing the accumulation of dead fuel in chamise. The opportunistic fungal pathogen *Botryosphaeria dothidea* has also been implicated as a primary cause of branch dieback of drought stressed shrubs, especially *Ceanothus* spp. (Riggan et al. 1994).

Although much work has been focused on chaparral fuel and biomass, land managers and scientists currently lack the means to estimate reliably fuel loading, fuel structure, and biomass components of specific chaparral sites, or how these characteristics of sites will change as a stand regenerates and matures following fire. The objective of this paper is to present an overview of our ongoing research into the estimation of chaparral fuels and biomass components, including some preliminary results, and to discuss gaps in our knowledge that need to be addressed in future research.

Methods

Study Sites

We have acquired data on chaparral biomass components and fuels from 16 sites in southern California over the past several years, as parts of several different studies. These studies have been conducted to assess smoke emissions from prescribed burning of chaparral, describe chaparral water use in relation to soil and weathered rock water holding capacity, determine efficient sampling and estimation procedures for quantifying chaparral biomass

and fuels, and to obtain ground-based data for calibration of remotely sensed data to chaparral stand characteristics including species composition, canopy water content, and fuel and biomass loading and structure. These sites span a broad range of geographic distribution, species composition, and years since last fire. Eight sites were sampled in each of two of the most important general types of chaparral communities, chamise (*Adenostoma fasciculatum*) chaparral and mixed chaparral, which is commonly dominated by members of the genus *Ceanothus*.

Sampling and Estimation Procedures

The specific data collection, processing, and analytical procedures differ somewhat among sites because these data were collected as part of several different studies. Detailed descriptions of methodology and rationale for each study is beyond the scope of this paper, but we will briefly describe in general terms the different approaches used. The methods used in all of the studies allow estimation of total aboveground biomass of the dominant shrub community, and the partitioning of this biomass into live wood, dead wood, and foliage components. Herbaceous plants are not common under mature chaparral (Hanes 1971), so we made no attempt to quantify them in our study. Accumulated surface litter, or forest floor, also tends to be very sparse under many mature chaparral stands, particularly stands dominated by *A. fasciculatum*. Although litter accumulations are greater in stands dominated by *Ceanothus* spp. and *Quercus* spp. we were primarily interested in canopy fuels which dominate fire behavior, so we did no sampling of surface litter. Because one of the goals of our ongoing research into chaparral ecosystems is to quantify patterns of fuel loading with respect to species composition, site factors, and age, we further partitioned the live and dead woody material of a subsample of shrubs into size classes related to fuel particle surface to volume ratio (Burgan and Rothermel 1984). This partitioning allows the development of site-specific, or more general, fuel models for chaparral sites that can be used to simulate fire behavior with the Rothermel fire spread model (Rothermel 1972) using the BEHAVE system (Andrews 1986), or the spatially explicit implementation of the Rothermel model, FARSITE, (Finney 1994). Detailed analyses comparing various fuel models is beyond the scope of this paper, although some general fuel parameters will be discussed, such as total fuel loading, fuel dead fraction, and foliage fraction. We used the definition of total fuel available for fire propagation described in Burgan and Rothermel (1984), i.e., dead woody material less than 76 mm (3 in) in diameter, live wood less than 6.3 mm (.25 in) in diameter, and foliage. We acknowledge that in some stands, such as those dominated by scrub oak (*Quercus berberidifolia*), accumulated leaf litter may be an important component of the available fuel, as would be grasses and other herbaceous

plants in very young stands, up to 5 to 10 years old. However, these issues are not a concern for many chaparral sites, including those we sampled.

We used two general approaches to sampling. One approach involved destructive sampling of all shrubs in fixed area plots, and using the plot area to put biomass and fuels estimates on a unit area basis. All shrubs were tallied by species, and whether the plant was alive or dead, and total fresh mass was determined by a tripod mounted spring scale. A subsample of live and dead shrubs of each species were partitioned into live wood, dead wood and foliage components, with the woody material being further partitioned into size classes as described in Burgan and Rothermel (1984). These shrubs were oven dried to constant mass at 85 °C, and the average ratio of dry mass to fresh mass, by species and status (live or dead shrub) was used to adjust field fresh weights to a dry mass basis. The ratio of the means estimator (Cochran 1963) was used to estimate the fraction of each biomass and fuel component as a proportion of the total mass of each shrub. Separate ratio of the means estimators were calculated for shrubs of each species and status. Biomass and fuel components were summed for all shrubs in each plot, and av-

eraged across plots to yield estimates of average biomass components for each site. Number and size of plots varied among sites sampled as parts of different studies, but the total area sampled at each site ranged from 36 to 50 m².

