

Biomass, productivity, and nutrient allocation in subalpine shrublands and meadows of the Emerald Lake Basin, Sequoia National Park, California

Philip W. Rundel¹

¹Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Box 95616, Los Angeles, California 90095, U.S.A., rundel@biology.ucla.edu

Abstract

The Emerald Lake Basin provides a long-term site for research on hydrology, ecology, and biogeochemistry, as well as baseline data for a representative subalpine watershed in the Sierra Nevada of California. Field studies provided quantitative data on the biomass, net primary production, and nutrient allocation of major subalpine shrub and meadow communities. Measurements carried out over two growing seasons found aboveground biomass per unit canopy area was 3857 g m⁻² in *Chrysolepis sempervirens*, 3360 g m⁻² in *Salix orestera*, and 1614 g m⁻² in *Phyllodoce breweri*. The biomass for *Chrysolepis* and *Salix* canopies were high compared to other published data for subalpine and alpine shrublands, but the *Phyllodoce* biomass was comparable to values for ericaceous heath in the Rocky Mountains and European Alps. Wet and dry meadows had 377 and 98 g m⁻², respectively, in aboveground living tissues, comparable to values from the Rocky Mountains and European Alps. Belowground biomass for shrub communities was the highest for *Phyllodoce* (3670 g m⁻²), followed by *Chrysolepis* (2400 g m⁻²) and *Salix* (2070 g m⁻²). The wet meadow community had a surprisingly high belowground biomass of 2897 g m⁻², reflecting the dominance of large perennial herb species. This resulted from a root:shoot ratio of 8.21 compared to 5.72 in the dry meadow community. Canopies of *Chrysolepis* and *Salix* had root:shoot ratios of 0.62 and 0.61, respectively, and *Phyllodoce* a ratio of 2.27.

DOI: <http://dx.doi.org/10.1657/AAAR0013-136>

Introduction

The biologically rich subalpine and alpine basins of the Sierra Nevada have had a long history of descriptive study, but more recently have served as important areas for quantitative research on the ecology and ecosystem processes in subalpine watersheds. These high mountain ecosystems are sensitive to small changes in growing season conditions of temperature and water availability, and their stability impacts hydrological conditions that provide a critical resource for downstream agriculture and urban development in California (Bales et al., 2006; Maurer, 2007; Trujillo et al., 2012). Despite a number of detailed studies of hydrology, and biogeochemical cycles of high mountain systems in the Sierra Nevada (Millar and Rundel, 2014), there has been relatively little study of the biomass and primary productivity of subalpine and alpine shrublands and meadows communities.

The Emerald Lake Basin in Sequoia National Park has served for more than three decades as a primary study site to understand the hydrology, ecology, and biogeochemistry of a representative subalpine watershed in the southern Sierra Nevada (Fig. 1). This work began in 1984 with funding from the California Air Resources Board to address concerns related to the influence of atmospheric inputs of nutrients to basin processes and ecosystem structure (Tonnessen, 1991). The ecological communities and floristic diversity of the Emerald Lake Basin have been described (Rundel et al., 2009). Watershed studies have continued up to the present day and have provided detailed and in many cases long-term and continuing databases to understand hydrologic flow and water balance (Kattelman and Elder, 1991; Huth et al., 2004), nutrient enrichment (Sickman et al., 2003a, 2003b), solute chemistry of snowmelt and runoff (Williams and Melack, 1991; Sadro and Melack, 2012), nitrogen fluxes and transformations (Williams et al., 1995; Miller

et al., 2009), and models of hydrochemical response (Wolford et al., 1996; Wolford and Bales, 1996; Meixner et al., 2004).

Relatively little is known about patterns of biomass distribution and rates of productivity for subalpine and alpine communities in the Sierra Nevada. Although there have been numerous studies in the Rocky Mountains and Europe describing the biomass and productivity of alpine and subalpine fellfield, sedgeland, and grassland meadow communities, there has been relatively little comparative study of subalpine shrublands, which often dominate extensive areas near treeline. Moreover, most of the existing subalpine and alpine meadow studies from Europe and the Rocky Mountains have focused on areas with a dominance of summer rainfall regimes where summer drought is not a strong limiting factor for growth.

The high mountains of California offer very different conditions, as late summer drought often limits growth before cold fall temperatures (Rundel et al., 2005). The objective in this paper has been to quantify the biomass, net primary production and nutrient allocation of major shrub and meadow communities of the Emerald Lake Basin, and compare and contrast these values with those for the summer-rainfall high mountain areas of the Rocky Mountains and Europe.

Methods and Materials

STUDY SITE

Field studies were carried out in the Emerald Lake Basin (Fig. 1), a subalpine watershed about 120 ha in area in the upper drainage of the Marble Fork of the Kaweah River above Tokopah Falls in Sequoia National Park (36°35'49"N, 118°40'30"W). The watershed is roughly triangular in shape trending northwest to southeast,

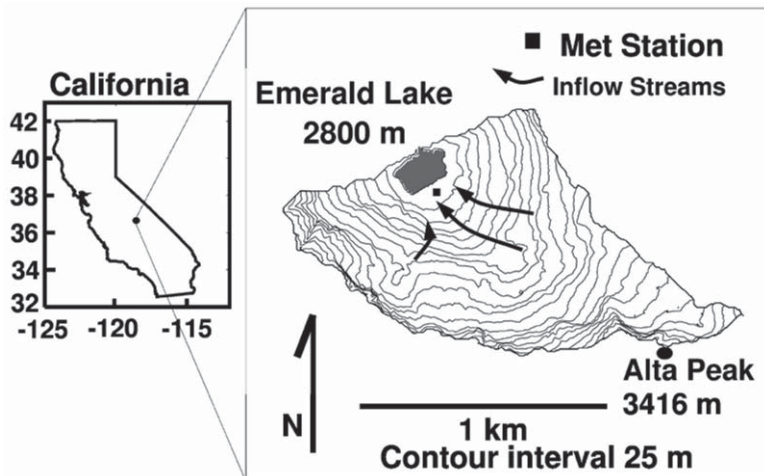


FIGURE 1. Map of the 120-ha Emerald Lake watershed, Sequoia National Park, California, U.S.A. Small map of California shows latitude and longitude.

with elevations ranging from 2804 m at Emerald Lake at the lower end of the basin to the apex of the triangle at the summit of Alta Peak at 3416 m (Rundel et al., 2009).

