

UC Berkeley

UC Berkeley Previously Published Works

Title

Allometric relationships and trade-offs in 11 common Mediterranean-climate grasses

Permalink

<https://escholarship.org/uc/item/2jq4b867>

Journal

Ecological Applications, 34(4)

ISSN

1051-0761

Authors

Gao, Xiulin

Koven, Charles D

Kueppers, Lara M

Publication Date

2024-06-01

DOI

10.1002/eap.2976

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

ARTICLE

Allometric relationships and trade-offs in 11 common Mediterranean-climate grasses

Xiulin Gao¹ | Charles D. Koven¹ | Lara M. Kueppers^{1,2} 

¹Climate and Ecosystem Sciences
Division, Lawrence Berkeley National
Laboratory, Berkeley, California, USA

²Energy and Resources Group,
University of California, Berkeley,
Berkeley, California, USA

Correspondence

Xiulin Gao
Email: xiulingao@lbl.gov

Funding information

Lawrence Berkeley National Laboratory;
U.S. Department of Energy; the Gordon
and Betty Moore Foundation

Handling Editor: Hinsby Cadillo-Quiroz

Abstract

Biomass allocation in plants is the foundation for understanding dynamics in ecosystem carbon balance, species competition, and plant–environment interactions. However, existing work on plant allometry has mainly focused on trees, with fewer studies having developed allometric equations for grasses. Grasses with different life histories can vary in their carbon investment by prioritizing the growth of specific organs to survive, outcompete co-occurring plants, and ensure population persistence. Further, because grasses are important fuels for wildfire, the lack of grass allocation data adds uncertainty to process-based models that relate plant physiology to wildfire dynamics. To fill this gap, we conducted a greenhouse experiment with 11 common California grasses varying in photosynthetic pathway and growth form. We measured plant sizes and harvested above- and belowground biomass throughout the life cycle of annual species, while for the establishment stage of perennial grasses to quantify allometric relationships for leaf, stem, and root biomass, as well as plant height and canopy area. We used basal diameter as a reference measure of plant size. Overall, basal diameter is the best predictor for leaf and stem biomass, height, and canopy area. Including height as another predictor can improve model accuracy in predicting leaf and stem biomass and canopy area. Fine root biomass is a function of leaf biomass alone. Species vary in their allometric relationships, with most variation occurring for plant height, canopy area, and stem biomass. We further explored potential trade-offs in biomass allocation across species between leaf and fine root, leaf and stem, and allocation to reproduction. Consistent with our expectation, we found that fast-growing plants allocated a greater fraction to reproduction. Additionally, plant height and specific leaf area negatively influenced the leaf-to-stem ratio. However, contrary to our hypothesis, there were no differences in root-to-leaf ratio between perennial and annual or C₄ and C₃ plants. Our study provides species-specific and functional-type-specific allometry equations for both above- and belowground organs of 11 common California grass species, enabling nondestructive biomass assessment in California grasslands. These allometric relationships and trade-offs in carbon allocation across species can

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2024 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

improve ecosystem model predictions of grassland species interactions and environmental responses through differences in morphology.

KEYWORDS

California grass, grass allometry, growth form, photosynthetic pathway, plant strategy

INTRODUCTION

Size-dependent allocation of carbon to different plant structures reflects the consequences of evolutionary and ecological influences and links morphology to function over a species' life history. Allometric relationships thus are important for understanding how species interact with changing environments and coexisting plants and the resulting impacts on community structure and ecosystem function (Bonser & Aarssen, 2003; Enquist et al., 1999; Niklas, 2004; Weiner, 2004). Past plant allometry studies have mainly focused on trees resulting in a now large database of tree allometric equations (Falster et al., 2015; Jucker et al., 2022), but relatively few studies have developed allometric equations for grasses (Chieppa et al., 2020; Irving, 2015; Mahood et al., 2021; Nafus et al., 2009; Oliveras et al., 2014; Youkhana et al., 2017). In addition to the lack of studies of grass allometry, existing work on grass allometry has rarely examined both aboveground and belowground components throughout the life cycle of a species.

The relative proportion of carbon that plants invest in building photosynthetic foliage, supporting structures, and roots can vary according to their functional types and strategies in coping with disturbances and competition with coexisting plants (McCarthy & Enquist, 2007; Poorter et al., 2012; Shipley & Meziane, 2002). While grasses and trees are two distinct groups in terms of allometric relationships (Chieppa et al., 2020; Niklas, 2004), variations in growth form (annual vs. perennial) and photosynthetic pathway (C_3 vs. C_4) among grass species can also lead to different strategies in carbon investment. For instance, fast-growing annual species often mature before the dry season in semiarid regions and produce a large number of seeds that will germinate in the next wet season to maintain their populations (de Ridder et al., 1981; Veenendaal et al., 1996; Vico et al., 2016). In fire-prone ecosystems, C_4 perennial grasses are thought to invest more in belowground carbon storage in order to survive defoliation by fire through resprouting (Pausas & Paula, 2020; Ripley et al., 2010). Increased root allocation in perennial species can also help resist recurrent drought events, enabling access to underground water by deep roots (Canadell et al., 1996; Monti & Zatta, 2009; Schenk & Jackson, 2002). While growing taller can be an

advantage for light competition, how to balance carbon allocation between photosynthetic foliage and supporting structures in order to achieve net carbon gain at the whole-plant level can be a question of both light use efficiency and leaf traits such as specific leaf area (SLA) and leaf spatial arrangement (Anten & Hirose, 1998; Mensah et al., 2016; Niinemets, 2010). The trade-offs in biomass allocation to different structures and the association between species' allocation strategies can provide valuable insights into plant–environment interactions.

Understanding how plants allocate their carbon to different structures is also crucial for projecting carbon cycle dynamics into the future, yet it remains a particularly large uncertainty in land models (De Kauwe et al., 2014). Cohort-based or individual-based process models such as vegetation demography models track the growth of plants across their life cycles and, thus, treat allocation as a function of allometric growth curves, which can vary as a function of plant traits (Koven et al., 2020; Martínez Cano et al., 2020; Moorcroft et al., 2001). In ecosystem models where size-dependent allometric relationships are not incorporated, knowing how plants vary in proportional carbon investment to leaf, stem, and root are still important for tracking carbon fluxes between different carbon pools (Running & Gower, 1991). However, current vegetation dynamic models and ecosystem models have poorly constrained allometric models to parameterize carbon allocation for grass functional types or apply the same allometric relationships to different grass functional types (e.g., C_3 vs. C_4 grass; Bonan et al., 2003; Clark et al., 2011). Such misrepresentation of grass growth and development can lead to poor model projections of the future of the carbon cycle in response to changing climate and disturbance regimes in grassy ecosystems. This is particularly the case for models that try to project coupled fire and ecophysiological dynamics (Koven et al., 2020; Medvigy et al., 2009; Sitch et al., 2003) since the aboveground to belowground partitioning of grassland net primary productivity is a key determinant of fuels for wildfire. Therefore, empirical data quantifying size-dependent biomass allocation processes for different species and plant functional types are important for model development and parameterization.

Grasslands and tree–grass savannas are important ecosystems in semiarid regions such as California given

their effects on regional fire regime and carbon and water cycling. Due to the Mediterranean climate, where most rainfall occurs in winter and early spring, these grassy ecosystems in California mainly consist of cool-season C₃ grasses, especially annual species from the Pooideae lineage with Mediterranean origins (Stromberg et al., 2007). Surrounding the central valley region are California’s C₃ annual grasslands, in which *Bromus* spp., *Avena* spp., and *Distachyon* spp. often dominate (Biswell, 1956; Stromberg et al., 2007). In less disturbed areas, native C₃ perennial species such as *Nassella pulchra*, *Elymus glaucus*, and *Poa secunda* can outcompete exotic annual species to have higher ground covers (Bartolome & Gemmill, 1981; Hobbs & Mooney, 1991; Seabloom et al., 2003; Stromberg et al., 2007). Despite the dominant distributions of C₃ grasses in California, C₄ grasses are one of the main community components in the southern warm desert region and occasionally in the valley floor grasslands (Stromberg et al., 2007). Species including *Sporobolus airoides* and *Aristida purpurea* are relatively common in these communities (Beetle, 1947; Stromberg et al., 2007).

