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RESEARCH PAPER

Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems

Richard M. Cowling[1,*], Fernando Ojeda[2], Byron B. Lamont[3], Phillip W. Rundel[4] and Richard Lechmere-Oertel[1]

[1]*Botany Department, Terrestrial Ecology Research Unit, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa,* [2]*Departmento de Biología, CASEM, Universidad de Cádiz, Campus Río San Pedro, E-11510 Puerto Real, Spain,* [3]*Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth 6845, Australia,* [4]*Department of Organismic Biology, Ecology and Evolution, University of California (UCLA), Los Angeles, CA 90095, USA*

ABSTRACT

Aim Rainfall reliability has been neglected as a determinant of plant trait convergence and divergence in mediterranean-climate ecosystems. This paper reports on patterns of rainfall reliability — quantified as interannual variation in monthly and seasonal rainfall, and as the frequency of individual events in terms of their size, duration and intensity — for four fire-prone mediterranean-climate ecosystems.

Location The four mediterranean-climate regions of the world with fire-prone ecosystems, namely SW Cape (South Africa), SW Australia, California and the Mediterranean Basin (Andalusia, Spain).

Methods Using long-term monthly rainfall data from stations dispersed across the four regions, we computed monthly means and interannual variation for each month of the year — the latter quantified as the coefficient of variation (CV) — and divided these into winter and summer seasons. We also computed the mean number of rainfall events, the mean frequency in various categories of event duration (days), the amount of rainfall per event (mm) and the rainfall intensity per event (mm/day) per year for winter and summer seasons for a subset of the rainfall stations.

Results The fraction of rain falling in summer was lowest in California (5%) and similarly low (*c.* 25%) in the other three regions. The hierarchy of values of coefficient of variation (CV) of monthly rainfall during the winter period was as follows: California > Andalusia >> SW Cape > SW Australia; results for summer were: California > > Andalusia >> SW Australia ~ SW Cape. SW Australian sites experienced the greatest frequency of short, small and low-intensity rainfall events in both seasons; patterns in the SW Cape were intermediate between Australia and the two northern hemisphere sites which both received fewer, larger and more intense events. Overall, the two southern hemisphere regions (SW Australia and the SW Cape) had significantly more reliable regimes than the two northern hemisphere ones (Mediterranean Basin and California).

Main conclusions These differences in rainfall reliability regimes may provide a novel perspective on the distribution of certain plant life-history traits in mediterranean-climate ecosystems. Less reliable regimes would select for germination and seedling survival traits that enable persistence of genets in the face of uncertain moisture conditions during the winter and spring establishment phase. Study systems that accommodate for phylogenetic constraints, namely invasive species derived from mediterranean-climate ecosystems, as well as shared lineages, provide good opportunities to develop and test hypotheses on the implication of different rainfall reliability regimes. One of the novel implications of this study is that the distinctive trait of assemblages in the southern hemisphere regions may be a consequence not so much of their shared nutrient-poor soils as of their similarly reliable rainfall regimes.

Keywords

California, convergence, Mediterranean Basin, mediterranean-climate ecosystems, plant traits, rainfall reliability regimes, SW Australia, SW Cape.

*Correspondence: Richard M. Cowling, Botany Department, Terrestrial Ecology Research Unit, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa. E-mail: rmc@kingsley.co.za

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INTRODUCTION

Since Schimper's (1903) account, mediterranean-climate ecosystems have been cited as classic examples of convergence in ecosystem structure and function, owing to their shared summer-dry, winter-wet climates (e.g. Specht, 1969; Cody & Mooney, 1978). During the 1980s, it became clear that there were also many convergences and divergences resulting from differences and similarities in soil nutrient status, the intensity of summer drought and fire regimes. Markedly lower soil fertility, larger amounts of summer rain, and more frequent fires were invoked to explain differences in plant traits and community structure between the mediterranean-climate ecosystems of south-western (SW) Australia and the SW Cape on the one hand, and the climatically analogous areas of California, Chile and the Mediterranean Basin, on the other (Cody & Mooney, 1978; Cowling & Campbell, 1980; Barbour & Minnich, 1990; Keeley, 1992). Vegetation in SW Australia and the SW Cape, occurring in areas experiencing similar edaphic and climatic regimes, shows remarkable convergence of plant traits and community structure (Milewski, 1983; Lamont *et al.*, 1985; Cowling & Witkowski, 1994). There is also considerable convergence in plant diversity patterns on edaphically and climatically matched sites in the SW Cape and western Mediterranean Basin (Ojeda *et al.*, 2001).

Almost all research on convergence in mediterranean-climate ecosystems has used mean annual rainfall as the climatic basis for selecting environmentally analogous sites for comparative studies (e.g. Parsons & Moldenke, 1975; Cowling & Campbell, 1980; Milewski, 1982; Ojeda *et al.*, 2001). Moving beyond annual means, the importance of summer drought intensity has been cited as an important factor for distinguishing mediterranean-climate environments (e.g. di Castri, 1981). However, only Lamont *et al.* (1985) and Keeley (1992) have invoked this as a factor leading to divergence in trait representation between regions. Rainfall reliability — measured as interannual variation in annual and monthly rainfall, and as the frequency of different sized rainfall events — has attracted surprisingly little interest as a factor that could explain convergence or divergence among mediterranean-climate ecosystems. Milewski (1981) has suggested that more intense rainfall events in SW Australia than the Cape explain the taller vegetation in the former region. Variation in annual rainfall is seldom mentioned in comparative studies and when it is (Zedler, 1990; Keeley, 1992), the ecological and evolutionary implications are not discussed.

