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Rainfall seasonality determines annual/perennial grass balance in vegetation of Mediterranean Iberian

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Abstract Much recent attention has been focused on the invasion and dominance of annual grass species in areas thought to have been historically dominated by perennial life forms. Explanations of this phenomenon in the literature have focused on two mechanisms favoring annuals: ruderal strategy associated with disturbance, and stress escaping associated with dry sites or deserts. Here I present evidence from vegetation surveys at 50 sites across a 1,200 km band of the Iberian Peninsula—a source region for many invasive annuals—showing that relative annual versus perennial grass composition is not well correlated with degree of disturbance or average annual precipitation. However, annual dominance is strongly and significantly linked to the seasonality of precipitation, in particular the relative intensity of summer drought. Disturbance was significantly associated with annual grass dominance in Iberia, but with much less explanatory power than summer drought intensity. Slope, aspect, and soil parent material were not significantly correlated with annual versus perennial grass dominance. These results suggest that subtle differences in rainfall seasonality largely drive grass composition in herbaceous Mediterranean vegetation. Furthermore, the patterns of annual grass invasion observed in the world's other Mediterranean climate regions may be associated with similar climatic drivers.

Keywords Iberian Peninsula · Mediterranean climate · Annual grass · Perennial grass · Disturbance · Precipitation · Invasion

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Introduction

Annual dominance is generally associated with habitats that are unpredictable and ephemeral, either edaphically, as in desert and dune settings (Raunkiaer 1934; Grime 1977), or successionally, as where disturbance opens sites for colonization by ruderal species (Stearns 1976). In either case, annual species dominance would not be expected in sites where annual rainfall is relatively abundant and predictable, soils are well developed, and disturbance is light to moderate. Mediterranean climate zones can support a full range of plant functional types. Nevertheless, annual grasses sometimes dominate plant communities under such conditions in the world's Mediterranean climate zones, which are characterized by mild moist winters and hot dry summers. Herbaceous vegetation is dominated by perennial herbs in South Africa, southwest Australia and most of the Mediterranean Basin (Bews 1971; Specht and Specht 1999), but by annual grasses and forbs in California and Chile (Crampton 1974; Figeroa et al. 2004). The dominant annuals of California and Chile are introduced species of Mediterranean Basin origin.

Mediterranean grasslands are a common and physiognomically consistent habitat type on the Iberian Peninsula. Usually occupying sites that were historically cleared or degraded, they are dominated by annual or perennial grasses (sometimes both) and a few shrubs, but they are quite heterogeneous in their overall plant composition, especially in the high diversity of forbs they harbor (Ramírez-Sanz et al. 2000). In spite of the wide distribution of this vegetation type, interactions between annual and perennial grasses have been little studied in these systems, likely because the species are usually considered early successional.

Within the Mediterranean Basin, disturbance is key in creating sites where herbaceous vegetation can dominate (Joffre et al. 1988), but less clear is its importance in maintaining grass dominance and in favoring annual versus perennial life histories. In eastern Spain annual grasses colonize and dominate only highly disturbed sites such as field edges and roadsides (Rivas Goday and Rivas Martínez 1963; San Miguel 2003), while in the southwest annuals are much more widespread, tending to dominate herbaceous vegetation as long as moderate disturbance in the form of livestock grazing is present (Joffre 1990; Figeroa and Davy 1991). More generally, disturbances such as brush-clearing, tilling, burning, and livestock grazing have been emphasized as factors that favor annual species dominance on the Iberian Peninsula (Rossiter 1966; Stoddart et al. 1975; Leiva et al. 1997). Similarly, disturbance from livestock grazing, perhaps combined with long-term drought, has often been cited as having favored the invasion of Mediterranean annual grasses into the Mediterranean-climate zones of California and Chile (Heady et al. 1992; Burcham 1957), where disturbance has also been credited with maintenance of annual dominance (Crampton 1974).

Highly seasonal rainfall regimes may also favor the dominance of annuals in some herbaceous Mediterranean plant communities (Raunkiaer 1934; Jackson 1985; Jackson and Roy 1986; Blumler 1993). As evidence for the potential of climatic seasonality to drive herbaceous composition, Jackson (1985) suggested (but did not quantify) that across the Mediterranean Basin, annual grasses appear to be the important plant community components mostly in regions with the longest and driest summers. Bartolome (1989) and Blumler (1984) both suggested that the long, intense summer drought characteristic of California might explain the success of Mediterranean annual invaders independent of disturbance. Though a simple climatic explanation of annual grass dominance in Mediterranean systems is intuitively appealing, little data exists to confirm climate's action in these systems.

