Received: 16 June 2020 | Revised: 13 October 2020 | Accepted: 21 October 2020

DOI: 10.1111/geb.13223

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

Rainfall continentality, via the winter Gams angle, provides a new dimension to biogeographical distributions in the western United States

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Editor: Jose Eduardo Meireles

Abstract

Aim: Drought stress has focused on water availability during the growing season, thus primarily on summer. However, variation in rainfall continentality can produce striking vegetation differences. We aim to disentangle summer water balance from winter rainfall continentality, to better understand how climate regulates the distributions of woody plants in the western USA.

Location: Western USA.

Time period: Actual.

Major taxa studied: Angiosperms and conifers.

Methods: We used redundancy analysis (RDA) to investigate correlations between rainfall continentality, summer water balance, minimum winter temperature and length of growing season on the distributions of 130 tree and shrub species in 467 plots. Rainfall continentality was calculated using the Gams index, modified for winter precipitation, and summer water balance with the ratio of summer precipitation to temperature. We estimated actual evapotranspiration (AET), deficit (DEF), mean annual temperature and rainfall from global gridded data sets and correlated them with RDA axes.

Results: Rainfall continentality measured with the Gams index and minimum temperatures best explained the contrast between oceanic vegetation in the Pacific Coast Ranges and continental vegetation in the Intermountain Region and Rocky Mountains. Growing season length (GSL) was the second strongest factor correlated with vegetation distributions. Summer water balance, despite being the most widely used climatic factor to assess drought stress in biogeography, was the third strongest factor correlating with vegetation classes of the western US. AET was equally correlated with RDA axes 1 and 3, and, thus, could not discriminate between the contrasts in the RDA.

Main conclusions: Rainfall continentality measured with the winter Gams index provides a more precise metric than summer water balance for understanding the biogeography of woody plants in the western USA. Broadly integrating the Gams index

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This paper is dedicated to the memory of Prof. Paul Ozenda (1920–2019), University Grenobles Alpes (France), Member of the French Academy of Sciences, a leading scientist in plant biogeography and mountain biodiversity who inspires this work on the importance of the Gams angle in mountain biogeography.

of continentality into plant distributions may improve our understanding of biogeographical distributions and predictions of responses to climate change.

KEYWORDS
drought, growing season length, minimum temperature, rain shadow effects, rainfall continentality, water balance, western USA, winter rainfall

1 | INTRODUCTION

For decades, water balance during the growing season has been the key measurement used to quantify drought stress in ecological, biogeographical, physiological and climate change studies, likely due to the primary objective of pioneer biogeographers to separate Mediterranean from temperate climates (Rueda et al., 2018; Stephenson, 1990; Walter & Lieth, 1960; Williams et al., 2020). For example, the ombrothermal diagram proposed by Bagnouls and Gaussen (1953) for the Mediterranean Basin, in Europe and northern Africa, has been widely and successfully used worldwide to describe biogeographical distributions (Walter & Lieth, 1960). Stephenson (1990, 1998) proposed measurements of actual evapotranspiration (AET) and deficit (DEF), which integrate evaporative demand with available water for plant performance. AET and DEF indices have been applied to water balance in several biological and ecosystem processes and to simulate climate change (Franck & Inouye, 1994; Rehfeldt et al., 2006).

However, indices quantifying water balance during the growing season might be limited in biogeographical explanatory power when growing season length exceeds 7 to 8 months, because they integrate both the effects of summer water balance and the effects of

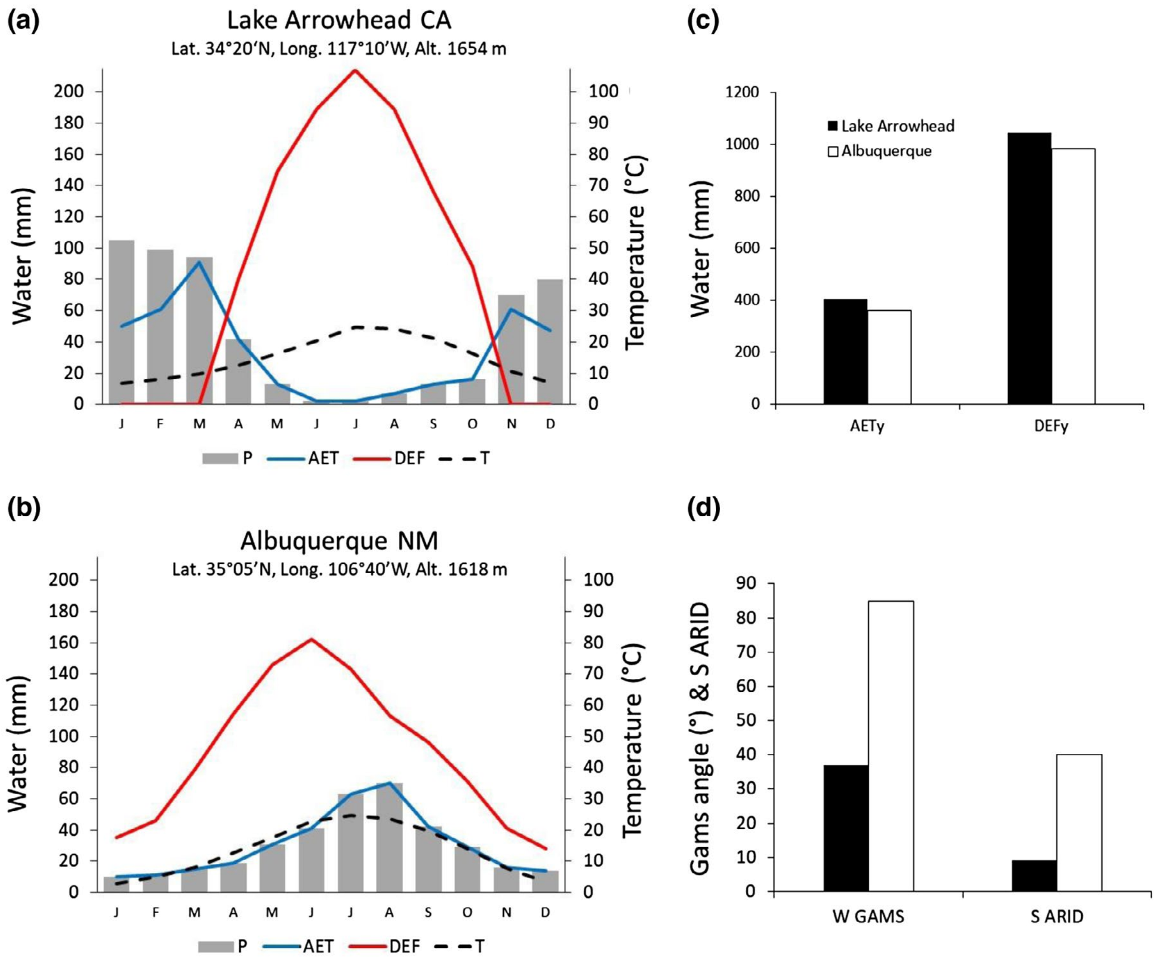

FIGURE 1 Left: ombrothermal diagrams and actual evapotranspiration (AET) and deficit (DEF) of weather stations with oceanic Mediterranean (a) and continental subtropical (b) climates from similar latitude and altitude. Right panels show that annual AET (AETy) and DEF (DEFy) (c) are very similar, although rainfall continentality (W GAMS) and summer water balance (S ARID) (d) are very different. Note that the vegetation of stations (a) and (b) were classified in clusters 11 and 5 in Table 2, that is, CA evergreen oaks and eastern evergreen oak woodlands, respectively. P, precipitation; T, temperature [Colour figure can be viewed at wileyonlinelibrary.com]

