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REVIEW ARTICLE

Fire regimen and spread of plants naturalized in central Chile

Régimen de incendios y expansión de plantas naturalizadas en Chile central

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ABSTRACT

Setting fires is an old practice of land management in the Mediterranean region of central Chile. Fire in the region is currently of predominantly human origin and previously published material suggests that the scheduling of these activities is associated with the spread of naturalized exotic species. Research into the effects of fire on both native and exotic Mediterranean vegetation in central Chile has increased notably over recent years. The objective of our review is to highlight new knowledge in this area of research from the last 30 years and to contribute to systematization and an explicit conceptual model which takes into account the effect of a fire regimen on the spread of exotic plants and the mechanisms involved. We begin with analyses of the fire regimen which is currently observed in one Region of central Chile and a subsequent exploration of the literature to identify the attributes mainly of the germination of seeds which are sensitive to fire and which apply to the exotic species that are abundantly naturalized in central Chile. According to the studies consulted, diverse mechanisms have been described which involve the effect of fire on the spread of exotic plants in central Chile. Life-history traits, tolerance, facilitation, and positive feedback between exotic plants and fire frequency have been mechanisms reported in the literature. Finally, we propose a conceptual model which represents dispersal assisted by humans of exotic species and the spread of species naturalized by the effect of fire regimens, which helps explain the composition and structure of the matorral of central Chile in an early successional state.

Key words: central Chile, exotic plant, fire, germination, naturalized plant.

RESUMEN

Los incendios son una antigua práctica del uso del suelo en la región mediterránea de Chile central. Actualmente en esta región, los incendios son principalmente de origen humano y los antecedentes publicados permiten sugerir que su régimen está asociado a la expansión de especies exóticas naturalizadas. Las investigaciones sobre el efecto de los incendios sobre la vegetación mediterránea tanto nativa como exótica en Chile central ha incrementado notablemente durante los últimos años. El objetivo de nuestra revisión fue resaltar los nuevos conocimientos en esta área de la investigación durante los últimos 30 años y contribuir a una sistematización y a un modelo conceptual explícito que incorpore los efectos del régimen de incendios en la expansión de plantas exóticas y en los mecanismos involucrados. Para ello se describe el régimen de incendios que actualmente se presenta en una región de Chile central y se realiza una exploración de la literatura para conocer principalmente los atributos de la germinación de las semillas sensibles a incendio que se encuentran en especies exóticas que están naturalizadas abundantemente en Chile central. De acuerdo a los estudios abordados, se han descrito diversos mecanismos que involucran el efecto de los incendios sobre la expansión de plantas exóticas en Chile central. Rasgos de historia de vida, tolerancia, facilitación y retroalimentación positiva entre plantas exóticas y frecuencia de incendios son los mecanismos que han sido documentados en la literatura. Finalmente, proponemos un modelo conceptual que representa la dispersión de especies exóticas asistida por los seres humanos y la expansión de especies naturalizadas por el efecto de los regímenes de incendios, que ayuda a explicar la composición y estructura del matorral de Chile central en un estado inicial de la sucesión.

Palabras clave: Chile central, incendio, germinación, plantas exóticas, plantas naturalizadas.

INTRODUCTION

In Chile, the number of naturalized exotic species has increased greatly over the last century (Matthei 1995, Castro et al. 2005), currently reaching approximately 700 species (Matthei 1995, Figueroa et al. 2004b). More than 65 % of naturalized species in continental Chile are propagated throughout the region of central Chile (Teillier et al. 2010), where the area below 2000 masl. has a Mediterranean climate (Di Castri & Hajek 1976). In terms of its biogeographic origin, approximately 70 % of the naturalized plants are of Eurasian origin, specifically from the Mediterranean Basin and North Africa (Arroyo et al. 2000).

The flora of central Chile diversified and spread through an environment which was not naturally exposed to periodic fire (Villagrán et al. 1996). Nevertheless, over the last centuries the vegetation in the region has been subjected to a human-imposed fire regimen with the aim of clearing land for multiple uses (Lara et al. 2003), a practice that has not been evaluated and analyzed in terms of all its ecological consequences (Fernández et al. 2010).