To what extent do climate, disturbance, and other environmental variables drive annual and perennial grass dominance in Mediterranean systems? To quantify the contributions of these factors, I surveyed grass-dominated plant communities along a 1,200 km belt of the Mediterranean climate zone of the Iberian Peninsula. Survey sites were chosen to be near long-term meteorological stations so vegetation patterns could be related to local climate. Within Mediterranean Iberia, there is a strong gradient of precipitation seasonality, from a relatively short summer drought in northeastern Spain to a much longer and dryer summer in the southwestern corner of the peninsula (Fig. 1); total precipitation is highly variable along the gradient, but with highest rainfall totals in the extreme southwest. Disturbance history varies greatly between individual sites, as do site characteristics such as slope, aspect, bare soil, and rock cover. Soil parent material is largely calcareous and basic in eastern Spain but siliceous and acidic on the western half of the peninsula. These variables were assessed at 50 sites and analyzed for their correspondence to annual grass dominance in Mediterranean grassland patches.

A close correspondence of annual grass dominance to seasonality in precipitation would support the hypothesis that climate, in particular summer drought intensity, plays a lead role in the annual/perennial grass dynamics in Mediterranean Iberia. On the other hand, if annual grass distribution were linked more closely to observed disturbance, a ''ruderal strategy'' explanation of annual dominance would be favored. Alternatively or concurrently, site-specific characteristics that modify plants' local environments, such as slope, aspect and soil characteristics, could affect community annual/perennial dynamics. Finally, if climatic factors play a central role in driving annual

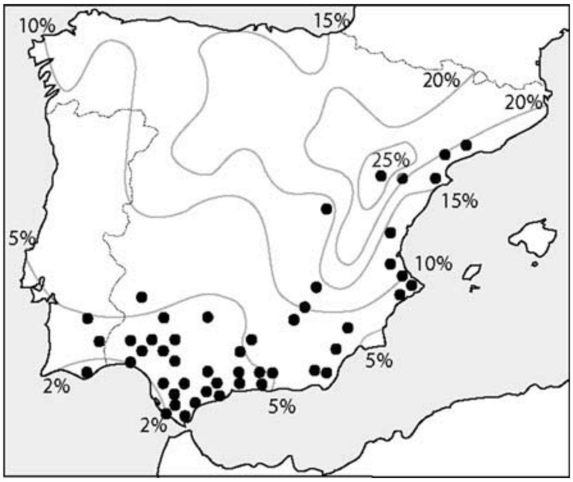


Fig. 1 Points represent locations of Iberian Peninsula sampling sites. Contours delineate percentage of total annual rain falling between June 21 and September 21 (adapted from Linés Escardó 1970), illustrating the overall gradient in precipitation seasonality on the Peninsula. The precipitation seasonality gradient is even stronger when all warm season rainfall (between May 1 and September 30) is taken into account, as in Fig. 2

dominance, regions of the Peninsula most similar in climate to other Mediterranean climate regions that are invaded by Mediterranean annuals, such as California and Chile, should show higher cover of these species.

Methods

Site selection

The geographic region under consideration was the southern and eastern coastal belt of the Iberian Peninsula, stretching from the Algarve of Portugal to the northern Mediterranean coast of Spain. I selected this region for its conformance to traditional definitions of Mediterranean climate—hot dry summers and mild wet winters—and because several grass species native to the zone are important invaders of natural areas in other Mediterranean-climate regions.

A list of meteorological stations throughout the region was assembled from publications of the Spanish Ministry of Agriculture. From this list, a subset of weather stations was chosen to be well dispersed throughout the study area, to represent a wide range of total precipitation values (240 mm/year to 1,010 mm/year), and to encompass wide variation in the seasonality of precipitation between the sites. Only stations with >20 years of meteorological records were used. All selected stations were <750 m in elevation, in order to minimize potential altitudinal effects on climate near each station.

I located a single site for vegetation sampling within a few kilometers of each previously selected weather station. Sampling sites were accepted wherever plant cover was at least 30% graminoid, provided that: (1) vegetation was natural, as opposed to planted; (2) the site had no signs of recent plowing or disking; (3) the site was not forested or heavily wooded; (4) the site was not enclosed by a fence. The site chosen for sampling was the first accessible site encountered meeting these selection criteria within 10 km of each weather station.

Sampling methods

Vegetative cover estimates were obtained at a total of 50 sites (Fig. 1). All sampling along the Mediterranean coast was performed between February 10 and February 19, 2003. Sites farther inland were sampled in February 24–March 6, 2003. The sampling order was intended to capture warmer coastal areas first and cooler inland areas later, to minimize effects of phenological differences in grass development between regions. Autumn and winter of 2002–2003 were close to long-term norms in rainfall and temperature throughout the region sampled (IRI Climate Information Digest).