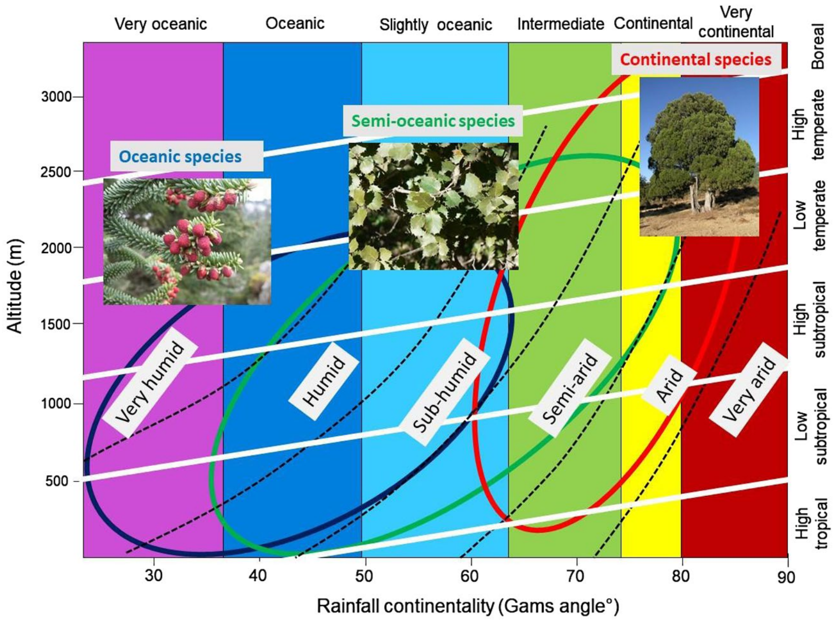

FIGURE 2 Distribution of oceanic (in blue, from high to low altitude *Abies pinsapo* ssp. *marocana* in the picture and *Quercus canariensis*, *Quercus suber* and *Quercus coccifera*), semi-oceanic (in green, from high to low altitude *Cedrus atlantica*, *Quercus rotundifolia* in the picture and *Tetraclinis articulata*) and continental species (in red, from high to low altitude *Juniperus thurifera* in the picture, *Juniperus phoenicea* and *Stipa tenacissima*) from Morocco within the climagram of Michalet (1991). The climagram includes a horizontal axis for the rainfall continentality gradient quantified with the annual Gams-angle index [driving vapor-pressure deficit (VPD) and cold stresses], a vertical axis for the altitudinal gradient (driving the length of the growing season) and, in an oblique dimension, the water balance gradient calculated with the Emberger (1930) index. The latter was inspired by the De Martonne (1926) aridity index and is primarily based on the ratio of annual precipitation to mean temperature. Coloured frames along the horizontal axis represent the different zones of continentality delimited using the annual Gams-angle index and oblique plain white lines along the vertical axis delimit the vegetation belts in relation to altitude and latitude [see also legend of Table 2 for growing season length (GSL)]. Oblique dashed lines delimit the aridity zones of Emberger (1930) indicated with white frames [Colour figure can be viewed at wileyonlinelibrary.com]

winter and early spring rainfall. This is particularly important in areas with both Mediterranean and highly continental climates, such as the western USA. In oceanic Mediterranean climates annual AET (AETy) is highly influenced by the high winter and spring rainfall but not by the very low summer rainfall (AET in winter and in spring contributes to 39 and 36 vs. 2.7% of AETy, respectively, in southern California, USA; Figure 1a). In contrast, in continental subtropical climates, AETy is weakly influenced by the low winter and spring rainfall but strongly influenced by the high summer rainfall (AET in winter and in spring contributes to 9.7 and 18 vs. 48.2% of AETy, respectively, in New Mexico, USA; Figure 1b). These two regions, located at similar latitude and altitude, have very similar AETy and DEFy (Figure 1c), but they have strikingly different climates in terms of summer water balance and rainfall continentality (Figure 1d).

Rainfall continentality effects, in which continental interior regions are insulated from oceanic influences, are decreases in precipitation induced by the penetration of low pressure air on a continent (Bach et al., 2013; Schermerhorn, 1967). Most low atmospheric air pressure systems have oceanic origins, but they can also originate on inland seas, such as the Mediterranean, Black and Caspian seas in Europe (Caccianiga et al., 2008; Michalet, 1991; Pache, Michalet, et al., 1996). In temperate and Mediterranean climates, rainfall continentality primarily affects winter precipitation, whereas in tropical monsoon climates these effects can also be strong in summer (Bach et al., 2013; Michalet, 1991). Rainfall continentality effects are much stronger where mountain ranges are adjacent to oceans, due to the increase in precipitation with increasing altitude on the windward sides of mountains (orographic effect, Browning & Hill, 1981) and a decrease on their leeward sides (rain shadow effect, Roe, 2005). Since vapor-pressure deficit (VPD) increases and cloudiness decreases along gradients of increasing rainfall continentality, temperature range increases in continental climates, due to increasing irradiance, with colder winter nights and warmer days than in oceanic climates (Bach et al., 2013; Waring & Franklin, 1979). The increase in day temperature, in particular in the spring, increases growing season length, which explains shifts in vegetation belts to higher altitudes in continental mountain ranges than in oceanic ranges (Desplanque et al., 1998; Grace, 1987; He et al., 2016; Michalet, 1991; Michalet et al., 2003; Ozenda, 1985 and see Figure 2).

Precipitation-based continentality creates striking differences in vegetation in a wide range of climates, and this has major ecological and evolutionary consequences. One of the best examples is in the temperate climate of northwestern America, where mountains and distance from ocean creates the difference between the rain forests of the Pacific Coast and the dry coniferous forests of the Rocky Mountains (Daubenmire, 1946; del Moral & Watson, 1978; Franklin & Dyrness, 1973; Waring & Franklin, 1979). This difference in vegetation is a major component of classification in the US

(Brown et al., 1998). Similar differences, though less strong, occur at the same latitudes in temperate Europe between the mixed deciduous-evergreen beech-fir (*Fagus sylvatica-Abies alba*) forests of the external (oceanic) Alps and the larch-pine (*Larix decidua-Pinus sylvestris-Pinus uncinata*) forests of the inner (continental) Alps (Gams, 1932; Michalet et al., 2003; Ozenda, 1985; Pache, Michalet, et al., 1996).

Although precipitation-based, or rainfall continentality and rain shadow effects, produce striking vegetation patterns on several continents, there has been little attention to winter precipitation in biogeographical patterns, likely because plants are generally dormant during the cold season. An important exception is the use of winter versus summer precipitation to predict shrub versus grass dominance, respectively, in US deserts and shrub steppe (Munson et al., 2013; Neilson, 1986, 1987; Paruelo & Lauenroth, 1996; Reinhardt et al., 2019). The most direct physiological stress associated with rainfall continentality is likely the much higher VPDs in continental climates that affect stomatal conductance, water uptake and carbon assimilation (Muhamed et al., 2013; Novick et al., 2016; Simonin et al., 2009). Also, the frequency of freezing temperatures increases substantially in dry continental air (Bach et al., 2013), and together with higher irradiances, increase photo-inhibition (Manuel et al., 1999). This is highly detrimental for species with high leaf area and specific leaf area (SLA) (Waring et al., 1978). Importantly, plants must cope with these constraints during the growing season, since the low cloudiness of continental climates is observed yearlong (Peyre, 1983). *Sequoia sempervirens*, in northern California, is tightly correlated with overcast conditions (Barbour et al., 2014; Waring & Franklin, 1979), perhaps an example of distributional limits imposed by high VPD in continental climates through leaf physiological traits.

