

Fire regimes and vegetation responses in two Mediterranean-climate regions

Regímenes de incendios y respuestas de la vegetación en dos regiones de clima Mediterráneo

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ABSTRACT

Wildfires resulting from thunderstorms are common in some Mediterranean-climate regions, such as southern California, and have played an important role in the ecology and evolution of the flora. Mediterranean-climate regions are major centers for human population and thus anthropogenic impacts on fire regimes may have important consequences on these plant formations. However, changes in fire regimes may have different impacts on Mediterranean type-ecosystems depending on the capability of plants to respond to such perturbations. Therefore, we compare here fire regimes and vegetation responses of two Mediterranean-climate regions which differ in wildfire regimes and history of human occupation, the central zone of Chile (matorral) and the southern area of California in United States (chaparral). In Chile almost all fires result from anthropogenic activities, whereas lightning fires resulting from thunderstorms are frequent in California. In both regions fires are more frequent in summer, due to high accumulation of dry plant biomass for ignition. Humans have markedly increased fires frequency both in the matorral and chaparral, but extent of burned areas has remained unaltered, probably due to better fire suppression actions and a decline in the built-up of dry plant fuel associated to increased landscape fragmentation with less flammable agricultural and urban developments. As expected, post-fire plant regeneration responses differs between the matorral and chaparral due to differences in the importance of wildfires as a natural evolutionary force in the system. Plants from the chaparral show a broader range of post-fire regeneration responses than the matorral, from basal resprouting, to lignotuber resprouting, and to fire-stimulated germination and flowering with fire-specific clues such as heat shock, chemicals from smoke or charred wood. Plants from the matorral have some resprouting capabilities after fire, but these probably evolved from other environmental pressures, such as severe and long summer droughts, herbivory, and volcanism. Although both Mediterranean-type ecosystems have shown to be resilient to anthropogenic fires, increasing fire frequency may be an important factor that needs to be considered as it may result in strong negative effects on plant successional trends and on plant diversity.

Key words: human impacts, plant regeneration, matorral, chaparral.

RESUMEN

Los incendios forestales originados por tormentas estivales son una característica común en la mayoría de las regiones con clima Mediterráneo, tal como el sur de California, y han jugado un rol importante en la ecología y evolución de su flora. Las regiones con clima Mediterráneo han sido, además, centros importantes para el establecimiento de poblaciones humanas, las que al alterar los regímenes de incendios podrían producir efectos negativos importantes en este tipo de formaciones vegetales. Sin embargo, los efectos antrópicos sobre el régimen de incendios podrían tener impactos distintos en ecosistemas Mediterráneos cuya vegetación ha evolucionado naturalmente con este tipo de perturbación. Así, en este trabajo comparamos los regímenes de incendios y la capacidad de respuesta de la vegetación de dos regiones con clima Mediterráneo que han tenido historias distintas en cuanto a la ocurrencia natural de incendios forestales y de ocupación humana, tales como la zona central de Chile (matorral) y el sur de California (chaparral). En Chile, casi todos los incendios forestales son el resultado de actividades antrópicas, mientras que en California los incendios producidos por el hombre se suman a los producidos por tormentas estivales. En ambas regiones, los incendios son más frecuentes en verano debido a la acumulación de biomasa vegetal seca altamente combustible. El hombre ha incrementado significativamente la frecuencia de incendios tanto en el matorral como en el chaparral en las últimas décadas, pero la extensión de los incendios no se ha incrementado en forma importante, probablemente debido a mejores sistemas de supresión del fuego y a la menor acumulación de biomasa vegetal seca por el aumento de la