The Emerald Lake Basin is a glacial cirque (Fig. 2), carved from granitic parent material and representative of many subalpine and alpine basins in the Sierra Nevada, with lakes exhibiting weakly buffered calcium bicarbonate surface waters (Williams and Melack, 1991). The climate of the Emerald Lake Basin is typical of the mediterranean-type regime of the southern Sierra Nevada, with 75%–90% of the annual precipitation falling as snow in the winter months (Stephenson, 1990). At this site specifically, rainfall composes only about 10% of annual precipitation and occurs predominantly in the autumn, with winter snows the predominant form of precipitation. Based on limited long-term data on precipitation levels, mean annual precipitation is about 1600 mm, but amounts are highly variable between years (Sickman et al., 2003a). Snowmelt typically begins in April with peak flow of runoff water occurring in June (Sickman et al., 2003b). Summers are generally dry except for an occasional convective storm associated with monsoonal air masses from the east (Sadro and Melack, 2012).

Because bedrock exposed by glacial scouring and frost action covers nearly half of the surface area of the Emerald Lake Basin, with the remaining half covered by talus and thin soils in approximately equal proportions, with soils present over only about 20% of the watershed surface (Sisson and Moore, 1984; Tonnessen, 1991), vascular plant cover is relatively sparse. Thin soils and fractures in the granite surface, however, do support a wide distribution of both wet and dry meadow communities throughout the basin as well as extensive woody shrub growth in local areas of the lower basin with more soil development and in rocky fracture lines across the basin where soil and moisture are available.

A low-growing ericaceous heath dominated by *Phyllodoce breweri* (Ericaceae) is widely distributed in the basin, but covers only about 0.73 ha of area. Also present in these heath stands are the evergreen *Arctostaphylos nevadensis* (Ericaceae) and the winter deciduous *Amelanchier utahensis*, *Prunus emarginata*, and *Sorbus californica* (all Rosaceae). However, *Phyllodoce* is the major element of this community and forms relatively extensive local populations in granite fracture zones across the basin. Species names used in this paper follow those in Baldwin et al. (2012).

Willow thickets are widespread and cover 8.55 ha within the basin. Along with *Salix orestera*, the dominant species, which reaches 1–2 m in height, there are a characteristic set of understory shrubs that typically cover 100% of the ground surface. These species include evergreen ericaceous shrubs such as *Rhododendron columbianum* (formerly *Ledum glandulosum*), *Kalmia polifolia*, *Phyllodoce breweri*, and *Vaccinium cespitosum* (Rundel et al., 2009).

The understory of open conifer forest stands in the lower elevations of the Emerald Lake Basin is locally dominated by an open shrubland of *Chrysolepis sempervirens* (Fagaceae), an evergreen shrub 1–1.5 m in height. This shrubland may locally exhibit dense ground cover up to 80%–100%, but is also present in more open stands with an understory of typical dry meadow herbs such as *Achillea millefolium* (Asteraceae) and *Ivesia santalinoides* (Rosaceae).

Wet meadows form diverse communities in the watershed and cover 4.1 ha of area. These include a number of distinctive associations largely distributed in relatively flat areas on west-facing slopes above Emerald Lake where soils accumulate to moderate depths and remain moist for much or all of the growing season (Rundel et al., 2009). Variations in soil texture, soil organic matter content, and soil moisture dynamics appear to be the primary physical factors separating different wet meadow associations.

Dry meadow communities occupy about 7.7 ha of the Emerald Lake watershed, most notably in the relatively flat plateau and benches below the northeast ridge and boundary of the basin. In these sites, soils are formed of shallow layers of decomposed granite with low organic matter, and typically dry early in the growing season, as indicated by the early senescence of herbaceous species (Rundel et al., 2009).

SAMPLING BIOMASS AND PRODUCTIVITY

Detailed measurements of stand biomass and productivity were carried out over two growing seasons (1985–1986) in three shrub species and wet and dry meadow communities in the Emerald Lake Basin. These shrubs were *Chrysolepis sempervirens*, *Phyllodoce breweri*, and *Salix orestera*. The differing structure and composition of each community type required the use of multiple sampling methodologies. Both *Salix* and *Chrysolepis* are large shrubs. For canopies of these species, we utilized a series of nine 1 m² canopy plots



FIGURE 2. Emerald Lake watershed, looking southeast toward Alta Peak (3416 m). Emerald Lake (2800 m) is in the foreground, with willow thickets along the far end of the lake and wet meadows beyond.

located in three different sites within the basin. For each plot, all biomass was clipped and sorted, separating current growth, previous year growth, and standing dead biomass. Understory herbs were harvested and surface litter collected. A standardized root core of 20 cm diameter (0.0314 m²) and 30 cm deep was taken from the center of each of these plots. Because of the shallow granitic soils, this depth of core was sufficient to sample virtually all roots.

For the *Phyllodoce* heath and wet meadow communities, three canopy areas of 20 cm diameter in each of three sites were clipped and tissues separated by species and by biomass categories of current and older growth. Surface litter was collected in the same plots. A root core of 20 cm diameter was taken from each of these nine plots, as above.