Fire provides an opportunity for colonization and persistence of some plants, as it frees up spaces and nutrients where invasive species can successfully establish themselves (Richardson et al. 1990, Hobbs 2000, D'Antonio et al. 2001). Consequently, it has been suggested that the common practice of the use of fire in central Chile may be a cause of the spread of naturalized plants with colonizing attributes (Pauchard et al. 2008, Figueroa et al. 2009). For example, fire may permit the spread of species with morpho-physiological traits, such as seeds which are sensitive to heat, smoke, chemical compounds found in post-fire soils or it may facilitate the spread of species with ecological traits that are susceptible to changes in the abundance of species affected by the fire (Brose et al. 1999, Sax 2002, Pauchard et al. 2008, Figueroa et al. 2009).

Considering that fire, regardless of its origin, is a frequent event both in the Mediterranean Basin and in central Chile; several authors have suggested that in the latter region fire may generate opportunities for the spread of plants, particularly Eurasian plants, because they come from environments where fire occurs naturally as part of the Mediterranean climate (Richardson et al. 1990, Trabaud 1991, Keeley et al. 2003, Castro et al. 2005).

In different plant communities in Mediterranean climates (Southeast Australia, South Africa, the Mediterranean Basin, and California) fire regimes have a long history as part of biota diversification, which may have led to the selection of adaptive attributes in plants for post-fire regeneration (Cody & Mooney 1978). For example, resprouting of roots, lignotubers, stem buds and bulbs after combustion of the aerial part of the plant, flowering (anthesis), seed spread and germination by exposure to smoke and/or by exposure to high temperatures for brief periods of time (thermal shock), are some of these attributes that have been described in Mediterranean regions which allow plants to regenerate after part or all of the vegetation has been destroyed by fire (Vázquez-Yanes & Orozco-Segovia 1998, Montenegro et al. 2002).

In the specific case of the Mediterranean Basin, in the maquis vegetation in the south of France fire promotes recursive colonization of exotic therophytes (Trabaud 1991) by releasing resources which are used by short-life species. On the other side of the world, in the fynbos in South Africa, highly intense fires, which are frequent among native plant species and allow self-perpetuation of serotinous species, have been proved to favor invasive behavior in exotic woody plants of European origin. Exotic plants of European origin in the Cape find a fire perturbation regimen which is similar to that of their original ecosystem (Jones 1963, Kruger & Bigalke 1984, Richardson et al. 1994). Furthermore, on the American continent, fire in the Californian chaparral inhibits reproduction of naturalized exotic species, even when the source of the propagules of the exotic species is close to fire (Keeley et al. 2003). Though the exotic species in the chaparral are abundant during the first year after a fire, affected sites are subsequently found to be free of naturalized species. The high intensity fires in the chaparral destroy a high proportion of organic material and most of the seeds of exotic species that are stored in the soil. However, these fires promote regeneration of native woody shrubs with serotinous characteristics. In the chaparral the sites under the closed canopy of the native shrubs do not provide favorable conditions for exotic species to grow, but they are favorable for the native species which grow in this shade (Keeley et al. 2003). Towards the southern end of the American continent, in central Chile, fire may facilitate colonization by both some native grasses and mainly exotic annual grasses with high growth rates (Sax 2002, Gómez-González et al. 2011). In this region high intensity fire may even stimulate germination of some colonizing native woody species (Muñoz & Fuentes 1989, Gómez- González et al. 2008) and its action may even generate conditions for the perpetuation of invasive exotic woody species (Pauchard et al. 2008).

In summary, according to the available literature, in communities in regions with a Mediterranean climate, including central Chile, fire may facilitate the establishment of exotic plants with colonizing traits and their spread into new areas, at least in the initial stage of the succession of the plant community. However, later stages in the plant succession are more complex and have diverse results over different Mediterranean-type regions throughout the world (Table 1), a phenomenon that is dependent on the interaction of factors that cause succession in the area (Keeley et al. 1999, Pignatti et al. 2002, Capitanio & Carcaillet 2007, Gómez-González et al. 2011).

