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ESTIMATING BIOMASS IN CALIFORNIA'S CHAPARRAL AND COASTAL SAGE SCRUB SHRUBLANDS

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ABSTRACT

Despite being one of the most extensive vegetation types in the North American Mediterranean Climate Zone, information on the amount of biomass and carbon stock associated with shrubland vegetation is still largely unknown. Efforts to quantify shrubland biomass through fieldwork consist of either direct measurement using destructive vegetation sampling or indirect measurement through the combined use of stem measurements and allometric equations. Both methods have their own benefits and shortcomings, resulting in substantial variation in how shrubland biomass is reported. Here we aim to provide a comprehensive review and synthesis of available shrubland biomass data from studies based in California to provide a concise and reliable source for natural resource managers. We conducted a literature review of 37 studies published over a span of 72 yrs to compile estimates of aboveground biomass (live, dead, and total), leaf biomass, stem biomass (live, dead, and total), litter biomass, and belowground biomass for three prominent shrubland communities and four shrubland species in the California Floristic Province. Overall aboveground biomass in shrub communities was greatest in mixed chaparral (3461 g/m^2), followed by chamise chaparral (2114 g/m^2), and coastal sage scrub (1583 g/m^2). In each community total aboveground biomass increased with the age of the stand. Leaf, stem, and litter biomass estimates were also highest for mixed chaparral compared to the other communities. Of the four shrub species we summarized biomass data for, *Ceanothus greggii* A. Gray (Rhamnaceae) had the highest average aboveground biomass, followed by *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae), *Quercus berberidifolia* Liebm. (Fagaceae), and *C. cuneatus* (Hook.) Nutt. By compiling these studies and summarizing the biomass data reported in them, we provide a single resource to characterize the amount of biomass of three different shrublands and four species over their life cycle. This is an essential resource for land managers and practitioners who need field-based biomass and carbon stock figures for monitoring and reporting purposes.

Key Words: Aboveground biomass, *Adenostoma fasciculatum* Hook. & Arn., belowground biomass, California, carbon storage, *Ceanothus* sp., chaparral, coastal sage scrub, North American Mediterranean Climate Zone, *Quercus berberidifolia* Liebm.

Shrublands cover extensive areas of the North American Mediterranean Climate Zone (also known as the California Floristic Province), which includes most of California, southwestern Oregon, northwestern Baja California, Mexico, and a sliver of western Nevada. However, despite their large spatial extent there is little appreciation of the contribution shrublands make to carbon storage and carbon sequestration (Di Castri et al. 1981, Luo et al. 2007). Chaparral and coastal sage scrub are two highly characteristic shrubland types of the lowland and middle elevation of this Mediterranean Climate Zone, especially in the southern portions of California and northwest Baja California. These ecosystems support high levels of plant species richness and endemism (Burge et al. 2016), as do their analogues in other Mediterranean-type ecosystems globally (Cowling et al. 1996, Myers et al. 2000). However, very little is known of their contributions to carbon storage or cycling other than the fact that many species have extensive and deep root systems that can provide substantial belowground carbon storage (Kummerow et al. 1977, Luo et al. 2007).

Studies and data for estimating biomass and carbon storage for major habitat types dominated by forest, such as tropical rainforests, are routinely conducted and reported. For example, some early studies providing image-derived biomass estimates for tropical rainforests were instrumental in highlighting their critical role in the global carbon cycle (e.g., Foody et al. 2001, Saatchi et al. 2007, Propastin 2013).Within the North American Mediterranean Climate Zone, studies estimating biomass for forested portions of the landscape have been conducted, for example, for the Sierra Nevada of California (McGinnis et al. 2010, Zhang et al. 2014) and forests of northern California and southwestern Oregon (Hudiburg et al. 2009). However, studies estimating biomass of shrublands in Mediterranean climates, either in North America or in the four other regions of the world where this climate occurs, are comparatively rare (e.g., Cerrillo and Oyonarte 2006).

At the continental scale in the USA, shrubland mapping efforts generally underestimate the amount of biomass in shrublands. National scale datasets such as the National Biomass and Carbon Dataset (http://www.whrc.org/mapping/nbcd/) and LandCarbon (http://landcarbon.org/) use USDA Forest Service Forest Inventory and Analysis (FIA) plot data alongside Landsat imagery and occasionally radar remote sensing imagery. The FIA database includes shrubland plots but unlike in forest plots, aboveground biomass is not measured in shrub plots, thus carbon mapping relying on the FIA dataset shows shrubland carbon storage as zero. At the California state scale, efforts to map carbon include the California Department of Forestry and Fire Protection's biomass assessment of forests and shrublands (FRAP 2005). Estimates are based on integrating data from land cover datasets, fuel models, as well as other spatial data on slope, land cover, ownership and fire threat (Anderson 1982, FRAP 2002, 2003, 2005).

Alternatively, the California Forest and Rangeland Greenhouse Gas Inventory assessment (Battles et al. 2014) used USGS Landfire data (30m) on Existing Vegetation Type (EVT) and the associated information on vegetation height and cover, and generated biomass densities by shrub-height classes based on the literature. Note that none of the mapping efforts described above address biomass stored belowground, which can be substantial, accounting for up to 41% of the species biomass in *Adenostoma fasciculatum* Hook. & Arn. (Kummerow et al. 1977) and 47% in *Arctostaphylos glauca* Lindl. (Miller and Ng 1977). At finer spatial scales, studies reporting field measurements of biomass in shrublands are characterized by a lack of consistency in the data collection methods and reporting. These inconsistencies are largely due to the variation in the focus of different studies and the research questions they aim to answer. Field studies vary in plot and sample size and biomass is reported using a variety of different metrics making extrapolations over larger shrubland areas challenging, given the variation in elevation (300–3000 m), soils, topography, aspect, coastal or desert exposure, and disturbance history.

Site specific influences on biomass make generalizations over large landscapes difficult. Plant community composition and structure are largely a direct reflection of the environment. At the regional scale, precipitation drives the distribution of mixed chaparral, chamise, and sage scrub, with mixed chaparral found in comparably wetter areas than both chamise and sage scrub (Conrad et al. 1986). In more productive sites, for example, with higher annual precipitation, higher annual production drives higher biomass accumulation (Gray 1982, Keeley and Keeley 1988, Schlesinger and Gill 1980, Uyeda et al. 2016). At a local scale, these differences in productivity can be due to slope, aspect, elevation, and soil characteristics (Hellmers 1955, Keeley and Keeley 1988, Regelbrugge and Conard 1996, Riggan and Dunn 1982, Schlesinger et al. 1982).