fragmentación del paisaje con desarrollos urbanos y agrícolas con menor potencial de combustión. Como se esperaba, las respuestas de regeneración de las plantas después de los incendios son distintas en el matorral y en el chaparral. Las plantas del matorral muestran un rango de respuestas regenerativas mayor, las que van desde el rebrote basal, al rebrote desde el lignotuber y a la germinación y floración estimuladas por el fuego, con estímulos fuego-específicos tales como shock térmico, químicos presentes en el humo y en la madera quemada. Las plantas del matorral tienen cierta capacidad de regeneración después del fuego, pero estas probablemente evolucionaron como consecuencia de otras presiones ambientales, tales como las severas y largas sequías de verano, la herbivoría y el volcanismo. Aunque ambos ecosistemas de tipo Mediterráneo han mostrado ser resistentes a los incendios de origen antrópico, el marcado aumento en la frecuencia de estos puede constituir un aspecto muy importante de considerar, ya que puede resultar en efectos negativos importantes tanto en los patrones sucesionales como en la diversidad vegetal.

Palabras clave: impactos antrópicos, regeneración vegetal, matorral, chaparral.

INTRODUCTION

Mediterranean-climate regions occupy less than 5 % of the Earth's surface, yet they contain about 20 % of the world's flora (Cowling et al. 1996). These regions are also major centers of human population growth and thus anthropogenic impacts on natural ecosystems have been a matter of concern, particularly because of the potential for introducing new disturbances or altering the frequency and intensity of the existing ones (Mooney et al. 1986, Fuentes et al. 1990, 1995).

Wildfires are a common feature of some Mediterranean-climate regions and they have long played an important role in the ecology and evolution of the flora. The autumn, winter, and spring rains, coupled with mild temperatures, support the growth of a diversity of shrubs, herbs and grasses thus resulting in a continuous stand of vegetation. The long summer drought produce extensive areas of dry biomass with highly flammable conditions and once ignited, the stand structure contributes to rapid fire spread. However, human settlement and associate activities have impacted natural fire regimes in these landscapes (Keeley et al. 1989, Minnich 1989). For instance, continuous and successful fire prevention practices in some Mediterranean-climate regions have resulted in important effects on ecosystem function, but on the other hand, prolonged buildup of fuel have resulted on highly destructive fires (Keeley & Keeley 1986).

We contrast here the role of natural (lightning-ignited) wildfires and the impact of anthropogenic fires on vegetation of two contrasting Mediterranean-climate regions, the Chilean matorral and the Californian chaparral, because of their differences in natural fire regimes and land use histories (Mooney 1977). Europeans colonized central Chile several centuries earlier than California. While relatively little exploitation of natural resources

occurred prior to the industrial revolution in California, strong impacts on natural ecosystems associated to subsistence lifestyles of rural populations have played an important role on the structure and function of the Chilean matorral (Bahre 1979, Aschmann 1991).

Fire regimes in Chile and California

Influence of the Mediterranean climate on timing of wildfires is clear from their seasonal distribution in Chile and California (Fig. 1 and 2). Fires are more frequent on summer months in both regions, but a significant fire hazard is also present throughout the year in California. One possible explanation for this may lie on sociological patterns associated to holiday travels; massive population movements from main cities to rural areas and coastal towns are concentrated in summer months in Chile (summer holiday), while travels associated to holidays are often spread out over the year in California. A complementary explanation may also lie in the causes of wildfires.

In Chile, wildfires are almost all result of anthropogenic activities and "natural" lightning-ignited fires are very rare in the official records (Table 1). Lightning fires, with ignitions resulting from thunderstorms, are clearly not described for Chile as they are for other areas with similar climates around the world, such as California, the southwestern Cape of Africa, southwestern Australia and the Mediterranean Basin (Aschmann & Bahre 1977, Araya & Avila 1981, Rundel 1981, Avila et al. 1988, Montenegro et al. 2002). Although, it has been hypothesized that other natural sources of fire may have been rare in Chile, (Mooney 1977, Armesto & Gutiérrez 1978), Fuentes & Espinoza (1986) have argued that volcanism, an unusually frequent phenomenon in Chile, may have served as a non-human ignition source, based on published botanical paleontological and geological evidence. However, California