Biomass samples collected at the end of the growing season in the first year of the study were separated into categories of current-year foliage, old foliage, reproductive tissues, current year twigs, older woody tissues, and dead biomass. In order to determine the increment of current-year woody tissue growth on older stems, woody tissues were first cut and separated into a series of diameter size classes. For the larger *Salix* and *Chrysolepis*, up to ten size classes were used. Only a single size class was necessary for the small and relatively uniform stems of *Phyllodoce*. The

total length (L) and mean diameter of each stem size class were measured to 0.1 and 1.0 mm accuracy, respectively. Ten twigs of each size class were subsampled, and measurements were made using a dissecting microscope of overall branch diameter, total wood diameter (D_n), and wood diameter beginning with the previous year (D_{n-1}). The volume of current-year wood increment (V_n) was calculated as:

$$V_n = \Pi/4 L (D_n - D_{n-1}). \quad (1)$$

The biomass increment of current-year woody growth on these stems was then the product of this volume calculated and summed for all of the sampled length of stems, times the mean wood density. Experimental trials demonstrated that wood density was not a function of stem diameter. Current-year bark biomass was included in the current-year twig pool, while bark on older twigs was included in the pool of older wood tissues. The reproductive pool for *Salix* and *Phyllodoce* included only current-year tissues, and with sampling occurring after some of the tissues had senesced. For *Chrysolepis*, the great bulk of the reproductive tissues were matured fruits from the previous growing season.

Prostrate rooted stems were commonly encountered in both *Salix* and *Chrysolepis*, apparently the result of snow compaction and subsequent layering of the tissues. For the purposes of this study, these rooted stems were classified as root tissues. Such stems formed the major part of the >20 mm diameter root pool as well as a smaller portion of the 10–20 mm diameter pool of roots.

The distribution of dead tissues on the aboveground stems was highly variable between species and within communities. Virtually all of this pool consisted of dead stem material from the growth of previous years, but small amounts of dead foliage and dried reproductive structures from previous years were also included when encountered. For *Salix*, dead aboveground tissues formed by large dead branches were uncommon and highly scattered in occurrence. The situation was very different in *Chrysolepis*, where large areas of dead canopy were localized in distribution.

NUTRIENT CONTENT AND ALLOCATION

The nitrogen, phosphorus, potassium, calcium, and magnesium contents of each major aboveground tissue were analyzed from individual biomass samples for *Phyllodoce breweri* and *Salix orestera*. These samples were divided into two groups, which were analyzed separately to provide replication in analyses for nitrogen and phosphorus. Samples of root tissues in three size classes were collected and analyzed for *Salix*, while only fine roots 0–2 mm in diameter were collected and analyzed for wet meadow canopies. Total nitrogen and total phosphorus were analyzed by the plant tissue laboratory of the University of Alaska, Anchorage, using Kjeldahl digestions and a Technicon colorimetric autoanalyzer using standard procedures and calibration, with mean values reported here. Cations (K, Ca, and Mg) were analyzed by optical emission spectroscopy at the then Laboratory of Biomedical and Environmental Sciences at UCLA, following procedures described by Alexander and McAnulty (1981) with subsamples run with ten replicates.

Results

BIOMASS

Shrub cover in the Emerald Lake basin totaled about 9% of the surface area, with willow thickets making up the great majority of this cover. The total aboveground biomass per unit canopy area of shrub cover, including both living and dead tissues, was highest among the canopies studied for *Chrysolepis sempervirens*, with a mean biomass of 3857 g m⁻², with 2747 g m⁻² (71%) of this in living tissues. Thickets of *Salix orestera* were a close second, with 3360 g m⁻², and 2230 g m⁻² (66%) of this in living tissues. Stands of the less woody and smaller stature *Phyllodoce breweri* had 1614 g m⁻² in aboveground tissues, with 1409 g m⁻² (87%) of this in living tissues (Table 1). Wet and dry meadow communities had 377 and 98 g m⁻² in aboveground living tissues, respectively.

Despite these differences in aboveground biomass, belowground biomass was much more consistent between communities. Estimated values of belowground biomass were high in the *Phyllodoce* heath, with an estimated 3670 g m⁻². The woodier *Chrysolepis* and *Salix* stands had a lower belowground biomass of 2400 and 2070 g m⁻², respectively. Including all tissues, living and dead, these values gave mean root:shoot ratios of 0.62 and 0.61 for the *Chrysolepis* and *Salix* stand canopies, respectively, and 2.27 for *Phyllodoce*. The wet meadow community, reflecting the dominance

of large perennial herb species, had a root:shoot ratio of 7.68, while this ratio was lower at 5.72 for the dry meadow community.

Litter biomass was highest in the *Chrysolepis* stands, with a mean of 4553 g m⁻², a value three times higher than that of any other community (Table 1). The *Phyllodoce* and *Salix* stands had 1618 and 1441 g m⁻², respectively, while the wet and dry meadow communities had much smaller amounts of litter. These values produced a ratio of aboveground biomass to litter of 0.85 and 1.00 in the *Chrysolepis* and *Phyllodoce* canopies and 2.33 in the *Salix* canopy (Table 1).

The woody growth of *Chrysolepis* and *Salix* did not allow for the survival of a significant biomass of herbaceous species below their canopies. However, we sampled a mean aboveground herb biomass of 54 g m⁻² below the more open canopy of *Phyllodoce* heath.

NET PRIMARY PRODUCTION AND BIOMASS ALLOCATION

Annual patterns of net primary production in the four study communities showed a different pattern than that seen in the biomass data. Despite its lower stature, the aboveground net primary production was highest in the *Phyllodoce* heath, with a mean of 499 g m⁻² y⁻¹ (Table 1). The *Chrysolepis* canopies were a close second in productivity, with 443 g m⁻² y⁻¹, followed by the *Salix* thickets with a relatively low annual productivity of 227 g m⁻² y⁻¹. The wet and dry meadow communities had rates of aboveground productivity very close to that of their biomass, reflecting the herbaceous growth forms that dominate these communities and die back to ground level each winter. A small amount of perennial aboveground tissues in wet meadow community was contributed by low-growing perennials such as *Vaccinium cespitosum*, *Penstemon heterodoxus*, *Eriogonum incanum*, and *Kalmia pohlifolia*.