The second approach involved measuring basal diameters of shrubs in fixed area plots, and destructively sampling shrubs outside of the plots, but in the contiguous stand. The destructively sampled shrubs were partitioned into fuel and biomass components as described above, and were used to develop estimators of biomass and fuel components as a function of shrub cross-sectional area of shrub stem diameters. Regression analysis using ordinary and weighted least squares was used to estimate total aboveground biomass of shrubs, and the ratio of the means estimator was used to estimate that proportion of shrub biomass in a particular fuel or biomass component. These estimators were then applied to the dimensional data recorded on the plots, summed within plots, and averaged across plots to obtain stand-level estimates. Estimators were developed separately for each species and status found at a given site. Figure 2 shows examples of estimators developed for *A. fasciculatum* at the North Moun-

Adenostoma fasciculatum North Mountain

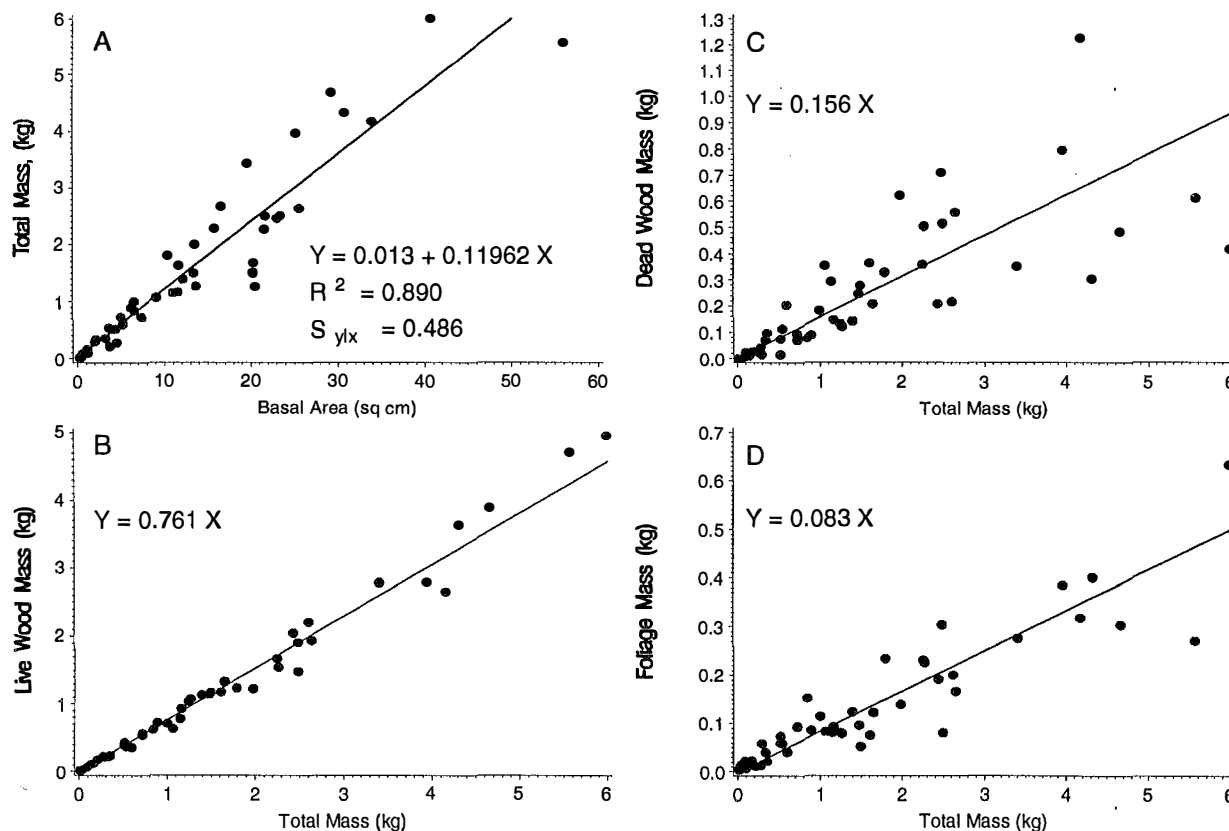


Figure 2. An example of the use of linear regression and ratio of the means estimators to estimate biomass components of *Adenostoma fasciculatum* at the North Mountain Experimental Area in the San Jacinto Mountains of southern California. Linear regression of stem biomass as a function of stem basal area (A), and ratio of the means estimates of mass of live wood, dead wood and foliage (B,C,D respectively) as a fraction of total biomass. For all graphs points show observed values and lines show estimated values.

tain Experimental Area in the San Jacinto Mountains. These relationships are fairly typical of those observed at other sites as well. Sample size varied among sites, but shrub dimensions were measured on at least 120 m² of plot area per site, and at least 10 shrubs per dominant species and status were harvested at each site.

Results and Discussion