In Europe there is a history of using variation in annual rainfall as an indicator of rainfall continentality in mountains (Gams, 1932; Ozenda, 1985). In the Alps of Switzerland, Gams (1932) proposed a rainfall continentality index, based on the rate of increase in precipitation with elevation and quantified with the angle of which the co-tangent is equal to the ratio of annual precipitation to elevation. It allows researchers to compare the rainfall continentality of sites differing in elevation, a task that cannot be accomplished with the comparison of only the precipitation of the sites. This is crucial since altitude and rainfall continentality are complex factors that drive different direct factors for plants, both for temperature and humidity. Thus, one main added value of the Gams-angle index is to disentangle in mountain ranges the effects of rainfall continentality from those of decreased precipitation with decreasing altitude (i.e., orographic effect). Gams (1932) showed that the distribution of European beech (*Fagus sylvatica*) was tightly related to variation in the index, with values below 45° in the external Alps where beech dominates the mountain belt, versus above 45° in the inner Alps where beech is replaced by Scots pine (*Pinus sylvestris*) and European larch (*Larix decidua*). Ozenda (1985) generalized the 'Gams-angle' approach throughout the Alpine Chain (see also Michalet et al., 2003 and Caccianiga et al., 2008) and Michalet (1991) applied the Gams-angle index to the Mediterranean climate of Morocco.

Michalet (1991) also proposed a climagram combining three important dimensions of mountain biogeography (rainfall continentality, altitude and aridity) that depicts the distribution of plant species both in the geographical and ecological spaces (Figure 2). Interestingly, plant species have an oblique distribution in the climagram in direct relation with the aridity zones of Emberger (1930), due to their occurrences at lower elevations in oceanic than continental climates. This means that, consistent with Emberger (1930), species have specific water balance requirements, from very humid to sub-humid for oceanic species, humid to semi-arid for semi-oceanic species and sub-humid to arid for continental species (Figure 2). These specific water balance conditions can occur at low altitude in oceanic climates, due to high precipitation occurring at low altitude, but only at high altitude in continental climates, due to a lower rate of increasing precipitation with increasing altitude. Thus, this climagram allows a better understanding of the link existing between the humidity (VPD) and cold stress that is only captured by the Gams index of rainfall continentality. Oceanic species are adapted to warmer climates than continental species since the specific water balance requirements can be found at lower elevation for the former than for the latter. Additionally, this climagram allows a display of the above-mentioned shift of vegetation belts to higher altitudes with increasing continentality. This shift likely contributes to the strong vegetation turnover occurring from oceanic to continental climates, since nights are colder in continental than oceanic climates, thus amplifying cold stress for oceanic species. Crucially, Pache, Michalet, et al. (1996) proposed a seasonal modification of the Gams-angle index that targeted winter precipitation (December to February), which provided a precipitation-based continentality index. We propose that this index provides a better metric than indices of growing season precipitation for assessing biogeographical patterns from areas with high seasonal variation in rainfall due to large ranges in latitude, like those from the Mediterranean Basin in Europe and Africa or from western North America.

Our main objective is to assess the relative importance of rainfall continentality and summer water balance in driving biogeographical distribution in areas subject to strong variation in winter and summer rainfall. The western USA has striking vegetation contrasts on gradients of rainfall continentality. Rainfall continentality occurs across a seasonal latitudinal gradient in rainfall, temperate in the north, Mediterranean in the southwest and with subtropical influences in the southeast. Thus, this system is very appropriate for assessing our main objective. We sampled vegetation throughout the 11 states of the western USA, establishing 467 vegetation plots near climate stations from which we extracted several climate indices to correlate them to vegetation composition using redundancy analysis (RDA). We partitioned vegetation plots in 16 groups with a cluster conducted on RDA results and mapped their distribution throughout the 11 states. We also extracted data from the Worldclim database for regional spatial variation in the main climate variables, including the Gams index for rainfall continentality in the winter (Pache, Michalet, et al., 1996). We finally analysed the relationship between the Gams-angle index and AETy, DEFy (Stephenson, 1998), mean annual precipitation (MAP) and mean annual temperature (MAT), which are commonly used in the literature. We had two main hypotheses: (a) variation in rainfall continentality quantified by the Gams-angle index provides a better metric for quantifying vegetation in the western USA than summer water balance; (b) variation in rainfall continentality quantified by the Gams-angle index provides a better metric for quantifying vegetation in the western USA than the current accepted metric of water availability during the growing season (AETy and DEFy).

2 | MATERIAL AND METHODS

2.1 | Study area

We focused on 11 states in the western USA (Figure 2). This geographical area, well separated from the American Prairie further east, may be subdivided into three main geographical units: (a) the western Pacific Coast Ranges *sensu lato*, located in the western parts of Washington State (WA), Oregon (OR) and California (CA) and including the coastal ranges *sensu stricto* and the Cascade and Sierra Nevada ranges; (b) the Intermountain Region, including the Great Basin, Colorado Plateau and southern deserts, mostly located in the eastern parts of the former states and southwest Idaho (ID), Nevada (NV), Utah (UT) and Arizona (AZ); (c) the Rocky Mountains to the east of the study area, in eastern ID, Montana (MT), Wyoming (WY), Colorado (CO) and New Mexico (NM). When considering seasonal rainfall distribution and mean temperatures, five main climatic influences characterize the study area following Walter and Lieth (1960), temperate oceanic in the northwest, mostly limited to WA, OR and ID, Mediterranean in the southwest, only in western CA, continental temperate in the northeast, in MT, WY and CO, continental and slightly subtropical in the southeast, in AZ and NM, and arid-desert in the southern parts of the Intermountain Region, in UT, NV, eastern CA, and southern AZ and NM.

2.2 | Climatic data and vegetation sampling

We collected climate data from 800 weather stations in the Western Regional Climate Center (https://wrcc.dri.edu/) for the study area. We used the elevation of the stations and, for the period 1971–2000, the precipitation and minimum and maximum temperatures over 12 months. To address our main goal, separating rainfall continentality from summer water balance, we calculated for each weather station the Gams-angle rainfall continentality index using winter (December, January and February) precipitation (W GAMS, Pache, Michalet, et al., 1996), and a summer water balance index, S ARID, calculating the ratio between the precipitation and the mean of maximum temperatures of the three summer months (June, July and August). For cold stress, we used the minimum temperature of the coldest month for cold-tolerance (Tmin), and the number of months with a maximum temperature above 12.5 °C for the growing season length (GSL). For rainfall continentality, we calculated W GAMS with winter precipitation using three different formulas depending on elevation (after Michalet et al., 2003), which accounted for nonlinearity in increasing precipitation with increasing elevation (Michalet, 1991):

- From 900 to 1,600 m, we used the original formula of Gams (1932):

$$\mathrm{Cotg}\ \alpha = 4\mathrm{P}/\mathrm{A}. \tag{1}$$

where α is the W GAMS index and P is the winter precipitation in millimetres and A the elevation in metres.

- Below 900 m, we used a modified Gams formula (Michalet, 1991):

$$\mathrm{Cotg}\ (\alpha) = (4\mathrm{P} - ((900 - \mathrm{A})/100) * (4\mathrm{P}/10))/\mathrm{A} \tag{2}$$

with A = 100 m when elevation below 100 m.

- Above 1,600 m, we used a second modified Gams formula (Pache, Aimé, et al., 1996):

$$\mathrm{Cotg}\ (\alpha) = (4\mathrm{P} + ((\mathrm{A} - 1,600)/100) * (4\mathrm{P}/20))/\mathrm{A}. \tag{3}$$

For vegetation sampling, we selected 467 plots near weather stations (see Statistical analyses) in order to get the vegetation composition of sites where climate variables were really measured. This sampled the climatic diversity of the total study area, while spatially distributing the sampling. Fieldwork was carried out between 2000 and 2010, at different times of the year depending on the growing season length and leaf phenology of the deciduous species in different areas. We recorded the presence or absence of all tree species and dominant shrubs at less than 5 km from each corresponding weather station, taking care not to sample species at more than 100 m of elevation higher or lower than the weather station. Considering the scale of the study, we sampled at all exposures and on all soil types within the plots.