Plant cover at each site was estimated using a point-intercept technique. I laid out 10 transects of 20 m length, each was separated by at least 2 m, at each location. A thin rod was dropped from a tape at 1 m intervals along the transect and the plant, or plants intercepted were identified to species where possible and to functional group when the species was unknown. Points not intersecting a plant were classified as hitting rock, bare soil, or plant litter. Thus, I collected data from a total of 210 points at each site to estimate cover of the various plant functional groups. At five of the sampling locations, only a half-set of the transect, for a total of 105 points, was performed, due to either limited area of the vegetated site or to time constraints.

In addition to vegetative composition, the slope and aspect of each sampling site were measured, using a clinometer and a compass respectively. For statistical analysis, sites were assigned to one of four slope categories (0–5%, 6–20%, 21–35%, and >35% slope), and one of five aspect categories, approximating increasing solar and thermal exposure (east, southeast, west, south or no slope, or southwest). Grass-dominated vegetation rarely occurs on more northerly facing slopes, and such slopes were not sampled in this survey. Finally, each sampling site was assigned to a ''calcareous'' or ''siliceous'' soil category, determined from soil maps, to account for the gradient in soil parent material across the sampling region.

Each sampling site was assigned to a recent disturbance category, based on observations of site characteristics independent of vegetative composition: (1) no evidence of recent disturbance; (2) signs of grazing activity, such as animal dung, clipped leaves, and animal trails; or (3) important soil disturbance such as churning by pigs or cattle.

Statistical analyses

Plant guild cover data and environmental variables—including average annual, cool season, and warm season precipitation—were analyzed with least-squares regression (SAS Institute 2002). These climatic variables, plus the parameters ''percent of average precipitation falling during the warm season,'' disturbance category, slope category, aspect category, and soil category were included as explanatory variables in forward stepwise regression analysis (SAS Institute 2002); the response variable was ''percent of total grass cover that is annual,'' an index of the relative dominance of annual to perennial grasses. This parameter was bounded by the values 0% and 100%, and was therefore an appropriate candidate for the logit transformation (Neter et al. 1996). Because this index contained values of zero that could not be logit transformed, the data were slightly compressed with the formula:

$$\text{Adjusted ``\% of grass cover that is annual''} = (\text{``\% of grass cover that is annual''} + 0.001)*0.998$$

Statistical analyses on data with this adjustment did not differ importantly from those on other data compressions that bring the extreme values closer to zero.

I performed principal component analysis (PCA) (SAS Institute 2002) on plant guild cover data, in which I assigned all data points to the categories annual or perennial grass, annual or perennial forb, herbaceous or woody legume, non-leguminous woody plants, bare soil, or exposed rock. I then calculated correlation coefficients of the first two ordination axes to each of the environmental variables included in the regression analyses.

Results

A relatively short list of grass species dominated most sites. The most common perennial grasses encountered were *Brachypodium retusum* (Pers.) P. Beauv., *Dactylis glomerata* L., *Hyparrhenia hirta* (L.) Staph, *Stipa tenacissima* L., and *Brachypodium phoenicoides* L.. The most commonly encountered annual grasses were *Bromus madritensis* L., *Bromus diandrus* Roth, *Avena* spp, and *Vulpia myuros* L.

Eight sites had no evident disturbance, 29 showed evidence of recent grazing, and 13 had grazing and widespread soil disturbance.

Annual grass cover was positively associated with average annual precipitation and average cool season (October–April) precipitation, but negatively associated with warm season (May–September) precipitation (Table 1). Perennial grass cover was positively related to warm season precipitation, but not signif-

Table 1 Relationship of annual and perennial grass cover on the Iberian Peninsula to average annual precipitation, cool season (October–April) precipitation, and warm season (May–September) precipitation

Variable	Annual grass cover			Perennial grass cover		
	Relationship	R^2	P	Relationship	R^2	P
Mean annual precipitation	+	0.18	0.002	n/a	0.02	0.347
Mean cool season precipitation	+	0.35	<0.0001	–	0.12	0.149
Mean warm season precipitation	–	0.23	0.0004	+	0.34	<0.0001

Values are from least-squares regression of cover onto each variable

Table 2 The environmental parameters most linked to the relative dominance of annual to perennial grasses at 50 Iberian Peninsula grassland sites