Total Biomass

Total aboveground biomass of all sites ranged between 16 and 118 Mg/ha (Figure 3A), with an overall mean of $50 (\pm 7.5, \text{standard error of the mean (SE)})$ Mg/ha ($1 \text{ Mg/ha} = 1000 \text{ kg/ha}$). Aboveground biomass of *A. fasciculatum*-dominated stands ranged from 16 to 40 Mg/ha, with an average of $26 (\pm 2.6, \text{SE})$ Mg/ha, while *Ceanothus*-dominated chaparral had much higher biomass, ranging from 50 to 118 Mg/ha, with an average of $74 (\pm 8.6, \text{SE})$ Mg/ha (Figure 3A). Age of the stands sampled ranged from 10 to 55 years (Figure 3A), with stands of both species spanning a similar range. Any clear rela-

tionship between biomass and age is not apparent, which may not be surprising given the broad range of site conditions these stands are growing on. These stands represent a broad geographic range, with some stands being within a few kilometers of the Pacific Ocean, and others lying as much as 200 km inland. Average annual rainfall within the study area may vary between 300 and 800 mm/yr, depending on the site. Differences in site factors such as aspect may be reflected in species composition, but other authors have noted large differences in total stand biomass among sites of identical age and species composition (Schlesinger and Gill 1980, Riggan et al. 1988). We suspect that water balance and nutrients may account for differences in site productivity which are reflected in the wide variability in stand biomass. These factors will be related to soil depth, soil chemical and physical properties, and topographic influences such as slope aspect, inclination, and position, as well as rainfall. The manner in which site factors influence productivity, and therefore biomass yield, is understood only in a general sense for chaparral. Although further analysis of our data and that found in the literature (e.g. Schlesinger and Gill 1980, Riggan et al. 1988) will help to elucidate the relationship