With regard to central Chile, over the last 10 years knowledge of the effect of fire on naturalized exotic plants has increased greatly (Holmgren et al. 2000. Montenegro et al. 2002, 2004, Pauchard et al. 2008, Figueroa et al. 2009, Gómez-González & Cavieres 2009, Gómez-González et al. 2011). Nevertheless, there are still improvements to be made in the characterization of the fire regimen in central Chile in order to better understand its role in exotic plant invasion (Figueroa et al. 2009). Similarly, more information is needed on the presence of morpho-physiological traits that are sensitive to fire in naturalized exotic plants in central Chile, information that has been published but is dispersed over different scientific media.

The objective of this review is to contribute to improve the characterization of fire regimens of anthropogenic origin in central Chile through the specific analysis of the Region of Valparaíso, while at the same time contributing to systematize the information available in the literature in relation to the presence of attributes that are sensitive to the effect of fire in naturalized exotic plants in central Chile.

Although there are similar studies in Chile at a national scale (Fernández et al. 2010), there are few studies which focus on the central region of the country (Villaseñor & Sáiz 1993, Sáiz 1993). Many of the characteristics of the fire regimen in the Region of Valparaíso are unique, since in Chile fire mainly depends on human activities, which vary from one Region to the next.

TABLE 1

Fire effect on the spread of exotic plant naturalized in Mediterranean-type regions of the world.

Efecto del fuego sobre la expansión de plantas exóticas naturalizadas en regiones Mediterráneas del planeta.

Region	Vegetation	Fire effect	References
Australia's South West	Sclerophyllous shrub	Exotic perennial grasses are favored	Milberg & Lamont (1995)
Cape of South Africa	Fynbos	Woody exotic are favored	Richardson et al. (1994)
Basin of the Mediterranean	Maqui	Exotic annuals are favored	Trabaud (1991)
California	Chaparral	Exotic recruitment is inhibited	Keeley et al. (2003)
Central Chile	Sclerophyllous forest	Annuals are favored (mainly exotics)	Figueroa et al. (2009), Gómez-González et al. (2011)

CAUSES OF FIRE IN THE VEGETATION OF THE REGION OF VALPARAÍSO

Practically all fires in the Valparaíso Region are currently caused by human activity (Fig. 1) (CONAF 2008), as are fires throughout Chile (Montenegro et al. 2004), unlike other Mediterranean-type ecosystems, where a significant percentage of fires occur naturally (e.g., storms and electric discharges from the atmosphere; Cody & Mooney 1978). For example, in the Region of Valparaíso, in central Chile, vehicular transport is the main cause of fires, causing 44 % of the fires between 1997 and 2007 (Fig. 1). Fires along road sides and highways are mainly caused by motorists who throw lit cigarettes and matches from vehicles in motion. Recreational activities cover 27 % of fires, which include, for example, campfires which are not carefully extinguished by users of established camping sites and other informal sites. A significant 18 % of fires are intentional, mainly involving arsonists. All other causes represent a minor contribution of 2 % (Fig. 1).

In the southern-central region of Chile the intentional use of fire has a long history. There is much evidence of the use of fire by Amerindian cultures, though with limited effects over time and also possibly over a limited space (Moreno & León 2003, Abarzúa & Moreno 2008). Subsequently, the colonial years saw the beginning of farming practices in the European tradition, which considered fire as a technique for clearing land to prepare the soil for planting (Aronson et al. 1998, Sanhueza 2001). In the 19th century, fire was used predominantly to free up sites for cattle farming (Sanhueza 2001) and during the 20th century it was used to establish plantations of exotic trees (Lara et al. 2003). Agricultural, cattle farming, and forestry activities currently contribute only 11 % of fires in Chile (INE 2009) and only 2 % of fires in the Region of Valparaíso (Fig. 1).