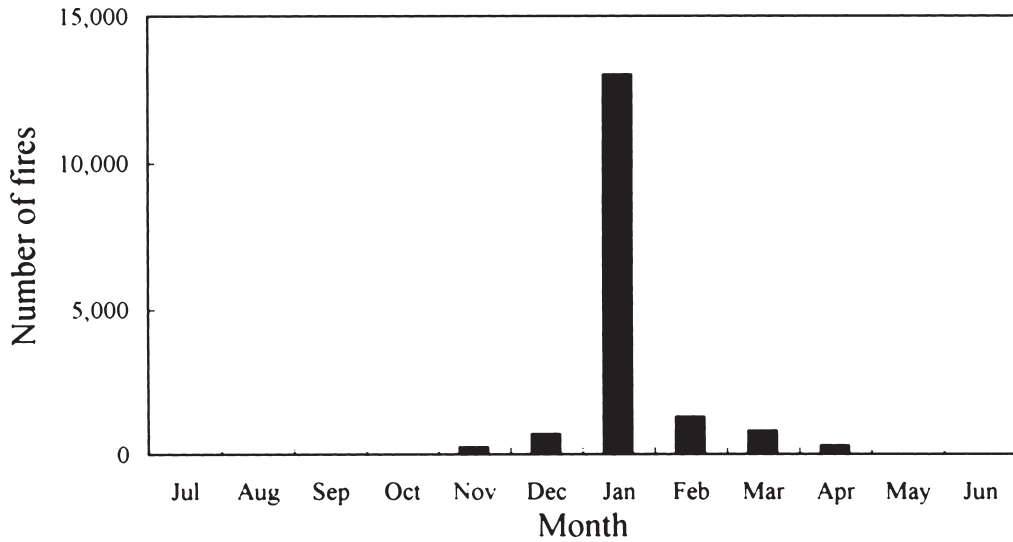


Fig. 1: Seasonal distribution of fires in Chile between 1978 and 1995 (data from CONAF 1995).

Distribución estacional de los incendios en Chile entre 1978 y 1995 (datos de CONAF 1995).

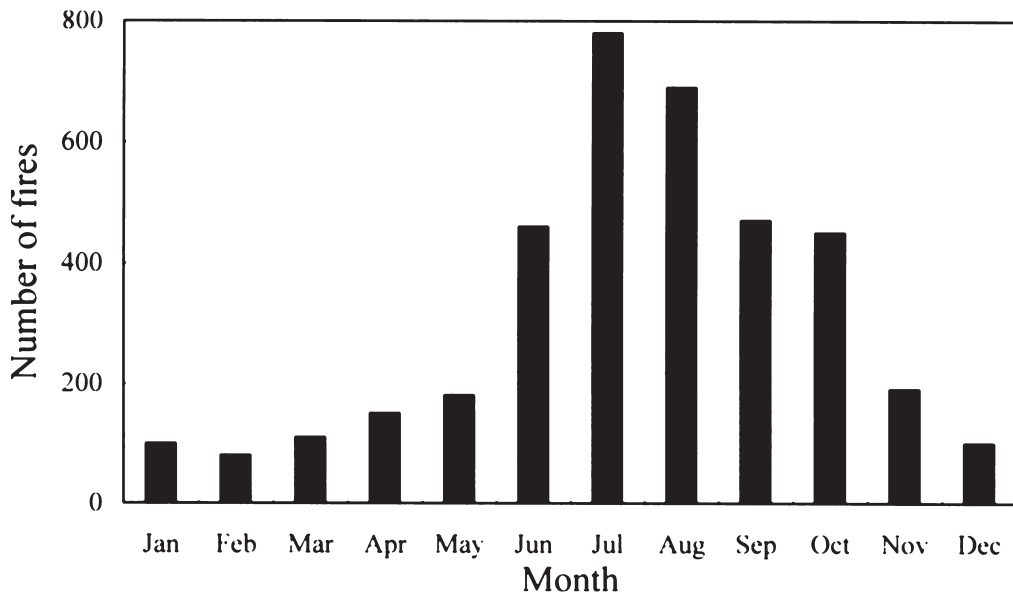


Fig. 2: Seasonal distribution of fires in southern and central California for the period 1910-1997 (data from Keeley et al. 1999).