One reason for the lack of comprehensive data on shrubland biomass is the physical difficulty of conducting fieldwork in these systems. Dense stands of shrublands, particularly chaparral, are often described as 'impenetrable' and slopes are often steep, consequently undertaking systematic fieldwork requires substantial resources and effort (Uresk and Menke 1977). Executing full shrub harvests to directly measure above- and belowground biomass requires excessive time and resources and is not feasible to do at a large scale. A more common field method for assessing biomass combines destructive and non-destructive sampling. First, shrubs representative of the stand are selected and all aboveground biomass is collected. Plant material is then dried and weighed, occasionally being broken down into different stem size classes, plant parts and/or live and dead material. These shrub samples are then used to build species-specific regression equations that relate more easily measured variables (e.g., stem diameter, cover) to overall biomass. Ideally the roots are also excavated, however in most cases belowground biomass is either ignored or calculated based on pre-determined root:shoot ratios (Mooney and Rundel 1979).

The variation in the locations and site specific characteristics of field studies combined with the lack of accurate image-derived maps at a useful scale, create a need for the available biomass data to be synthesized in a concise and comprehensive way. From a resource management perspective, there is an increasing need to be able to accurately quantify biomass in shrubland landscapes and understand how it is impacted by management actions or by disturbance events such as wildfire. Similarly, information on the projected recovery of biomass post disturbance allows resource managers to anticipate the return of carbon storage ecosystem services and also the return of other services associated with vegetation and biomass, such as wildlife habitat or an established root system for retaining sediment, which is otherwise eroded from denuded slopes (Wohlgemuth et al. 1999). If disturbances become too frequent in shrubland communities (e.g., extremely short fire-return intervals) they can result in vegetation type-conversions, changing the nature of carbon storage and sequestration on the landscape as biomass values differ substantially between shrublands and non-native annual grasses (Keeley et al. 2005, Lippitt et al. 2013).

From a policy perspective, federal agencies such as the USDA Forest Service are now required to record and report information on carbon stocks. The Climate Change Scorecard for example, requires the quantity of carbon stocks under Forest Service management to be reported as well as the estimated impact of disturbance and management activities on these carbon stocks (http://www.fs.fed.us/climatechange/advisor/scorecard/carbon-assessment-stewardship.html). There is also increasing interest in mapping and quantifying the ecosystem services that natural landscapes provide, which can – among other things – provide the basis for developing market based approaches such as Payment for Ecosystem Services (Chan et al. 2006). In this paper we review and summarize the available literature on above- and belowground biomass of shrublands from studies based in California with the intention of providing a concise and reliable resource for natural resource managers.

METHODS

To compile the available data on biomass we carried out an extensive literature search online. We used the Web of Science and Google Scholar search engines specifying key words that included 'chaparral', 'shrubland', 'biomass', 'chamise', 'sage scrub', and 'California'. In addition, more general web searches were conducted to locate government documents or conference and symposium proceedings. From the relevant literature we extracted all reported biomass values and associated details including location (general and specific coordinates), sample size, parent material, elevation, aspect, age, stand height, unit of measurements, and species mix (when specified). In some cases biomass values were presented in graphical form rather than tables in which case it was necessary to approximate the actual values. We also recorded specific details of the biomass measurements, for example, whether reported values were calculated using destructive sampling, allometric equations, and/or whether dead material was included in the total biomass values. Studies that reported biomass values in a format that did not allow for comparisons with other studies were excluded (e.g., biomass per plant versus biomass per area).

To synthesize the array of different datasets we made the following assumptions. When only certain biomass components were reported we calculated the missing components when feasible. For example, if live and dead biomass values were reported without reporting a total aboveground biomass, we summed live and dead to report total aboveground biomass. Alternately, if a total aboveground biomass value and a live aboveground biomass value were reported without a value for dead biomass, we subtracted live from the total to provide a value for dead biomass. Finally, if aboveground biomass was reported without specifying live or dead, we assumed both were included. This last assumption may lead to an underestimate of total aboveground biomass, with combined live and dead averages occasionally exceeding total aboveground averages. Similarly for species-level data, when only live aboveground biomass was reported, we included it when averaging total aboveground biomass which may cause minor underestimates of species-level total aboveground biomass due to the missing dead biomass component. Consequently, in using these data we caution that some interpretation was necessary where the published material was unclear.

Once collected, we summarized the studies based on community type, age of shrubland and species. Community type was determined based on either the designation provided by the authors of the given study or assigned based on the shrub species reported for the given stand. Mixed chaparral stands varied in the number of species present and at times were largely dominated by one or two chaparral species such as *Ceanothus greggii* A. Gray or *Quercus berberidifolia* Liebm. Only pure stands of *Adenostoma fasciculatum* or stands that were explicitly dominated by *A. fasciculatum* were classified as chamise chaparral. In some cases, biomass averages of monospecific shrub communities were included in the species breakdown. It was assumed that the stand level biomass per unit area was the same as the shrub level biomass per unit area when there was only one species present in the stand. For example, a pure stand of *A. fasciculatum* included in the chamise chaparral summaries, was also included in the species summary for *A. fasciculatum*.

We summarized data for shrub communities and species that were sufficiently documented in the literature. Shrub communities with less than three studies reporting overall biomass, such as desert shrubland, are not reported. Data were grouped into different age classes (e.g., 1–10, 11–20, 21–30, >30 yr) and summarized accordingly. When shrubland age was not provided, effort was made to determine the general age of the stand through descriptions in the text. For instance, if a stand was described as "mature" but not assigned a specific age, it was placed in the oldest age class. If no age was provided nor was there sufficient information to assign an age class, the associated data were included in the overall averages but not in a specific age class. It is important to note that in most studies, the age of shrubland was determined by the time of last fire. Furthermore, biomass metrics reported in different studies varied widely with little consistency in the units of measurement used, which included tons/acre, lbs/acre, g/m^2, kg/m^2, Mg/ha, kg/ha, and tonnes/ha. We standardized all biomass units to g/m^2.

We report the available biomass studies at two spatial scales. First by community type: mixed chaparral, chamise chaparral, and coastal sage scrub; and second, at a higher resolution using four dominant shrubland species: *Adenostoma fasciculatum*, *Ceanothus greggii, Quercus berberidifolia,* and *C. cuneatus*. Subdividing the data by stand age, we summarize total aboveground biomass and range and the live and dead aboveground biomass and range (for the community level only).These were the most commonly reported variables in the studies reviewed. Other data we present include annual aboveground biomass increment, a breakdown of live and dead stem biomass, leaf biomass, litter biomass, and root-to-shoot ratios.