With regard to naturally occurring fires, in south-central Chile occasional fires are seen which are caused by volcanic activity (Fuentes & Espinoza 1986) and countrywide statistics indicate that naturally occurring fires are practically non-existent, as only 0.1 % of all fires occurring between 1987 and 2007 were considered natural (Fernández el at. 2010). This low frequency of natural fires in central Chile considered within an evolutionary temporal scale means that it is highly unlikely that such fires could have had a determinant role in the selection of adaptive traits for post-fire regeneration. However, Muñoz & Fuentes suggested that fire caused by volcanoes may have represented a selective pressure on woody plants in central Chile, though the arguments and evidences are weakened by the absence of continuous volcanic records in an evolutionary temporal scale.

The evidence shows that the current intentional fire regime in central Chile is a relatively recent event and plants that have proliferated and spread are those with life history traits that are appropriate for recurrence. In this context, naturalized plants, mostly of European origin, have come to the region and spread rapidly in areas with recurrent perturbation by fire and agricultural activity (Matthei 1995, Castro et al. 2005).

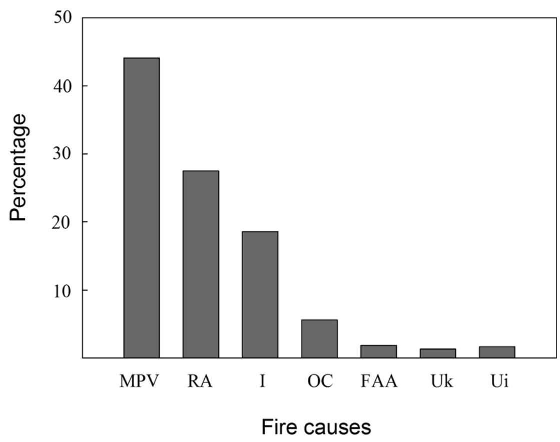

Fig. 1: Causes of fires between 1997 and 2007 in the Region of Valparaíso, central Chile. MPV = movement of people and vehicles, RA = recreational activities, I = intentional, OC = other causes, FAA = forestry and agriculture activities, Uk = unknown, Ui = unidentified.

Causas de incendios entre 1997 y 2007 en la región de Valparaíso, Chile central. RA = actividades recreativas, I = intencional, OC = otras causas, FAA = actividades forestales y agrícolas, Uk = desconocida, Ui = no identificada.

FIRE REGIMEN IN CENTRAL CHILE

Regardless of its origin, the incidence of fire in a given area presents regularities that are defined by a fire regimen (Morgan et al. 2001, Chuvieco et al. 2008). This regimen exhibits traits which are defined in a similar way to the attributes of several different types of perturbation, for example, tornadoes, wind storms, landslides, avalanches, volcanic activity, pests, and others (White & Pickett 1985). One of these traits is frequency, that is, the average time between incidents occurring in a given area, also known as return interval (Gurevitch et al. 2002). Another trait is fire intensity, which is calculated as the amount of destruction of organic material caused by the fire or, analogously, the amount of energy produced by the combustion of organic material, and is determined by the composition of the vegetation (e.g., grasses, shrubs, trees), the characteristics of the soil (e.g., water content, porosity, stored chemical compounds), and the atmospheric conditions (e.g., humidity, wind). Other traits are related to the size of the affected area and the season of the year in which incidence is most frequent (D'Antonio & Vitousek 1992).

Below is a description and analysis of the characteristics of the fire regimen in the Region of Valparaíso over the course of a decade, followed by consideration of some of its possible consequences on the spread of naturalized plants. Over the last decade the Region of Valparaíso has occupied the third place in terms of the highest number of fires in Chile, representing approximately 15 % of the total (INE 2009). The regions that are most affected by fires are Bio-Bio and Araucanía, which represent 32 and 22 %, respectively, of all fire incidents in Chile (INE 2009). The data on fires for the Valparaíso Region were obtained from a CONAF (2008) database, which was begun in 1997 in Valparaíso.