We also extracted from the Worldclim2 database (Fick & Hijmans, 2017) the former selected variables for estimating annual actual evapotranspiration (AETy), annual deficit (DEFy), mean annual temperature (MAT) and mean annual precipitation (MAP) for post-analysis correlations. The water balance-related variables (AETy and DEFy) were calculated according to Stephenson (1990). The available water capacity (AWC) was retrieved from the United States Department of Agriculture (USDA) State Soil Geographic Database (Miller & White, 1998). AWC data for the first 100 cm have been used.

2.3 | Statistical analyses

We conducted a principal component analysis (PCA) on the 800 weather stations and four climate indices extracted from the Western Regional Climate Center (W GAMS, S ARID, Tmin and GSL). A cluster analysis was conducted on PCA scores in order to select 467 stations among the climate types. We then performed a RDA—also known as a multivariate analysis with respect to instrumental variables—to study species–environment relationships. RDA is a two-table ordination technique in which the environmental table—that is, the predicting set of variables—is analysed by a PCA of a correlation matrix, and the floristic table—that is, the response set of variables—is analysed by a PCA of a covariance matrix. The algorithm searches for the linear combination of environmental variables that best capture community structure (Dray et al., 2003). The environmental table included the same four climate variables as in the PCA, plus winter precipitation (W PREC). Plant species with a frequency lower than 5 out of the 467 plots were excluded from the analysis. The final floristic table contained 130 species. To benchmark our results with other studies, we projected AETy, DEFy, MAT and MAP on the three first RDA axes. Multivariate analyses were conducted in R (R Core Team, 2017) with the library ade4 (Dray & Dufour, 2007).

The partitioning of vegetation plots was performed on a dissimilarity matrix estimated with the Jaccard's index (Jaccard, 1901). We used the partitioning around medoids (PAM) technique (Kaufman & Rousseeuw, 2009) implemented in the library CLUSTER (Maechler et al., 2019) to search for *k* representative objects or medoids among the observations. The algorithm assigns each observation to the nearest medoid with the objective of minimizing the sum of dissimilarities between groups. The method utilizes a prescribed number of medoids. We found that the value $k = 16$ provided an ecologically and biogeographically meaningful partition of relevés while retaining a sufficient number of relevés per group.

3 | RESULTS

In the RDA, the total unconstrained inertia was 5.55 and the sum of eigenvalues was 1.13, indicating that 20.4% of the total floristic variance was explained by environmental variables (Supporting Information Appendix S1). The RDA axes accounted for 40, 29, 20, 8 and 3% of the explained variance. Given the drop between Axis 3 and Axis 4, we did not consider the last two RDA axes in further analyses. In agreement with our first hypothesis, RDA Axis 1 was more positively correlated with rainfall continentality quantified by the Gams-angle index (W GAMS; $r = .99$) than any other variable, negatively with winter precipitation (W PREC; $r = -.87$) and less so with minimum temperatures (Tmin; $r = -.63$) (Figure 4a, Table 1). RDA Axis 2 was highly negatively correlated with growing season length (GSL; $r = -.87$) and less with cold temperature (Tmin; $r = -.72$).

RDA Axes 1–2 were also highly correlated with the plant biogeography of the western USA. The temperate rain forests of the Pacific Coast Ranges and Mediterranean evergreen oak forests (cluster groups 1 and 11, respectively) aggregated on the extreme left of Axis 1. In contrast, the coniferous forest and woodland communities from central Montana and eastern pinion-juniper woodlands in the central and southern Rocky Mountains aggregated on the extreme right of Axis 1 (cluster groups 6 and 10, respectively, Figures 3a and 4a,b, Tables 1 and 2). The upper end of Axis 2 was occupied by the northwestern and eastern subalpine coniferous forest communities (cluster groups 12 and 9, respectively) and the lower end by the subtropical desert communities of the Sonoran Desert and evergreen oak woodlands of AZ and NM (cluster groups 4 and 5, respectively, Figures 3a and 4a,b, Tables 1 and 2). The west–east climatic contrast on Axis 1 can be seen on the W GAMS and Tmin maps and the north–south contrast on Axis 2 on the Tmin map only (Figure 3b,c). The contrast between the oceanic vegetation of the Pacific Coast Ranges and the continental vegetation of the Rocky Mountains and Intermountain Region was distinct, with few species in common between the two zones or in intermediate positions on the gradient (see Supporting Information Appendix S2, and the low number of communities occurring at intermediate position along Axis 1 in Figure 4b, i.e., only 12, 16, 8). Species occurring along the whole gradient of continentality were represented by different subspecies in each zone, for example, *Pinus ponderosa* var. *ponderosa*, *Pseudotsuga menziesii* var. *menziesii* and *Pinus contorta* var. *murrayana* in the west versus *P. ponderosa* var. *scopulorum*, *P. menziesii* var. *glauca* and *P. contorta* var. *latifolia* in the east.

RDA Axis 3 was strongly correlated with summer water balance (S ARID; $r = -.86$, Supporting Information Appendix S3, Figure 4c)

TABLE 1 Regression coefficients of the five variables (five first) of the redundancy analysis (RDA) for the three axes and post-RDA correlations of the variables (four last) extracted from Worldclim with RDA scores

Climate variables	RDA Axis 1	RDA Axis 2	RDA Axis 3
w.GAMS	.99***	−.06	.05
w.PREC	−.87***	.12**	−.01
Tmin	−.63***	−.72***	.18***
GSL	−.33***	−.87***	.14**
s.ARID	.07	.27***	−.86***
MAT	−.22***	−.89***	.22***
MAP	−.80***	.19***	−.18***
AETy	−.54***	.30***	−.54***
DEFy	.30***	−.76***	.38***

Note: w.GAMS = rainfall continentality index; w.PREC = winter precipitation; Tmin = minimum temperature of the coldest month for cold-tolerance; GSL = growing season length; s.ARID = summer water balance; MAT = mean annual temperature; MAP = mean annual precipitation; AETy = annual actual evapotranspiration; DEFy = annual deficit.

$^{**}p < .01$; $^{***}p < .001$.

TABLE 2 Vegetation labels, dominant species, continentality [position on redundancy analysis (RDA) Axis 1, Supporting Information Figure S3.3a], locations and vegetation zones (position on RDA Axis 2, Supporting Information Figure S3.3b) of the 16 cluster groups