In this work, we aimed to fill a gap in grass allometry studies by collecting data on biomass growth rates in leaf, stem, fine root, and reproductive tissues for 11 common California grass species. By collecting biomass and plant size data, we aimed to develop size-dependent allometric equations for both carbon allocation and canopy architecture by choosing the best independent variables for each and testing if species and functional types vary significantly in their allometric relationships. In addition, we examined trade-offs in biomass allocation across species by determining the correlations between allometric parameters across species and between these parameters and SLA. We further examined how biomass allocation between root and leaf, relative allocation to reproductive tissues, and the partitioning between leaf and stem varied across species by testing three hypotheses: (1) that perennial and C₄ grasses will have higher root-to-leaf carbon ratios than annual and C₃ grasses; (2) that fast-growing species will invest more carbon in reproduction; and (3) that taller plants will have lower leaf-to-stem ratios due to more carbon investment in stem biomass rather than in leaf biomass as plant height increases; SLA will also be negatively correlated with leaf-to-stem ratio due to the lower amount of carbon required for building the same leaf area per unit canopy area in plants with broader and thinner leaves.

MATERIALS AND METHODS

We conducted a greenhouse experiment using seeds from 11 common California grass species that vary in both photosynthetic pathway (C₃ vs. C₄) and growth form

(annual vs. perennial). We tracked species growth and changes in allometry during the period March–October 2022 by measuring basal and canopy diameter and plant height and periodically harvesting a subset of individuals to quantify both aboveground and belowground biomass. We then developed size-dependent allometric equations by choosing the best predictors for each allometric relationship through model selection. Last, we built linear mixed-effects models to test the three hypotheses.

Study species

We selected 11 grass species that (1) are common in California ecosystems, including the valley, coastal, and warm desert grasslands based on the distribution and occurrence of each species according to Calflora (<https://www.calflora.org/search.html>) and (2) had seed available by request. Selected species varied in both photosynthetic pathway and growth form to represent different potential functional types, with at least two species for each combination (Table 1). Although C₄ annual grasses are minor components of California grasslands, we decided to include this particular functional type as the data can be useful to studies that focus on C₄ annual grass-dominant habitats. Seeds of each study species were requested from the National Plant Germplasm System, United States Department of Agriculture (<https://www.ars-grin.gov/npgs/>), by primarily choosing collections

TABLE 1 Study grass species that vary in both photosynthetic pathway and growth form.

Species	Photosynthetic pathway	Growth form
<i>Avena barbata</i> Pott ex Link	C ₃	Annual
<i>Brachypodium distachyon</i> (L.) P. Beauv.	C ₃	Annual
<i>Bromus hordeaceus</i> L.	C ₃	Annual
<i>Vulpia myuros</i> (L.) C. C. Gmel.	C ₃	Annual
<i>Elymus glaucus</i> Buckley	C ₃	Perennial
<i>Nassella pulchra</i> (Hitchc.) Barkworth	C ₃	Perennial
<i>Aristida oligantha</i> Michx.	C ₄	Annual
<i>Setaria pumila</i> (Poir.) Roem. and Schult.	C ₄	Annual
<i>Aristida purpurea</i> Nutt.	C ₄	Perennial
<i>Muhlenbergia rigens</i> (Benth.) Hitchc.	C ₄	Perennial
<i>Sporobolus airoides</i> (Torr.) Torr.	C ₄	Perennial

from California or other Mediterranean regions if the Californian source was not available.

Greenhouse methods

Seeds were germinated on a flat tray without stratification in mid-February 2022 at the Oxford greenhouse facility at the University of California, Berkeley. All seeds germinated within 2 weeks. Once seedlings reached a minimum height of 5 cm, we transplanted 30 or 35 seedlings of each species into either nursery cones (7 cm in diameter \times 25.5 cm in depth) or deep pots (15 cm in diameter \times 42 cm in depth) with regular greenhouse potting soil. We used nursery cones because of limited greenhouse space. To minimize effects of small pots on plant growth, we harvested all plants from nursery cones within 1.5 months after potting. In total, we had 15 replicates growing in nursery cones and 15–20 replicates growing in large pots for each of our studied species.

We split our experimental plants evenly by species into five blocks in the same room. All plants were randomly placed on the workbench within each block and relocated every other month throughout the course of the experiment. We watered the plants frequently to maintain a moist soil surface during the wet months (February–May) in California and changed watering frequency to every other day in the dry season (June–October) to reproduce potential effects of precipitation seasonality on plant carbon allocation but also to ensure the growth and survival of potted plants. Fertilizer, 100 ppm N 20-20-20 $\text{Ca}(\text{NO}_3)_2$, which is within the range of field observations (Parker & Muller, 1982), was applied once each month to all plants. Metal halide growth lights with a 16-h photoperiod setting were applied for the entire period.

All destructive measurements were made on harvested plants, beginning in March 2022. We first harvested plants growing in nursery cones. We measured basal diameter by taking both the widest diameter and its orthogonal diameter at the base of each plant. We used the same method for canopy diameter measurements at the top of each plant. We calculated canopy area using the average canopy diameter by assuming that the shape of each canopy was close to a circle. We measured plant height as the distance between the soil surface and the highest point of the plant under its natural resting condition, which included the inflorescence when it was present. Following the size measurements, plants were clipped at the soil surface and separated into leaf, stem, and reproductive tissues, if any were present. We then unearthed the root biomass and washed it in a large plastic tub to carefully remove all soil particles and organic

debris. The biomass of each organ was bagged, transported to the laboratory, oven-dried at 60°C for 3 days, and weighed. Our first harvest included all species, with one replicate of each species per block being randomly selected with five replicates per species each time. As each species grew at different rates, measurements after the first sampling were taken on different species at different times in order to capture changes in plant size and biomass allocation of each species during the course of the experiment. We used the presence of reproductive tissues, including flowers and seeds, to define the end of the experiment for a species. Therefore, we last sampled all annual species in mid-June 2022 and finished sampling all perennial species in October 2022. Two perennial species, *M. rigens* and *N. pulchra*, did not produce any reproductive tissues by October 2022. For annual grasses that only live for one growing season and senesce after seed production, data collected during this time period and the associated results thus refer to the entire life cycle of the studied annual species but may only represent the early life stage of the studied perennial grasses. In addition to size and biomass measurements, we also measured SLA by taking one fully expanded leaf from five randomly selected individuals of each species during mid-May in 2022. Leaf samples were collected on the same day for all studied species, with sampled individuals varied in the status of sexual maturity, but all plants were actively growing with no sign of senescence. We scanned each leaf using a flatbed scanner at a fixed resolution and size, then calculated leaf area using ImageJ (Abràmoff et al., 2004). The leaf sample was then oven-dried and weighed for biomass measurement. Measured SLA was then averaged to estimate species-level mean SLA.

Data analysis

We assumed a power law relationship to build the allometric equations for leaf, stem, and root biomass and canopy architecture, including plant height and canopy area (West et al., 1997). To calculate both the exponent and coefficient of each equation, we fit linear regressions using natural log-transformed plant biomass and size data. To select the best model and determine species differences in allometric relationships, we compared models that included species as another independent variable along with basal diameter and/or height to ones without species, using the Akaike information criterion (Bozdogan, 1987). For fine root allometry, both plant size and leaf biomass were included as candidate predictors (Chen et al., 2019). When both plant basal diameter and height were included in the regression, we did not

include an interaction term between the two, since including the interaction improved adjusted R^2 by only 1% in all cases. Therefore, we dropped such interaction effects in favor of model parsimony. For allometric relationships with significant species differences, we then fit another linear regression model using the structure of the best model selected but including photosynthetic type and growth form instead of species to further determine whether allometric relationships generalized by grass functional types were better than those resolved by species. We did not include the interaction between photosynthetic type and growth form, as there were only two species in the C_4 annual and C_3 perennial functional groups. Allometry equations are reported according to the model selection results: (1) species-specific allometric equations using species-level data if the species effect was significant or generalized grass allometric equations using the entire data set otherwise and (2) functional-type-specific allometric equations using data grouped by photosynthetic type and growth form if the effects of functional group were significant and the model was better than the species-specific model. We corrected the intercept term of each linear regression for error due to log-transformation of the data (Mascaro et al., 2011; Sprugel, 1983). The slope of each predictor and the corrected intercept term were then used as the exponent associated with the corresponding predictor and the coefficient of the allometry equation, respectively. To explore how species-specific allometric relationships correlated with one another and with SLA, we created a Pearson correlation matrix for the traits, including the exponents and coefficients for each allometric relationship and SLA, and calculated the significance of each correlation.

To test the three hypotheses, we fit a linear mixed-effects model for each. To determine whether perennial and C_4 grasses allocated more biomass to belowground tissue for a given amount of leaf carbon than annual or C_3 grasses do, we included the root-to-leaf ratio as the dependent variable and the photosynthetic pathway and growth form as two fixed effect variables with no interaction between the two. To test whether fast-growing species invested more in reproduction, we included only growth rate as the fixed effect and reproduction investment as the dependent variable. We calculated growth rate by fitting a linear model with log-transformed total biomass as the dependent variable and time as the independent variable for each species. We then used the slope of each linear regression as the species growth rate. Reproductive investment is calculated by dividing reproductive biomass by total biomass (aboveground plus belowground biomass), to control for plant size effects. Finally, to test whether the leaf-to-stem ratio was inversely related to plant height and SLA, we built a

linear mixed-effects model including both plant height and species-level mean SLA as fixed effects and leaf-to-stem ratio as the dependent variable. A two-way interaction term was included. For all three linear mixed-effects models, we included species as the random term to account for the potential effects of unmeasured species-specific traits.