Fire frequency

In the Region of Valparaíso, over the decade of 1997 to 2007, the average fire frequency was 915 events per year in an area of 1602856.2 ha (approximately one fire per 1752 ha per year). This frequency varies between 630 fires in 1997 and 1334 fires in 2002 (Fig. 2), which represent

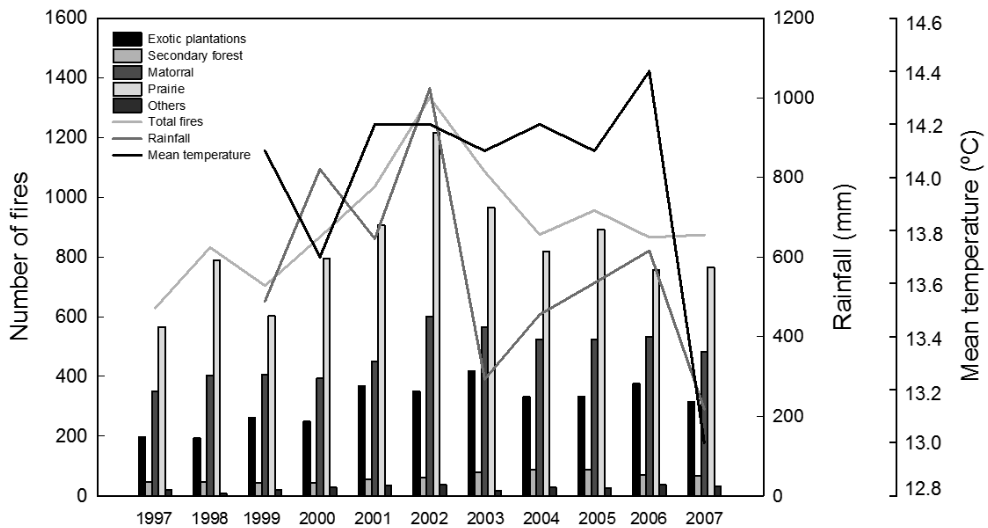

Fig. 2: Number of fires in the 1997 to 2007 period in the Region of Valparaíso, central Chile. Total number of fires, number of fires by land use, accumulated rain during the year, and average annual temperature are shown. The sum of the fires per plant community is greater than the total recorded number of fires because a single event can affect more than one plant community.

Número de incendios entre 1997 y 2007 en la región de Valparaíso, Chile central. Se señala el número total de incendios, incendios registrados por uso de suelo, precipitaciones acumuladas durante el año y la temperatura promedio anual. La suma de los incendios por comunidad vegetal es mayor al total de eventos registrados porque un evento de fuego puede afectar a más de una comunidad de planta.

12 % and 21 %, respectively, of all fires in Chile (Fernández et al. 2010). The distribution pattern of the number of fires in different types of vegetation is significantly different (Kruskal-Wallis, H = 51; 4 Gl; P < 0.001). Grasslands (cattle-rearing or farming pastures) are the type of vegetation which experienced the highest frequency of fires in the Region, followed by matorral and exotic tree plantations. The grasslands were affected by approximately 90 % of all fires registered annually (Fig. 2). Matorral also has a high frequency of fires, as it is affected by approximately 52 % of the annual fires in the Region (Fig. 2). Plantations of exotic trees, mainly *Eucalyptus* spp., are affected by 34 % of annual fires, and secondary sclerophyllous forests by only 7 %, approximately (Fig. 2). The sum of these percentages is greater than 100 %, since an important number of fires affected two or more types of vegetation (Fig. 2).