Cluster groups	Label Vegetation	Dominant species	Continentality Location	Vegetation zone
11	Californian evergreen oak forests	*Quercus agrifolia, Q. douglasii, Q. wislizenii, Q. kelloggii. Q. chrysolepis*	Oceanic CA, OR	High subtropical and low temperate
1	Coastal rain temperate forests	*Pseudotsuga menziesii m., Thuja plicata, Tsuga heterophylla*	Oceanic WA, OR, CA	Low and high temperate
8	Southern California Chaparral	*Quercus agrifolia, Q. douglasii, Ceanothus* sp. *Pseudotsuga macrocarpa*	Intermediate CA	Low and high subtropical
12	Northwestern Rocky Mt. subalpine forests	*Thuja plicata, Abies grandis, Pinus monticola, Pseudotsuga menziesii g., Larix occidentalis*	Intermediate ID, MT	High temperate and boreal
16	Northwestern Rocky Mt. mountain forests	*Pseudotsuga menziesii g., Larix occidentalis, Pinus ponderosa p.*	Intermediate MT, WA, ID	High temperate
4	Sonoran Desert	*Cercidium microphyllum, Olneya tesota, Prosopis velutina, Opuntia* sp.	Continental AZ	High tropical and low subtropical
5	Eastern evergreen oak woodlands	*Quercus emoryi, Q. arizonica, Yucca* sp., *Agave* sp.	Continental NM, AZ	Low and high subtropical
14	Mojave Desert	*Larrea tridentata, Ambrosia dumosa, Yucca brevifolia, Yucca schidigera*	Continental CA, NM, UT	Low and high subtropical
10	Rocky Mt. pinion-juniper woodlands	*Pinus edulis, Juniperus osteosperma, Quercus gambelii, Artemisia tridentata*	Continental UT, NM, CO, AZ	High subtropical and low temperate
3	Great Basin pinion-juniper woodlands	*Pinus monophylla, Juniperus osteosperma, Artemisia tridentata*	Continental UT, NV, WY, CA	Low temperate
2	Great Basin mountain woodlands	*Pinus ponderosa p., Juniperus occidentalis, Artemisia tridentata,*	Continental CA, OR, NM, ID	Low and high temperate
13	Northeastern mountain woodlands	*Pinus ponderosa s., Juniperus scopulorum, Artemisia frigida, Artemisia cana*	Continental MT, WY	Low and high temperate
15	Great Basin sagebrush steppe	*Artemisia tridentata, Chrysothamnus nauseasus*	Continental ID, OR, WA	Low and high temperate
6	Northeastern Rocky Mt. woodlands	*Pseudotsuga menziesii g., Pseudotsuga flexilis, Artemisia tridentata, Juniperus scopulorum*	Continental MT, WY, CO, ID	Low and high temperate
7	Southern Rocky Mt. mountain forests	*Pinus ponderosa s., Pseudotsuga menziesii g., Picea pungens, Abies concolor*	Continental NM, CO, AZ	High temperate
9	Eastern Rocky Mt. subalpine forests	*Abies lasiocarpa, Picea engelmannii, Pseudotsuga menziesii g., Pinus contorta*	Continental MT, WY, CO	Boreal

Note: Vegetation zones correspond to growing season length (GSL): high tropical: 10 months, low subtropical: 9 months, high subtropical: 8 months, low temperate: 7 months, high temperate: 6 months, boreal: 5 months. Abbreviations: Rocky Mt. = Rocky Mountains; *Pseudotsuga menziesii m.* or *g.* = *Pseudotsuga menziesii* var. *menziesii* or var. *glauca*; *Pinus ponderosa p.* or *s.* = *Pinus ponderosa* var. *ponderosa* or var. *scopulorum.*

and also weakly with Tmin and GSL (Table 1). Within oceanic climates, that is, on the left of Axis 1, Axis 3 separated Mediterranean communities with a dry summer (clusters 11 and 8—CA evergreen oak forests and southern chaparral, respectively) from temperate communities with a wet summer (clusters 1 and 12—coastal temperate rain forests and northwestern subalpine forests, respectively). Within continental climates, that is, on the right of Axis 1, Axis 3 separated communities of the Great Basin with a dry summer, the mountain Ponderosa pine woodlands and the pinion-juniper woodlands (clusters 2 and 3, respectively), from mountain and subalpine coniferous forest communities of the Rocky Mountains (cluster groups 9 and 7, respectively) with wet summers (Figures 3a and 4d, Table 2, Supporting Information Table S2.1).

Oceanic climates with low W GAMS values always had high Tmin, but continental climates with high W GAMS values were highly variable in Tmin (Figure 5a), consistent with the high positive correlation with RDA Axis 1 (Table 1, Figure 3b,c). In contrast, there was no correlation between W GAMS and S ARID (Figure 5b), which is consistent with the collinearity with the two different RDA Axes, 1 and 3, respectively (Table 1, Figure 4). MAP and MAT were only correlated with Axes 1 and 2 ($r = -.80$ for the former and $r = -.89$ for the latter). Consistent with our second hypothesis, the Gams-angle index provided a better metric than AETy and DEFy. AETy was correlated with both Axes 1 and 3 but with lower correlations coefficients than W GAMS and S ARID ($r = -.54$ and $-.54$, respectively, Figure 4a and c). DEFy was primarily correlated with Axis 2 ($r = -.76$) and less with

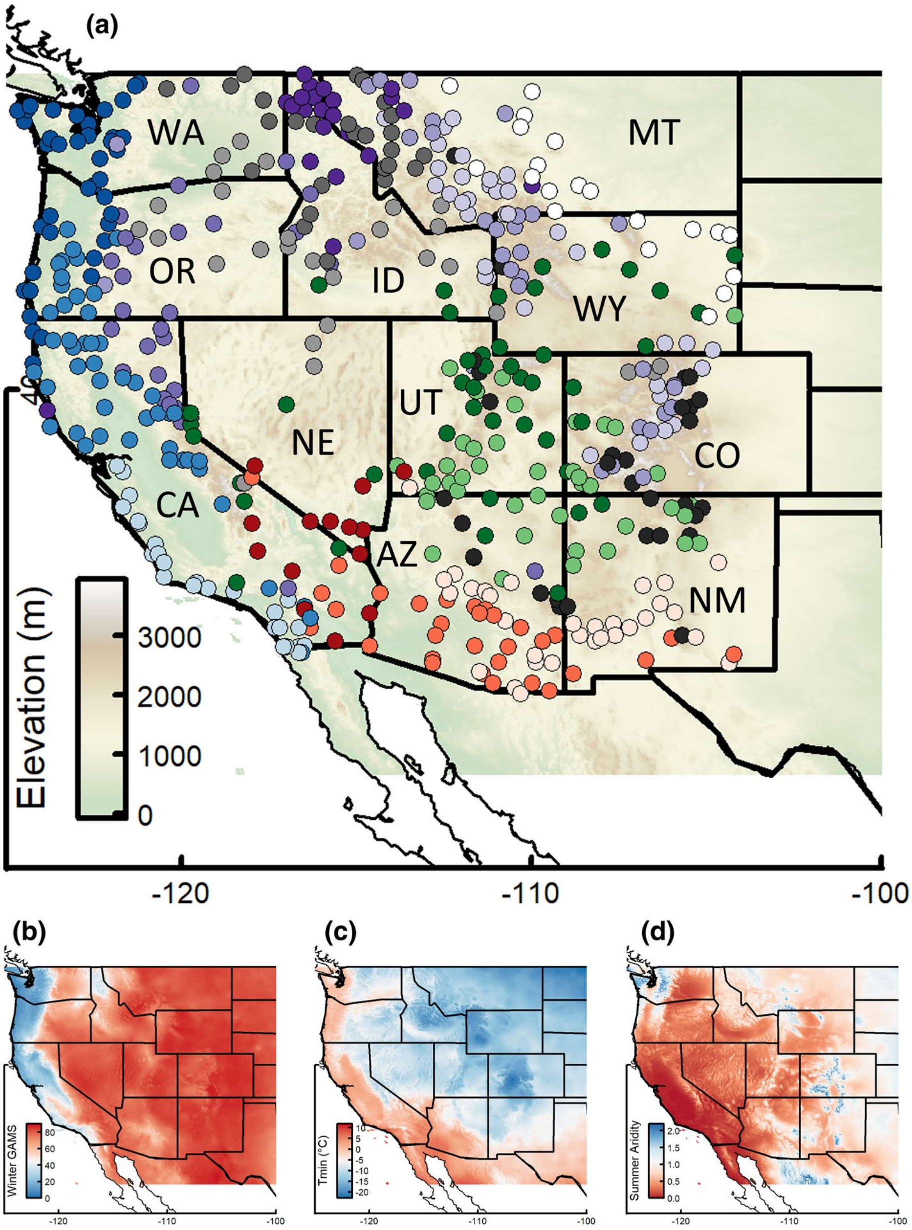

FIGURE 3 Location of our 467 plots and 16 cluster groups in the 11 states of the western USA (a), and maps of rainfall continentality index (W GAMS index; b), minimum temperature of the coldest month for cold-tolerance (Tmin; c) and summer aridity (d). Colour legends of symbols of cluster groups are in Figure 4. Abbreviations: AZ = Arizona; CA = California; CO = Colorado; ID = Idaho; MT = Montana; NE = Nevada; NM = New Mexico; OR = Oregon; UT = Utah; WA = Washington State; WY = Wyoming [Colour figure can be viewed at wileyonlinelibrary.com]