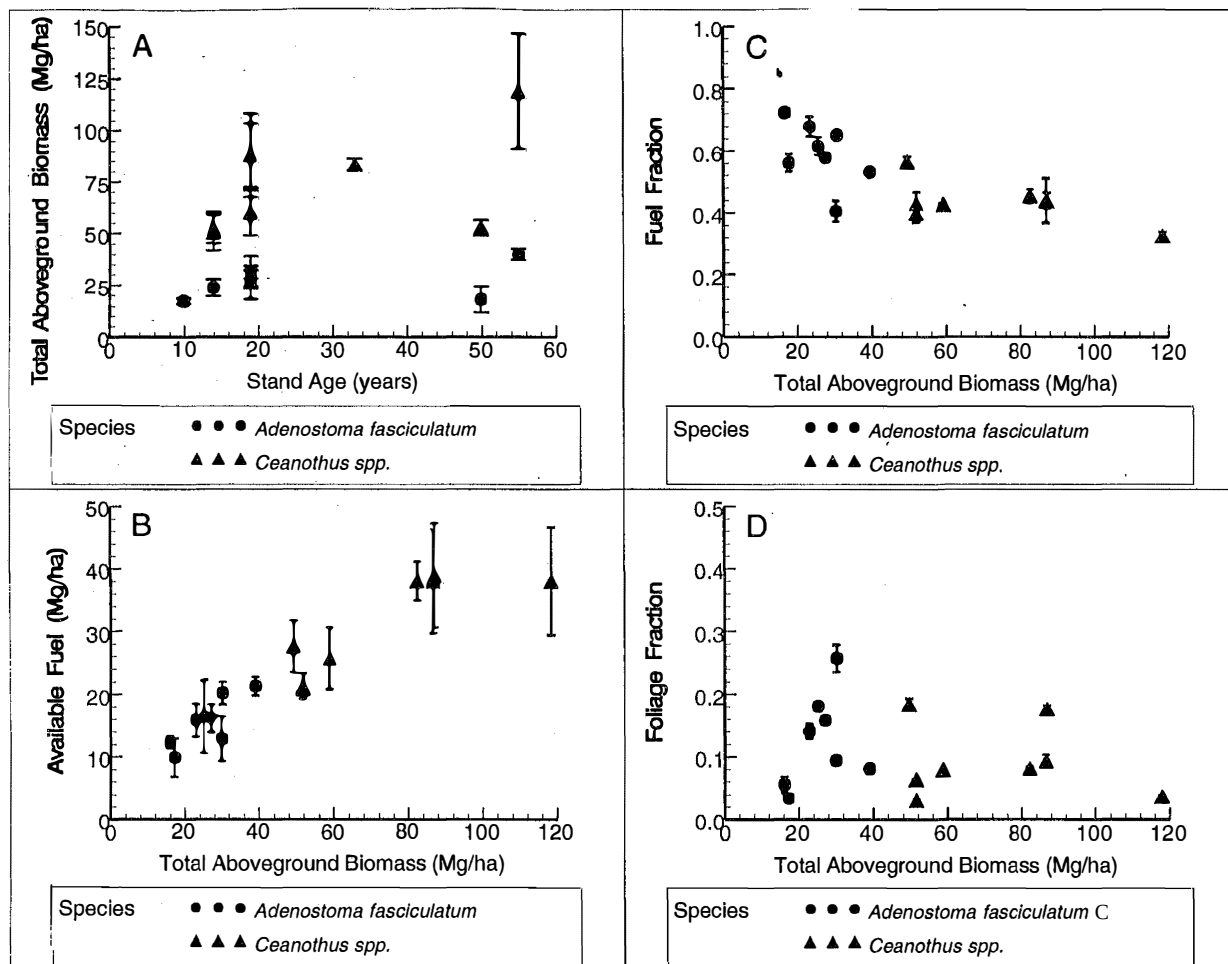


Figure 3. Total aboveground biomass versus stand age (A), and available fuel (B), fraction of stand biomass that constitutes available fuel (C), and foliage as a fraction of stand biomass (D) versus total aboveground biomass for 16 chaparral sites in southern California, USA.

of site factors and productivity, we feel that additional data need to be collected to address this question specifically.

Available Fuel

Because available fuel contains only dead wood less than 76 mm in diameter, live wood less than 6.3 mm in diameter, and foliage, total available fuel is somewhat less than total aboveground biomass for most stands, but otherwise displays similar trends with respect to stand age. An important question is what fraction of total biomass comprises available fuel, and is this fraction related to variables like species composition, stand age, or total stand biomass. These relationships could be exploited to provide estimates of total fuel, or perhaps fuel components, without the need for costly, labor intensive partitioning of shrub samples into components. Total available fuel increases with total biomass (Figure 3B), but total available fuel does not appear to be a constant proportion of total biomass (Figures 3B and 3C). *Ceanothus* species tend to grow larger diameter stems and branches than does *A. fasciculatum*, and this is illustrated in the lower fuel fraction in *Ceanothus*-dominated stands (Figure 3C), where more of the total stand biomass is concentrated in large diameter woody material which is not considered to be available fuel. Average fuel fraction was 59 (± 4 , SE) percent for *A. fasciculatum* stands, and 43 (± 2 , SE) percent for *Ceanothus*-dominated stands (Figure 3C). We suspect that the relative dominance, i.e., proportion of total biomass, of species with different physical structure, in stands of mixed composition will be related to the fuel fraction. For example, the *Ceanothus*-dominated stand with the highest fuel fraction in our study, 56 percent, had a larger *A. fasciculatum* component than any other *Ceanothus* stands we observed (Figure 3C). Future analyses will incorporate any published data available to investigate variability in fuel fraction within species, and in relation to species proportion in mixed stands.