Thus, as stated above, plants which regenerate in an accelerated manner after a fire must have adequate traits from their life history in order to respond to the frequency of a fire regimen (Table 1) which frees up sites and resources during an expected return interval. For example, there is evidence from garden experiments (Contreras 2009) that growth of aerial tissue of the naturalized *Bromus scoparius* (L) and the native *Bromus berteroanus* (Colla) grasses increases biomass in soils recently affected by fire in central Chile (Fig. 3). The positive response of both annual grasses in soils recently subjected to a fire may indicate that the fire regimen can modify soil quality (e.g., nutrients, oxygenation, water retention, and pH). It is known, for example, that fire can release nutrients into the soil (such as Ca, K and Mg) which come from the ash of the burnt vegetation (Chandler et al. 1983, Kruger 1983). These nutrients can be used efficiently by fast growth species which are established in the grasslands and matorral of central Chile. Hence, if fire frequency is very low, the quality of the soil would diminish, affecting the regeneration of species requiring these nutrients. In line with this, both *Bromus* grasses are highly abundant in areas recently affected by fire and in fertilized farming lands (Matthei 1995), although the effect of light after fire on the establishment of shade-intolerant grasses, when the sclerophyllous woody matorral canopy in central Chile is absent, should be considered (Fuentes et al. 1986).

In summary, the Region of Valparaíso is subject to a high annual frequency of fires of human origin, a level which has remained rather constant at least over the last 30 years (Sáiz 1993). Approximately 90 % of these fires affect grassland communities and 50 % affect matorral communities. Fires produced in forest vegetation are low in frequency; they include plantations of exotic tree (mainly *Eucalyptus* spp. and *Pinus* spp.) which are affected by no more than 35 % of all fires recorded. This is most likely due to the fire prevention measures created and applied in these areas by forestry companies.

Fire size

Over the decade from 1997 to 2007, in the Valparaíso Region an average of 6000 ha were burnt per year (CONAF 2008). This area corresponds to only 0.3 % of the total surface area of the Region. However, inter-annual

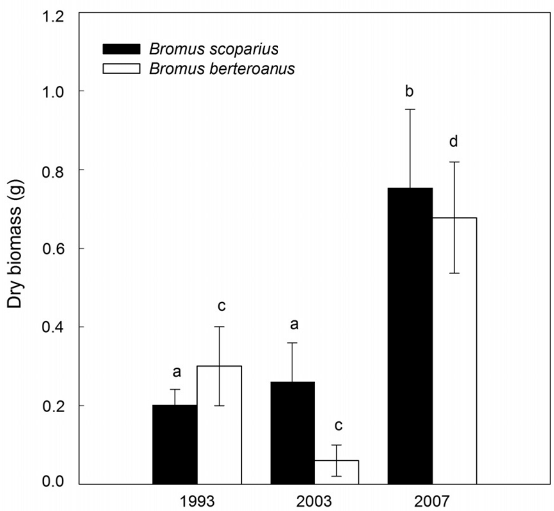

Fig. 3: Average dry aerial biomass of *Bromus scoparius* and *B. berteroanus* (in 2008), grown in soils subjected to fires during 1993, 2003, and 2007. Biomass is significantly different between years in both plant species (Kruskal-Wallis, P < 0.01). The bars indicate ± 1 SE.

Biomasa seca del tejido aéreo de *Bromus scoparius* y *B. berteroanus* producidos en ensayos de crecimiento (en 2008) en suelos que fueron sometidos a fuego durante 1993, 2003 y 2007. La biomasa en ambas especies de plantas es significativamente diferente entre años (Kruskal-Wallis, P < 0.01). Las barras indican ± 1 EE.

variation is very high. During the 2004 season approximately 15500 ha were burnt (1 % of the total surface area of the Region), while in 2001 only 2200 ha were burnt. Of the 10059 fires recorded over the 10 seasons, 92.6 % were small in size, less than 5 ha (Fig. 4), 6.8 % were between 5 and 200 ha in size, and only 0.6 % of the fires were greater than 200 ha in size. The latter are classified by CONAF as high risk and they occurred at a very low frequency between 1997 and 2007. For example, the highest frequency in fires over 200 ha was recorded during 2004, when there were nine events with these characteristics, while the lowest frequency for fires of this size was recorded in 1999 and 2006, when only one such event was seen during each year (CONAF 2008).

With respect to the distribution of the burnt surface over the different soil uses, the analysis show that the incinerated surface of native and exotic forests was more than twice that expected for forests that are distributed randomly over the Region's soil uses (Cochran's Linear Trend = 4343, d.f. = 2, P < 0.001). During the analyzed decade 18 % of the total burnt area corresponded to native forests and 14 % to exotic plantations, although both types of forests combined cover only 11 % of the Region's total area.