Finally, as a case study, we examined the relationship between aboveground biomass and one of the key drivers in productivity – precipitation. We mapped a subset of study locations (n = 36) and display these with annual mean precipitation from the Basin Characterization Model (BCM) dataset (1981–2010, Flint et al. 2013). Where a single location had multiple biomass measurements for different age classes of chaparral, we averaged measurements of stands >10 yr old (this allowed us to keep most of the plots except for the very young ones). For these 36 plots we identified mean annual precipitation values and assessed the correlation with mean aboveground biomass.

RESULTS

We reviewed 37 studies published between 1944 and 2016 with the majority published in the 1970s and 1980s. While we did our best to capture as much of the relevant literature as possible using the keyword searches described, it is inevitable that some studies might have been missed owing to time and resource constraints. Just over half of these documents (51%) were published in peer-reviewed journals and sources for the remaining documents included conferences and/or symposium proceedings (14%), government documents (14%), dissertations (11%), book chapters (8%), and university reports (3%). The most common shrub community types reported in the literature were mixed chaparral and chamise chaparral, followed by coastal sage scrub and desert shrublands. Many studies also reported biomass at the species level, with 75% of these sudies reporting biomass values for *A. fasciculatum*. Other species such as *Q. berberidifolia*, *C. greggii*, and *C. cuneatus* were less prevalent in the literature, each reported in 15% of the studies. There were 21 additonal species reported on but much less frequently.

Of the biomass metrics reported in the 37 studies, total aboveground biomass was reported most frequently (almost 90% of the studies), followed by live aboveground biomass, and dead aboveground biomass. Litter biomass, leaf biomass, live and dead stem biomass, and aboveground annual increment of biomass (i.e., accumulated biomass per yr) were less commonly reported (< 33% of the studies). Belowground biomass was the least common biomass metric, reported in only 16% of the studies.

Aboveground Biomass Estimates

Biomass at the community level. Mixed chaparral was the most widely reported shrub community in the literature. Summaries show that average total, live, and dead aboveground biomass were all lowest in 1–10 yr old stands (Table 1, Fig. 1). In these young stands total aboveground biomass on average was 861 g/m^2 with an average of 792 g/m^2 of live aboveground biomass and 300 g/m^2 of dead aboveground biomass. Total and dead aboveground biomass was the highest on average in stands >30 yr old with 4931 g/m^2 and 1575 g/m^2 respectively. Live aboveground biomass was the highest on average in 21–30 yr old stands with 4674 g/m^2 (Table 1, Fig. 1). The highest aboveground biomass reported among studies focusing on mixed chaparral was 11,800 g/m^2 in a 55 yr old *Ceanothus*-dominated stand (Regelbrugge and Conard 1996). Average annual aboveground biomass increment was highest in 21–30 year old stands at 952 g/m^2, however annual increment data reported for older stands (>30 yr old) were limited to only one study (Riggan and Lopez 1982; average biomass increment 67 g/m^2), so this value is unlikely to be representative of older mixed chaparral stands as a whole.

Chamise chaparral was the second most commonly reported shrub community in the literature (Table 2). There were no studies that report comparable biomass values for chamise chaparral in the 21–30 yr age class. Due to the lack of data for this age class, it was necessary to combine the 11–20 and 21–30 age classes. The lowest values for average aboveground total, live and dead biomass were found in the youngest stands (1–10 yr; Fig 2). Average total aboveground biomass in this age class was very similar to that of the young mixed chaparral stands with a value of 923 g/m^2. On average, total, live and dead aboveground biomass were all highest in >30 yr old stands. The highest reported total aboveground biomass was 4909 g/m^2 in a 37 yr old *A. fasciculatum* stand with a small component of *Ceanothus crassifolius* Torr. present (Specht 1969). Average biomass in >30 yr old chamise chaparral stands was about half that reported in equivalent stands of mixed chaparral (2787 g/m^2 and 4931 g/m^2 respectively).

In contrast, biomass data from coastal sage scrub stands were relatively limited and data only supported a breakdown into two age classes, 1–10 yr and >10 yr (Table 3). Average total and live aboveground biomass were both lowest in 1–10 yr old stands with 598 g/m^2 and 409 g/m^2 respectively (Fig. 3). Dead aboveground biomass for this age group was not reported in the literature. Average total and live aboveground biomass were highest in stands >10 yr old (the oldest stand reported on was 40 yr). Total aboveground biomass for older stands averaged 1901 g/m^2, with average live of 995 g/m^2 and average dead of 555 g/m^2.

Data on leaf, stem, and litter biomass were less commonly reported in the studies reviewed. Leaf

TABLE 1. SUMMARY OF CALIFORNIA MIXED CHAPARRAL BIOMASS DATA BASED ON 25 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2016 IN THE AVAILABLE LITERATURE [REFERENCES 1–7, 9–12, 17, 20–25, 27, 28, AND 32–36 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from ≤ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live aboveground biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment (g/m^2/yr.)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	861.4	120–1814	791.5	200–2055	300.0	40–700	201.9	197.0	998.5[i]	–	1205.0[i]	–	–
11–20	3473.8	411–8740	3417.9	1000–7644	422.4	0–1520	850.0[i]	336.0[i]	2896.0[i]	–	–	–	–
21–30	4352.5	1912–8290	4673.5	2012–6680	955.3	400–1610	951.9	388.2	5167.5[i]	1304.0[i]	5244.1	2108.0	–
>30	4931.0	1730–11800	3999.7	1850–10000	1574.9	0–4500	66.5[i]	200.0[i]	1580.0[i]	1165.7[i]	2870.0[i]	5300.0[i]	1330.0[i]
Total	3460.5	120–11800	3166.3	200–10000	688.8	0–4500	427.0	303.0	2801.3	1257.9	4198.8	2541.3	1330.0[i]

TABLE 2. SUMMARY OF CHAMISE CHAPARRAL BIOMASS DATA BASED ON 13 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2012 IN THE AVAILABLE LITERATURE [REFERENCES 1–3, 5, 10, 12, 17, 21, 23, 27, 30, 31, AND 35 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from ≤ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live Aboveground Biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment (g/m^2/yr.)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	922.6	175–1636	670.4	115–1054	451.7[i]	158–583[i]	110.0[i]	–	–	762.2[i]	–	–	–
11–30	2536.7	1440–3050	1921.1	1400–2530	583.4	40–920	–	–	–	–	–	–	–
> 30	2787.2	1510–4909	2129.9	1400–3049	711.0	200–2184	–	–	–	560.4[i]	–	–	–
Total	2114.4	175–4909	1687.5	115–5600	642.4	25–2184	110.0[i]	–	–	661.3[i]	–	1277.8[i]	–