Distribución estacional de los incendios en California central y sur para el período 1910-1997 (datos de Keeley et al. 1999).

markedly contrasts with Chile where lightning is a frequent and significant source of ignitions (Table 2). Nonetheless, humans account for a substantial number of ignitions in California as well as in Chile.

Further suggestion for the importance of humans on fire regimes in these regions is the

significant increase of wildfires in recent decades, both in Chile (Fig. 3) and in California (Fig. 4). Although the Chilean data shown here is for the whole country, the trend is very similar when restricted to the central region with temperate Mediterranean climate-type (Zunino & Riveros 1990). The increase in

TABLE 1

Causes of wildfires in Chile for the period 1986-1990 (n = 3955). Data from CONAF
 Causas de los incendios forestales en Chile para el período 1986-1990 (n = 3955). Datos de CONAF

Cause	Percentage (%)
Transportation	30
Forestry/agriculture	20
Recreation	19
Military	12
Incendiary	14
Unknown	5

TABLE 2

Frequency and extent of burning by natural lightning fires and anthropogenic causes on
 State and federal wildlands in California (1970-1979) (from Keeley 1982)

Frecuencia y extensión de los incendios forestales producidos por causas naturales y antropogénicas
 en áreas silvestres de California (1970-1979) (Keeley 1982)

Jurisdiction	Fires (10^6 ha yr $^{-1}$)		Hectares burned (10^6 ha year) $^{-1}$	
	Humans	Lightning	Humans	Lightning
State of California,				
Division of Forestry	541	31	3347	416
United States Forest Service	134	129	669	189

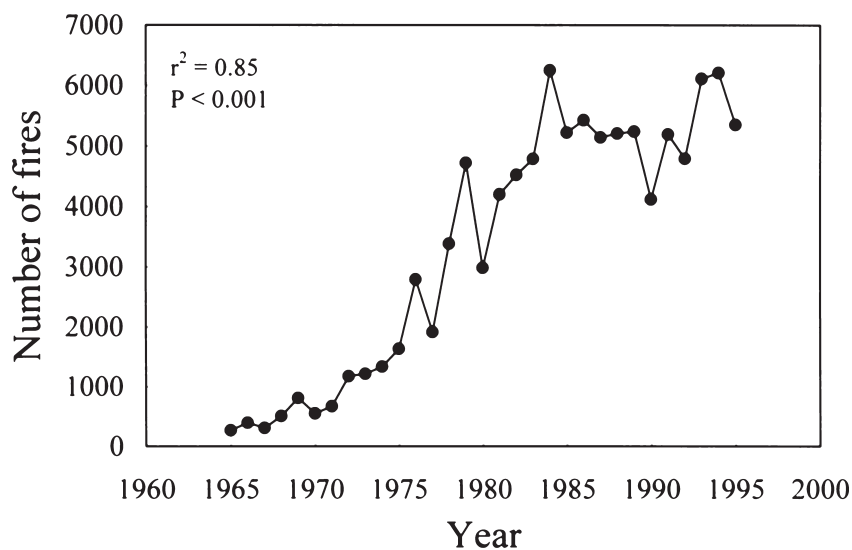


Fig. 3: Annual fire frequency in Chile for the period 1965-1994 (data from CONAF 1995).

Frecuencia anual de incendios en Chile para el período 1965-1994 (datos de CONAF 1995).