We performed all data analysis using R (R Core Team, 2019). All mixed-effects models were built with the lme4 package (Bates et al., 2015). We examined the significance of fixed effects using the “Anova()” function in the car package (Fox et al., 2013). To test hypotheses with interaction effects, we calculated type 3 sums of squares; type 2 sums of squares were calculated otherwise (Hector et al., 2010; Shaw & Mitchell-Olds, 1993). We estimated approximate df and p -values using the Kenward–Roger approximation to avoid unacceptable type I errors (Luke, 2017).

RESULTS

The selected best model for allometric relationships differed between belowground and aboveground structures. The best single predictor for leaf and stem biomass, plant height, and canopy area was plant basal diameter. Including plant height as a second predictor improved model performance for leaf and stem biomass and canopy area (Figure 1 and Appendix S1: Table S1). In contrast, the best independent variable selected for fine root biomass was leaf biomass, indicating that carbon investment in belowground growth was proportional to that of photosynthetic tissues. In addition, models in which species identity was included as another variable to account for species-specific effects were better than models without species as one of the predictors in all cases (Appendix S1: Table S1). Therefore, we developed species-specific allometric relationships for leaf, stem, and root biomass, plant height, and canopy area (Tables 2 and 3). Although the models that included photosynthetic type and growth form were not better than species-specific models, we still developed allometric equations for each of the four functional types and for the most general allometric relationships across all species for two reasons: (1) the effects of photosynthetic type and/or growth form were significant and (2) these functional-type-specific allometric relationships are needed for vegetation demography models when they do not resolve individual species and, thus, can be of interest to other studies (Tables 2 and 3). Moreover, as canopy cover and plant height are easier to measure than basal diameter in field surveys or can be estimated via remote sensing technology at large spatial scales, allometry

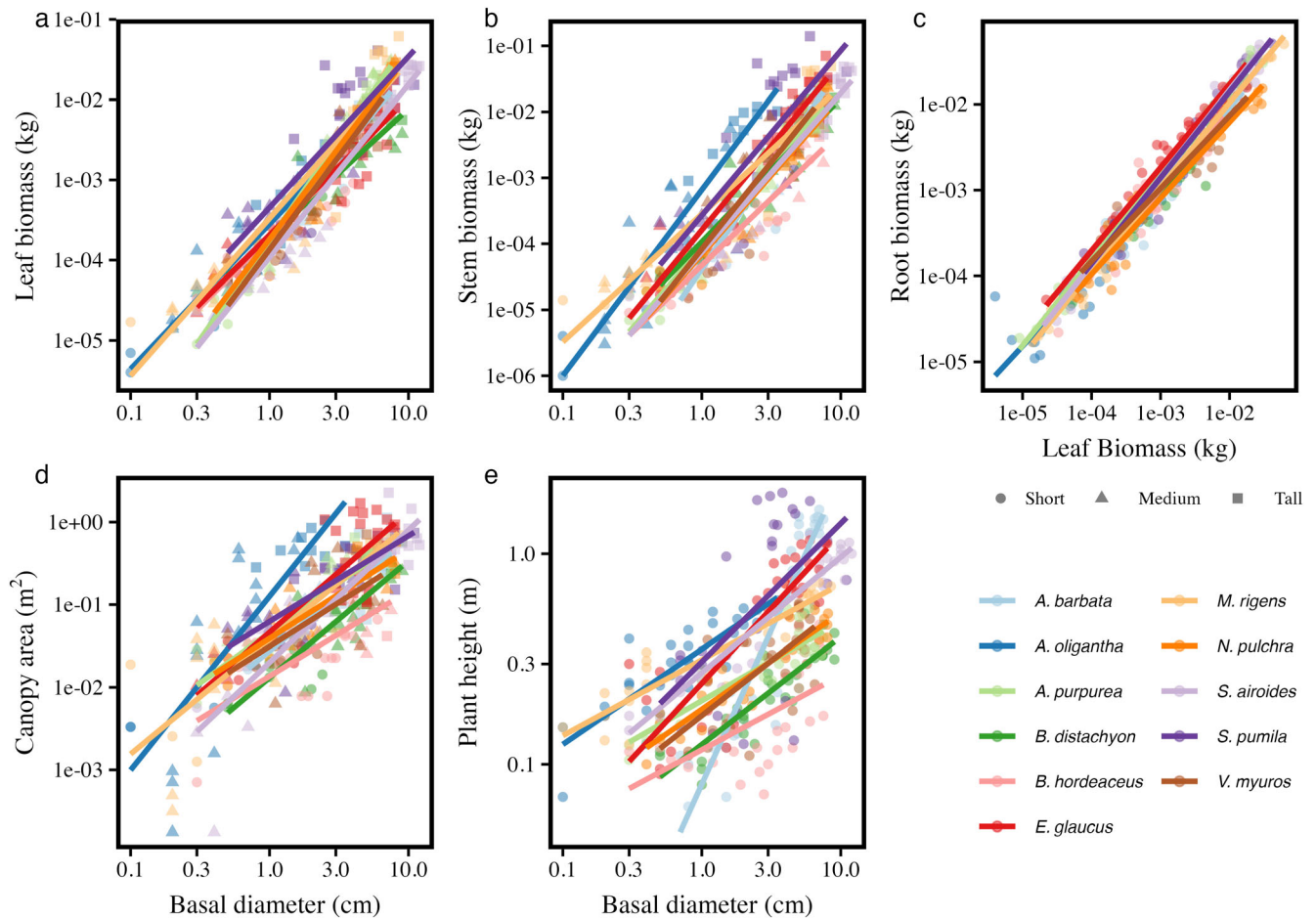


FIGURE 1 Best predictors in each allometric relationship and variations in allometric relationships across 11 grass species. Points are original observations; lines are best-fit linear models. Points and lines are both color-coded by species. For leaf biomass, stem biomass, and canopy area, both basal diameter and height were included as predictors (Table 2). We thus used different shapes to visualize the effects of height using cutoff values to group height into three groups: short (height ≤ 0.165 m), medium (0.165 m < height ≤ 0.406 m), and tall (height > 0.406 m). Cutoff values were chosen to ensure each group has a similar number of plant individuals. Height was included as a continuous variable in the model.

equations including canopy area and plant height are also provided (Appendix S1: Table S2) to facilitate biomass estimation at broader scales.

The trade-offs in biomass allocation across species were complicated, with both positive and negative correlations found (Figure 2). Exponents and coefficients for leaf and stem biomass allometries were positively correlated across species, suggesting that carbon investment in foliage and supporting structures changed in a similar way in response to changes in plant size. Negative correlations were found between leaf biomass and stem biomass allometry, canopy area and height allometry, and fine root biomass and canopy area allometry, indicating trade-offs. These relationships showed that exponents associated with basal diameter for stem allometry were negatively correlated with coefficients of leaf allometry; that species with larger exponents associated with height and coefficients for canopy area allometry tended to have

lower exponents for basal-diameter-dependent height allometry; and that a larger coefficient for fine root allometry often suggested a smaller coefficient for canopy area allometry of the species. Within allometric equations, exponents associated with height for stem and leaf biomass and canopy area allometry and exponent associated with leaf biomass for fine root allometry were positively correlated with the corresponding coefficients, respectively. This correlation was much stronger for fine root and leaf biomass allometry than for stem biomass and canopy area allometry. Moreover, species having a larger exponent associated with height and a larger coefficient tended to have a smaller exponent associated with basal diameter for its leaf allometry.

The results of the linear mixed-effects models suggested the rejection of the first hypothesis that perennial and C_4 grasses tend to have higher root-to-leaf ratios than annual and C_3 grasses. Instead, we found no

TABLE 2 Species-specific and functional-type-specific allometric equation for leaf, stem, and root biomass of studied grass species.