Several studies have commented on the ecological and evolutionary significance of variation in rainfall reliability *within* mediterranean-climate ecosystems. Lamont and Markey (1995) and Ojeda (1998) have shown that fire-killed shrubs (non-sprouters) in *Banksia* (Proteaceae) and *Erica* (Ericaceae) are proportionally more diverse than sprouters in areas receiving the most reliable winter rains, in SW Australia and the Cape Floristic Region, respectively. Cowling *et al.* (1997) and Cowling and Lombard (2002) showed that regional-scale plant richness was twofold higher in the western part of the Cape, which receives reliable winter rainfall, compared with the eastern, non-seasonal part, where winter rain is much less reliable. They argued that reliable winter rainfall, by selecting for the obligate seeding life history, promotes high speciation rates — and depresses extinction rates, owing to the larger population sizes of non-sprouters. Procheş *et al.* (2005) also concluded that higher richness of Cape geophytes in the reliable winter-rainfall region of the west is a consequence of higher speciation and lower extinction rates than in the less reliable, non-seasonal rainfall zone in the east. In the eastern Mediterranaean Basin, Aronson and Shmida (1992) reported highest plant diversity in a biogeographical transition zone characterized by the highest interannual rainfall variation amongst the sites they studied. In California, Minnich and Howard (1984) have posited that the coastal concentration of non-sprouters in certain shrub lineages is less related to lower fire frequency there (Keeley, 1977) than to the higher reliability of winter rains in coastal than in interior ranges.

Rainfall reliability has been invoked to explain ecosystem structure and function and the frequency of traits and processes across the world's arid and semiarid regions (e.g. Le Houérou *et al.*, 1988; Wiens, 1991; Esler *et al.*, 1999; Davidowitz, 2002). For example, Cowling *et al.* (1999) and Esler *et al.* (1999) have argued that the more reliable rainfall in the winter-rainfall desert of southern Africa (Namaqualand) than North America (Mohave and western Sonoran) is a key factor in explaining the shorter shrub stature, greater population turnover and higher regional diversities in the former region.

Given these ecological–rainfall reliability relationships, it seemed appropriate to us to compare patterns among different mediterranean-climate ecosystems, which is the topic of this paper. Since fire plays an important role in selecting for plant reproductive traits in mediterranean-climate ecosystems (e.g. Kruger, 1983), and the likelihood of fire–rainfall reliability interactions, we excluded Chile from the analysis, as fire is not a component of the region's selective regime (Muñoz & Fuentes, 1989; Arroyo *et al.*, 1995). Much of our discussion is devoted to identifying opportunities for researching the implications of patterns of rainfall reliability for divergence and convergence of plant life-history traits and processes in mediterranean-climate ecosystems.

DATA AND METHODS

Rainfall stations

We sourced from various electronic databases rainfall data from the four mediterranean-climate ecosystems (Fig. 1) where fire is a natural part of the disturbance regime (Table 1). Because the Mediterranean Basin encompasses a wide climatic heterogeneity (Blondel & Aronson, 1999), we chose an area of this region that is adjacent to the Atlantic Ocean, in order to improve comparability with the three other regions, all of which have extensive coastlines and associated maritime influence. The area we chose is Andalusia in Spain (NW Mediterranean Basin) (Fig. 1).

Within each region, we chose rainfall stations using the criteria listed below. Owing to the constraints associated with these, we were not able to select stations randomly.

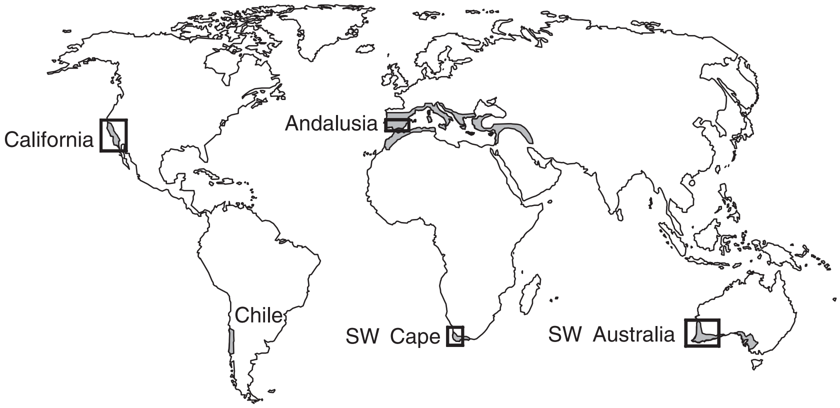

Figure 1 Location of the world's five mediterranean-climate ecosystems.