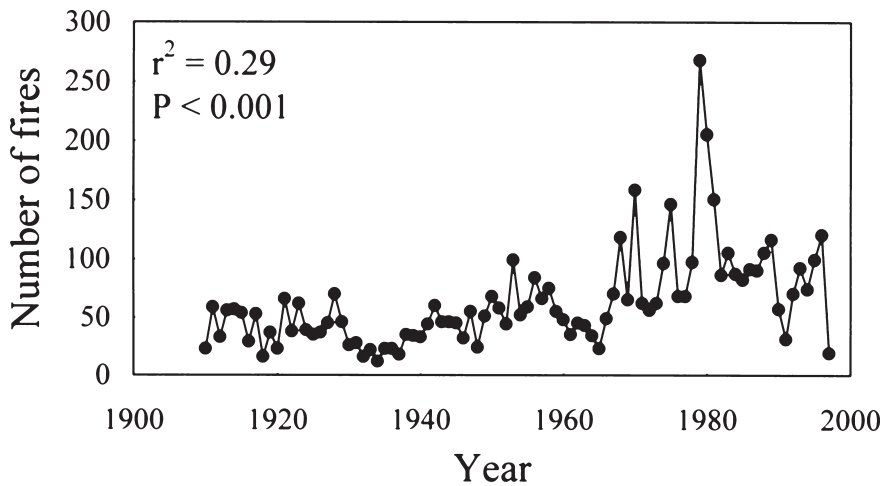


Fig. 4: Annual fire frequency of southern and central California for the period 1910-1997 (data from Keeley et al. 1999).

Frecuencia anual de incendios en el centro y sur de California en el período 1910-1997 (datos tomados de Keeley et al. 1999).

fire frequency closely follows the accelerate population growth produced in both Mediterranean regions over the same period (Palmer 1993).

Although fire frequency has increased in both regions, there is no evidence that the total area burned has increased over the same period in Chile (Fig. 5) and in California (Fig. 6). Reasons for the lack of correlation between fire frequency and surface of burned area are many and complex, but the obvious one may be that average fire size has declined with time due to

effective fire suppression (Keeley & Keeley 1986). Furthermore, the increased fragmentation of wild habitats that has accompanied accelerated population growth and development (Lepart & Debussche 1992) also reduce surface of wild areas that can be potentially burned. In Chile and California, Mediterranean landscapes have been altered by replacing vast stretches of contiguous wild ligneous vegetation for patches of vegetation dispersed in a mosaic interspersed with less flammable agricultural, weedy herbaceous

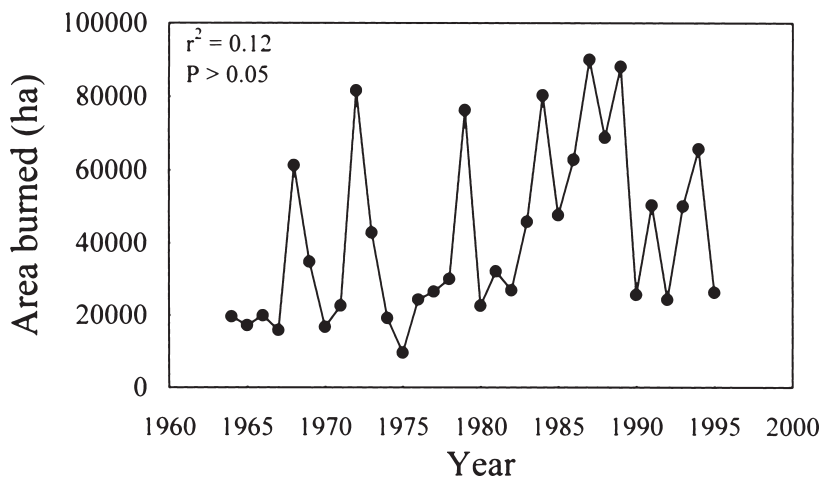


Fig. 5: Annual area burned in Chile for the period 1965-1994 (data from CONAF 1995).

Área anual quemada en Chile en el período 1965-1994 (datos de CONAF 1995).