Species/PFT	Leaf biomass (kg)	Stem biomass (kg)	Root biomass (kg)
<i>Avena barbata</i>	$0.0013616179 \times \text{bd}^{0.9632224} \times \text{hgt}^{0.7695094}$	$0.0018430602 \times \text{bd}^{0.9188281} \times \text{hgt}^{1.4638936}$	$0.6145165 \times \text{leaf}^{0.8924402}$
<i>Aristida oligantha</i>	$0.0011134586 \times \text{bd}^{1.2979848} \times \text{hgt}^{1.1237133}$	$0.0059751386 \times \text{bd}^{2.0865629} \times \text{hgt}^{1.6162808}$	$0.4127416 \times \text{leaf}^{0.8708756}$
<i>Aristida purpurea</i>	$0.0001699565 \times \text{bd}^{2.4627071} \times \text{hgt}^{-0.1000366}$	$0.0003542401 \times \text{bd}^{2.0669758} \times \text{hgt}^{0.7826914}$	$1.3998147 \times \text{leaf}^{0.9887286}$
<i>Brachypodium distachyon</i>	$0.0017642697 \times \text{bd}^{1.0823284} \times \text{hgt}^{1.0078166}$	$0.0117671970 \times \text{bd}^{1.0510878} \times \text{hgt}^{2.2098905}$	$0.6920349 \times \text{leaf}^{0.9400956}$
<i>Bromus hordeaceus</i>	$0.0010856761 \times \text{bd}^{1.4757366} \times \text{hgt}^{0.7545222}$	$0.0009265308 \times \text{bd}^{1.5573795} \times \text{hgt}^{1.3254468}$	$0.8690024 \times \text{leaf}^{0.9597882}$
<i>Elymus glaucus</i>	$0.0003452391 \times \text{bd}^{1.3573965} \times \text{hgt}^{0.2883154}$	$0.0015066543 \times \text{bd}^{1.3824217} \times \text{hgt}^{1.4991645}$	$2.8875124 \times \text{leaf}^{1.0454835}$
<i>Muhlenbergia rigens</i>	$0.0073154333 \times \text{bd}^{1.1105775} \times \text{hgt}^{2.3644061}$	$0.0077778084 \times \text{bd}^{1.0404906} \times \text{hgt}^{2.4904269}$	$1.0004837 \times \text{leaf}^{0.9811488}$
<i>Nassella pulchra</i>	$0.0014412579 \times \text{bd}^{1.5889337} \times \text{hgt}^{1.1031745}$	$0.0008209071 \times \text{bd}^{1.2950947} \times \text{hgt}^{1.3740156}$	$0.7845209 \times \text{leaf}^{0.9599259}$
<i>Sporobolus airoides</i>	$0.0006953617 \times \text{bd}^{1.4411525} \times \text{hgt}^{1.2956815}$	$0.0013878175 \times \text{bd}^{1.2705902} \times \text{hgt}^{2.0754241}$	$1.6598366 \times \text{leaf}^{1.0168490}$
<i>Setaria pumila</i>	$0.0024560125 \times \text{bd}^{0.9937094} \times \text{hgt}^{1.3501222}$	$0.0029060531 \times \text{bd}^{1.2559667} \times \text{hgt}^{1.8889166}$	$1.5087865 \times \text{leaf}^{1.0016670}$
<i>Vulpia myuros</i>	$0.0002713855 \times \text{bd}^{2.1743119} \times \text{hgt}^{0.2854919}$	$0.0029818582 \times \text{bd}^{1.6266470} \times \text{hgt}^{1.9410848}$	$0.3899739 \times \text{leaf}^{0.8474375}$
C ₃ annual grass	$0.0005851419 \times \text{bd}^{1.569265} \times \text{hgt}^{0.4954871}$	$0.00103039 \times \text{bd}^{1.614535} \times \text{hgt}^{1.209238}$	$0.6032279 \times \text{leaf}^{0.9077466}$
C ₃ perennial grass	$0.0001848569 \times \text{bd}^{2.063426} \times \text{hgt}^{-0.1716052}$	$0.00140364 \times \text{bd}^{1.572202} \times \text{hgt}^{1.536391}$	$0.8548639 \times \text{leaf}^{0.9187837}$
C ₄ annual grass	$0.0016160522 \times \text{bd}^{1.30174} \times \text{hgt}^{1.282181}$	$0.004138626 \times \text{bd}^{1.482047} \times \text{hgt}^{1.810899}$	$1.3178439 \times \text{leaf}^{0.9905364}$
C ₄ perennial grass	$0.0004260698 \times \text{bd}^{1.981073} \times \text{hgt}^{0.255733}$	$0.001124235 \times \text{bd}^{1.611751} \times \text{hgt}^{1.269692}$	$1.4337324 \times \text{leaf}^{1.0034105}$
Generalized grass	$0.0006890597 \times \text{bd}^{1.669976} \times \text{hgt}^{0.5895024}$	$0.001809336 \times \text{bd}^{1.507866} \times \text{hgt}^{1.480002}$	$1.033965 \times \text{leaf}^{0.9654983}$

Note: All coefficients were corrected for error that is due to log transformation of the data. Abbreviations: bd, basal diameter (in centimeters); hgt, height (in meters); leaf, leaf biomass (in kilograms).

TABLE 3 Species-specific and functional-type-specific allometric equation for canopy architecture of studied grass species.

Species/PFT	Canopy area (m ²)	Height (m)
<i>Avena barbata</i>	$0.04514152 \times \text{bd}^{1.1733757} \times \text{hgt}^{0.1345857}$	$0.08811922 \times \text{bd}^{1.4651031}$
<i>Aristida oligantha</i>	$1.13077752 \times \text{bd}^{1.5347793} \times \text{hgt}^{1.2594413}$	$0.36481456 \times \text{bd}^{0.4515522}$
<i>Aristida purpurea</i>	$0.26502260 \times \text{bd}^{0.8960342} \times \text{hgt}^{0.9815189}$	$0.20401990 \times \text{bd}^{0.3734491}$
<i>Brachypodium distachyon</i>	$0.20612150 \times \text{bd}^{0.7844884} \times \text{hgt}^{1.2328798}$	$0.12812118 \times \text{bd}^{0.5109920}$
<i>Bromus hordeaceus</i>	$0.20742634 \times \text{bd}^{0.6398081} \times \text{hgt}^{1.1070299}$	$0.12966407 \times \text{bd}^{0.3531690}$
<i>Elymus glaucus</i>	$0.17841370 \times \text{bd}^{0.9941569} \times \text{hgt}^{0.6546150}$	$0.27203321 \times \text{bd}^{0.6946629}$
<i>Muhlenbergia rigens</i>	$0.65598468 \times \text{bd}^{0.6927433} \times \text{hgt}^{1.9273278}$	$0.32349678 \times \text{bd}^{0.3596250}$
<i>Nassella pulchra</i>	$1.11711962 \times \text{bd}^{0.2636253} \times \text{hgt}^{1.9180868}$	$0.18642472 \times \text{bd}^{0.4827293}$
<i>Sporobolus airoides</i>	$0.01025025 \times \text{bd}^{2.0454243} \times \text{hgt}^{-0.8063971}$	$0.27771970 \times \text{bd}^{0.5494034}$
<i>Setaria pumila</i>	$0.15005544 \times \text{bd}^{0.6391970} \times \text{hgt}^{0.6066071}$	$0.42498205 \times \text{bd}^{0.6573687}$
<i>Vulpia myuros</i>	$0.27128106 \times \text{bd}^{0.5265581} \times \text{hgt}^{1.0404903}$	$0.18469213 \times \text{bd}^{0.5201388}$
C ₃ annual grass	$0.12826361 \times \text{bd}^{0.7134629} \times \text{hgt}^{0.7576721}$	$0.1476171 \times \text{bd}^{0.6995105}$
C ₃ perennial grass	$0.23702483 \times \text{bd}^{0.72682} \times \text{hgt}^{0.9459644}$	$0.2329925 \times \text{bd}^{0.619077}$
C ₄ annual grass	$0.25749493 \times \text{bd}^{1.0866763} \times \text{hgt}^{0.5700335}$	$0.4204882 \times \text{bd}^{0.5194908}$
C ₄ perennial grass	$0.06669907 \times \text{bd}^{1.3043469} \times \text{hgt}^{0.2002879}$	$0.2776634 \times \text{bd}^{0.4176197}$
Generalized grass	$0.191594 \times \text{bd}^{0.8377013} \times \text{hgt}^{0.8555644}$	$0.2717316 \times \text{bd}^{0.4532469}$

Note: All coefficients were corrected for error that is due to log transformation of the data. Abbreviations: bd, basal diameter (in centimeters); hgt, height (in meters).

difference in the root-to-leaf ratios between functional types (Figure 3 and Appendix S1: Table S3). As expected in the second hypothesis, there was a positive effect of

species growth rate on proportional reproduction allocation (Figure 4 and Appendix S1: Table S4). Also, consistent with the third hypothesis, we found negative