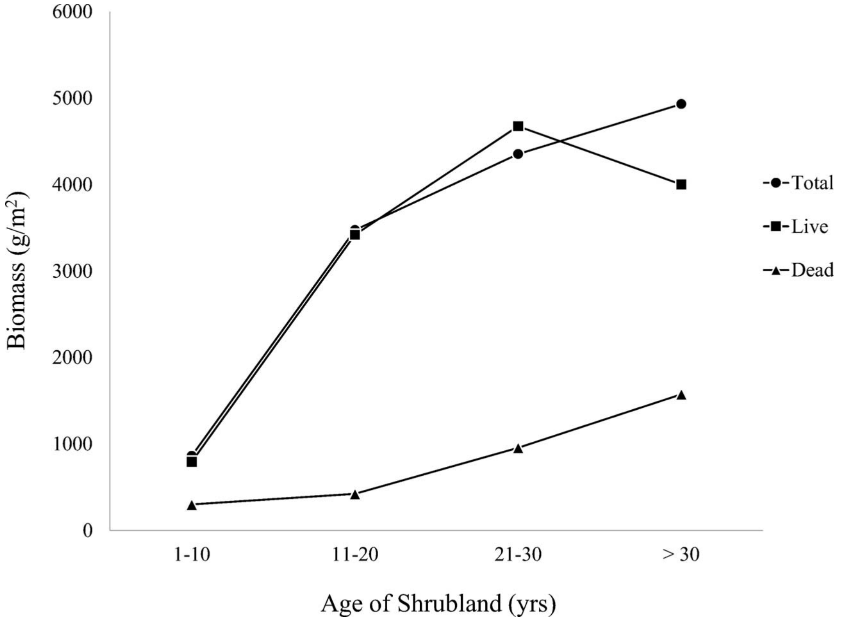

FIG. 1. Estimates of aboveground biomass (g/m^2) for mixed chaparral by age class based on 25 studies with biomass measurements from 1944–2016. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

biomass in mixed chaparral was approximately twice that of coastal sage scrub communities (303 g/m^2 compared to 141 g/m^2; Tables 1 and 3). Similarly, total stem biomass was about four times greater in mixed chaparral compared to coastal sage scrub (4199 g/m^2 compared to 1120 g/m^2). The amount of litter across all age classes was highest in mixed chaparral followed by coastal sage scrub and then chamise chaparral communities (2541 g/m^2, 1392 g/m^2, and 1278 g/m^2 respectively).

FIG. 2. Estimates of aboveground biomass (g/m^2) for chamise chaparral by age class based on 13 studies with biomass measurements from 1944–2012. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

TABLE 3. SUMMARY OF COASTAL SAGE SCRUB BIOMASS DATA BASED ON 10 STUDIES WITH BIOMASS MEASUREMENTS FROM 1981–2012 IN THE AVAILABLE LITERATURE [REFERENCES 2, 3, 5, 7, 8, 10, 14, 21, 35, AND 37 IN APPENDIX 1]. Note: average total aboveground biomass does not equate to live plus dead because not all studies report all three variables. Total includes all age classes as well as studies that did not provide a shrubland age. [i]Values averaged from $\leq$ 2 studies.

Age class (yrs.)	Total aboveground biomass (g/m^2)		Live aboveground biomass (g/m^2)		Dead aboveground biomass (g/m^2)		Avg biomass increment (g/m^2/yr.)	Avg leaf biomass (g/m^2)	Avg live stem biomass (g/m^2)	Avg dead stem biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Avg belowground biomass (g/m^2)
	Avg	Min-Max	Avg	Min-Max	Avg	Min-Max							
1–10	597.8[i]	255–958[i]	409.4[i]	200–630[i]	–	–	306.9[i]	–	–	–	–	–	–
> 10	1901.1	1172–2800	995.0	400–1300	555.4	247–852	305.1[i]	140.8[i]	867.3[i]	253.1[i]	1120.4[i]	1370.9[i]	–
Total	1582.7	255–3094	660.3	200–2200	617.7	247–919	306.5	140.8[i]	867.3[i]	253.1[i]	1120.4[i]	1392.2[i]	–

TABLE 4. SUMMARY OF BIOMASS MEASUREMENTS FOR 4 DOMINANT CHAPARRAL SPECIES BASED ON 20 STUDIES WITH BIOMASS MEASUREMENTS FROM 1944–2012 IN THE AVAILABLE LITERATURE [REFERENCES 4, 7, 9, 12, 13, 15, 16, 18–20, 22, 25–32, AND 35 IN APPENDIX 1]. Note: some ages inferred based on stand age or age of surrounding shrubs. [i]Values averaged from $\leq$ 2 studies.

Species	Age range of shrubs included (yrs)	Total aboveground biomass (g/m^2)		Avg annual biomass increment (g/m^2/yr.)	Avg leaf biomass (g/m^2)	Avg total stem biomass (g/m^2)	Avg litter biomass (g/m^2)	Total belowground biomass (g/m^2)		Avg root:shoot ratio
		Avg	Min-Max					Avg	Min-Max	
Adenostoma fasciculatum	1–60+	1957.6	198–6818	252.8	246.7	1136.3	–	1632.7	90.3– 4789	0.6[i]
Ceanothus greggii	21–24	4876.8[i]	1109–10139[i]	595.5[i]	–	1275.3[i]	2217.3[i]	798.4[i]	154.8–1442[i]	0.3[i]
Quercus berberidifolia	23–35+	1709.5	1233–2046	238.2[i]	310.0[i]	1695.7[i]	5300.0[i]	1330.0[i]	–	–
Ceanothus cuneatus	15–25	880.6	814–990	–	46.9[i]	767.0[i]	–	–	–	–

FIG. 3. Estimates of aboveground biomass (g/m^2) for coastal sage scrub based on 10 studies with biomass measurements from 1981–2016. Note: average total aboveground biomass does not equate to live plus dead because not all studies reported all three variables.