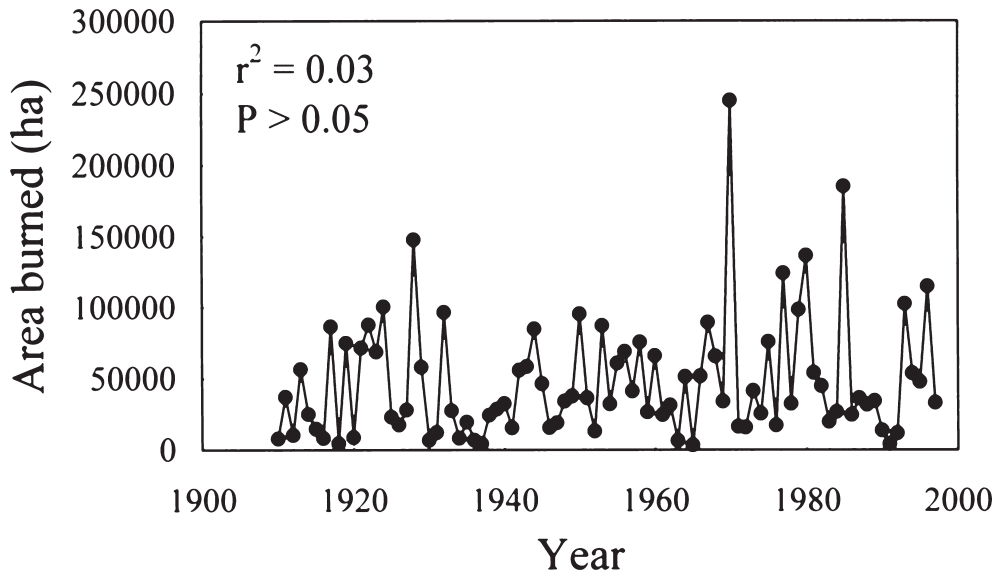


Fig. 6: Annual area burned in southern and central California for the period 1910-1997 (data from Keeley et al. 1999).

Área anual quemada en el centro y sur de California en el período 1910-1997 (datos tomados de Keeley et al. 1999).

communities and suburban vegetation, as well as non-flammable urban developments. Therefore, if the total area burned has remained the same then it is likely that the effective fire suppression, particularly near urban centers, and the heterogeneity in burning of the mosaics generated from the landscape fragmentation has led to differences in the fire return interval. For instance, in areas near urban centers a low return interval of fire may be expected due to less flammability of developments and effective fire suppression while a high return interval may be expected in other areas.

The net effect would appear to largely offset increased fire incidence and thus it would appear that despite increased fire incidence there has been no net impact on fire regime. However, this notion needs to be tempered by recognition that while burned area may, broadly speaking, be roughly the same over time, the surface extent of natural vegetation has declined. As a consequence, for any given parcel of natural vegetation, fire frequency has likely increased in recent decades. As a consequence, dry plant fuel built-up has likely declined, further reducing flammability of stands, thus contributing to a reduction in fire spread and ultimate fire size.

Vegetation response to fires in Chile and California

The marked similarity in vegetation structure and function between the Mediterranean-climate regions of Chile and California has been well described (Mooney & Parsons 1973, Parsons & Moldenke 1975, Parsons 1976, Mooney 1977). This applies at the landscape level, where resemblance exists between sclerophyllous shrublands and woodlands of central Chile and California (Mooney et al. 1970), besides similar vegetation patterns of polar-versus equator-facing aspects (Armesto & Martínez 1978). However, differences in the importance of wildfires as an evolutionary force for plant formations may have resulted in different post-fire regeneration strategies in the chaparral and the matorral.

Post-fire plant regeneration responses are summarized in Table 3. Comparison between both Mediterranean regions has been focused on chaparral and matorral plant formations and not on the whole sclerophyllous Mediterranean-type vegetation. Fire regimes in both regions essentially preclude epicormic sprouting. Stand structure and fuel loads may generate catastrophic stand-replacing fires,

TABLE 3

Post-fire regeneration responses and their relative importance in Californian chaparral and Chilean matorral (++++, frequent response shown by plants; ++, less frequent response; +/- uncommon response; -, not found response)

Respuestas de regeneración post-fuego y su importancia relativa en el chaparral californiano y el matorral chileno (++++, respuesta frecuente; ++, respuesta menos frecuente; +/- respuesta poco común; -, respuesta no detectada)