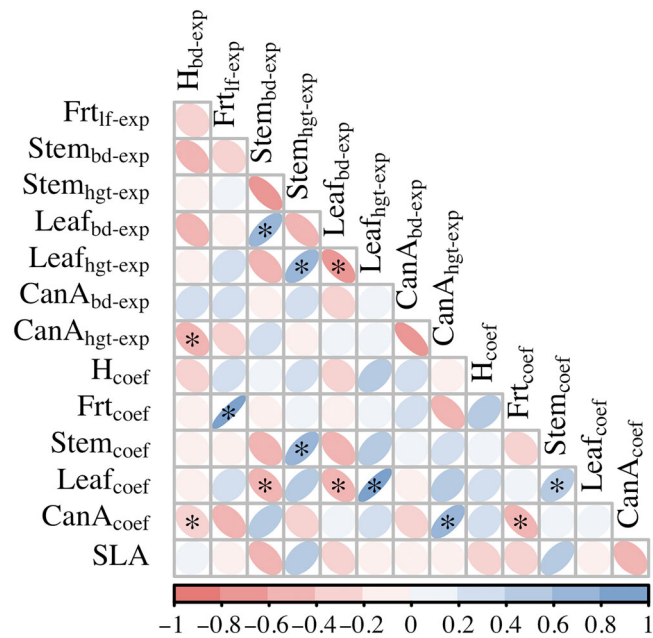


FIGURE 2 Correlations among allometric parameters and with specific leaf area across species. Significant correlations with $p < 0.05$ are marked with asterisk. $\text{Stem}_{\text{bd-exp}}$: exponent associated with basal diameter for stem biomass allometry; $\text{Stem}_{\text{hgt-exp}}$: exponent associated with height for stem biomass allometry; $\text{Stem}_{\text{coef}}$: coefficient for stem biomass allometry. H: height; Frt: fine root; CanA: canopy area. All other abbreviations in this figure follow the same labeling pattern as for stem biomass allometry.

correlations between the leaf-to-stem ratio and plant traits including plant height and SLA. The negative effect of plant height on the leaf-to-stem ratio was much stronger for plants with larger SLA, a negative interaction effect between the two plant traits on the leaf-to-stem ratio (Figure 5 and Appendix S1: Table S5).

DISCUSSION

We developed allometric equations of leaf, stem, and root biomass, plant height, and canopy area for 11 common California grasses and tested the generality of each allometric relationship by examining species and functional type effects. The results demonstrated that both basal diameter and plant height were important size measurements for predicting changes in biomass allocation throughout the life cycle of annual grasses and during the early life stage of perennials, which is consistent with previous studies (Alamgir & Al-Amin, 2008; Guevara et al., 2002; Kenzo et al., 2022; Nafus et al., 2009; Oliveras et al., 2014). While species varied in their allometric relationships, species differences mainly occurred in canopy architecture including plant height, canopy area, and

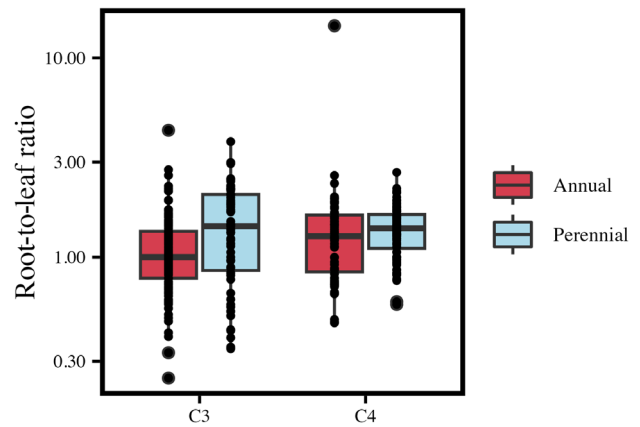


FIGURE 3 Root-to-leaf ratio comparison between annual and perennial and C_3 and C_4 grasses. The extreme value of >10 was from a seedling of *Aristida oligantha*. As a reference, the mean root-to-leaf ratio of C_3 annuals is 1.12.

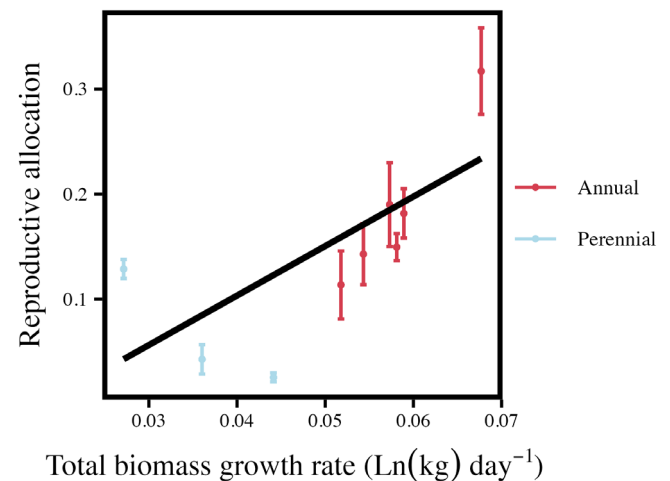


FIGURE 4 Relationships between total biomass growth rate and reproductive allocation. Line is best-fit model. Points are mean proportion allocated to reproduction by species, and bars are \pm one SE. Species are color-coded by their growth form.

stem biomass allocation, with both leaf and fine root allocation being relatively well conserved across species (Figure 1; also, see Garnier, 1992; Poorter et al., 2012). Such patterns are likely due to the large variation in plant height and the intrinsic correlation between height, canopy area, and stem biomass: An increase in height reflects the elongation in the stem, which in turn leads to a spreading, larger canopy, since grass stems are not as rigid as those of woody plants (Table 2). In addition to species variation in height, variations in tillering pattern can also contribute to changes in stem biomass allocation and canopy area (Nelson & Moore, 2020). For instance, *A. oligantha* has a height similar to or shorter than that

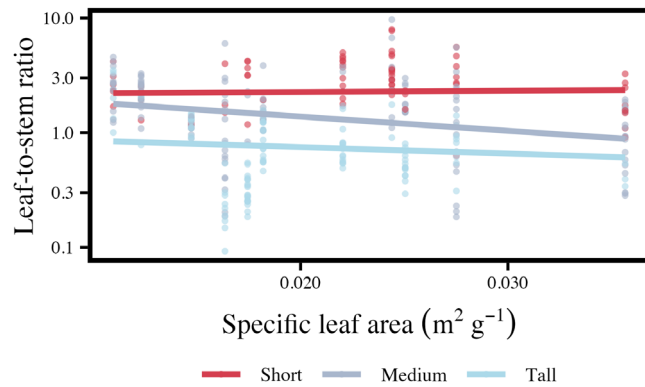


FIGURE 5 Relationships between leaf-to-stem ratio and specific leaf area (SLA) and plant height. Points are original observations, and lines are best-fit models. Points and lines are color-coded by plant height. Height was included as a continuous variable in the model, but in order to visualize the height effect on the leaf-to-stem ratio, we grouped plants into three height categories: short (height ≤ 0.165 m), medium ($0.165 < \text{height} \leq 0.406$ m), and tall (height > 0.406 m). Cutoff values were chosen to ensure each group has a similar number of individuals. Species mean SLA is plotted on the X-axis.

of *S. pumila* at a basal diameter less than 4.0 cm (Appendix S1: Figure S1). However, both stem biomass and canopy area of *A. oligantha* were greater than those of *S. pumila* (Figure 1b,d). This inconsistency in size-dependent structure change may be due to the large number of fine tillers in *A. oligantha* compared to the few but wider tillers in *S. pumila* (personal observation), especially when those fine tillers mainly expanded horizontally instead of occupying the vertical space (Appendix S1: Figure S2). The tillering pattern can also contribute to species variations in leaf biomass allocation. With more fine tillers, species such as *A. purpurea* tended to have a higher leaf biomass allocation, even though they were shorter in height compared to species such as *A. barbata* (Figure 1).

The best-conserved allometric relationship across species was the fine root allocation; most species maintained a relatively constant carbon partition between their leaves and roots as the plant size changed, as indicated by an exponent that was close to one (Table 2) (Chen et al., 2019; Poorter et al., 2012). Therefore, an isometric or nearly isometric scaling between leaf and fine root biomass can be used to simplify the prediction of root development in grass functional types such as C_4 annuals (scaling exponent between leaf and root biomass is 0.99 (Table 2)). However, the observation period was relatively short for perennial grasses in our work. Also, perennials can have more belowground biomass allocation later during their life due to ontogenetic drift and change in growing conditions (Geng et al., 2007; Pitelka,

1977; Poorter et al., 2015), shifting the scaling exponent as plants grow older.