Table 1 Annual rainfall characteristics for each of the four mediterranean-climate regions used in this study. SW = south-western, Med = Mediterranean Basin, Cal = California and Aust = Australia. MAR = mean annual rainfall calculated as the mean of the mean annual rainfall across all sites; $n < 25$ years. Percentage winter is expressed as the proportion of the MAR across all sites that falls in the 6 winter months (April–September in the southern hemisphere and October–March in the northern hemisphere)

	No. of stations	MAR (mm)	SD	Median	Range	% winter	Data source
SW Med	40	602.5	280.1	530.5	330–1783	75.0	SinambA
Cal	22	492.1	266.5	452.2	294–1382	95.2	National Oceanic and Atmospheric Administration
SW Cape	25	682.2	383.4	563.2	366–1607	75.2	Computing Centre for Water Research
SW Aust	26	539.7	276.1	432.9	310–1238	74.5	Bureau of Meteorology

(1) Mean annual rainfall must exceed 250 mm, as below this amount, mediterranean-type ecosystems are replaced by transitional or pure semidesert ecosystems under most circumstances in all four regions (Milewski, 1979; Cowling & Campbell, 1980; Keeley, 1992; Blondel & Aronson, 1999).
(2) More than 70% of annual rain must fall in the 6 winter months (April–September in the southern hemisphere and October–March in the northern hemisphere). This excluded many sites in the southern and eastern parts of the Cape Floristic Region (Deacon *et al*., 1992).
(3) They needed to be spread over the entire region to ensure a representative sample of rainfall totals.
(4) Rainfall records must exist for at least 25 consecutive years.

For the analysis of rainfall events (see below), in addition to the criteria constraining the choice of stations in the larger data set, we further constrained the choice by including only those stations with the longest recording period and with the most complete records (i.e. sites with much missing data were excluded). Nine sites were selected from west Andalusia, 12 from California, 10 from the SW Cape, and 11 from SW Australia.

Interannual variation

We computed interannual variation for each month of the year and divided these into winter (April–September in the southern hemisphere and October–March in the northern hemisphere) and summer (October–March in the southern hemisphere and April–September in the northern hemisphere) seasons. We calculated interannual variation as the coefficient of variation (CV) of monthly rainfall. Differences in monthly CVs between regions were explored using one-way analysis of variance (ANOVA) and subsequent Tukey tests.

Rainfall events

We defined a rainfall event as any period ≥ 2 consecutive days in which some rain was recorded, either as a continuous event or as discrete events. We reasoned that events of this duration, comprising follow-up rains, were likely to trigger biological responses such as germination and seedling growth, especially in the winter growing season. We excluded events associated with a single day, because in all regions, the majority of these comprised rainfall events of < 5 mm, an amount that is not regarded as biologically significant (Cerda, 1997; Henkin *et al*., 1998). Note that all rainfall events were included in the analyses comparing yearly and seasonal rainfall totals, as well as interannual variation for monthly rainfall. We computed the mean number of events, and the mean frequency in various categories of event duration (days), the amount of rainfall per event (mm) and the rainfall intensity per event (mm/day) per year for winter and summer seasons (defined previously) for selected sites in all four regions.

We used analysis of covariance (ANCOVA) to explore if there was any difference between the four mediterranean-climate ecosystems in mean number of rainfall events per year across all sites. We did this separately for the winter and summer seasons (defined previously) using mean seasonal rainfall as a covariate.

Table 2 Results of a one-way ANOVA on monthly rainfall (mm) for selected localities in four mediterranean-climate regions (see Table 1 for explanation of abbreviations for regions). Northern hemisphere winter is October–April and summer is April–September; the southern hemisphere winter is April–September and summer is October–March. Data are the mean values for all localities within a region. Values sharing the same superscripts are not significantly different ($P > 0.05$) after Tukey test

Month	SW Med	Cal	SW Cape	SW Aust	*F*	*P*
Winter						
Oct/Apr	66.56*	21.23†	54.98*	30.28†	21.90	< 0.0001
Nov/May	89.98*	57.22†	89.83*	74.73*	3.12	< 0.05
Dec/Jun	93.70*	85.06*	110.90*	87.58*	1.02	> 0.05
Jan/Jul	78.97*	101.90*	99.22*	88.93*	1.21	> 0.05
Feb/Aug	75.08*	89.47*	98.63*	72.13*	1.84	> 0.05
Mar/Sep	47.72*	75.53†	56.69*,†	48.26*	4.42	< 0.01
Summer						
Apr/Oct	58.90*	36.25†	45.22*†	32.65†	8.28	< 0.0001
May/Nov	40.05*	11.23†	31.42*,‡	29.18‡	15.82	< 0.0001
Jun/Dec	19.43*	3.74†	23.64*	18.00*	18.21	< 0.0001
Jul/Jan	4.33*	0.97*	19.53†	17.26†	36.70	< 0.0001
Aug/Feb	7.11*	2.43*	20.98†	20.96†	47.43	< 0.0001
Sep/Mar	20.90*	7.04†	28.20‡	20.04*	24.31	< 0.0001

The use of the latter as a covariate is legitimate as: (1) there was a positive significant relationship between it and the number of rainfall events (both variables log-transformed) for all regions in both seasons, and (2) the slopes of the relationships between these variables were homogeneous for all regions in both seasons (winter: $F_{3,34} = 0.83$, $P = 0.49$; summer: $F_{3,34} = 2.61$, $P = 0.067$).

We used Kruskal–Wallis and Dunn post-tests to assess the significance of differences in mean frequency per year across regions within categories (bins) of event duration, rainfall amount per event, and rainfall intensity per event.

RESULTS

Annual and monthly means

There was no significant difference in mean annual rainfall across all sites in the four regions ($F = 1.79$, $P = 0.15$). The lowest value was recorded for California and the highest for the SW Cape (Table 1). The winter rainy season starts one month later in California than in the other regions (Table 2). The fraction of rain falling in summer was lowest in California (5%) and similarly low (*c.* 25%) for the other three regions. However, while early summer rainfall (April–May) was highest in Andalusia, and late summer (September) rainfall was similar in amount to that recorded in the southern hemisphere regions, peak summer (July–August) rainfall was not significantly different from the very low values recorded in California. The amount of summer rain recorded in SW Cape and SW Australia was similar for all months except March, when significantly more rainfall was recorded in the SW Cape.