Response	Chaparral	Matorral
Resprouting from epicormic stem buds	-	-
Resprouting from roots or the root crown	++++	++++
Resprouting from lignotuber	++++	++
Resprouting from deeply buried bulbs or corms	++	+++
Fire-stimulated flowering	++	++?
Release of seeds from serotinous cones or fruits	+/-	-
Germination of dormant soil-seed banks stimulated by heat shock	++++	+
Germination of dormant soil-seed banks stimulated by chemicals from smoke or charred wood	++++	-?

leaving scarce aboveground living tissues. This contrast with woodland communities, where thick bark and self-pruning of hardwood trees, such as *Quercus agrifolia* in California and *Cryptocarya alba* in Chile, make epicormic sprouting a viable option.

Basal resprouting is common in the woody flora of both regions. Indeed, this is the primary mechanism responsible for persistence of many species in the face of frequent fires. In other words, in both regions a large proportion of the dominant woody flora fail to recruit seedlings immediately after fire and would be locally extinct from the site if not for vegetative regeneration. While resprouting is clearly adaptive in this context, it is a matter of some debate whether or not resprouting was initially selected for as a response to fire. Deposition of adventitious buds in the root crowns of woody plants is a nearly ubiquitous trait in dicotyledonous plants (Wells 1969). Although wildfires are an important feature of many ecosystems worldwide and have been present since the early evolution of angiosperms, there are other disturbance factors that could select for this trait, such as extended drought and herbivory.

Chilean matorral differs significantly from Californian chaparral in that all woody species can resprout after fire (Parsons 1976, Mooney 1977, Araya & Ávila 1981, Montenegro et al. 1983), while a substantial proportion of the Californian chaparral shrub species fail to resprout, even after low intensity fires (Wells 1969). These non-sprouters or obligate seeders recruit massive seedling populations after fire

and are considered highly specialized “fire-dependent” species (Keeley 1986).

Another common fire adaptation is the presence of swollen “basal burls” or lignotubers, which are structures, composed of many adventitious buds from which resprouts may arise. Such structures are produced by a number of widely distributed shrub species in both the Californian chaparral and the Chilean matorral. Storage of carbohydrates is an important role for such structures, and there is strong experimental evidence showing that seasonal depletion of carbohydrates may strongly affect regenerative power from lignotubers (Rundel et al. 1987). For example, it has been shown that the starch stored in lignotubers of *Cryptocarya alba*, a tree from the central zone of Chile, is used as an effective energy source for the built-up of a new canopy after the fire (Gómez 2003). The starch content in lignotubers of burned trees decreases 70 % during the first month of regeneration after fire and it does not recover until the next plant-growth season. However, only a small percentage of woody plants found in the Mediterranean climate-type ecosystems has lignotubers. These structures are ontogenetic features that are programmed to be developed in the early seedling growth (Wells 1969, Montenegro et al. 1983). This contrast with lignotuber development detected in most non-Mediterranean-climate species, where the basal swelling is a wound response to strong damage in aboveground stems (Keeley 1981).

Geophytes are a diverse and abundant component of all Mediterranean climate-type

regions (Dafni et al. 1981, Rundel 1996). In some respects their life cycle pre-adapts them to fires, since their seasonal cycle involves a dormancy period where aboveground tissues die back. The dormancy period of these plants coincides with the fire season of Mediterranean climate-type regions, and thus geophytes are well buffered against fires, as it seems likely that the deeply buried corms and bulbs are not negatively affected by fire. Furthermore, such species positively respond to fire by virtue of having much greater frequency of flowering (Stone 1951, Rundel 1981, Le Maitre & Brown 1992), stimulated perhaps by enhanced nutrients and light availability after fire. One very extreme example of fire-following flowering is the geophyte *Cyrtanthus ventricosus*, which flowers immediately (and only) after fire, being triggered by smoke (Keeley 1993). Chile and California are remarkably similar in the proportion of their flora comprised of geophytes, 5.4 % in both regions (Rundel 1996).