Parameter	Slope of relationship to annual dominance	P	R^2 contribution of parameter in stepwise multiple regression
% Precipitation falling in summer	–	<0.0001	0.59
Disturbance category	+	0.01	0.05
Aspect	n/a	0.15	0.02
Silicaceous or calcareous soils	n/a	0.23	0.01
Total annual precipitation	n/a	0.32	0.01

Parameters were selected by forward stepwise regression, with probability to enter = 0.40 and probability to leave = 0.10. For significant variables ($P < 0.05$), the sign of the slope of the relationship between the variable and annual dominance is given

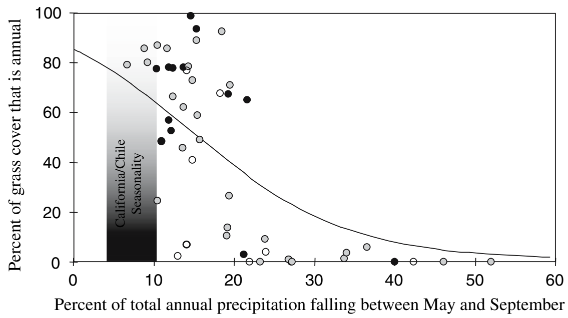


Fig. 2 Best-fit curve of percent of grass cover that is annual against percent of average annual precipitation falling in the warm season (May–September). Shading of points indicates disturbance category of each site sampled: unfilled represent the least disturbed category, gray the intermediate disturbance category, and black the highly disturbed category. Shaded bar approximates where the Mediterranean climate zones of California and Chile would fall with respect to rainfall seasonality

icantly linked to cool season and total annual precipitation (Table 1).

Table 2 presents the five environmental parameters, selected by forward stepwise regression, that explain the most variation in the percent of grass cover that is annual in the survey region. Only the percent of average precipitation falling in summer and the disturbance category were significantly linked to annual versus perennial dominance (graphed in Fig. 2). In contrast, average annual precipitation, slope, aspect, total cool-season precipitation, and soil category were not significantly correlated with the relative dominance of annual grasses.

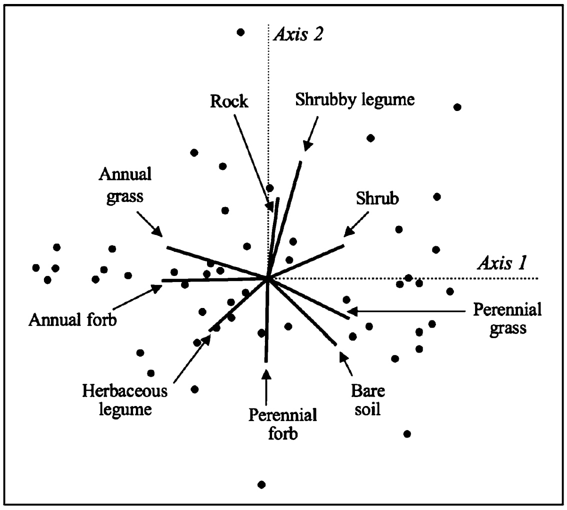
Principal component analysis of plant functional group cover (plus bare soil and rock cover) situated perennial grasses and annual grasses and forbs near opposite poles of the first axis, which explained 34.6% of variance in the ordination (eigenvalue = 3.11) (Fig. 3). Other plant cover groups separate away from the first axis to varying degrees; perennial forbs and woody legumes were distinguished mostly along the second axis, which explained 16.0% of variance in the ordination (eigenvalue = 1.44). The first axis was strongly correlated with the percent of annual precipitation falling in summer, and to a lesser degree with other measures of rainfall seasonality and disturbance. The second axis was not strongly correlated with any measured environmental parameters.

Discussion

Climate seasonality

Rainfall seasonality, measured as the percentage of average annual precipitation falling in the warm season, was a powerful predictor of annual grass dominance in Mediterranean Iberian grassland patches, explaining almost 60% of variance in annual/perennial grass composition. Annual grasses made up 80% or more of grass cover at all three sites where average summer rainfall was less than 10% of total annual precipitation. In contrast, annuals were never greater than 6% of grass cover at the nine sites where more than 25% of total precipitation falls as summer rain. Between these two end ranges of summer precipitation, relative annual grass cover varied greatly; Fig. 2 makes apparent that a small part of the variation within that range was associated with observed level of disturbance at the sites.