Foliage Biomass

Foliage of chaparral plants has very high surface-to-volume ratios (σ), which means it is rapidly dehydrated and ignited by a flame front, and is therefore a very important fuel for fire propagation in chaparral. Foliage as a fraction of total stand biomass ranged from 3 to 25 percent, with an average of 11 (± 2 , SE) percent, (Figure 3D), and did not appear different between *A. fasciculatum* and *Ceanothus* stands. However, the two *Ceanothus* stands with the lowest foliage fractions, about 3 percent, were composed of *Ceanothus oliganthus* and *Ceanothus spinosus*, species with very thin, mesophytic leaves compared to the thick, sclerophyllous leaves of many *Ceanothus* species (Figure 3D). Foliage has high σ compared to woody fuels, which gives foliage strong influence on fire behavior in simulations, so it may be neces-

sary to consider the influence of leaf morphology on foliage biomass if constructing site-specific fuel models. Observations of actual fires also indicates that propagation of fire through the chaparral canopy is strongly dependent on foliage.

Dead Fraction

Dead woody biomass in chaparral originates from two distinctly different sources. The first, and that most commonly described in the literature, is from mortality of branches and plants during stand development. This mortality likely results from shading and competition for soil water, and perhaps nutrients. The other source is from residual "skeletons" of shrubs that were not burned in the last fire. Dead biomass varied widely in our study, ranging from 12 to 46 percent of total stand biomass (Figure 4A), and showed no clear trends with respect to species composition or stand age. Although several authors have previously indicated that chaparral dead fraction increases strongly as stands age, (e.g. Rothermel and Philpot 1973; Green 1981), our data are consistent with the findings of Paysen and Cohen (1990), that chaparral dead fraction is not reliably predicted by age. Distinguishing whether dead fuel is expressed as a fraction of total fuel, or of total stand biomass, is important for clarity, but this distinction is rare in the literature. In our study, virtually all dead wood was within the size range to be considered fuel, but if this dead fuel mass is expressed as a fraction of available fuel we get a range of 27 to 72 percent, considerably higher than dead fuel as a fraction of stand biomass (Figure 4B). We do not know whether this ambiguity in terminology is responsible for part of the confusion over dead fuel fraction in the literature, but hope that future authors will define and use terminology clearly. While most dead fuel is assumed to result from branch and shrub mortality during stand development, we caution that this may not always be the case. The youngest stand in our study appears to have an extremely high proportion of dead fuel, 63 percent of total fuel (Figure 4B). We observed that this stand contained many dead shrub stems 25 to 76 mm in diameter, with no fine branchwood attached, that appeared to be residual from a fire 10 years earlier. While this situation may be atypical, it will influence fuel bed geometry in potentially significant ways.

Spatial Variation of Biomass and Fuels

Although variation in biomass and fuels among chaparral sites has been well documented, much less information has been published on variability within a site. Several of our studies have involved sampling multiple plots within a given stand. Compared to surrounding areas, these stands were relatively homogeneous within an area between 0.5 and 5 ha. The coefficient of variation among plots in estimated stand biomass was often as high as 25