The biomass accumulation ratio, aboveground living biomass divided by productivity, was relatively high in the woody *Chrysolepis* and *Salix* stand canopies, with values of 6.2 and 9.8, respectively. This ratio was 2.8 in the *Phyllodoce* heath, and only about 1.1 in the wet and dry meadow communities.

As expected, the proportion of dry weight biomass within new tissues was lowest in the woody *Chrysolepis* and *Salix* canopies, with 12.7% and 8.5%, respectively (Table 2). In *Phyllodoce* canopies, new growth for the current year made up 32.9% of the biomass. The relative allocation of new growth to leaves in the evergreen *Chrysolepis* and *Phyllodoce* was quite similar, with a relative allocation to leaf production of 49.8% and 50.6%, respectively. Deciduous *Salix* canopies allocated a significantly lower 30.9% of new growth to leaves, but a higher fraction to new twigs. The three species did not differ significantly in allocation to new wood on old branch tissues (Table 2).

NUTRIENT CONTENT AND ALLOCATION

Nutrient contents on a dry weight basis for each tissue type of *Phyllodoce breweri*, *Salix orestera*, and wet and dry meadows are presented in Appendix Table A1. New leaves of *Salix* had a relatively high nitrogen content of 28.2 mg g⁻¹, compared to only 14.9 mg g⁻¹ in *Phyllodoce*. Phosphorus concentration levels in new leaves were less different with 1.9 mg g⁻¹ in *Salix* and 1.7 mg g⁻¹ in *Phyllodoce*.

The relative amount of aboveground nitrogen pools contained in new tissues of *Phyllodoce* closely matched the proportional biomass of these tissues. The situation was very different in *Salix* where current year tissues composed less than 10% of the total

Table 1

Biomass and productivity parameters for three subalpine shrub species and wet meadows in the Emerald Lake Basin of Sequoia National Park. All values are based on units of canopy cover for the shrub species. For wet meadows, cover was taken as 100% of the mapped community, while for more open dry meadows cover was measured as 38% of the mapped community. NP indicates tissue not present.

| | <i>Chrysolepis sempervirens</i> | <i>Phyllodoce breweri</i> | <i>Salix orestera</i> | Wet meadow | Dry meadow |
|---|---------------------------------|---------------------------|-----------------------|------------|------------|
| Aboveground biomass (g m ⁻²) | | | | | |
| Live | 2746 | 1409 | 2230 | 377 | 98 |
| Dead | 1111 | 205 | 1130 | 0 | 0 |
| Total | 3857 | 1614 | 3360 | 377 | 98 |
| Aboveground productivity (g m ⁻² y ⁻¹) | 443 | 499 | 227 | 318 | 88 |
| Biomass accumulation ratio (Biomass/productivity) | 6.2 | 2.8 | 9.8 | 1.2 | 1.1 |
| Belowground biomass (g m ⁻²) | 2400 | 3670 | 2070 | 2897 | 561 |
| Root:shoot | 0.60 | 2.27 | 0.61 | 7.68 | 5.72 |
| Herb biomass (g m ⁻²) | 0 | 54 | 0 | 377 | 98 |
| Litter | 4553 | 1618 | 1441 | 137 | 77 |
| Aboveground biomass/litter | 0.60 | 0.87 | 1.55 | 2.75 | 1.27 |

plant biomass, but held 44% of the nitrogen (Table 3). This pattern is repeated in concentrations of phosphorus, potassium, calcium, and magnesium. Among new tissues, *Phyllodoce* with evergreen leaves allocated 60% of its nitrogen to leaf tissues compared to a biomass proportion of 51%, while *Salix* with deciduous leaves allocated 55% of nitrogen compared to a proportional biomass of

31% for leaf tissues. Similarly, *Salix* allocated proportionally larger relative amounts of phosphorus, potassium, calcium, and magnesium to new leaf tissues than to biomass, although the proportion is less for phosphorus.

Discussion

Data on the biomass and productivity of subalpine and alpine shrubland communities are relatively few in the literature. The shrub tundra at Niwot Ridge in Colorado, a community of low willows less than 50 cm in height, has an aboveground biomass of about 1500 g m⁻², an aboveground net primary production of about 300 g m⁻², and a belowground biomass of about 5000 g m⁻², for a root:shoot ratio of 3.3 (May and Webber, 1982). More parallel with our research are data collected on mountain heath communities dominated by *Phyllodoce empetriformis*, *Cassiope metensisana*, and *Vaccinium deliciosum* in the Cascade Range of Washington by Grier (1973) who looked at patterns of organic matter and nitrogen distribution in three differing areas of geomorphic condition. The standing crop of aboveground biomass ranged from 740 to 2380, and root:shoot ratios were 0.37 and 0.38, respectively, in organic-rich and colluvial soils but 1.00 in residual soils. Our results for aboveground biomass in *Phyllodoce breweri* lie within this range, but we found greater biomass in *Castanopsis sempervirens* and *Salix orestera*. The relatively high biomass of these latter two species likely results from the more moderate conditions of winter temperatures in the Sierra Nevada and the heavy snowpack that protects soils from deep frosts and canopies from winter desiccation.