Biomass at the species level. At a finer species-level scale, we report on four dominant chaparral species based on their prevalence in the literature (Table 4). We only report total aboveground biomass, excluding a breakdown of live and dead aboveground biomass due to insufficient data. The most frequent shrub species measured was *A. fasciculatum*. Average total aboveground biomass for *A. fasciculatum* was 1958 g/m^2 (Table 4). The lowest reported biomass in the literature was 198 g/m^2 for a 1 yr old individual (Sparks and Oechel 1993) and the highest was 6818 g/m^2 reported by Kummerow et al. (1977) for a 2 yr old individual. Kummerow et al. (1977) note that this individual was resprouting and had numerous dead stems resulting in a root:shoot ratio of 0.7. The next highest biomass reported in the literature for *A. fasciculatum* was for a mature individual with a biomass of 4260 g/m^2 (3,363 g/m^2 of which was live; Green 1970). Average total aboveground biomass was the highest for *C. greggii*, which also had the maximum biomass reported at 10,139 g/m^2 for one individual (no age provided), although 20–30% of this biomass was from dead stems (Kummerow et al. 1977). Biomass reported for *Q. berberidifolia* was lowest in a mature shrub at 1233 g/m^2 (Green 1970) and highest in a 23 yr old shrub at 2046 g/m^2 (Mooney et al. 1977). *C. cuneatus* had the lowest average total aboveground biomass as well as the smallest range of biomass values reported with 814 g/m^2 as the minimum reported biomass (Parsons and Stohlgren 1986) and 990 g/m^2 as the maximum reported biomass (Stohlgren et al. 1989). Of the species reported, *Q. berberidifolia* had slightly higher leaf biomass compared to *A. fasciculatum* (310 g/m^2 compared to 247 g/m^2), and *C. cuneatus* the least (47 g/m^2). *Q. berberidifolia* also had the highest stem biomass and litter biomass, although litter biomass at the species level was only available for *Q. berberidifolia* and *C. greggii* (Table 4).

Patterns of aboveground biomass with precipitation. The 36 plots we mapped ranged from coastal locations in Ventura County to higher elevation areas in the Angeles National Forest. It is these higher elevation areas where mean annual precipitation is also highest (Fig. 4). The correlation of mean aboveground biomass with mean annual precipitation showed a positive relationship with biomass increasing with greater mean precipitation ($R^2 = 0.23$, Fig. 5).

Belowground Biomass Estimates

Belowground biomass was by far the least reported metric in the literature. Only four studies reported belowground biomass values determined via direct measurements. Two were published in the late 1970's, one in the early 1980's and one in 2004, all in southern California. The most detailed studies were

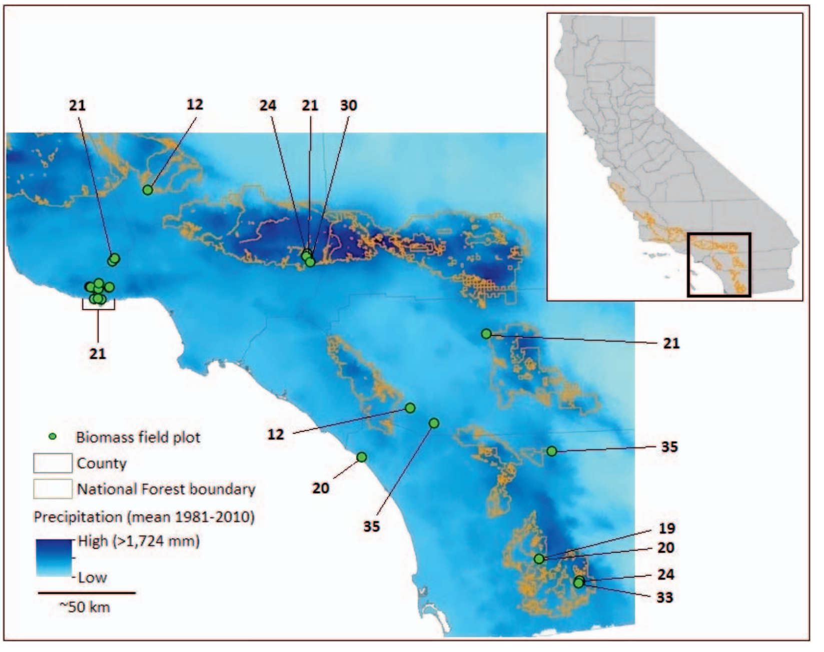

FIG. 4. Location of 36 field plots mapped with mean annual precipitation. Inset map shows enlarged area outlined in black. Numbered plot locations correspond to references listed in Appendix 1. Note: (a) a number of plots in the map overlap making them difficult to distinguish and (b) plots with multiple stand values were averaged where stands were >10 yr olds.

undertaken by Kummerow et al. (1977) and Miller and Ng (1977). In a 70 m^2 mixed chaparral stand dominated by *A. fasciculatum*, Kummerow et al. (1977) wired shrubs into place and hydraulically excavated the roots. Biomass as well as root:shoot ratios were determined for each individual shrub excavated and belowground biomass values ranged from about 1402 g/m^2 to 4789 g/m^2 for *A. fasciculatum*, 2028 g/m^2 for *Arctostaphylos pungens*, and 1442 g/m^2 for *Ceanothus greggii*. An average

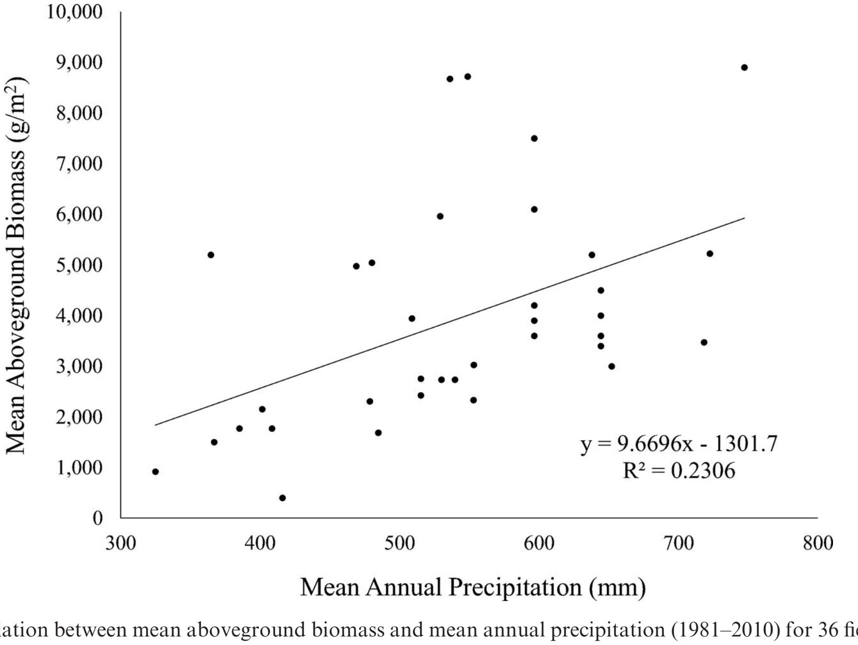

FIG. 5. Correlation between mean aboveground biomass and mean annual precipitation (1981–2010) for 36 field plots with precise coordinates.

overall root:shoot ratio of 0.6 was determined for all species included in the study. Species-specific root:-shoot ratios included 0.44 for an *Arctostaphylos pungens* individual and 0.7 for an *A. fasciculatum* individual (Kummerow et al. 1977). Similarly, Miller and Ng (1977) hydraulically excavated individual shrubs in a 21 yr old mixed chaparral stand. Biomass values reported were per shrub only, however, and varied greatly depending on shrub size. *A. fasciculatum* was the main shrub analyzed in the study (4 individuals total) and had a root:shoot ratio ranging from 0.49 to 0.69.