Axis 3 (*r* = .38; Table 1, Figure 4a and c), as shown by the two climagrams of Figure 6 where aridity zones delimited using DEFy were highly correlated with the vertical axis (growing season length, i.e., RDA Axis 2), both in the dry- and wet-summer climagrams (Figure 6a and b, respectively). Thus, the two 3-D climagrams proposed here for the western USA are conceptually very similar to the climagram proposed by Michalet (1991) for Morocco, with rainfall continentality distributed horizontally on the climagram, growing season length distributed vertically, and water balance distributed obliquely on the climagram.

4 | DISCUSSION

We found that rainfall continentality and summer water balance captured two different facets of plant stress. In agreement with our first hypothesis, across the entire breadth of climate we measured, rainfall continentality corresponded much better with vegetation distribution, and took priority over the length of the growing season and summer water balance. These results are of paramount importance, both for our understanding of the relationship between drought-related climate variables and plant physiology, and

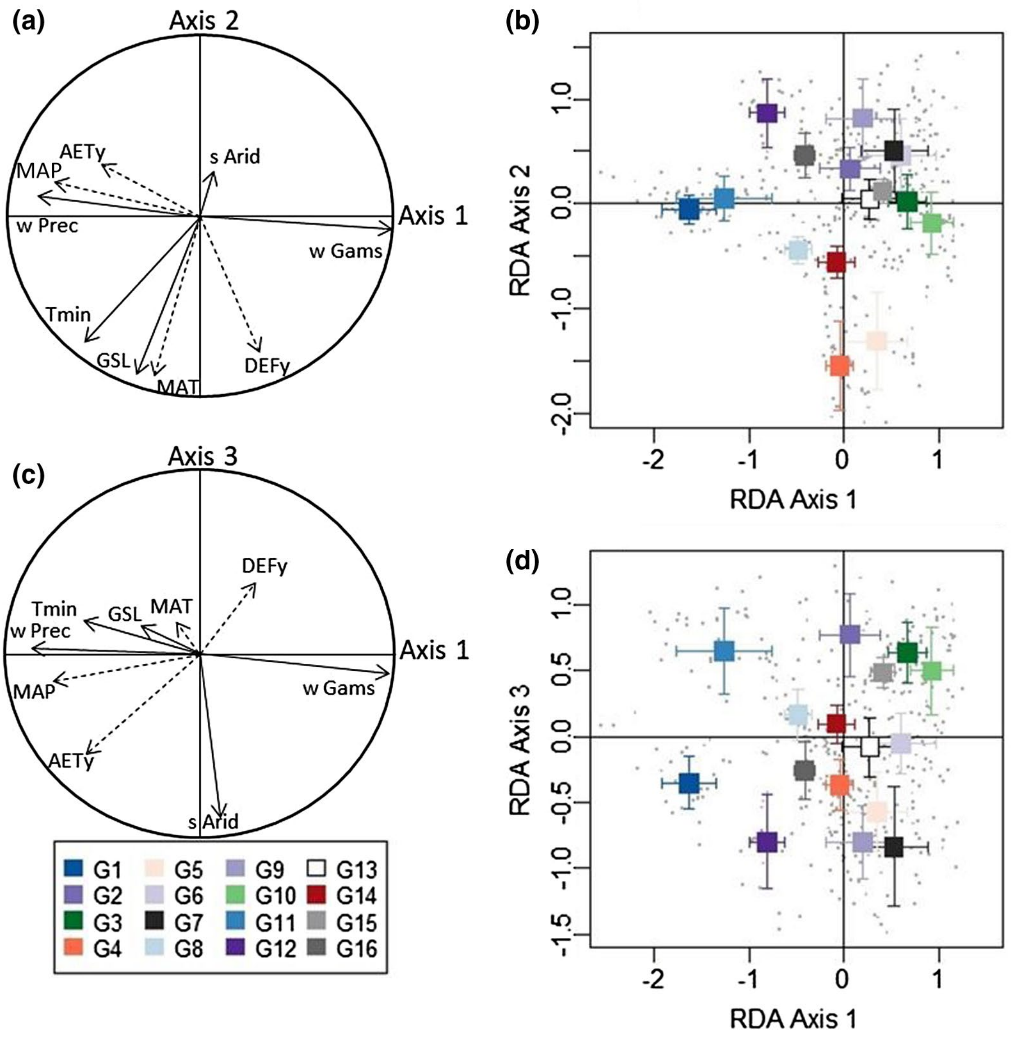

FIGURE 4 Redundancy analysis (RDA) results, with in (a) 1–2 diagram for climate variables, in (b) for mean scores (± 1 *SE*) of the 16 cluster groups, in (c) 1–3 diagram for climate variables and in (d) for mean scores (± 1 *SE*) of the 16 cluster groups. Dashed arrows in panels (a) and (c) show correlations for supplementary variables not included in the RDA. Abbreviations: GSL = growing season length; MAP = mean annual precipitation; MAT = mean annual temperature; DEFy = annual deficit; AETy = annual actual evapotranspiration; w Prec = winter precipitation; s Arid = summer water balance; w Gams = rainfall continentality index. [Colour figure can be viewed at wileyonlinelibrary.com]

for predicting the ecological and evolutionary responses of plant species to changing climate.

4.1 | Rainfall continentality and low water balance in the growing season, two different stresses for plants

The rainfall continentality Gams index adjusted for winter precipitation (Pache, Michalet, et al., 1996) was highly predictive of vegetation types—strongly separating those in the Pacific Coast Range, from woodlands and desert communities in the Intermountain Region and Rocky Mountains (see Daubenmire, 1946; Franklin & Dyrness, 1973; Waring & Franklin, 1979). These vegetation types are the foundation for classification in the western USA (Brown et al., 1998). This dramatic rainfall continentality gradient is induced by both a steep orographic effect on the windward sides of the coastal ranges and a strong rain shadow effect occurring on their leeward sides (Bach et al., 2013). Crucially, this continental/rain shadow-driven contrast is independent of the summer water balance contrast of the northwest temperate climate (wet summer) of western WA and OR to the southwestern Mediterranean climate of CA (dry summer) and the southeast subtropical climate of AZ and NM (wet summer) to the desert Mediterranean climate (dry summer) of the Mojave Desert in eastern CA and Great Basin in NE and eastern OR.