There have been numerous studies of subalpine *Vaccinium* and *Rhododendron* heaths in the European Alps, and these have generally reported aboveground biomass of 1200–1900 g m⁻² (Körner, 2003; Gerdol et al., 2004). Another synthesis reported a mean of 1163 g m⁻² (Elzein et al., 2011), while similar values have been published for dwarf shrub communities on both acidic and calcareous soils from the eastern Alps (Tappeiner et al., 2008). Belowground biomass for dwarf shrub communities in the European

TABLE 2

Relative aboveground biomass allocation (%) and relative allocation of new aboveground growth (%) in three species of subalpine shrubs in the Emerald Lake Basin, Sequoia National Park. Values shown in parentheses are standard deviations of measurements.

| | <i>Chrysolepis sempervirens</i> | <i>Phyllodoce breweri</i> | <i>Salix orestera</i> |
|-----------------------------------|---------------------------------|---------------------------|-----------------------|
| Relative biomass allocation | | | |
| New leaves | 6.5 (3.1) | 15.5 (3.4) | 2.7 (1.7) |
| New twigs | 1.2 (0.4) | 4.7 (1.3) | 1.8 (0.9) |
| New wood | 4.5 (1.1) | 9.8 (1.6) | 3.8 (1.3) |
| New reproduction | 0.3 (0.4) | 0.5 (0.5) | 0.1 (0.1) |
| Old leaves | 3.5 (2.4) | 14.5 (3.7) | 0 |
| Old wood (live and dead) | 83.8 (5.3) | 52.6 (3.5) | 91.5 (2.4) |
| Relative allocation of new growth | | | |
| Leaves | 49.8 (9.6) | 50.6 (5.5) | 30.9 (13.9) |
| Twigs | 10.0 (1.3) | 15.3 (3.3) | 20.9 (7.1) |
| Wood | 37.1 (8.2) | 32.7 (7.0) | 45.7 (11.3) |
| Reproduction | 3.0 (3.9) | 1.8 (1.7) | 2.5 (3.4) |

TABLE 3

Relative allocation of macronutrients in total aboveground biomass and the relative allocation of these nutrients to aboveground new growth in *Phyllodoce breweri* and *Salix orestera*. NP indicates tissue not present; ND = no data.

| | Nitrogen | Phosphorus | Potassium | Calcium | Magnesium |
|--|----------|------------|-----------|---------|-----------|
| <i>Phyllodoce breweri</i> | | | | | |
| Relative nutrient allocation in biomass (%) | | | | | |
| New leaves | 29.6 | 32.4 | 21.4 | 21.2 | 25.0 |
| New twigs | 6.0 | 9.2 | 6.5 | 6.3 | 5.7 |
| New wood | 12.6 | 19.1 | 13.6 | 13.1 | 11.8 |
| New reproduction | 0.8 | 0.9 | 0.7 | 0.7 | 0.7 |
| Old leaves | 20.4 | 14.8 | 21.9 | 20.0 | 24.8 |
| Old wood (live) | 30.6 | 23.5 | 35.9 | 38.7 | 31.2 |
| Relative nutrient allocation in new growth (%) | | | | | |
| Leaves | 60.3 | 52.5 | 50.8 | 51.3 | 58.9 |
| Twigs | 12.3 | 14.9 | 15.4 | 15.2 | 12.9 |
| Wood | 25.7 | 31.0 | 32.2 | 31.8 | 26.7 |
| Reproduction | 1.7 | 1.5 | 1.6 | 1.7 | 1.5 |
| <i>Salix orestera</i> | | | | | |
| Relative nutrient allocation in biomass (%) | | | | | |
| New leaves | 29.6 | 7.4 | 15.1 | 10.1 | 11.6 |
| New twigs | 6.0 | 5.1 | 7.6 | 3.1 | 5.5 |
| New wood | 12.6 | 6.1 | 5.4 | 6.1 | 5.5 |
| New reproduction | 0.8 | 0.7 | 0.8 | 0.1 | 0.4 |
| Old leaves | NP | NP | NP | NP | NP |
| Old wood (live) | 30.6 | 80.7 | 71.1 | 80.7 | 77 |
| Relative nutrient allocation in new growth (%) | | | | | |
| Leaves | 55.2 | 38.3 | 52.1 | 52.1 | 50.5 |
| Twigs | 21.6 | 26.4 | 26.2 | 15.8 | 23.9 |
| Wood | 21.1 | 31.6 | 18.7 | 31.4 | 23.9 |
| Reproduction | 2.1 | 3.6 | 2.9 | 0.7 | 1.8 |

Alps range from 2400 to 2800 g m⁻², giving root:shoot ratios of 2.0–2.3 (Tappeiner et al., 2008).

Studies of aboveground production in alpine and subalpine shrublands in the central Rocky Mountains and the European Alps have generally found rates of 100–400 g m⁻² yr⁻¹, with typical values closer to 200 g m⁻² yr⁻¹ (see Bowman and Fisk, 2001; Körner, 2003). However, these mean values mask the high spatial heterogeneity in rates of aboveground net primary productivity, with plot level values ranging from as low as 50 g m⁻² yr⁻¹ to as much as 500 g m⁻² yr⁻¹ or more (Bowman et al., 1993; Walker et al., 1994). This heterogeneity is strongly influenced by topographic controls on microclimate conditions as well as biotic impacts from grazers and burrowing animals (Scott and Billings, 1964). Interannual variation in productivity is also characteristic with summer temperatures, patterns of snowmelt,

and levels of summer drought having a strong influence on the length of growing season (Billings and Bliss, 1959).

Extensive studies on aboveground biomass and primary production of alpine meadows have been carried out at Niwot Ridge in Colorado, with net aboveground primary production of herbaceous alpine communities varying between about 120 and 171 g m⁻² yr⁻¹ (Bowman and Fisk, 2001). These values for herbaceous communities are similar to those reported for other herbaceous subalpine and alpine communities in North America (Billings and Bliss, 1959; Scott and Billings, 1964; Klikoff, 1965; Bliss, 1966, 1985; Kuramoto and Bliss, 1970; Anderson et al., 1979). Higher values with means of 542–684 g m⁻² have been described for alpine meadows in the European Alps (Tappeiner et al., 2008). Older data on aboveground biomass are in subalpine and alpine *Carex*

heath and wet meadows in Europe present values from 240 to 800 g m⁻² (Brzoska, 1973; Wielgolaski, 1975; Rehder, 1976; Rehder and Schäfer, 1978). These values are lower than what we have measured in our subalpine wet meadow where large upright herbaceous perennials contain significant amounts of biomass, but higher than our low-growing dry meadow community (Table 1).