Interannual variation

The hierarchy of values of CV of monthly rainfall during the winter period was as follows: California > Andalusia > > SW Cape > SW Australia (Fig. 2, Table 3). The differences between the northern and southern hemisphere regions were most clear-cut in the mid-winter months (December–February and June–August, respectively). Early winter rainfall (October–November) was especially unreliable in California, as was mid-winter rainfall (December–February) in Andalusia. In the southern hemisphere regions, mid-winter rainfall (June–August) was the most reliable.

Table 3 Results of a one-way ANOVA on the coefficient of variation (CV) of monthly rainfall of selected localities in four mediterranean-climate regions (see Table 1 for explanation of abbreviations for regions). Northern hemisphere winter is October–March and summer is April–September; the southern hemisphere winter is April–September and summer is October–March. Data are the mean values for all localities within a region. All results $P < 0.001$. Values sharing the same superscripts are not significantly different ($P > 0.05$) after Tukey test

Month	SW Med	Cal	SW Cape	SW Aust	*F*
Winter					
Oct/Apr	0.88*	1.30†	0.82*	0.76*	44.42
Nov/May	0.94*	1.06*	0.71†	0.60‡	53.54
Dec/Jun	1.05*	0.83†	0.63‡	0.43§	108.20
Jan/Jul	0.99*	0.88†	0.57‡	0.39§	121.4
Feb/Aug	0.73*	0.90†	0.61‡	0.47§	35.33
Mar/Sep	0.83*	0.90*	0.70†	0.50‡	32.45
Summer					
Apr/Oct	0.72*	1.07†	0.76*	0.58*	43.43
May/Nov	1.01*,‡	1.69†	1.16‡	0.81*	46.89
Jun/Dec	1.35*	2.14†	1.15*	1.14*	30.29
Jul/Jan	3.51*	2.43†	1.26‡	1.74‡	40.57
Aug/Feb	1.96*	3.09†	1.15‡	1.08‡	59.27
Sep/Mar	1.33*	2.50†	0.98‡	1.12*,‡	29.04

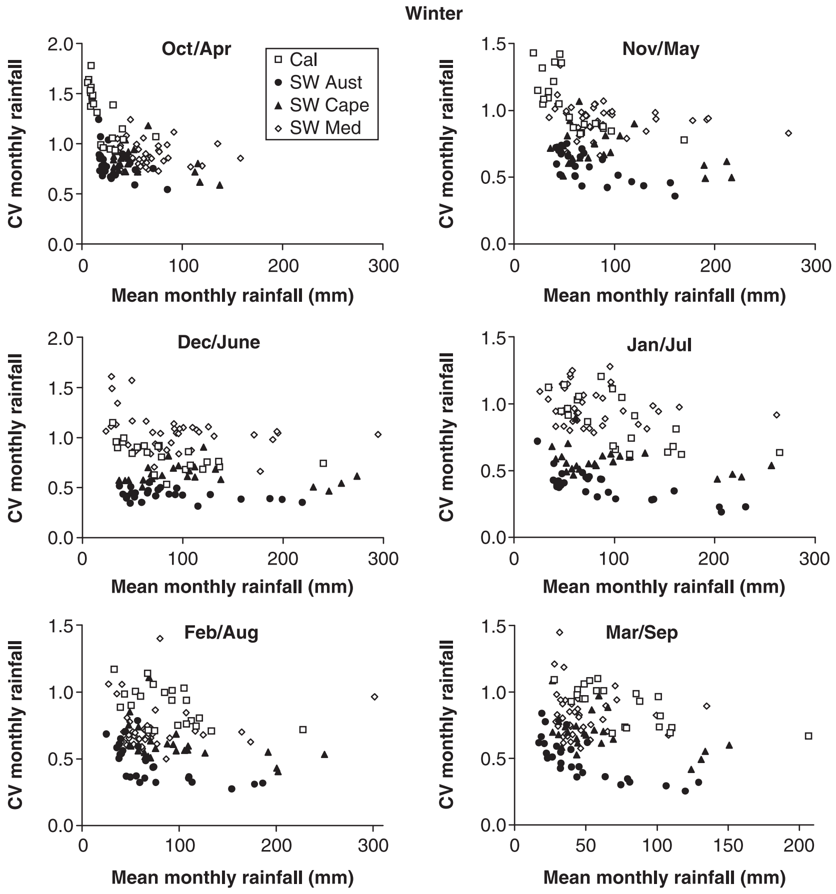

Figure 2 Relationship between the coefficient of variation (CV) of monthly rainfall and mean monthly rainfall in the winter months for selected localities in four mediterranean-climate ecosystems. The northern hemisphere winter is defined as October–March and the southern hemisphere as April–September.

The hierarchy of values of CV of monthly rainfall during the summer period was as follows: California > > Andalusia > > SW Australia ~ SW Cape (Fig. 3, Table 3). Whereas relative reliability was lowest in midsummer months (December–February) in the southern hemisphere regions, highest CV values were recorded in the later summer months (July–September) in the northern hemisphere.