Trade-offs in carbon allocation patterns across species, as demonstrated by negative correlations between allometric parameters, suggest that these grasses prioritize investments in different structures to compete for resources such as space, light, and nutrients (Blanchard et al., 2016; McCarthy & Enquist, 2007; Poorter et al., 2012; Schenk & Jackson, 2002; White et al., 2012). For instance, the exponent of the basal diameter-dependent height allometry was negatively correlated with both the exponent associated with height and the coefficient for canopy area allometry (Figure 2), which suggests that when growth in height was large for a given change in basal diameter, the plants tended to have smaller canopy area (Poorter et al., 2006) and, thus, a strategy to grow taller rather than wider to occupy the canopy layer (Archibald & Bond, 2003; Blanchard et al., 2016). In addition, species with a larger exponent for basal-diameter-dependent stem biomass allometry had a smaller coefficient for leaf biomass allometry, suggesting that seedlings with less leaf biomass tended to have more allocation to stem biomass per unit change in basal diameter. Moreover, seedlings with a larger belowground root allocation had a narrower canopy, reflecting a trade-off between root and canopy structures at an early stage. Within the same allometric equation, a negative correlation between exponents associated with different predictors can indicate the main variable that drives the growth of the corresponding organ. For instance, a larger exponent associated with height and a larger coefficient often corresponded to a smaller exponent associated with basal diameter in leaf allometry across species. Such negative correlations suggest that increases in leaf biomass were mainly determined by an increase in height rather than an increase in basal diameter if their seedlings started with a larger leaf biomass. A potential explanation of this is the continuous growth in plant height at the later stage of development once basal diameter reached a threshold size and tillering ceased. For example, *A. barbata* has a unique canopy architecture with mostly short tillers centered around a few main stems at the base of the plant. Leaves of *A. barbata* seedlings were relatively larger in comparison to most of the other species. During the later stage of plant development in *A. barbata*, only the main stems continued to grow into the vertical space and contribute to increase in leaf biomass.

When the growth of two different organs is intrinsically linked with one another, a positive correlation between each parameter of the two allometric relationships is present. For instance, the positive correlations

between leaf and stem allometric parameters as a function of both basal diameter and height suggests that an increase in tiller numbers, which expanded basal diameter, and height resulted in an increase in both leaf and stem biomass simultaneously, as the growth of both height and tillers involved the development of both leaf and stem (Ackerly & Donoghue, 1998; Xiang et al., 2009). We also found positive correlations within the same allometric equation between the exponent and coefficient in fine root allometry as a function of leaf biomass and between exponents associated with height and the coefficients in leaf, stem, and canopy area allometry. The former indicates that species that had higher allocation to roots at an early stage also tended to increase their root biomass per unit leaf biomass more rapidly over their life cycle, meaning a starter effect. The latter indicates that species starting at larger leaf and stem biomass and canopy area often tended to invest more carbon in growing leaf and stem and building a wider canopy as per unit change in height.

Contrary to our hypothesis, we did not find greater belowground allocation per unit leaf biomass in C_4 and perennial grasses compared to C_3 and annual species (Figure 3). While this is consistent with some previous findings (Garnier, 1992; Pitelka, 1977; Poorter et al., 2015), there is also a large body of work showing more extensive root systems in C_4 or perennial plants (DuPont et al., 2014; Holmes & Rice, 1996; Taylor et al., 2010). Despite the contrasting patterns documented, the result we observed here can be due to the fact that over the course of our short experiment, it is impossible to observe a significant deviation in root-to-leaf ratios between annual and perennial functional groups, especially when all plants were regularly watered and fertilized. It is also important to point out that with the small number of species we have here, difference between functional groups may not be detectable, so further evidence is required.

As expected, fast-growing species invested more carbon in reproduction, and this positive effect of growth rate on reproductive allocation was driven mainly by annual species (Figure 4 and Brock, 1983; Pitelka, 1977; Wilson & Thompson, 1989), supporting the foregoing hypothesis. Having an annual life history strategy is a known strategy to avoid stresses such as drought (Fernández Ales et al., 1993; Sherrard & Maherali, 2006; Volis et al., 2002). Annual plants usually grow at a higher rate than coexisting perennial species, so that they can reach a reproductive stage earlier and produce a large number of seeds before the dry season starts. A greater allocation to seed production allows for persistence and even expansion of their populations in the local community (Veenendaal et al., 1996; Volis et al., 2002). Although

not all perennial grasses reproduced during our experiment, past work shows generally lower reproductive allocations in perennial grasses compared to annual grasses (Wilson & Thompson, 1989). We thus believe this positive correlation between growth rate and reproductive allocation holds true for studied species even with limited data from perennial species.

Finally, in keeping with our hypothesis, as plants grew taller and for species with higher SLA, less carbon was allocated to leaves than to stems, and such negative effects of plant height on the leaf-to-stem ratio was stronger in plants with higher SLA (Figure 5). Since height was defined as the distance between the soil surface and the highest point a plant can reach, an increase in height should require more support structure rather than leaves and, therefore, a decreased leaf-to-stem ratio. The negative effect of SLA and its interaction with plant height to further reduce the leaf-to-stem ratio could be a result of the reduced carbon demand to fill a unit canopy area when SLA is large. However, unmeasured traits such as light use efficiency and leaf spatial arrangement may also affect carbon partitioning between photosynthetic tissues and support structures (Niinemets, 2010).

Our study provides allometry equations for leaf, stem, and root biomass, plant height, and canopy area for 11 common California grasses; it is also the first work to determine allometric relationships for both aboveground and belowground components of each species. With species-specific allometry equations, it is now possible to estimate both the aboveground and belowground biomass of California grasslands or other Mediterranean grasslands with similar species composition without performing destructive measurements. It also helps better understand the growth and development in grass species, which can improve model accuracy in representing carbon allocation. In particular, we show that allometric relationships based on a plant's basal diameter is a robust method for understanding plant growth over the life cycle and early life stage of annual and perennial species, respectively, and this supports the use of basal diameter as the basic index of plant size for grasses in vegetation demographic models, just as stem diameter at breast height is widely used as an index of plant size for trees in such models. Both species and plant functional type had significant effects on allometric relationships, but variations were relatively subtle in leaf and root allometry. Instead of using species-specific allometry for leaf and root, usage of more generalized functional type allometric equations is reasonable in vegetation demographic models, in particular for root allometry. To choose between species-specific and functional-type-specific allometric equations for stem biomass, height, and canopy

area, modelers should consider both the scale of the study and the dominant species in the study region: At the site level species composition can be simpler than that at the regional level, and species-specific allometry of the dominant species can be applied, while for regional studies, generalized functional-type allometry of the dominant function type in the region is better for representing the average growth and development of different grass species that belong to the same functional group. Lastly, the trade-offs in biomass allocation that we explored here shed light on understanding plant–environment interactions and species competition by defining different plant strategies according to reproduction and water and light competition. Future work with more species to account for potential phylogenetic effects on grass allometric relationships (Ackerly & Donoghue, 1998; Griffith et al., 2020) and a longer observation period with field data is required to further confirm the results we observed here. In addition, studies to quantify the response of carbon allocation to changes in environmental factors such as nutrients, precipitation, and CO₂ in observations combined with model simulations at larger spatial and temporal scales can help better understand future ecosystem dynamics under global change.

AUTHOR CONTRIBUTIONS

All authors contributed equally to the idea and experimental design. Xiulin Gao led the data collection, data analysis, and writing of the first draft, with advice from Charles D. Koven and Lara M. Kueppers. All authors contributed equally to the editing of the manuscript.

ACKNOWLEDGMENTS

This research was supported by the Laboratory Directed Research and Development Program funded by Lawrence Berkeley National Laboratory, the Gordon and Betty Moore Foundation, and the U.S. Department of Energy, Office of Biological and Environmental Research, Regional and Global Model Analysis through the Early Career Research Program. We would like to thank undergraduate research assistants including Declan Farriday, Jackie Fenner, Paige Lund, and Spencer Goldstein for their help on data collection. In addition, we thank staff at the Oxford greenhouse facility at University of California, Berkeley, in particular Tina Wistrom, for their help taking care of our plants.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Gao et al., 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10655820>.