Belowground biomass has also been quantified in a number of alpine meadow studies. Research at Niwot Ridge has reported total root biomass in herbaceous alpine communities from about 1500 to 5700 g m⁻², with associated root:shoot ratios of 2.5–5.6 (May and Webber, 1982; Fisk et al., 1998). The Emerald Lake belowground biomass for wet and dry meadows lies within this range for belowground biomass. However, while the root:shoot ratios in dry meadows at Emerald Lake lie at the upper end of values for Niwot Ridge, the wet meadow ratios are higher at 7.68. The relative absence of deep soil freezing in the Sierra Nevada likely leads to the ability to form larger amounts of storage tissue, a beneficial trait under conditions of summer drought. Root:shoot ratios for alpine meadows in the European Alps have been reported to average about 2.2–2.4 (Tappeiner et al., 2008). Root:shoot ratios are expected to increase with decreasing temperature (Körner, 2003; Friend and Woodward, 1990) and with decreasing availability of water or nutrients (Chapin, 1980; Fonseca et al., 2000).

Conclusions

Despite extensive research on alpine meadows in both North America and Europe, there remain relatively few published data on biomass, primary production, and nutrient pools and fluxes in shrublands, communities that cover significant areas of subalpine watersheds in the Sierra Nevada. The existing data come largely from older studies in the European Alps (e.g., Rehder, 1976; Larcher, 1977; Rehder and Schäfer, 1978; see summary in Tappeiner et al., 2008). Ericaceous subalpine shrublands in the Sierra Nevada have comparable values of biomass and productivity to those in the Pacific Northwest and European Alps. However, willow shrublands in the Sierra Nevada contain far more biomass and higher productivity than low-growing alpine willow stands in the Rocky Mountains. Subalpine meadows in the Sierra Nevada have biomass and productivity relationships similar to those found in subalpine and alpine meadows of the Rocky Mountains at Niwot Ridge, but wet Sierran meadows possess higher biomass and root:shoot ratios than those reported for Niwot Ridge and the European Alps.

Subalpine shrublands and meadows appear to be highly sensitive to small alterations in the seasonality of temperature and hydrology, and thus play a major role in biogeochemical cycles. There have been clear indications for the Sierra Nevada that there has been a significant upward elevational shift in range over the past century for a number of species of birds and mammals (Moritz et al., 2008; Tingley et al., 2009). Subalpine and alpine ecosystems will likely be impacted by other attendant factors as declining snowpack, earlier spring runoff, and earlier phenology (Cayan et al., 2001; Mote et al., 2005; Stewart et al., 2005; Maurer, 2007; Millar and Rundel, 2015). The structure and stability of these high mountain biotic systems form critical components of alpine and subalpine ecosystems in a world with rapid global change (Theurillat and Guisan, 2001; Millar and Rundel, 2015).

Acknowledgments

I thank the California Air Resources Board for funding this research. Peter Rabenold, Mike Neuman, Gail Baker, Evan Edinger,

Carmen Crivellone, and Karen Poulin provided major assistance in carrying out the field work for the project. The support of Kathy Tonnessen, Dave Parsons, the staff of Sequoia and Kings Canyon National Parks, and colleagues from many universities working in the Emerald Lake Basin is gratefully acknowledged with thanks.

References Cited

- Alexander, G. V., and McAnulty, L. T., 1981: Multi-element analysis of plant-related tissues and fluids by optical emission spectroscopy. *Journal of Plant Nutrition*, 3: 51–59.
- Anderson, D. C., Hoffman, R. S., and Armitage, K. B., 1979: Aboveground productivity and floristic structure of a high subalpine herbaceous meadow. *Arctic and Alpine Research*, 11: 467–476.
- Baldwin, B. G., Goldman, D. H., Keil, D. J., Patterson, R., and Rosatti, T. J., 2012: *The Jepson Manual: Vascular Plants of California*. Second edition. Berkeley: University of California Press.
- Bales, R. C., Molotch, N. P., Painter, T. H., Dettinger, M. D., Rice, R., and Dozier, J., 2006: Mountain hydrology of the western United States. *Water Resources Research*, 42: W08432, <http://dx.doi.org/10.1029/2005WR00438>.
- Billings, W. D., and Bliss, L. C., 1959: An alpine snowbank environment and its effect on vegetation, plant development, and productivity. *Ecology*, 40: 389–397.
- Bliss, L. C., 1966: Plant productivity in alpine microenvironments on Mount Washington, New Hampshire. *Ecological Monographs*, 36: 125–155.
- Bliss, L. C., 1985: Alpine. In Chabot, B. F., and Billings, W. D. (eds.), *Physiological Ecology of North American Plant Communities*. New York: Chapman and Hall, 41–65.
- Bowman, W. D., and Fisk, M. C., 2001: Primary production. In Bowman, W. D., and Seastedt, T. R. (eds.), *Structure and Function of an Alpine Ecosystem: Niwot Ridge, Colorado*. Oxford: Oxford University Press, 177–197.
- Bowman, W. D., Theodose, T. A., Schardt, J. C., and Conant, R. T., 1993: Constraints of nutrient availability on primary production in two alpine communities. *Ecology*, 74: 2085–2098.
- Brzoska, W., 1973: Dry matter production and energy utilization of high mountain plants in the Austrian Alps. *Oecologia Plantarum*, 8: 63–70.
- Cayan, D. R., Kammerdiener, S. A., Dettinger, M. D., Caprio, J. M., and Peterson, D. H., 2001: Changes in the onset of spring in the western United States. *Bulletin of the American Meteorological Society*, 82: 399–415.
- Chapin, F. S., III, 1980: The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, 11: 233–260.
- Elzein, T. M., Blarquez, O., Gauthier, O., and Carcaillet, C., 2011: Allometric equations for biomass assessment of subalpine dwarf shrubs. *Alpine Botany*, 121: 129–134.
- Fisk, M. C., Schmid, S. K., and Seastedt, T. R., 1998: Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology*, 79: 2253–2266.
- Fites-Kaufman, J. A., Rundel, P., Stephenson, N. L., and Weixelman, D. A., 2007: Montane and subalpine vegetation of the Sierra Nevada and Cascade ranges. In Barbour, M. G., Keeler-Wolf, T., and Schoenherr, A. A. (eds.), *Terrestrial Vegetation of California*. Third edition. Berkeley: University of California Press, 456–501.
- Fonseca, C. R., Overton, J. M., Collins, B., and Westoby, M., 2000: Shifts in trait-combinations along rainfall and phosphorus gradients. *Journal of Ecology*, 88: 964–977.
- Friend, A. D., and Woodward, F. I., 1990: Evolutionary and ecophysiological responses of mountain plants to the growing season environment. *Advances in Ecological Research*, 20: 59–124.
- Gerdol, R., Anfodillo, T., Gualmini, M., Cannone, N., Bragazza, L., and Brancaleoni, L., 2004: Biomass distribution of two subalpine dwarf-shrubs in relation to soil moisture and nutrient content. *Journal of Vegetation Science*, 15: 457–464.