Lipson et al. (2004) undertook a study of the effects of long-term elevated atmospheric CO_2 on root growth among other variables in an 11 yr old *A. fasciculatum* dominated stand. Samples were collected for root biomass measurements using a 10 cm diameter metal soil coring device to a depth of 30 cm, and reported a root biomass of 250 m/g^2 in the control, which is likely an underestimate of the total belowground biomass due to sampling methods. Riggan and Lopez (1982) assessed nitrogen relations in a 35 yr old *Q. berberidifolia* dominated chaparral stand and report the pre-fire burl biomass of *Q. berberidifolia* as 1330 g/m^2 but did not assess the biomass of the entire root system.

There were also several studies that looked at root:shoot ratios of shrub seedlings (<12 months old) to assess nitrogen fertilization and allocation tradeoffs among life history traits, among other things. Padgett and Aleen (1999), for example, assessed biomass accumulation in coastal sage scrub species after growing for three months in pots and found that *Artemisia californica* root:shoot ratios range from 0.12 to 0.48 depending on the amount and type of nitrogen added. In a study comparing biomass allocation in shrubs exhibiting three different life history traits, Pratt et al. (2012) found that non-sprouting shrubs (e.g., *Ceanothus megacarpus*, *C. cuneatus*) had an average root:shoot ratio of 0.77 when grown in the sun and 0.44 when grown in the shade. Facultative sprouters (e.g., *C. spinosus*, *C. leucodermis*) had an average root:shoot ratio of 0.84 in the sun and 0.31 in the shade and lastly, obligate seeders (e.g., *Rhamnus ilicifolia, R. californica*) had an average root:shoot ratio of 1.7 in the sun and 0.89 in the shade (Pratt et al. 2012).

Discussion

Our review included 37 studies over 72 yrs from which we compiled summary estimates on total, live and dead biomass by age class, as well as information on leaf biomass, live and dead stem biomass, and belowground biomass from a subset of these studies. Key findings were that overall total aboveground biomass in the shrub communities reported was greatest in mixed chaparral (3461 g/m^2), followed by chamise chaparral (2114 g/m^2), and coastal sage scrub with a total aboveground biomass less than half that of mixed chaparral (1583 g/m^2). In each community total average aboveground biomass generally increased with the age of the stand. Other variables measured included leaf biomass, stem biomass and litter biomass which were also all highest in mixed chaparral compared to chamise chaparral or coastal sage scrub communities. By species, *C. greggii* had the highest average aboveground biomass (4877 g/m^2) and *C. cuneatus* had the least biomass with 881 g/m^2. *Q. berberidifolia* had the highest leaf, total stem, and litter biomass of the four species reported and *A. fasciculatum* had the highest belowground biomass of the two species where reporting was possible, with an average root:shoot ratio of 0.6.

Although we summarized available data on the annual net growth of shrubland communities and individual species, we did not include biomass estimates for annual flower and fruit production in our summaries due to the lack of information on this biomass component in the literature as well as the ephemeral nature of reproductive structures. Reproductive output, however, can be quite substantial, especially for non-sprouting shrub species (e.g., over 150 g/m^2 for *Arctostaphylos glauca*; Keeley and Keeley 1977). While this biomass does not remain as standing biomass on individual shrubs over time, it is likely accounted for indirectly through estimates of biomass present in the litter layer. Annual reproductive output is important to take into consideration but it may not be relevant when estimating long-term carbon storage.

This review provides a summary of biomass at the community and species level, however, levels of biomass vary considerably acoss the landscape, most notably with water availability and associated plant water stress during the summer drought (Mooney 1977a). Areas with higher annual precipitation and at higher elevations, e.g., mesic north-facing slopes, and slopes with deeper soils, have sustained high rates of production (Riggan and Dunn 1982). The example we provide using the 36 plots which had precise coordinates supports this point, and shows that mean aboveground biomass has a positive correlation with mean annual precipitation in southern California. Miller (1947) estimated that north facing slopes have roughly 30% more water available in the soil, and consequently chaparral communities on these aspects develop a larger leaf area and higher rates of production than those on south facing slopes (Krause and Kummerow 1977).

A noteable point from these summaries is the amount of dead aboveground biomass reported. Dead biomass accounts for approximately one-half the total biomass in coastal sage shrub, one-third in chamise chaparral, and one-fifth in mixed chaparral. The ratio of live to dead biomass in a stand is often related to the stand's fire history. Chaparral species typically have one of three life history strategies: obligate seeder, obligate resprouter, or faculative seeder. Of these three strategies, obligate resprouters and facultative seeders are capable of regenerating vegetatively after fire (Keeley and Keeley 1988). Shrubs that resprout typically have belowground lignotubers, also called burls, that store carbohydrates and send out sprouts when burned. The biomass of these burls can make up a significant portion of the overall biomass of an individual shrub (Kummerow et al. 1977, Miller and Ng 1977). Additionally, recently burned stands tend to have a higher ratio of dead to live aboveground biomass due to the original stems not being fully consumed by the fire. Alternatively, during long fire-free periods, slow decomposition rates can lead to dead material accumulating in these stands and if fire has not entered into a stand for long enough, it is possible for more competitive, disturbance-free taxa to replace disturbance-dependant taxa, altering the type and amount of biomass in the system (Keeley and Keeley 1988, Hilbert and Larigauderie 1990).

Using simulation modeling, Hilbert and Larigauderie (1990) investigated the mechanisms behind stand senescence in Mediterranean-climate shrublands using available data in the literature. The authors developed two versions of a general model based on dynamics observed in pure stands of *Adenostoma fasciculatum*: one that accounts for individual shrub senescence (e.g., accelerated mortality of mature plants) and one that does not. According to the model results, live biomass and cover tends to peak at about 25–30 yr and litter biomass peaks at about 40 yr after fire, while standing dead biomass shows a slow increase over a 100 yr period. With the incorporation of shrub senescence in the model these trends were accelerated. The authors concluded that the two main factors leading to a decline in biomass and cover over time in shrubland stands are the absence of recruitment and the limit of individual shrub growth (Hilbert and Larigauderie 1990).