ORCID

Lara M. Kueppers  <https://orcid.org/0000-0002-8134-3579>

REFERENCES

- Abramoff, M. D., P. J. Magalhães, and S. J. Ram. 2004. “Image Processing with imageJ.” *Biophotonics International* 11: 36–41.
- Ackerly, D. D., and M. J. Donoghue. 1998. “Leaf Size, Sapling Allometry, and Corner’s Rules: Phylogeny and Correlated Evolution in Maples (*Acer*).” *American Naturalist* 152: 767–791.
- Alamgir, M., and M. Al-Amin. 2008. “Allometric Models to Estimate Biomass Organic Carbon Stock in Forest Vegetation.” *Journal of Forestry Research* 19: 101–6.
- Anten, N. P. R., and T. Hirose. 1998. “Biomass Allocation and Light Partitioning among Dominant and Subordinate Individuals in *Xanthium canadense* Stands.” *Annals of Botany* 82: 665–673.
- Archibald, S., and W. J. Bond. 2003. “Growing Tall Vs Growing Wide: Tree Architecture and Allometry of *Acacia karroo* in Forest, Savanna, and Arid Environments.” *Oikos* 102: 3–14.
- Bartolome, J. W., and B. C. N. Gemmill. 1981. “The Ecological Status of *Stipa pulchra* (Poaceae) in California.” *Madrono* 28: 172–184.
- Bates, D., M. Mächler, B. M. Bolker, and S. C. Walker. 2015. “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software* 67: 1–48.
- Beetle, A. A. 1947. “Distribution of the Native Grasses of California.” *Hilgardia* 17: 309–357.
- Biswell, H. H. 1956. “Ecology of California Grasslands.” *Journal of Range Management* 9: 19.
- Blanchard, E., P. Birnbaum, T. Ibanez, T. Boutreux, C. Antin, P. Ploton, G. Vincent, et al. 2016. “Contrasted Allometries between Stem Diameter, Crown Area, and Tree Height in Five Tropical Biogeographic Areas.” *Trees* 30: 1953–68.
- Bonan, G. B., S. Levis, S. Sitch, M. Vertenstein, and K. W. Oleson. 2003. “A Dynamic Global Vegetation Model for Use with Climate Models: Concepts and Description of Simulated Vegetation Dynamics.” *Global Change Biology* 9: 1543–66.
- Bonser, S. P., and L. W. Aarssen. 2003. “Allometry and Development in Herbaceous Plants: Functional Responses of Meristem Allocation to Light and Nutrient Availability.” *American Journal of Botany* 90: 404–412.
- Bozdogan, H. 1987. “Model Selection and Akaike’s Information Criterion (AIC): The General Theory and its Analytical Extensions.” *Psychometrika* 52: 345–370.
- Brock, M. A. 1983. “Reproductive Allocation in Annual and Perennial Species of the Submerged Aquatic Halophyte *Ruppia*.” *The Journal of Ecology* 71: 811.
- Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. “Maximum Rooting Depth of Vegetation Types at the Global Scale.” *Oecologia* 108: 583–595.
- Chen, G., S. E. Hobbie, P. B. Reich, Y. Yang, and D. Robinson. 2019. “Allometry of Fine Roots in Forest Ecosystems.” *Ecology Letters* 22: 322–331.
- Chieppa, J., S. A. Power, D. T. Tissue, and U. N. Nielsen. 2020. “Allometric Estimates of Aboveground Biomass Using Cover and Height Are Improved by Increasing Specificity of Plant Functional Groups in Eastern Australian Rangelands.” *Rangeland Ecology and Management* 73: 375–383.

- Clark, D. B., L. M. Mercado, S. Sitch, C. D. Jones, N. Gedney, M. J. Best, M. Pryor, et al. 2011. "The Joint UK Land Environment Simulator (JULES), Model Description—Part 2: Carbon Fluxes and Vegetation Dynamics." *Geoscientific Model Development* 4: 701–722.
- De Kauwe, M. G., B. E. Medlyn, S. Zaehle, A. P. Walker, M. C. Dietze, Y. P. Wang, Y. Luo, et al. 2014. "Where Does the Carbon Go? A Model-Data Intercomparison of Vegetation Carbon Allocation and Turnover Processes at Two Temperate Forest Free-Air CO₂ Enrichment Sites." *New Phytologist* 203: 883–899.
- de Ridder, N., N. G. Seligman, and H. van Keulen. 1981. "Analysis of Environmental and Species Effects on the Magnitude of Biomass Investment in the Reproductive Effort of Annual Pasture Plants." *Oecologia* 49: 263–271.
- DuPont, S. T., J. Beniston, J. D. Glover, A. Hodson, S. W. Culman, R. Lal, and H. Ferris. 2014. "Root Traits and Soil Properties in Harvested Perennial Grassland, Annual Wheat, and Never-Tilled Annual Wheat." *Plant and Soil* 381: 405–420.
- Enquist, B. J., B. W. Geoffrey, L. C. Eric, and H. B. James. 1999. "Allometric Scaling of Production and Life-History Variation in Vascular Plants." *Nature* 401: 907–911.
- Falster, D. S., R. A. Duursma, M. I. Ishihara, D. R. Barneche, R. G. FitzJohn, A. Vårhammar, M. Aiba, et al. 2015. "BAAD: A Biomass and Allometry Database for Woody Plants." *Ecology* 96: 1445.
- Fernández Ales, R., J. M. Laffarga, and F. Ortega. 1993. "Strategies in Mediterranean Grassland Annuals in Relation to Stress and Disturbance." *Journal of Vegetation Science* 4: 313–322.
- Fox, J., M. Friendly, and S. Weisberg. 2013. "Hypothesis Tests for Multivariate Linear Models Using the Car Package." *R Journal* 5: 39–52.
- Gao, X., C. D. Koven, and L. M. Kueppers. 2024. "Allometric Relationships and Trade-offs in Eleven Common Mediterranean-Climate Grasses (Dataset); In Ecological Applications (EA-finals submission-V1.0)." Zenodo. <https://doi.org/10.5281/zenodo.10655820>.
- Garnier, E. 1992. "Growth Analysis of Congeneric Annual and Perennial Grass Species." *The Journal of Ecology* 80: 665.
- Geng, Y. P., X. Y. Pan, C. Y. Xu, W. J. Zhang, B. Li, and J. K. Chen. 2007. "Plasticity and Ontogenetic Drift of Biomass Allocation in Response to above- and below-Ground Resource Availabilities in Perennial Herbs: A Case Study of *Alternanthera philoxeroides*." *Ecological Research* 22: 255–260.
- Griffith, D. M., C. P. Osborne, E. J. Edwards, S. Bachle, D. J. Beerling, W. J. Bond, T. J. Gallaher, et al. 2020. "Lineage-Based Functional Types: Characterising Functional Diversity to Enhance the Representation of Ecological Behaviour in Land Surface Models." *New Phytologist* 228: 15–23.
- Guevara, J. C., J. M. Gonnet, and O. R. Estevez. 2002. "Biomass Estimation for Native Perennial Grasses in the Plain of Mendoza, Argentina." *Journal of Arid Environments* 50: 613–19.
- Hector, A., S. von Felten, and B. Schmid. 2010. "Analysis of Variance with Unbalanced Data: An Update for Ecology & Evolution." *Journal of Animal Ecology* 79: 308–316.
- Hobbs, R. J., and H. A. Mooney. 1991. "Effects of Rainfall Variability and Gopher Disturbance on Serpentine Annual Grassland Dynamics." *Ecology* 72: 59–68.
- Holmes, T. H., and K. J. Rice. 1996. "Patterns of Growth and Soil-Water Utilization in some Exotic Annuals and Native Perennial Bunchgrasses of California." *Annals of Botany* 78: 233–243.
- Irving, L. J. 2015. "Carbon Assimilation, Biomass Partitioning and Productivity in Grasses." *Agriculture* 5: 1116–34.
- Jucker, T., F. J. Fischer, J. Chave, D. A. Coomes, J. Caspersen, A. Ali, G. J. Loubota Panzou, et al. 2022. "Tallo: A Global Tree Allometry and Crown Architecture Database." *Global Change Biology* 28: 5254–68.
- Kenzo, T., R. Yoneda, and M. A. Alias. 2022. "Estimation of above and Belowground Biomass for Grass, Herb, and Fern Species in Peninsula Malaysia." *Tropical Ecology* 64: 500–510.
- Koven, C. D., R. G. Knox, R. A. Fisher, J. Q. Chambers, B. O. Christoffersen, S. J. Davies, M. Detto, et al. 2020. "Benchmarking and Parameter Sensitivity of Physiological and Vegetation Dynamics Using the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama." *Biogeosciences* 17: 3017–44.
- Luke, S. G. 2017. "Evaluating Significance in Linear Mixed-Effects Models in R." *Behavior Research Methods* 49: 1494–1502.
- Mahood, A. L., E. Fleishman, J. K. Balch, F. Fogarty, N. Horning, M. Leu, M. Zillig, and B. A. Bradley. 2021. "Cover-Based Allometric Estimate of Aboveground Biomass of a Non-native, Invasive Annual Grass (*Bromus tectorum* L.) in the Great Basin, USA." *Journal of Arid Environments* 193: 104582.
- Martínez Cano, I., E. Shevliakova, S. Malyshev, S. J. Wright, M. Detto, S. W. Pacala, and H. C. Muller-Landau. 2020. "Allometric Constraints and Competition Enable the Simulation of Size Structure and Carbon Fluxes in a Dynamic Vegetation Model of Tropical Forests (LM3PPA-TV)." *Global Change Biology* 26: 4478–94.
- Mascaro, J., C. M. Litton, R. F. Hughes, A. Uowolo, and S. Schnitzer. 2011. "Minimizing Bias in Biomass Allometry: Model Selection and Log-Transformation of Data." *Biotropica* 43: 649–653.
- McCarthy, M. C., and B. J. Enquist. 2007. "Consistency between an Allometric Approach and Optimal Partitioning Theory in Global Patterns of Plant Biomass Allocation." *Functional Ecology* 21: 713–720.
- Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. "Mechanistic Scaling of Ecosystem Function and Dynamics in Space and Time: Ecosystem Demography Model Version 2." *Journal of Geophysical Research* 114: G01002.
- Mensah, S., T. Seifert, and R. Glèlè Kakaï. 2016. "Patterns of Biomass Allocation between Foliage and Woody Structure: The Effects of Tree Size and Specific Functional Traits." *Annals of Forest Research* 59: 49–60.
- Monti, A., and A. Zatta. 2009. "Root Distribution and Soil Moisture Retrieval in Perennial and Annual Energy Crops in Northern Italy." *Agriculture, Ecosystems and Environment* 132: 252–59.
- Moorcroft, P. R., G. C. Hurtt, and S. W. Pacala. 2001. "A Method for Scaling Vegetation Dynamics: The Ecosystem Demography Model (ED)." *Ecological Monographs* 71: 557–586.
- Nafus, A. M., M. P. McClaran, S. R. Archer, and H. L. Throop. 2009. "Multispecies Allometric Models Predict Grass Biomass in Semidesert Rangeland." *Rangeland Ecology and Management* 62: 68–72.
- Nelson, C. J., and K. J. Moore. 2020. "Grass Morphology." In *Forages: The Science of Grassland Agriculture*, edited by K. J. Moore, M. Collins, C. J. Nelson, and D. D. Redfearn, 23–49. Hoboken, NJ: John Wiley & Sons, Inc.