- Grier, C. G., 1973: Organic matter and nitrogen distribution in some mountain heath communities of the Source Lake Basin, Washington. *Arctic and Alpine Research*, 5: 261–267.
- Huth, A. K., Leydecker, A., Sickman, J. O., and Bales, R. C., 2004: A two-component hydrograph separation for three high-elevation catchments in the Sierra Nevada, California. *Hydrological Processes*, 18: 1721–1733.
- Kattelmann, R., and Elder, K., 1991: Hydrologic characteristics and water balance of an alpine basin in the Sierra Nevada. *Water Resources Research*, 27: 1553–1562.
- Klikoff, L. G., 1965: Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. *Ecological Monographs*, 35: 187–211.
- Körner, C., 2003: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Second edition. Berlin: Springer Verlag.
- Kuramoto, R. T., and Bliss, L. C., 1970: Ecology of subalpine meadows in the Olympic Mountains, Washington. *Ecological Monographs*, 40: 317–347.
- Larcher, W., 1977: Ergebnisse des IBP-Projekts ‘Zwergstrauchheide Patscherkofel.’ *Sitzungsberichte der Österreichischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Abteilung I*, 186: 301–371.
- Maurer, E. P., 2007: Uncertainty in hydrologic impacts of climate change in the Sierra Nevada, California, under two emissions scenarios. *Climatic Change*, 82: 309–325.
- May, D. E., and Webber, P. J., 1982: Spatial and temporal variation of vegetation and its productivity on Niwot Ridge, Colorado. In Halfpenny, J. (ed.), *Ecological Studies in the Colorado Alpine: A Festschrift for John W. Marr*. Boulder: University of Colorado, Institute of Arctic and Alpine Research, Occasional Paper No. 37, 35–62.
- Meixner, T., Gutmann, C., Bales, R., Leydecker, A., Sickman, J., Melack, J., and McConnell, J., 2004: Multidecadal hydrochemical response of a Sierra Nevada watershed: sensitivity to weathering rate and changes in deposition. *Journal of Hydrology*, 285: 272–285.
- Millar, C. I., and Rundel, P. W., 2015: The subalpine forest and treeline zone. In Mooney, H., and Zavaleta, E. (eds.), *Ecosystems of California—A Source Book*. Berkeley: University of California Press, in press.
- Miller, A. E., Schimel, J. P., Sickman, J. O., Skeen, K., Meixner, T., and Melack, J. M., 2009: Seasonal variation in nitrogen uptake and turnover in two high-elevation soils: mineralization responses are site dependent. *Biogeochemistry*, 93: 253–270.
- Moritz, C., Patton, J. L., Conroy, C. J., Parra, J. L., White, G. C., and Beissinger, S. R., 2008: Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science*, 322: 261–264.
- Mote, P., Hamlet, A. F., Clark, M. P., and Lettenmaier, D. P., 2005: Declining snowpack in western North America. *Bulletin of the American Meteorological Society*, 86: 39–49.
- Rehder, H., 1976: Nutrient turnover in alpine ecosystems. I. Phytomass and nutrient relations in four mat communities in the northern calcareous Alps. *Oecologia*, 22: 411–423.
- Rehder, H., and Schäfer, A., 1978: Nutrient turnover studies in alpine ecosystems. IV. Communities of the central Alps and comparative survey. *Oecologia*, 34: 309–327.
- Rundel, P. W., Gibson, A. C., and Sharifi, M. R., 2005: Plant functional groups in alpine fellfield habitats of the White Mountains, California. *Arctic, Antarctic, and Alpine Research*, 37: 358–365.
- Rundel, P. W., Neuman, M., and Rabenold, P., 2009: Plant communities and floristic diversity of the Emerald Lake Basin, Sequoia National Park, California. *Madroño*, 56: 184–198.
- Sadro, S., and Melack, J. M., 2012: The effect of an extreme rain event on the biogeochemistry and ecosystem metabolism of an oligotrophic high-elevation lake. *Arctic, Antarctic, and Alpine Research*, 44: 222–231.
- Scott, D., and Billings, W. D., 1964: Effects of environmental factors on standing crop and productivity of an alpine tundra. *Ecological Monographs*, 34: 243–270.
- Sickman J. O., Melack, J. M., and Clow, D. W., 2003a: Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. *Limnology and Oceanography*, 48: 1885–1892.
- Sickman J. O., Leydecker, A. C., Chang, C. Y., Kendall, C., Melack, J. M., Lucero, D. M., and Schimel, J., 2003b: Mechanisms underlying export of N from high-elevation catchments during seasonal transitions. *Biogeochemistry*, 64: 1–24.
- Sisson, T. W., and Moore, J. G., 1984: *Geology of Giant Forest–Lodgepole Area, Sequoia National Park, California*. Denver, Colorado: U.S. Geological Survey, Geologic Investigation Report OF 84-0254.
- Stephenson, N. L., 1990: Climatic control of vegetation distribution: the role of the water balance. *American Naturalist*, 135: 649–670.
- Stewart, I. T., Cayan, D. R., and Dettinger, M. D., 2005: Changes toward earlier streamflow timing across western North America. *Journal of Climate*, 18: 1136–1155.
- Tappeiner, U., Tasser, E., Leitinger, G., Cernusca, A., and Tappeiner, G., 2008: Effects of historical and likely future scenarios of land use on above- and belowground vegetation carbon stocks of an alpine valley. *Ecosystems*, 11: 1383–1400.
- Theurillat, J. P., and Guisan, A., 2001: Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, 50: 77–109.
- Tingley, M. W., Monahan, W. B., Beissinger, S. R., and Moritz, C., 2009: Birds track their Grinnellian niche through a century of climate change. *Proceedings of the National Academy of Science*, 106: 19637–19643.
- Tonnessen, K. A., 1991: The Emerald Lake watershed study: introduction and site description. *Water Resources Research*, 27: 1537–1539.
- Trujillo, E., Molotch, N. P., Goulden, M. L., Kelly, A. E., and Bales, R. C., 2012: Elevation-dependent influence of snow accumulation on forest greening. *Nature Geoscience*, 5: <http://dx.doi.org/10.1038/NGE01571>.
- Walker, D. A., Ingersoll, R. C., and Webber, P. J., 1994: Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology*, 75: 393–408.
- Wielgolaski, F. E., 1975: Primary productivity of alpine meadow communities. In Wiegolaski, F. E. (ed.), *Fennoscandian Tundra Ecosystems. Pt. I. Plants and Microorganisms*. Berlin: Springer-Verlag, 121–128.
- Williams, M. W., and Melack, J. M., 1991: Solute chemistry of snowmelt and runoff in an alpine basin, Sierra Nevada. *Water Resources Research*, 27: 1575–1588.
- Williams, M. W., Bales, R. C., Brown, A. D., and Melack, J. M., 1995: Fluxes and transformations of nitrogen in a high-elevation catchment, Sierra Nevada. *Biogeochemistry*, 28: 1–31.
- Wolford, R. A., and Bales, R. C., 1996: Hydrochemical modeling of Emerald Lake watershed, Sierra Nevada, California: sensitivity of stream chemistry to changes in fluxes and model parameters. *Limnology and Oceanography*, 41: 947–954.
- Wolford, R. A., Bales, R. C., and Sorooshian, S., 1996: Development of a hydrochemical model for seasonally snow-covered alpine watersheds: application to Emerald Lake Watershed, Sierra Nevada, California. *Water Resources Research*, 32: 1061–1074.