Species that accumulate seed banks between fires and produce a pulse of seedling recruitment in the first growing season after fire are common in Mediterranean-climate regions (Keeley 1994). However, Chile greatly differs from the other four regions in this respect, including California. Canopy storage of quiescent seeds in serotinous cones or fruits, which is well developed in South Africa and Australia, and present in California and the Mediterranean Basin, is unknown in Chile. Deeply dormant seeds stored in the soil are common and widespread in the other four regions, but only weakly developed in Chile. One species *Retanilla trinervia* (*Trevoa trinervis*), does commonly establish seedlings immediately after fire (Keeley & Johnson 1977), although the degree to which recruitment is disturbance or fire dependent is not known. "Fire-endemic" annuals common in chaparral are rare in the Chilean matorral (Keeley & Johnson 1977, Ávila et al. 1981). While fire-stimulated germination is common and widespread in the Californian chaparral, it is relatively rare in the Chilean matorral (Muñoz & Fuentes 1989, Keeley 1994). Based on seed coat characteristics and affinities, the Chilean shrub *Retanilla trinervia* (Rhamnaceae) is most likely stimulated to germinate by heat shock, as it is the case with all fire-stimulated chaparral species of *Ceanothus* and South African fynbos species of *Phyllic*, both of which are Rhamnaceae (JE Keeley personal communication).

Germination triggered by chemicals from charred wood or smoke is widespread in Californian chaparral, South African fynbos

and Australian kwongan, heath and other associations (de Lange & Boucher 1990, Brown 1993, Keeley 1994, Dixon et al. 1995, Keeley & Fotheringham 1997). It is clearly the most specialized cue tying germination to post-fire conditions. To date, this mechanism has not been reported for the Chilean flora. Based on the relatively scarce flora that recruit from seed banks after fire, it seems unlikely that this response is widespread in the Chilean matorral (Montenegro et al. 2002).

Vegetation resilience and dependence on fire in Chile and California

Models of community-level response to disturbance vary from situations where vegetation is totally replaced by temporary successional species, which colonize from outside the system, to communities where immediate post-disturbance regeneration is from the original *in situ* vegetation. Hanes (1971) termed this latter model "auto-successional," to describe post-fire Californian chaparral where the pre-fire flora is fully represented in the immediate post-fire flora. Nonetheless, fire does generate major structural and floristic changes in the chaparral community. In particular, the dominant shrubland communities are typically replaced by a short-lived herbaceous or sub-ligneous vegetation. The woody flora itself structurally changes, in that shrubs are replaced by either seedlings or herbaceous resprouts from basal lignotubers or roots. Evidence suggests that fires have been a natural part of the Californian Mediterranean climate-type ecosystems prior to anthropogenic influences, but the Chilean matorral appears to have had little evolutionary exposure to fires. As a consequence, we see that a substantial portion of the Californian flora is fire-dependent, and because of specific chemical germination cues requires the disturbance of fire to complete a life cycle. Such is not the case in the Chilean matorral, as all species appear to have some significant capacity for regeneration in the absence of fire, and thus represent a very different successional model than chaparral (Armesto & Pickett 1985).

The present anthropogenic impact on these regions appears to be one of increasing fire frequency (Fig. 1 and 2). The impact of fires on vegetation structure is, of course, a function of the perturbation frequency and intensity. Therefore, the impact of more frequent fires on the Californian chaparral is a function of whether or not repeated fires occur frequently enough to prevent the non-sprouting shrub

element from establishing a seed bank sufficient to regenerate the population. In Chile, this is apparently not a problem, though as with chaparral, high fire frequency may reduce survivorship of resprouting species and over time this may reduce plant population sizes. In Chile, there is also the confounding effect of additional pressures on the vegetation in the form of intensive browsing by domestic goats and wood gathering for charcoal production, two not important perturbations in the Californian chaparral. A consequence of these anthropogenic impacts in both Mediterranean regions is that areas in close proximity to urban developments often exhibit marked declines in the woody component of the flora and an increase in non-native annual grasses and forbs. Proyecto Fia CO1-1-G-002.

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