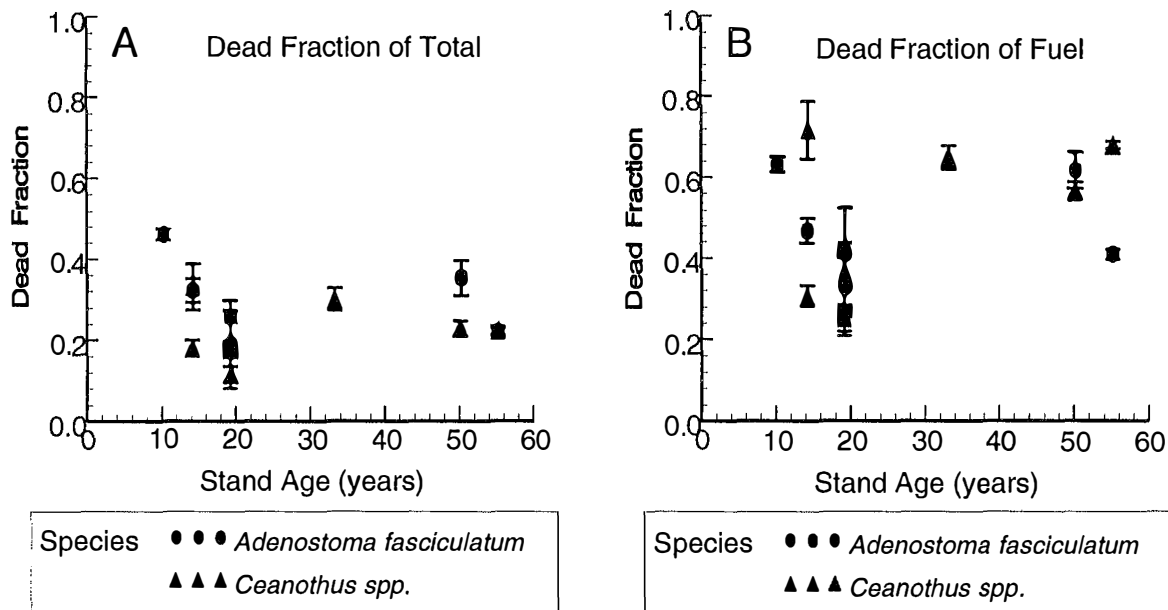


Figure 4. Dead biomass in relation to stand age, expressed as a fraction of total aboveground biomass, (A) and as a fraction of available fuel (B), of 16 chaparral sites in southern California.

or 30 percent (Figure 5); For the stand of *A. fasciculatum* with *Arctostaphylos glandulosa* (Eastwood manzanita) as an associated species at the North Mountain Experimental Area, biomass of 5m x 5m subplots ranged between 20 and 60 Mg/ha (Figure 5), with a mean of $39 (\pm 2.6, \text{SE})$ Mg/ha. This variability in biomass is readily apparent from the variable structure of the plant community as one explores this site. The topography of this area is highly dissected, and variability in soil depth to bedrock, and the degree of weathering of the bedrock are also quite variable (Sternberg et al. 1996). These factors could very well influence microsite productivity, and consequently, biomass and fuel accumulation, through their influence on water availability for plant growth.

Variable fuel structure may well have an important effect on both model predicted, and actual fire behavior (Fujioka 1985). The degree to which spatial variation in fuels will affect fire behavior is unclear for several reasons. Although it is possible to assess the sensitivity of the Rothermel model to changes in chaparral fuel, we still don't have a good sense of how well predictions from the Rothermel model correspond to actual fire behavior in chaparral fuels. This uncertainty is due at least in part to the difficulty of collecting data on fire spread where all of the required inputs for fire modeling are accurately known (Albini and Anderson 1982). Secondly, we don't know clearly at what spatial scale the variability in fuels becomes important. There may well be a spatial scale below which variability in fuels does not affect fire behavior in an observable manner, therefore the average condition of such a unit would be sufficient knowledge. Above this scale, however, variability could strongly in-

fluence fire behavior as the flame front moved through fuel zones with different physical structure. This topic requires much investigation to answer these questions.

Future Research Needs

A computerized fuels database with sufficient accuracy, accessibility, and geographic coverage is a necessary element for fire modeling for both strategic and tactical applications (Albini and Anderson 1982). To implement such a system, we need to elucidate further patterns of chaparral growth through time and in relation to site characteristics. We also need to correlate ground-based measures of chaparral fuels and biomass with remotely sensed data. This would allow mapping chaparral fuels at broad landscape levels, would facilitate incorporation of fuels data with other pertinent landscape attributes via GIS, and could allow relatively easy updating and modification of the database as needed to account for growth, or disturbances such as fires or episodes of dieback related to drought and pathogens such as *Botryosphaeria dothidea*. Although remote sensing is vital to the development of an extensive fuels database, several important knowledge gaps can be filled only through ground-based sampling. These questions mostly relate to quantifying the effects of site productivity on chaparral growth, and relating the accumulation of dead woody fuel to causal, or perhaps only associative, factors. Identifying the causal mechanism of deadwood accumulation would be ideal, but an associative relationship potentially could be exploited in a predictive manner as well.