MS accepted October 2014

APPENDIX

TABLE A1

Macronutrient content (mg g⁻¹dry weight) of tissues of *Phyllodoce breweri*, *Salix orestera*, and wet meadow tissues in the Emerald Lake Basin, Sequoia National Park. NP indicates tissue not present; ND = no data.

| | Nitrogen | Phosphorus | Potassium | Calcium | Magnesium |
|----------------------------------|----------|------------|-----------|---------|-----------|
| <i>Phyllodoce breweri</i> | | | | | |
| New leaves | 14.9 | 1.7 | 8.68 | 5.31 | 1.59 |
| New twigs | 10.5 | 1.65 | 9.1 | 5.42 | 1.2 |
| New wood | ND | ND | ND | ND | ND |
| New reproduction | 11.6 | 1.4 | 7.57 | 4.92 | 1.16 |
| Old leaves | 10.5 | 0.8 | 9.09 | 5.14 | 1.58 |
| Old wood (live) | 5.6 | 0.45 | 5.28 | 3.52 | 0.7 |
| Dead wood | 6.4 | 0.3 | 3.9 | 5.87 | 0.86 |
| Litter | 13.4 | 0.9 | 2.99 | 2.85 | 1.05 |
| <i>Salix orestera</i> | | | | | |
| New leaves | 28.2 | 1.9 | 8.72 | 11.01 | 2.02 |
| New twigs | 13.5 | 1.6 | 5.36 | 4.09 | 1.17 |
| New wood | 6.2 | 0.9 | 1.79 | 3.81 | 0.54 |
| New reproduction | 16.9 | 1.28 | 7.36 | 2.23 | 1.02 |
| Old leaves | NP | NP | NP | NP | NP |
| Old wood (live) | 6.3 | 0.8 | 1.59 | 3.42 | 0.52 |
| Dead wood | 5.2 | 0.2 | 2.1 | 7.77 | 0.78 |
| Roots (0–2 mm) | 14.9 | 14.4 | 25.52 | 5.66 | 2.74 |
| Roots (2–5 mm) | 8.6 | 8.49 | 8.04 | 6.99 | 1.35 |
| Roots (5–10 mm) | 8.7 | 11.8 | 27.08 | 3.28 | 1.57 |
| Litter | 25.4 | 1.00 | 3 | 5.91 | 1.32 |
| <i>Wet Meadow</i> | | | | | |
| Aboveground | 17.01 | 1.61 | 21.48 | 9.12 | 2.33 |
| Roots (0–2 mm) | 8.8 | 7.07 | 13.32 | 3.01 | 1.79 |
| Litter | 15.31 | 0.8 | 7.4 | 4.89 | 1.53 |
| <i>Dry Meadow</i> | | | | | |
| Aboveground | 8.38 | 1.92 | 19.4 | 10.59 | 2.52 |
| Roots (0–2 mm) | 10.73 | 1.01 | 15.61 | 5.00 | 1.60 |
| Litter | 7.54 | 1.02 | 6.68 | 5.68 | 1.65 |