- Niinemets, Ü. 2010. "A Review of Light Interception in Plant Stands from Leaf to Canopy in Different Plant Functional Types and in Species with Varying Shade Tolerance." *Ecological Research* 25: 693–714.
- Niklas, K. J. 2004. "Plant Allometry: Is there a Grand Unifying Theory?" *Biological Reviews of the Cambridge Philosophical Society* 79: 871–889.
- Oliveras, I., M. van der Eynden, Y. Malhi, N. Cahuana, C. Menor, F. Zamora, and T. Haugaasen. 2014. "Grass Allometry and Estimation of above-Ground Biomass in Tropical Alpine Tussock Grasslands." *Austral Ecology* 39: 408–415.
- Parker, V. T., and C. H. Muller. 1982. "Vegetational and Environmental Changes beneath Isolated Live Oak Trees (*Quercus agrifolia*) in a California Annual Grassland." *The American Midland Naturalist* 107: 69–81.
- Pausas, J. G., and S. Paula. 2020. "Grasses and Fire: The Importance of Hiding Buds: A Response to Moore et al. 'Effects of Drought and Fire on Resprouting Capacity of 52 Temperate Australian Perennial Native Grasses'." *New Phytologist* 226: 957–59.
- Pitelka, L. F. 1977. "Energy Allocation in Annual and Perennial Lupines (*Lupinus*: Leguminosae)." *Ecology* 58: 1055–65.
- Poorter, H., A. M. Jagodzinski, R. Ruiz-Peinado, S. Kuyah, Y. Luo, J. Oleksyn, V. A. Usoltsev, T. N. Buckley, P. B. Reich, and L. Sack. 2015. "How Does Biomass Distribution Change with Size and Differ among Species? An Analysis for 1200 Plant Species from Five Continents." *New Phytologist* 208: 736–749.
- Poorter, H., K. J. Niklas, P. B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. "Biomass Allocation to Leaves, Stems and Roots: Meta-Analyses of Interspecific Variation and Environmental Control." *New Phytologist* 193: 30–50.
- Poorter, L., L. Bongers, and F. Bongers. 2006. "Architecture of 54 Moist-Forest Tree Species: Traits, Trade-Offs, and Functional Groups." *Ecology* 87: 1289–1301.
- R Core Team. 2019. *A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.
- Ripley, B., G. Donald, C. P. Osborne, T. Abraham, and T. Martin. 2010. "Experimental Investigation of Fire Ecology in the C₃ and C₄ Subspecies of *Allotropis semialata*." *Journal of Ecology* 98: 1196–1203.
- Running, S. W., and S. T. Gower. 1991. "FOREST-BGC, A General Model of Forest Ecosystem Processes for Regional Applications. II. Dynamic Carbon Allocation and Nitrogen Budgets." *Tree Physiology* 9: 147–160.
- Schenk, H. J., and R. B. Jackson. 2002. "Rooting Depths, Lateral Root Spreads and below-Ground/above-Ground Allometries of Plants in Water-Limited Ecosystems." *Journal of Ecology* 90: 480–494.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. "Invasion, Competitive Dominance, and Resource Use by Exotic and Native California Grassland Species." *Proceedings of the National Academy of Sciences* 100(23): 13384–89.
- Shaw, R. G., and T. Mitchell-Olds. 1993. "ANOVA for Unbalanced Data: An Overview." *Ecology* 74: 1638–45.
- Sherrard, M. E., and H. Maherali. 2006. "The Adaptive Significance of Drought Escape in *Avena barbata*, an Annual Grass." *Evolution* 60: 2478–89.
- Shipley, B., and D. Meziane. 2002. "The Balanced-Growth Hypothesis and the Allometry of Leaf and Root Biomass Allocation." *Functional Ecology* 16: 326–331.
- Sitch, S., B. Smith, I. C. Prentice, A. Arneth, A. Bondeau, W. Cramer, J. O. Kaplans, et al. 2003. "Evaluation of Ecosystem Dynamics, Plant Geography and Terrestrial Carbon Cycling in the LPJ Dynamic Global Vegetation Model." *Global Change Biology* 9: 161–185.
- Sprugel, D. G. 1983. "Correcting for Bias in Log-Transformed Allometric Equations." *Ecology* 64: 209–210.
- Stromberg, M. R., J. D. Corbin, and C. M. D'Antonio. 2007. *California Grasslands: Ecology and Management* 21–24. Berkeley, CA: University of California Press.
- Taylor, S. H., S. P. Hulme, M. Rees, B. S. Ripley, F. Ian Woodward, and C. P. Osborne. 2010. "Ecophysiological Traits in C₃ and C₄ Grasses: A Phylogenetically Controlled Screening Experiment." *New Phytologist* 185: 780–791.
- Veenendaal, E. M., W. H. O. Ernst, and G. S. Modise. 1996. "Reproductive Effort and Phenology of Seed Production of Savanna Grasses with Different Growth Form and Life History." *Vegetatio* 123: 91–100.
- Vico, G., S. Manzoni, L. Nkurunziza, K. Murphy, and M. Weih. 2016. "Trade-Offs between Seed Output and Life Span—A Quantitative Comparison of Traits between Annual and Perennial Congeneric Species." *New Phytologist* 209: 104–114.
- Volis, S., S. Mendlinger, and D. Ward. 2002. "Adaptive Traits of Wild Barley Plants of Mediterranean and Desert Origin." *Oecologia* 133: 131–38.
- Weiner, J. 2004. "Allocation, Plasticity and Allometry in Plants." *Perspectives in Plant Ecology, Evolution and Systematics* 6: 207–215.
- West, G. B., J. H. Brown, and B. J. Enquist. 1997. "A General Model for the Origin of Allometric Scaling Laws in Biology." *Science* 276: 122–26.
- White, K. P., J. A. Langley, D. R. Cahoon, and J. P. Megonigal. 2012. "C₃ and C₄ Biomass Allocation Responses to Elevated CO₂ and Nitrogen: Contrasting Resource Capture Strategies." *Estuaries and Coasts* 35: 1028–35.
- Wilson, A. M., and K. Thompson. 1989. "A Comparative Study of Reproductive Allocation in 40 British Grasses." *Functional Ecology* 3: 297.
- Xiang, S., N. Wu, and S. Sun. 2009. "Within-Twig Biomass Allocation in Subtropical Evergreen Broad-Leaved Species along an Altitudinal Gradient: Allometric Scaling Analysis." *Trees—Structure and Function* 23: 637–647.
- Youkhana, A. H., R. M. Ogoshi, J. R. Kiniry, M. N. Meki, M. H. Nakahata, and S. E. Crow. 2017. "Allometric Models for Predicting Aboveground Biomass and Carbon Stock of Tropical Perennial C₄ Grasses in Hawaii." *Frontiers in Plant Science* 8: 1–9.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gao, Xiulin, Charles D. Koven, and Lara M. Kueppers. 2024. "Allometric Relationships and Trade-Offs in 11 Common Mediterranean-Climate Grasses." *Ecological Applications* 34(4): e2976. <https://doi.org/10.1002/eap.2976>