Rainfall events

There were significant differences in the number of rainfall events in both the winter and summer months across the four mediterranean-climate ecosystems, after controlling for mean seasonal rain (Table 4). SW Australia had significantly more rainfall events in winter than the other three mediterranean-climate regions (Tukey test) (Fig. 4). Differences were most pronounced for California, which had the lowest number of events overall, and least pronounced for the SW Cape, although differences among these three regions were not significant. Patterns were similar for the summer months. However, in this season there were significantly fewer events in California than in the SW Cape.

In all regions, most rainfall events — in both winter and summer — were of relatively short duration (≤ 3 days) and very few long events (≥ 7 days) were recorded (Fig. 5). SW Australian sites experienced significantly more events across all duration categories in winter, although differences were more marked for short (≤ 3 days) than longer categories (Fig. 5). The SW Cape had significantly more short events per year and significantly fewer very long events (≥ 7 days) than the two northern hemisphere regions, which had almost identical profiles for winter event duration. The overall pattern for summer was similar, although the total number of events was lower (Fig. 4). However, differences for short events between the SW Cape and the northern hemisphere regions were not significant and patterns for longer events were not consistent across all regions.

Table 4 Results of a one-way ANCOVA comparing the number of rain events per site (log-transformed) in the winter and summer seasons across the four mediterranean-climate regions. Northern hemisphere winter is October–March and summer is April–September; the southern hemisphere winter is April–September and summer is October–March. The covariate is mean seasonal rainfall per site (log-transformed)

Source	d.f.	MS	*F*	*P*
Winter				
Region	2	0.17	31.3	0.00001
Mean winter rainfall	1	0.23	41.2	0.00001
Error	37	0.005		
Summer				
Region	2	0.14	14.2	0.00001
Mean summer rainfall	1	0.73	73.6	0.00001
Error	37	0.01		

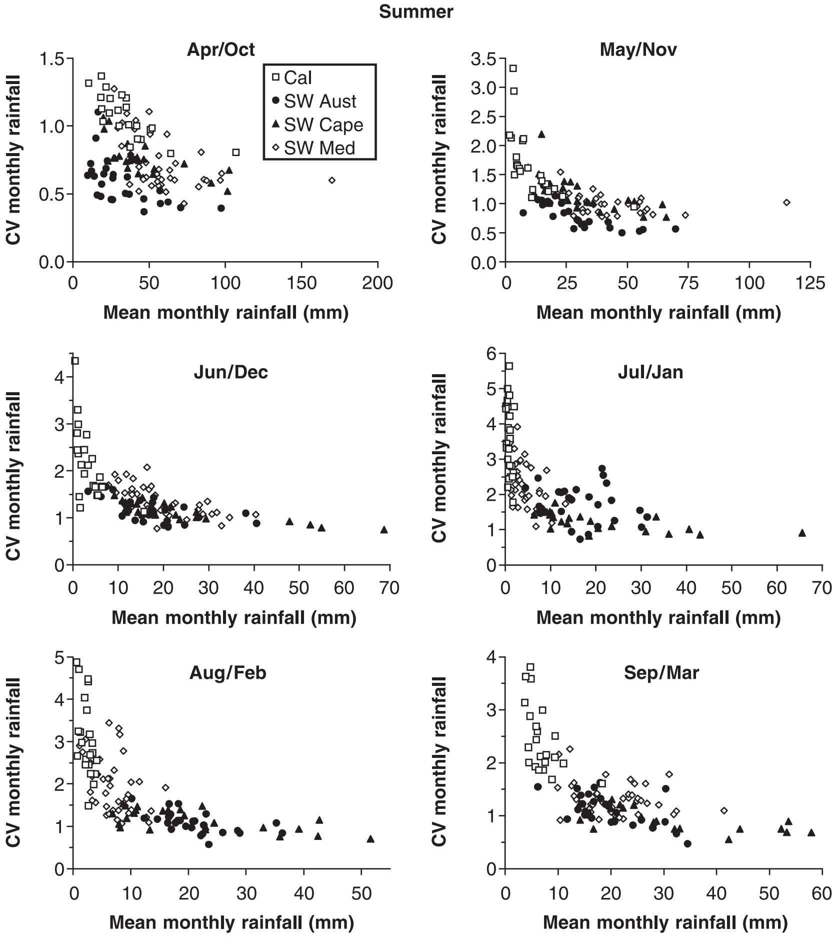

Figure 3 Relationship between the coefficient of variation (CV) of monthly rainfall and mean monthly rainfall in the summer months for selected localities in four mediterranean-climate ecosystems. The northern hemisphere summer is defined as April–September and the southern hemisphere as October–March.

All regions showed marked differences in the mean number of different sized rainfall events per winter (Fig. 5). SW Australia had significantly more small events (≤ 20 mm), and significantly more intermediate-sized events (> 10 ≤ 50 mm) were recorded in the SW Cape than in the northern hemisphere regions (but not SW Australia), and the northern hemisphere regions had significantly more large events (> 100 mm) than the southern hemisphere ones. Patterns were broadly similar in summer, although differences between the SW Cape and the northern hemisphere regions were not consistent across event size categories. However, Andalusian sites recorded significantly more large events (> 50 mm) than all other regions.

The patterns for mean frequency of different categories of rainfall intensity per event were similar to the profiles for rainfall per event (Fig. 5). In both seasons, most rainfall events were of low intensity, in the SW Cape most events were of intermediate intensity, whereas the two northern hemisphere regions — and especially Andalusia — had the highest frequency of high-intensity events.