The effect of seasonality on relative annual dominance had two distinct sources: the positive association of increasing cool-season precipitation with annual cover, and the positive correlation



Variable	Axis 1 Correlation	Axis 2 Correlation
% total mean rainfall falling in warm season	0.695	0.107
Average May-Sept rainfall	0.551	0.182
Average Oct-Apr rainfall	−0.549	0.068
Disturbance category	−0.467	−0.181
Total average precipitation	−0.359	0.136
Slope	0.152	0.143
Aspect	0.168	−0.012

Fig. 3 Principle Component Ordination of plant functional group data from all 50 sampling points. The first principle component axis (Axis 1) explains 34.5% of community variance, while the second principal component (Axis 2) explains 16.0%. The sidebar shows correlations between measured environmental variables and the first and second principle components

between warm-season precipitation and perennial grass cover (Table 1). It is unsurprising that cool-season annuals respond favorably to increasing resources during their growth period. Responses to warm-season precipitation may be more nuanced, since in much of the Iberian Mediterranean climate zone, the yearly overlap of drought with warm temperatures restricts most plant growth—including that of most perennials—to spring and autumn. Annuals escape the dry summer as seed, while perennials must possess (presumably) costly mechanisms for summer survival (Slatyer 1967). Where summer drought is consistently longer and dryer, perennial plants must invest progressively more of their resources into drought survival, thereby reducing allocations to growth and reproduction (Stearns 1976). Many perennial grasses are physiologically adapted to surviving even the harshest Mediterranean climate conditions, though in the context of competition from other plant functional groups, they may be unable to dominate or even persist (Joffre et al. 1987; Dyer and Rice 1999; Clary et al. 2004). Even where individual perennials can survive in the presence of annual competitors, under extremely seasonal conditions annuals will be better able to maintain their reproductive outputs than perennials; subsequent dispersal—mostly by grazing animals in the case of grasses—would then gradually permit increasing dominance by annuals (Russi et al. 1992). By either mechanism, along the continuum of increasing drought intensity, annual species escaping summer drought as seed should be progressively favored (the ‘‘therophyte’’ strategy; Raunkiaer 1934).

Principal component analysis ordination of plant guild cover was consistent with the role of precipitation seasonality in driving elements of community composition, since annual and perennial grasses fell at opposite poles of the first PCA axis, which was most correlated with precipitation seasonality. Annual forbs are closely grouped with annual grasses, suggesting a similar concentration on sites with the harshest summer conditions. Perennial forbs and legumes, however, separate along the second ordination axis and are not closely associated with either group of grasses.

Disturbance

The primary alternate hypothesis—that disturbance largely determines annual grass dominance in these systems—was not supported by the data. Though significantly associated with annual grass cover, observed recent disturbance played a relatively minor role in explaining overall grass composition, mainly contributing to variation in the ‘‘intermediate’’ climate seasonality region. At the least seasonal and most highly seasonal sites, disturbance had no apparent relation to annual dominance. This result is consistent with annuals acting as r-selected ruderals at the local scale in areas of intermediate seasonality, filling in open spaces created by disturbance. The ruderal strategy is insufficient to explain landscape-level variability in annual dominance.

Local site characteristics

Similarly, other environmental factors potentially affecting community dynamics at more local scales, such as slope, aspect and substrate origin, explained little annual/perennial grass variance. This finding could reflect a small effect size or a lack of consistent directional effects across such a large scale. Others working at smaller scales in Mediterranean climate systems have found that dryer south-facing microsites hosted a greater proportion of annuals than moister expositions (Litav 1967; Madon and Médail 1997), and that perennial grasses established more successfully on north-facing slopes in California grassland restoration (Lulow 2004). Similarly, steeper slopes usually lose more water to runoff and are thus more xeric. These effects may be more important at the local scale, where slope and aspect differentiate microsites under a more or less constant climate.

Correspondence to other Mediterranean systems

Regions of Mediterranean Iberia that are climatically most similar to highly annual-invaded areas of California and Chile showed the greatest dominance of annual grass species (Fig. 2). Overlaying the precipitation seasonality ranges for California and Chile against data from this study shows that the Mediterranean climates of these regions have longer and more intense summer droughts that most of the Iberian Peninsula. In these regions, Mediterranean annual grasses have invaded and replaced most of the original perennial-dominated herbaceous communities. Indeed, if precipitation seasonality correlates with annual dominance as closely in California as it did in this Mediterranean study, we would predict annual dominance in nearly all California herbaceous communities outside montane regions, as is now the case.

Conclusions

The results of this study provide strong evidence that annual grasses are favored over perennial grasses in Mediterranean-climate zones with high rainfall seasonality. Many other factors may be at play in invasive annual success in these systems, including release of invaders from herbivores or pathogens, invader traits that make them effective colonizers and competitors, and inherent invasibility of the recipient region based on biodiversity or evolutionary and disturbance history. In light of these results, however, these factors may be less important in highly seasonal Mediterranean climate zones than mechanisms allowing avoidance or tolerance of extreme summer drought.

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