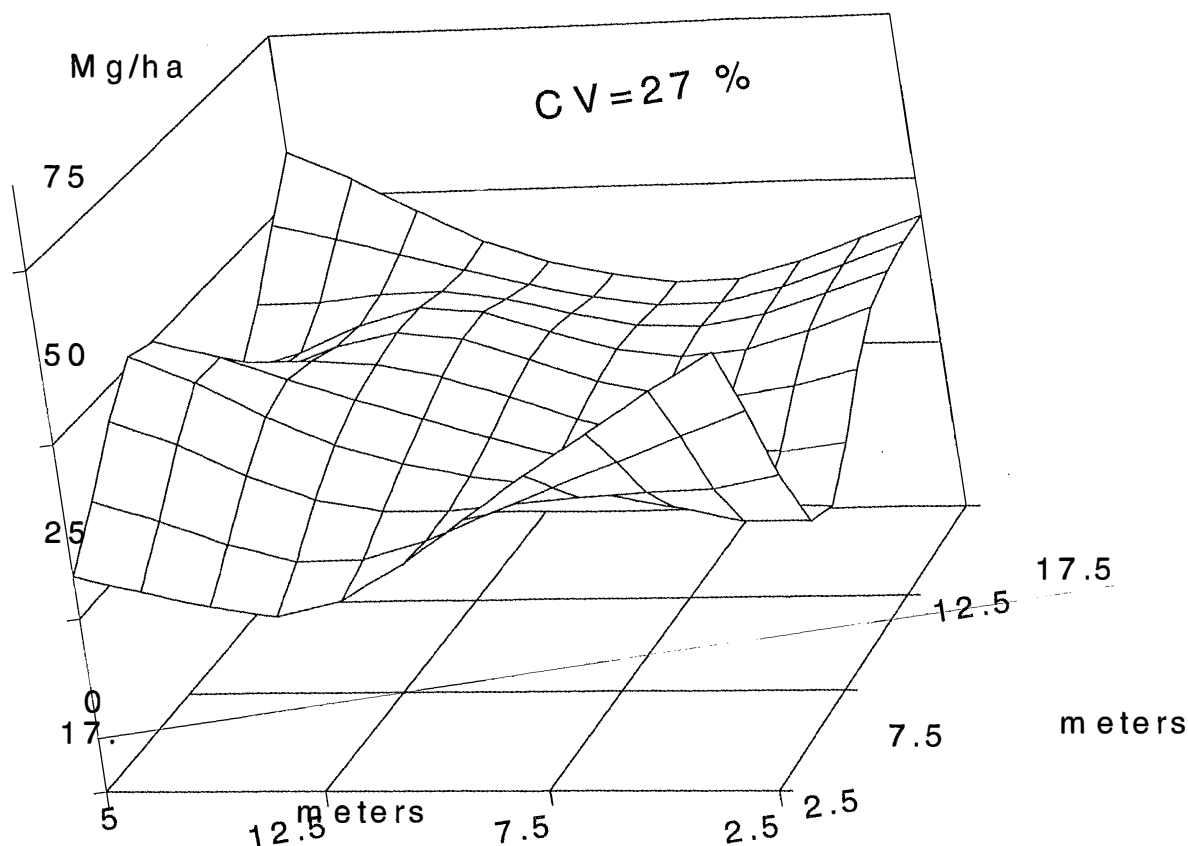


Figure 5. Spatial variation of aboveground biomass in an *Adenostoma fasciculatum* - *Arctostaphylos glandulosa* stand at the North Mountain Experimental area in the San Jacinto Mountains of southern California. The surface shows a spline interpolation of biomass values estimated for 16 contiguous subplots (5m by 5m in size), and the x and y axes show relative position of subplot centers at 2.5 m intervals. Coefficient of variation of total aboveground biomass among these subplots was 27 percent.