DISCUSSION

Rainfall regimes compared

Despite no differences in mean annual and winter rainfall across the four mediterranean-climate ecosystems, our data show that the rainfall regimes of the two southern hemisphere regions are fundamentally different from the northern hemisphere ones. The Australian and Cape regions have (1) substantially less variable between-year winter rain, (2) a higher frequency of rainfall events, especially small to moderate ones, in both winter and summer, and (3) higher overall summer rain. Of these two regions, Australia has the more reliable rainfall regime, measured as CV of monthly rain and the frequency of small, low-intensity events. Thus, our data provide no support for Milewski's (1979) hypothesis that SW Australia receives more intense rainfall events than the SW Cape. Of the two northern hemisphere regions, California has the most variable regime and more intense summer drought, whereas Andalusia has greater numbers of large and intense downpours, the latter being a notable feature of the Mediterranena Basin rainfall regime (Blondel & Aronson, 1999).

Caution must be exercised in generalizing our results from Andalusia for the entire Mediterranean Basin. Le Houérou *et al.* (1988) have shown that rainfall reliability varies greatly in different parts of the Mediterranean Basin. Also, there are pronounced differences in rainfall regimes within each of the regions studied here. Thus, Ojeda (1998) differentiated between southern and northern subregions of the SW Cape, based on the amount of summer rain and winter rainfall reliability (both higher in the south). Lamont and Markey (1995) documented a similar geographical trend in these variables in SW Australia. Minnich and

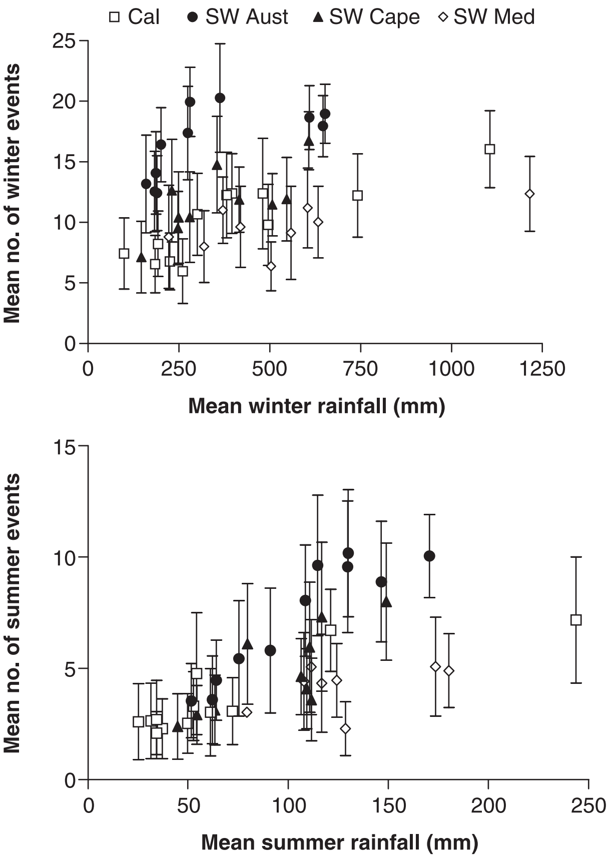

Figure 4 Relationship between mean number of rainfall events (see text for definition) and mean seasonal rainfall for selected localities in four mediterranean-climate ecosystems. See Table 3 for explanation of abbreviations for the regions and definition of winter and summer seasons. Error bars represent one standard deviation (SD).

Howard (1984) observed that winter rainfall reliability was higher in the coastal than the interior ranges of California. There is no clear geographical pattern of rainfall reliability within Andalusia (F. Ojeda, unpublished data).

The reasons for these intercontinental differences in rainfall regimes are probably complex and beyond the scope of this study. Nevertheless, we suspect that, apart from global climatic phenomena — such as the North Atlantic Oscillation (NAO) and the El Niño-Southern Oscillations (ENSO) — as main explanatory variables (e.g. Reason *et al*., 2000; Rodrigo *et al*., 2001; Haylock & Goodess, 2004), the influence of topography may account for differences among regions. Deacon *et al*. (1992) have suggested that the coastal ranges in the SW Cape play an important role in influencing the tracks of circumpolar, rain-bearing fronts. SW Australia has virtually no topography of significance, whereas Andalusia and California have ranges that exceed in height those in the Cape by 1.5 km and 2.5 km, respectively. This hierarchy in topography parallels the ones for winter rainfall reliability, event frequency, size and intensity: regions of low topography experience more reliable rain that falls in many more small and low-intensity events. We know of no studies in comparative frontology in mediterranean-climate ecosystems, other than that of Grab and Simpson (2000) who showed that southern Africa experiences an annual frequency of circumpolar westerly fronts that is about double that of the NW Mediterranean Basin.

The causes of differences in summer rainfall regimes are likely to be even more complex, as the synoptic conditions associated with summer events are likely to differ among regions. In the SW Cape, summer rain may be associated with circumpolar fronts, postfrontal conditions as moist air is advected over the warm Indian Ocean, cutoff lows and late summer thunderstorms (Deacon *et al*., 1992). Summer rain in SW Australia is largely a product of the deep penetration of tropical cyclones that develop over the north Indian Ocean (Milewski, 1979), whereas in California, a limited incursion of moist air from the Gulf produces thunderstorms in the interior mountains (di Castri, 1981). In the NW Mediterranean Basin, summer rain is associated with convective cloudiness favoured by thermal mesoscale depressions and the increase in temperature of the Mediterranean Sea (Llasat, 2001).