As noted, most correlations of vegetation distribution with climate in the western USA have used growing season or annual water balance indices such as AETy and DEFy (Stephenson, 1990, 1998). However, consistent with our second hypothesis these two metrics, commonly used in biogeography to quantify drought stress, had a lower and more complex explanative power than W GAMS. We found that AETy was correlated with both Axes 1 and 3, and DEFy with Axis 2. This may be due to the sensitivity of AETy to winter and spring precipitation and to summer precipitation, with the former

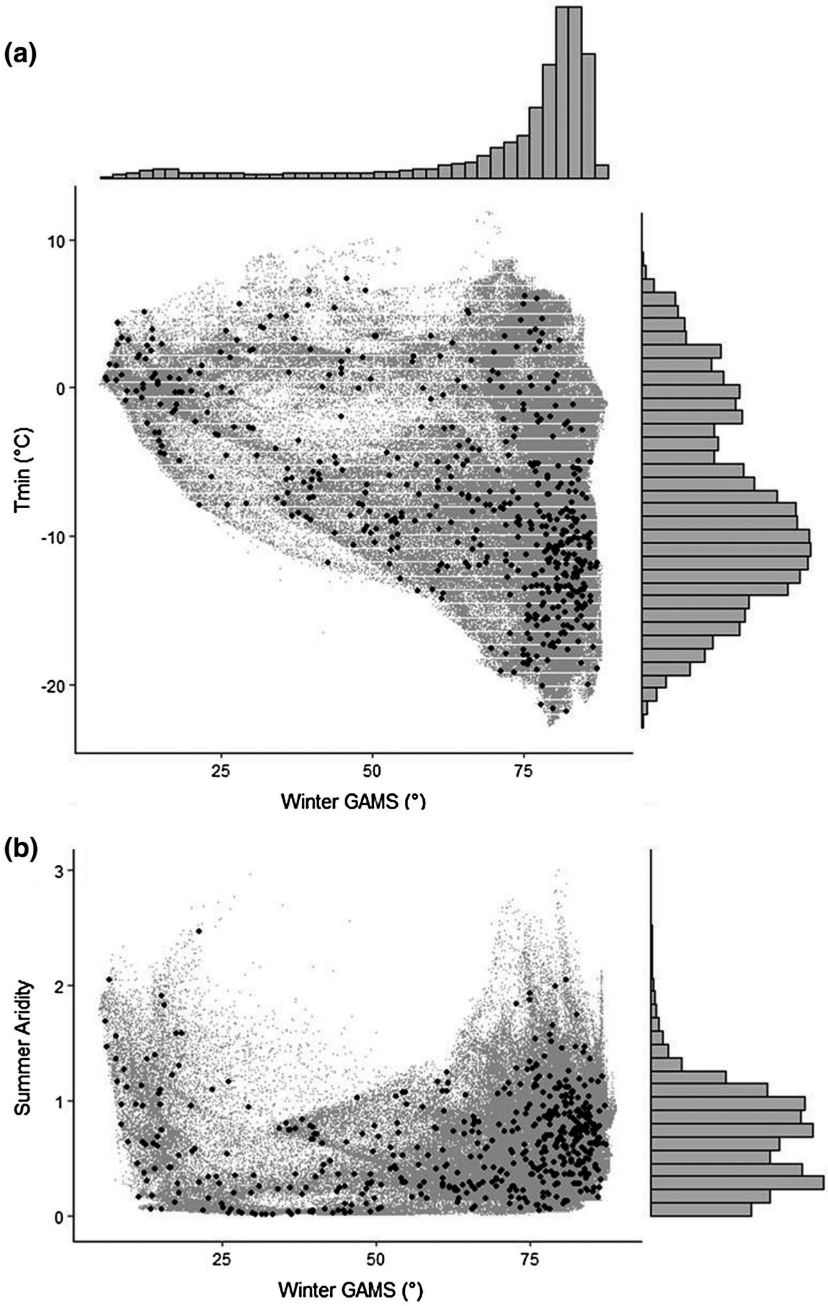

FIGURE 5 Relationships between minimum temperature of the coldest month for cold-tolerance (Tmin) and rainfall continentality index (W GAMS; a) and summer water balance (S ARID) and W GAMS (b) for the 467 plots (black dots) and Worldclim data (grey clouds)

increasing AETy in oceanic climates and the latter decreasing AETy in Mediterranean climates (see Figure 1). This explains why annual AETy does not capture key climate patterns (i.e., rainfall continentality and summer water balance) and the vegetation differences associated with it. The high correlation between DEFy and Axis 2 is due to the increase in precipitation and decrease in temperature with increasing altitude in mountain ranges, both contributing to decreasing DEFy, as also observed in the ombrothermal method (Bagnouls & Gaussen, 1953; Walter & Lieth, 1960). This latter result is also consistent with changes in aridity zones of Emberger (1930) and DEFy with increasing altitude in the climagram of Michalet (1991) for Morocco and the two climagrams for the western USA (Figure 6), respectively. However, altitude has very large effects on temperature (Rolland, 2003). Thus, it is not easy to disentangle the effects on vegetation of DEFy and length of the growing season (Grace, 1987; Ozenda, 1985).

Tmin was also strongly correlated with RDA Axis 1, which is consistent with the tight physical relationships between rainfall continentality, cloudiness, VPD and irradiance. Correspondingly, oceanic climates have high winter precipitation and high night temperatures in the winter (Bach et al., 2013; Waring & Franklin, 1979). High VPD and irradiance associated with rainfall continentality have strong effects on canopy microclimate and leaf physiology (Michalet et al., 2003; Novick et al., 2016; Simonin et al., 2009). This facet of drought is not captured in the index of soil water deficit during the growing season (Bagnouls & Gaussen, 1953; Stephenson, 1990). The winter Gams-angle index is a highly effective way to capture this VPD-related component of drought.

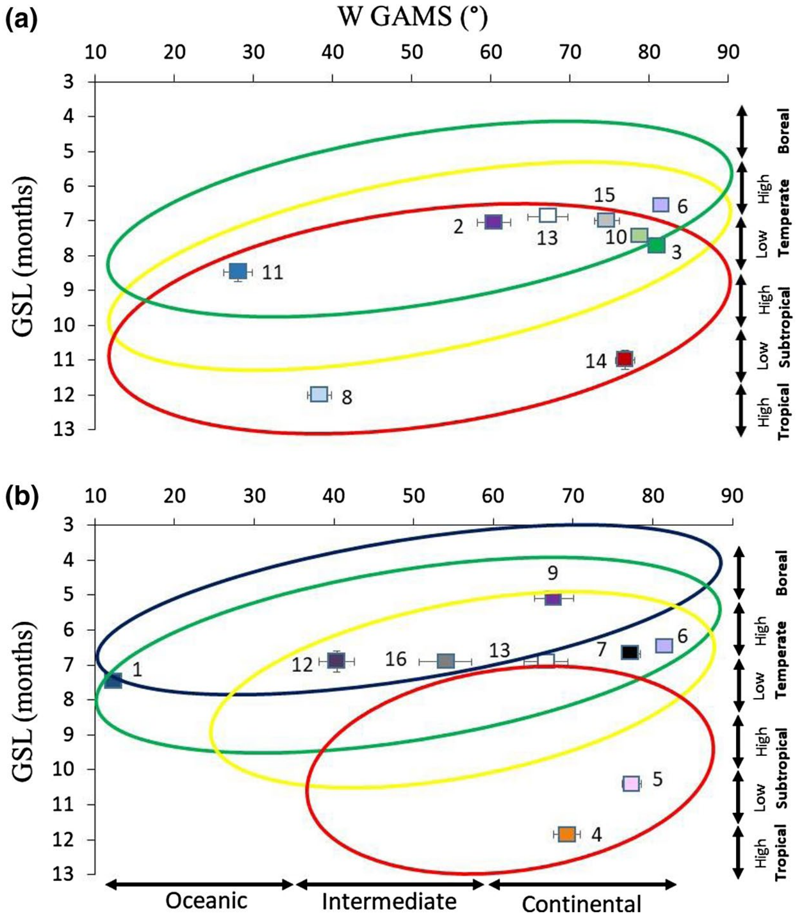

FIGURE 6 Mean (± 1 *SE*) positions of cluster groups from (a) dry-summer [upper part of redundancy analysis (RDA) Axis 3, Figure 3d] and (b) wet-summer sites (lower part of RDA axis 3, Figure 3d) along the rainfall continentality (W GAMS) and growing-season length (GSL) gradients. Ellipses delimit the positions of sites with increasing annual deficit (DEFy) following Stephenson (1998), with in blue humid (DEFy 38–200), green sub-humid (DEFy 201–640), yellow semi-arid (DEFy 640–820) and red arid sites (DEFy 821–1770). Legends of cluster groups are indicated by their numbers and colours (see Figure 4). Continentality zones are indicated below the horizontal axis and vegetation belts along the vertical axis (and see Table 2 for their delimitations) [Colour figure can be viewed at wileyonlinelibrary.com]