Fuelbed geometry is probably also very important to the manner in which fire propagates in chaparral. Unlike forest floor fuels, chaparral fuel particles typically are oriented vertically, and chaparral fuel beds have very high porosity compared to many other wildland fuel types. Fine twigs and foliage tend to be stratified vertically, and the height of greatest concentration of these most flammable fuels above the ground surface varies both within and among species. These and other structural properties of chaparral fuelbeds have only been described in a very cursory, simplistic fashion. Yet, practical experience indicates that these may have a profound influence on fire behavior. *A. fasciculatum* stands, with many fine branches in relatively compact crowns, which tend to be close to the ground, seem relatively easy to burn under prescribed burning conditions, while mature *Ceanothus* stands, with taller canopies composed of fuels with lower σ , often seem able to sustain combustion only under extreme conditions. Although many fire professionals have an intuitive sense of these types of phenomena, quantitative de-

scriptions of thresholds such as these have not been developed, in spite of their potential utility. Not only do we lack understanding of where spread thresholds may occur, we can't describe the relative influence of σ versus fuel bed porosity or fuel particle arrangement on spread thresholds. Experimental fires, in which fire behavior can be closely monitored and related to measured fuels and weather information would help to describe thresholds which separate conditions where fires either will or will not spread, and at what scale does variability in fuels affect fire spread and intensity in a detectable fashion.

References

- Albini, F. A., and E. B. Anderson. 1982. Predicting fire behavior in U.S. Mediterranean ecosystems. P. 483-489 in Proceedings of the Symposium on Dynamics and Management of Mediterranean-type Ecosystems. June 22-26, 1981, San Diego, CA.

- Andrews, P. L. 1986. BEHAVE: fire behavior prediction and fuel modeling system—BURN subsystem, part 1. USDA For. Serv. Gen. Tech. Rep. INT-194. 130 p.
- Burgan, R. E., and R. C. Rothermel. 1984. BEHAVE: Fire behavior prediction and fuel modeling system—FUEL subsystem. USDA For. Serv. Gen. Tech. Rep. INT-167. 126 p.
- Cochran, W. G. 1963. Sampling techniques. 2nd ed. New York: Wiley. 413 p.
- Finney, M. A. 1994. Modeling the spread and behavior of prescribed natural fires. P. 138-143 in Proceedings of the 12th Conference on Fire and Forest Meteorology, Oct. 26-28, 1993, Jekyll Island GA. Society of American Foresters.
- Fujioka, F. M. 1985. Estimating wildland fire rate of spread in a spatially nonuniform environment. *Forest Science* 31(1): 21-29.
- Green, L. R. 1981. Burning by prescription in chaparral. USDA Forest Service General Technical Report PSW - 51. 36 p.
- Gray, J. T. 1982. Community structure and productivity in *Ceanothus* chaparral and coastal sage scrub of Southern California. *Ecol. Monogr.* 52(4): 415-435.
- Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecol. Monogr.* 41(1): 27-52.
- Paysen, T. E., and J. D. Cohen. 1990. Chamise chaparral dead fuel fraction is not reliably predicted by age. *West. J. of Appl. For.* 5(4):127-131.
- Riggan, P. J., S. Goode, P. M. Jacks, and R. N. Lockwood. 1988. Interaction of fire and community development in chaparral of southern California. *Ecol. Monogr.* 58(3):155-176.
- Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service Research Paper INT 115. 40 p.
- Rothermel, R. C., and C. W. Philpot. 1973. Predicting changes in chaparral flammability. *J. For.* 71(1):640-643.
- Rundel, P. W., and D. J. Parsons. 1979. Structural changes in chamise (*Adenostoma fasciculatum*) along a fire-induced age gradient. *Jour. Range Manage.* 32(6):462-466.
- Schlesinger, W. H., and D. S. Gill. 1980. Biomass, production, and changes in the availability of light, water, and nutrients during the development of pure stands of the chaparral shrub, *Ceanothus megacarpus*, after fire. *Ecology* 61(14):781-789.
- Specht, R. L. 1969. A comparison of sclerophyllous vegetation characteristic of Mediterranean-type climates in France, California, and southern Australia. II. Dry matter, energy and nutrient accumulation. *Aust. J. Bot.* 48:293-308.
- Sternberg, P. D., M. A. Anderson, R. C. Graham, J. L. Beyers, and K. R. Tice. 1996. Root distribution and seasonal water status in weathered granitic bedrock under chaparral. *Geoderma* 72: 89-98.
- Stohlgren, T. J., D. J. Parsons, and P. W. Rundel. 1984. Population structure of *Adenostoma fasciculatum* in mature stands of chamise chaparral in the southern Sierra Nevada, California. *Oecologia* 64: 87-91. 9