Implications for divergence and convergence of plant life-history traits

In mediterranean-climate ecosystems, the incidence of plant life-history traits — and their evolutionary consequences — is controlled by fire regime (Kruger, 1983), soil fertility (Cody & Moody, 1978), climate (Barbour & Minnich, 1990) and phylogenetic factors (Cowling & Witkowski, 1994; Verdú *et al*., 2003). Because selective regimes vary markedly among mediterranean-climate ecosystems, as does the phylogenetic composition of their floras, testing hypotheses based on differences in rainfall reliability alone will be a difficult and risky task. It makes sense, as far as is feasible, to control for the other factors in selecting study systems.

An hypothesis worth testing is that reliable rain falling in many relatively small and low-intensity events after summer-autumn fires — the normal fire season in mediterranean-climate ecosystems (Kruger & Bigalke, 1984) — would select for plant traits that enhance germination in the immediate postfire period (Cowling *et al*., 2004). Thus, reliable soil moisture levels in the postfire environment would select for synchronous postfire germination, the rapid postfire growth of seedling populations, and enable early reproduction and a rapid build-up of seed banks prior to the next fire. These traits would be less advantageous where rain falls in few large events whose occurrence is unpredictable from year to year, because the resultant prolonged dry spells would result in high seedling mortality and therefore a high risk of extinction of seedling populations.

An epitome of fire-cued germination is serotiny — the retention on the plant of seeds in woody infructescences. Serotiny is most favoured where interfire recruitment is ineffective (e.g. when competition or predation is intense between fires) and where fire-induced seed release is followed by a reliably wet winter (Lamont *et al*., 1991; Lamont & Enright, 2000). Ecologists have struggled to explain the higher incidence and greater degree of serotiny in SW Australian vs. SW Cape Proteaceae (Lamont *et al*., 1985, 1991). Both regions have similarly infertile soils and fire regimes (Cowling & Witkowski, 1994) and phylogenetic factors

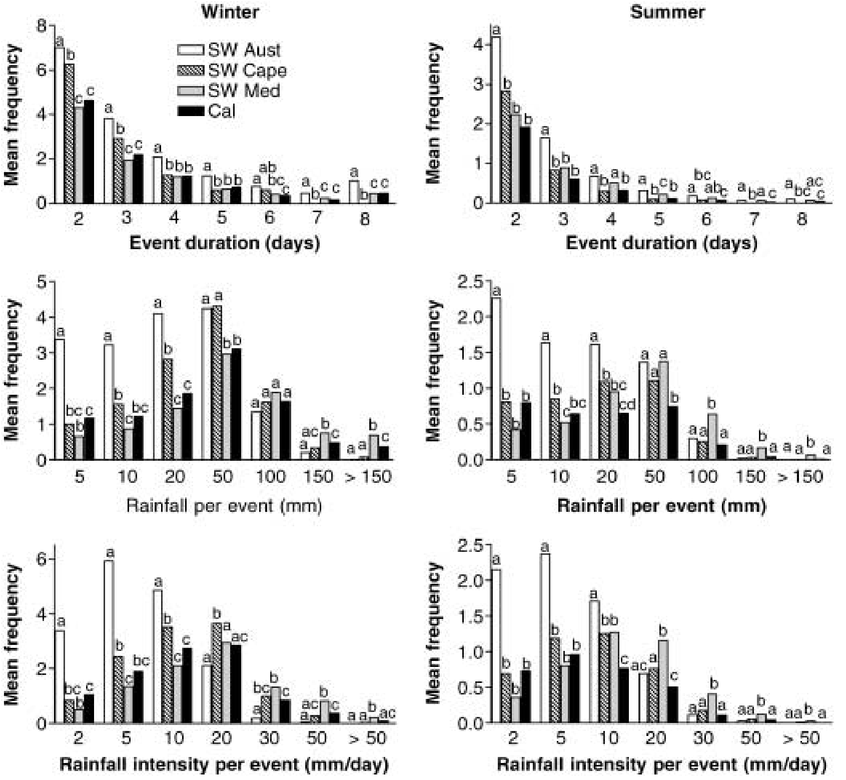

Figure 5 Mean frequency per year of event duration, rainfall per event and rainfall intensity per event for selected localities in four mediterranean-climate ecosystems. Shared letters above bars per event category indicate $P > 0.05$ (Dunn's test). See Table 3 for explanation of abbreviations for the regions and definition of winter and summer seasons.

are unlikely to be of significance, as this pattern is evident in the Proteoideae, which are represented in both regions. It is possible that this pattern is consistent with the rainfall reliability hypothesis presented above, given that winter (postfire) rainfall is significantly more reliable in SW Australia than in the SW Cape.