Pache, Michalet, et al. (1996) found that the geographical distribution of *Abies alba* in the European Alps was highly correlated with the W GAMS index, with no occurrence of this species in the most continental inner Central Alps. This is also the case for many *Abies* species in the Mediterranean Basin, which only occur in the hyper humid Mediterranean bioclimate characterized by high winter precipitation (Quezel & Médail, 2003 and see Figure 2). The common occurrence of North American *Abies* species in the oceanic cluster groups in our study is consistent with results from Europe and the Mediterranean Basin. Interestingly, the two larch species in the study area, *Larix occidentalis* and *Larix lyallii*, only occur in sites of intermediate continentality (cluster groups 12 and 16), whereas in Europe *Larix decidua* is common in the most continental inner zone of the European Alps. This may be due to the higher rainfall continentality in the Rocky Mountains (W GAMS is always lower than 70° in the Alps, versus often over 85° in the Rocky Mountains; Pache, Michalet, et al., 1996; see Figure S3.3a in Supporting Information Appendix S3).

Another ecological pattern that distinguishes rainfall continentality from summer water balance is the relationship between the climatic distribution of tree species and their responses to neighbours when seedlings. In the European Alps, Saccone et al. (2009) reported that *A. alba* tolerated low summer water balance but not high air atmospheric stress (high VPD) due to rainfall continentality. In this context, *A. alba* was facilitated by adult canopies during the August 2003 European heat-wave. In contrast, *Picea abies* tolerated high irradiance due to continentality, but was intolerant to low summer water balance. In turn, this species was negatively affected by competition for water during the heat-wave. Similar results were found by Muhamed et al. (2013) and Guignabert et al. (2020) for *Quercus suber* and *Pinus pinaster*, respectively, two Mediterranean species known for their oceanic distribution. In their experiments, seedlings of both species were facilitated by the shade of shrubs in gaps and forest dune communities from southwest France, correlated with lower VPD below shrubs despite lower soil water availability than where shrubs were experimentally removed.

4.2 | Relative importance of rainfall continentality and water balance in western USA

In the western USA, W GAMS values can be lower than 10° along the Pacific coast and exceed 85° in the eastern Rocky Mountains, whereas in the European Alps the lowest values are around 20° in the northwest and the highest values below 70° in the inner Central Alps (Michalet, et al., 2003; Pache, Michalet, et al., 1996). The very high level of rainfall continentality observed in CA and OR, immediately to the east of the Sierra Nevada and Cascade Ranges, only 300 km from the

Pacific Coast, has its only parallel in Europe at a distance of at least 3,000 km from the Atlantic Ocean, in the Ukraine. In contrast, except in western WA, summer water balance is very low in the western USA and thus varies much less spatially than in Europe. This may explain the much higher relative importance of rainfall continentality than summer water balance for vegetation distribution in the western USA than in Europe (Bagnouls & Gaussen, 1953). Additionally, the strong contrast existing along the Pacific coast between the high winter rainfall and low summer rainfall (see Figure 3b and d), and not in Europe along the Atlantic Ocean, may explain the rarity of deciduous tree species in western North America as compared to Europe and eastern North America (Waring & Franklin, 1979). One of the two deciduous oaks of the Rocky Mountains, *Quercus gambelii*, has been shown to occur in the southern Rockies but not the northern ones, because of the higher summer rainfall of the latter due to the American monsoon originating from the Gulf of Mexico (Neilson & Wullstein, 1983).

4.3 | Disentangling rainfall continentality from summer water balance for predicting responses to climate change

Disentangling rainfall continentality from low summer water balance is crucial for improving the accuracy of our predictions for the effects of climate change on species distributions. Our results indicate that many plant species, and in particular deep rooted woody species, in the western USA may respond differently to changes in winter versus summer precipitation. Neilson (1986, 1987) have shown that past low-frequency variations in winter and summer rainfall and temperatures drove the spatial dynamic of C3 and C4 species in the Chihuahuan Desert. Our results also showed the ability of rainfall continentality to be strongly associated with subspecies formation, with the three most common conifer species of the western USA (*Pinus ponderosa*, *Pinus contorta* and *Pseudotsuga menziesii*) represented by different subtaxa in oceanic and continental climates along RDA Axis 1. This supports Ikeda et al. (2017) who found that including genetically informed ecological niche models improved the accuracy of predictions of species distributions under climate change. Thus, if the future climate becomes drier in summer and thus more Mediterranean, or drier in winter and thus more continental, we might predict strikingly different responses among woody plant species and their subspecies. Most climate change studies have focused on summer, or growing season drought stress (Breda et al., 2006; Rehfeldt et al., 2006; Williams et al., 2020), even though recent studies also indicate a trend towards increasing winter precipitation, as in Scotland (UK) (Malby et al., 2007) and in western US deserts (Munson et al., 2013; Palmquist et al., 2016). Munson et al. (2013) have suggested that increasing winter precipitation in western deserts should favour shrubs over grasses, considering the current relative dominance of the former functional group in western deserts characterized by higher winter than summer precipitation (Paruelo & Lauenroth, 1996; but see Grover & Musick, 1990). In contrast, Palmquist et al. (2016) constructed models suggesting that the benefits of higher winter rainfall for shrubs induced by climate change should be overwhelmed by higher evaporative demand later in the growing season. Novick et al. (2016) estimated that soil moisture supply and atmospheric demand for water independently limit vegetation productivity and water use during periods of drought stress. The results of our study support their conclusion—conceptual and mathematical models that do not independently resolve VPD and soil moisture limitations (and thus rainfall continentality and low water balance) will not adequately capture the magnitude of ecosystem response to increasing climate stress. In conclusion, we argue that the Gams-angle index proposed here to disentangle water balance from rainfall continentality has exceptional potential for predicting species responses to climate change, as well as contributing to fundamental plant biogeography (Bell et al., 2014; Stevens et al., 2020; Violle et al., 2014).

ACKNOWLEDGMENTS

We thank Gilbert Billard, Camille Peyre, Edith Schaffter and Blaise Touzard for their contribution to vegetation sampling in the field and Jean-Christophe Domec for improving the manuscript.

AUTHOR CONTRIBUTIONS

R.M. designed the study and sampled vegetation; P.C. conducted the statistical analyses; R.M. wrote the manuscript with the help of P.C., R.C. and T.W.

DATA AVAILABILITY STATEMENT

Data will be available on Dryad (https://doi.org/10.5061/dryad.dbrv15f06) https://datadryad.org/stash/dataset/doi:10.5061/dryad.dbrv15f06.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

How to cite this article: Michalet R, Choler P, Callaway RM, Whitham TG. Rainfall continentality, via the winter Gams angle, provides a new dimension to biogeographical distributions in the western United States. *Global Ecol Biogeogr*. 2021;30:384–397. https://doi.org/10.1111/geb.13223