Studies varied in how biomass values were generated. The majority of studies utilized allometric equations to estimate biomass across a certain area. This method typically involves select whole shrub harvesting to create linear equations which are then used to calculate plot level biomass using stem diameter measurements. Very few of the studies included in this review carried out full plant harvests that included the root system. In general, the use of allometric equations and pre-determined root:shoot ratios appear to be the most popular methods for generating stand-level biomass. Species-level biomass studies, on the other hand, typically select several shrubs rather than a plot area, allowing a more thorough measurement of biomass for each individual. However, these studies are also extremely limited in the number extracting belowground biomass for direct measurements. Sample size and plot size varied widely in the identified literature, depending on the focus of a given study as well as the resources available to undertake it, sample size varied from n=1 to n=100 and the size of plots varied from 1 m^2 (Guo 2001) to 120 m^2 (Riggan et al. 1988). This is important to recognize as both the number of samples and the size of plots influence the amount of variation captured within a shrubland community. A larger plot (especially one that captures different slopes and aspects), for example, will likely capture openings within the shrubland as well as both live and dead shrubs, providing biomass values that are more representative across the landscape.

Of particular note in undertaking this review is the comparative lack of studies published in the last 10 yr. The majority of the field studies (60%) were carried out in the 1970's and 1980's, a time at which there was funding and great academic and practical interest in comparing the five Mediterranean-type climate regions of the world. For example, the United Nations Man and the Biosphere Programme (MAB) was launched in the early 1970's as an intergovernmental scientific program aiming to promote planning and implementation of research and training programs (http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/man-and-biosphere-programme/). As part of this program, in 1976 the San Dimas Experimental Forest (designated in 1933) in the San Gabriel Mountains of southern California was established as a biosphere reserve, which resulted in numerous experimental studies in chaparral landscapes. In the 1970s the US also joined the International Biological Program (IBP) which focused on documenting the productive capacity of different regions of the world. More specifically, as part of the IBP, a Convergent Evolution program was created to compare the productive structure of vegetation that evolved to meet the challenges of dry summer climates, for example between California and Chile (Mooney and Dunn 1970, Mooney 1977b). Additionally, the relative lack of more recent field studies, especially those that assess belowground biomass, may be due to a shifting focus towards using remote sensing tools to estimate biomass at much larger scales. These studies typically rely on previously established field-based biomass estimates and are often focused on making repeatable regional biomass estimates, often disregarding the importance of belowground biomass (e.g., Schmidt et al. 2016, Uyeda et al. 2017). While it is important to continue developing the most accurate and efficient methods for determining biomass at a landscape level, further work quantifying belowground biomass would strengthen our understanding of biomass accumulation in shrublands.

In this review, by parsing out biomass at the stand and species level and reporting on above- and belowground biomass, live and dead biomass, and leaf, litter and stem biomass, we provide a valuable resource for land managers and conservation practitioners who need estimates of shrubland biomass at different life stages. Understanding these biomass values is foundational information for mapping biomass and monitoring changes,and ultimately quantifying carbon storage ecosystem services (it is generally assumed that carbon makes up 45–50% of plant biomass; Kort and Turnock 2003, Schlesinger and Bernhardt 2013).

While much attention has focused on the role of forested landscapes as a sink of atmospheric CO_2, the contribution of Mediterranean climate shrublands to the global carbon cycle has received little attention (Evrendilek et al. 2006). Despite shrublands historically being considered overmature after reaching 60 yrs of age (Hanes 1971), shrublands over 100 yrs old have been reported as vigorous (Keeley 1992). Indeed, Luo et al. (2007) recorded a 100 yr old chamise-dominated chaparral stand to be a significant carbon sink (-155 g $C/m^2/yr$). In another study of Mediterranean climate shrublands in Italy, shrublands were reported to remove significant quantities of C from the atmosphere (2200 g $C/m^2/yr$; Gratani et al. 2013). Future changes in climate are likely to impact the capability of shrublands to store and sequester carbon, however there is considerable uncertainty surrounding this. For example, some studies predict that changes in temperature and precipitation may decrease the area of shrublands in the North American Mediterranean Climate Zone owing to expansion of grasslands (Hayhoe et al. 2004) while other studies predict an increase as shrublands encroach into areas currently dominated by conifers in California (Lenihan et al. 2008). In addition, climate changes may lead to variations of shrubland structure and productivity (Haase et al. 2000) and conseqently effect carbon sequestration and storage capabilities (Evrendilek et al. 2006). Luo et al. (2007), for example, recorded that after a period of severe drought the ability of the chaparral stand to sequester carbon was limited. Through increasing our knowledge surrounding biomass accumulation and associated carbon sequestration in shrublands, land managers will be better able to understand the potential for these stands to sequester carbon in the future and also provide the information necessary for embarking on Payment for Ecosystem Services schemes for carbon.

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APPENDIX 1. REFERENCES FOR LITERATURE INCLUDED IN SUMMARY TABLES. Table 1. References: 1–7, 9–12, 17, 20–25, 27, 28, 32–36. Table 2. References: 1–3, 5, 10, 12, 17, 21, 23, 27, 30, 31, 35. Table 3. References: 2, 3, 5, 7, 8, 10, 14, 21, 35, 37. Table 4. References: 4, 7, 9, 12, 13, 15, 16, 18–20, 22, 25–32, 35.

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APPENDIX 2. REPORTED ABOVEGROUND BIOMASS VALUES ORGANIZED BY COMMUNITY TYPE, GENERAL LOCATION, AND AGE OF STAND. Studies that did not report on total, live or dead aboveground biomass are excluded from this table. When a study provided multiple biomass values for the same age and location, we report the average of those values. [a]General locations are based on descriptions provided in the reference text, for more detailed information please refer to the original source; [b]References are listed in Appendix 1.