Overcoming phylogenetic constraints would be best achieved by comparing patterns of trait representation for closely related taxa along gradients of rainfall reliability within mediterranean-climate ecosystems. Such gradients exist in California (Minnich & Howard, 1984), SW Cape (Ojeda, 1998; Procheş *et al*., 2005), SW Australia (Lamont & Markey, 1995) and the Mediterranean Basin (Le Houérou *et al*., 1988). Mustart and Cowling (1993) have demonstrated that germination of serotinous Cape Proteaceae is highly sensitive to wet–dry cycles that correspond with the intervals between rainfall events. It would be interesting to compare patterns within species whose distributions span the rainfall reliability gradient (e.g. *Protea repens*, *Protea neriifolia*, *Leucadendron salignum*). We would predict a greater tolerance to prolonged dry spells of seeds from populations in the less reliable non-seasonal zone than the more reliable winter-rainfall one. SW Australian Proteaceae (and other taxa) afford the same opportunity. Similar patterns for phylogenetically related taxa along rainfall reliability gradients on both continents would provide powerful support for convergence theory.

Despite largely unrelated floras, phylogenetic factors need not constrain comparisons between northern and southern hemisphere mediterranean-climate ecosystems, which show the greatest differences in rainfall reliability regimes. Studies should select phylogenetically related taxa and explicitly avoid premediterranean lineages, namely species that have persisted since the onset of mediterranean climates in the terminal Pliocene (Axelrod, 1975; Herrera, 1992; Valiente-Banuet *et al*., 1998; Verdú *et al*., 2003; Cowling & Procheş, 2005). SW Cape–Mediterranean Basin comparisons should focus trait comparisons of shared genera, including *Erica* (Ericaceae) and the geophytic genera *Androcymbium* (Colchicaceae), *Gladiolus*, *Moraea*, *Romulea* (Iridaceae), and *Dipcadi*, *Drimia* and *Ornithogalum* (Hyacinthaceae). Traits that could be investigated include germination response to soil moisture regimes that reflect rainfall reliability patterns (Mustart & Cowling, 1993; Pérez-Fernández *et al*., 2000), allocation of resources to below- and above-ground biomass (Bell & Ojeda, 1999; Verdaguer & Ojeda, 2002), and seedling mortality in relation to short-term water stress.

Invasive alien species are potentially excellent study systems for future research. Annual grasses from the Mediterranean Basin (e.g. *Briza*, *Lagurus*, *Lolium*, *Lophochloa*, *Phalaris*, *Poa*), which are widely established weeds in all other mediterranean-climate ecosystems (Groves & di Castri, 1991), offer good opportunities to compare the germination and survival of seedlings, in response to soil moisture variation that simulates rainfall reliability regimes, of populations of known provenances from northern and southern hemisphere regions. The short generation times associated with the annual life cycle means that divergence may well have occurred in populations that have been isolated on different continents for 150 years or more (Groves & di Castri, 1991). Interestingly, Pérez-Fernández *et al*. (2000) showed that germination of Mediterranean Basin herbs is more rapid and more responsive to increased moisture than SW Australian ones, which is consistent with taking advantage of heavy but less reliable rainfall events experienced in the former region. However, this study did not correct for phylogenetic constraints, as its aim was to understand the mechanisms by which weed invasion into SW Australian vegetation occurred. Other research prospects include *Carpobrotus*, a SW Cape genus that is a member of the rapidly diversifying Ruschioideae clade in the Aizoaceae (Klak *et al*., 2004). *Carpobrotus* species are invasive in coastal ecosystems in both California (Weber & D'Antonio, 1999) and the Mediterranean Basin (Suehs *et al*., 2001). Another model system is the Mediterranean Basin pines — *Pinus pinaster* and *Pinus halepensis* — both serotinous species (Tapias *et al*., 2004) that are strongly and widely invasive in Cape fynbos ecosystems (e.g. Rouget *et al*., 2001).

Overall, patterns of rainfall reliability, in conjunction with other components of the selective regime — especially fire — may provide a novel perspective on the distribution of certain plant traits in mediterranean-climate ecosystems. Differences in rainfall reliability may explain convergence and divergence in many other ecological patterns and processes, including hydrology and the structure and function of lotic and wetland systems (Gasith & Resh, 1999). Ultimately, it may contribute to explaining, via differences and similarities in life-history traits, patterns of species richness in mediterranean-climate ecosystems (Aronson & Shmida, 1992; Cowling *et al*., 2004). One of the novel implications of this study is that the distinctive trait assemblages in the southern hemisphere regions — for example, the high incidence of serotinous and fire-killed shrubs (Lamont *et al*., 1985; Cowling & Witkowski, 1994) — may be a consequence not so much of their shared nutrient-poor soils, as of their similarly reliable rainfall regimes.

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BIOSKETCHES

Richard Cowling has had a long interest in plant ecology and evolution of mediterranean-climate shrublands and deserts. These days he spends most of his time researching ways of undertaking biodiversity and socioeconomic assessments for implementing conservation actions in South Africa's Cape fynbos, succulent karroo and subtropical thicket biomes.

Fernando Ojeda's research is focused in three principle areas: ecology and evolution of the genus *Erica*, the role of fire and rainfall patterns in the evolution of regeneration life histories in Mediterranean woody plants, and biodiversity and conservation of species-rich Mediterranean heathlands.

Byron Lamont has studied the ecology of the south-western Australian flora for 35 years. His main interest is plant population dynamics in relation to fire, drought and herbivory by kangaroos.

Phil Rundel has wide-ranging interests in the ecophysiology of plants growing in most of the world's biomes, but especially mediterranean-climate shrublands and deserts. Recent interests include conservation and urban ecology.

Richard Lechmere-Oertel is a plant ecologist with experience in landscape scale processes. He is currently developing biodiversity conservation planning and management tools for conservation agencies in the Maloti-Drakensberg bioregion of southern Africa.