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m^2)			Reference[b]
			Total	Live	Dead	
Mixed chaparral	Los Padres NF	5	–	2055	–	28
Mixed chaparral	Los Padres NF	12	–	3232	–	28
Mixed chaparral	Los Padres NF	21	6337	4871	1466	28
Mixed chaparral	Los Padres NF	25	3039	2012	1028	4
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	6	1430	1330	100	24
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	11	2817	2638	179	34
Mixed chaparral	San Dimas Experimental Forest, Angeles NF	21	5575	4838	743	24
Mixed chaparral	Angeles NF	33	8900	6008	2892	21
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	1	–	200	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	2	–	475	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	3	–	660	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	4	–	600	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	5	–	500	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	6	–	560	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	7	–	700	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	8	–	800	–	35
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	54	3005	–	–	17
Mixed chaparral	Sky Oaks Biological Field Sta., San Diego Co.	85	3085	–	–	17
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	4	1500	800	700	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	11	2600	2400	200	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	54	5000	3700	1300	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	80	4500	3500	1000	1
Mixed chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	85	4500	3700	800	1
Mixed chaparral	Descanso Ranger District, Cleveland NF	2	1813	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	3	199	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	5	540	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	10	1489	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	11	411	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	13	1639	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	18	1839	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	20	1418	–	–	36
Mixed chaparral	Descanso Ranger District, Cleveland NF	22	2813	–	–	36
Mixed chaparral	Kitchen Creek, Cleveland NF	1	–	280	–	24
Mixed chaparral	Kitchen Creek, Cleveland NF	7	1320	–	–	33
Mixed chaparral	Kitchen Creek, Cleveland NF	28	4140	–	–	33
Mixed chaparral	Kitchen Creek, Cleveland NF	35	–	2325	–	25
Mixed chaparral	Kitchen Creek, Cleveland NF	35	3000	3000	0	24
Mixed chaparral	Kitchen Creek, Cleveland NF	68	5060	–	–	33
Mixed chaparral	Camp Pendleton, San Diego Co.	–	6236	3853	890	2
Mixed chaparral	Camp Pendleton, San Diego Co.	–	9774	–	–	3
Mixed chaparral	Camp Pendleton, San Diego Co.	"mature"	9000	4500	4500	6
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	4	840	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	11	1873	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	54	2535	–	–	17
Mixed chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	80	3500	–	–	17
Mixed chaparral	Echo Valley International Biological Program	23	2308	–	–	20
Mixed chaparral	Leo Carrillo State Park, Santa Monica Mountains, Los Angeles Co.	22	7705	6482	1223	7
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	1	130	–	–	11
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	2	410	–	–	11

APPENDIX 2. CONTINUED

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m²) Total	Live	Dead	Reference[b]
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	3	590	–	–	11
Mixed chaparral	Stunt Ranch Santa Monica Mountains UC Reserve, Los Angeles Co.	4	855	–	–	11
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	5010	3945	1065	21
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	8730	7420	1310	5
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	8698	7420	1255	21
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	5920	4840	1080	5
Mixed chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	5963	4864	1098	21
Mixed chaparral	North Mountain Experimental Area, Riverside Co.	"mature"	7846	6165	1681	9
Mixed chaparral	Bear Creek, Riverside Co.	30-50	5201	4775	426	12
Mixed chaparral	Sequoia National Park, Tulare Co.	3	540	–	–	32
Mixed chaparral	Sequoia National Park, Tulare Co.	15	3020	–	–	32
Mixed chaparral	Sequoia National Park, Tulare Co.	24	3165	–	–	22
Mixed chaparral	Southern California	14	4900	–	–	23
Mixed chaparral	Southern California	19	7300	–	–	23
Mixed chaparral	Southern California	33	8200	–	–	23
Mixed chaparral	Southern California	50	5100	–	–	23
Mixed chaparral	Southern California	55	11800	–	–	23
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	1	127	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	2	204	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	3	433	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	4	629	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	5	1011	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	6	1088	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	7	1134	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	8	1186	–	–	27
Mixed chaparral	Mendocino Co.; Lake Co.; Shasta Co.	"Old stand"	3100	–	–	27
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	1	273	115	158	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	3	1087	521	566	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	9	–	863	–	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	18	2039	1659	380	30
Chamise chaparral	San Dimas Experimental Forest, Angeles NF	37	4909	2726	2184	30
Chamise chaparral	Sky Oaks Biological Field Sta., San Diego Co.	"pre-fire"	–	1686	–	35
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	4	1300	800	500	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	11	1440	1400	40	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	54	2050	1800	250	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	80	1600	1400	200	1
Chamise chaparral	Cleveland NF; Sky Oaks Biological Sta.; West of Anza-Borrego Desert	85	3400	2500	900	1
Chamise chaparral	Camp Pendleton, San Diego Co.	–	2843	1189	1015	2
Chamise chaparral	Camp Pendleton, San Diego Co.	–	3755	–	–	3
Chamise chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	4	770	–	–	17
Chamise chaparral	Puerta La Cruz Rd, Warner Springs, San Diego Co.	80	1510	–	–	17
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	13	2805	2085	720	5
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	13	2679	2074	605	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	2309	1547	762	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	3050	2170	880	5

APPENDIX 2. CONTINUED

Community type	General location[a]	Age (yrs)	Aboveground biomass (g/m^2)			Reference[b]
			Total	Live	Dead	
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	17	2735	2197	538	21
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	40	2760	2220	540	5
Chamise chaparral	Santa Monica Mountains National Recreation Area, Los Angeles Co.	40	2735	2219	516	21
Chamise chaparral	Newhall, Los Angeles Co.	35-50	1771	1569	202	12
Chamise chaparral	San Bernardino NF	55	3945	3049	897	21
Chamise chaparral	Santa Rosa Plateau Preserve, Riverside Co.	10	1636	1054	583	12
Chamise chaparral	Sequoia National Park, Tulare Co.	>60	3066	–	–	31
Chamise chaparral	Southern California	10	1600	–	–	23
Chamise chaparral	Southern California	14	2300	–	–	23
Chamise chaparral	Southern California	19	2800	–	–	23
Chamise chaparral	Southern California	50	1700	–	–	23
Chamise chaparral	Southern California	55	4000	–	–	23
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	1	175	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	2	309	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	3	465	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	4	740	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	5	1000	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	6	1130	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	7	1215	–	–	27
Chamise chaparral	Mendocino Co.; Lake Co.; Shasta Co.	8	1276	–	–	27
Coastal sage scrub	Camp Pendleton, San Diego Co.	–	2869	661	773	2
Coastal sage scrub	Camp Pendleton, San Diego Co.	–	2959	–	–	3
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	1	–	575	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	2	–	395	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	3	–	630	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	4	–	520	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	5	–	200	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	6	–	210	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	7	–	325	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	8	–	420	–	35
Coastal sage scrub	Santa Margarita Ecological Reserve, San Diego Co.	35	–	400	–	35
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	1750	1170	580	5
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	14	1771	1188	583	21
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	18	2152	1300	852	21
Coastal sage scrub	Santa Monica Mountains National Recreation Area, Los Angeles Co.	30	1502	986	516	21
Coastal sage scrub	Santa Monica Mountains, Los Angeles Co.	1	598	–	–	14
Coastal sage scrub	Leo Carrillo State Park, Santa Monica Mountains	22	1172	925	247	7
Coastal sage scrub	Leo Carrillo State Park, Santa Monica Mountains	22	1418	–	–	8
Coastal sage scrub	Robert J. Bernard Biological Field Sta., Los Angeles Co.	40	2725	–	–	37