In summary, over the 1997 to 2007 period the Valparaíso Region was subject to mainly small fires (< 5 ha), and fires classified as high risk by CONAF (> 200 ha) were very low in number. Native and exotic forests are the most threatened vegetations by fires in the Region of study.

Fire intensity

Due to the widespread opinion that directly recording the temperature of a fire is costly, and alternative indirect colorimetric methods based on estimates of origin of ash are available at low cost (Chandler et al. 1983), official statistics for the Region of Valparaíso from CONAF (2008) do not directly indicate fire intensity or the amount of energy released per unit of material burnt. However, intensity can be estimated indirectly from the type of vegetation that is burnt and the rate of spread of the fire, which is obtained by analyzing the CONAF database (2008). Thus, we can state that for the 1997 to 2007 period, in the Valparaíso Region approximately 67 % of the total surface area affected by fire was covered by prairies and matorral (Fig. 5). Similarly, 28 % of the total burnt surface area corresponds to exotic plantations and secondary sclerophyllous

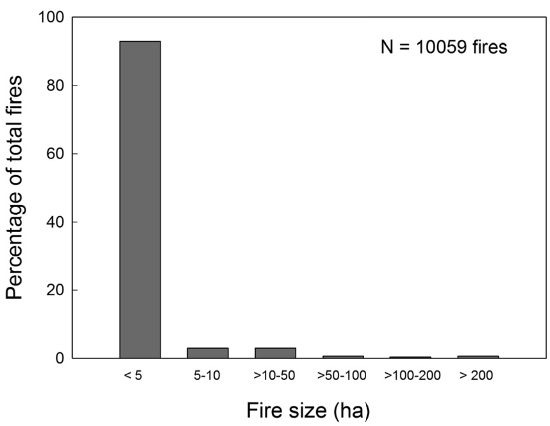

Fig. 4: Percentage of total fires by fire sizes (ha) recorded for 1997 to 2007 in the Region of Valparaíso, central Chile.

Porcentaje del total de incendios para cada tamaño de incendio (ha) registrados entre 1997 y 2007 en la región de Valparaíso, Chile central.

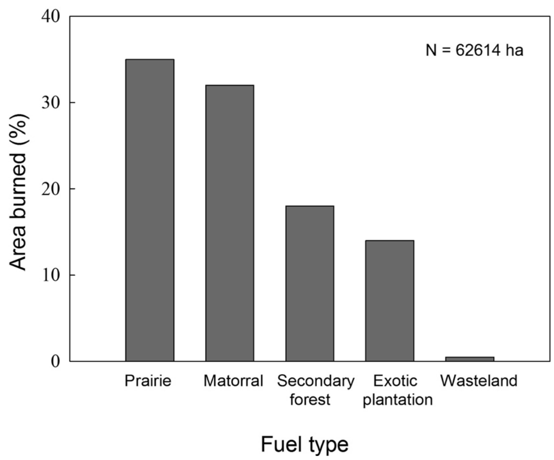

Fig. 5: Percent contribution of the five fuel types in the fires recorded for 1997 to 2007 in the Region of Valparaíso, central Chile.

Contribución porcentual de los cinco tipos de combustibles en los incendios registrados entre 1997 y 2007 en la región de Valparaíso, Chile central.

forests. In addition, when analyzing the fire spread rate from the same database (CONAF 2008), 75 % of the total during 1997 and 2007 in the Region of Valparaíso burnt less than 10 ha per day (Fig. 6). On the other hand, 25 % of the fires burnt more than 10 ha per day, and only 1 % of the fires burnt more than 100 ha per day (Fig. 6). These data show that most fires in the Valparaíso Region are of low or medium size and are probably of low and medium calorific power.

In summary, almost 2/3 of the areas affected by fire are covered by the annual grasses that dominate low density prairies and matorral, presenting lower calorific power than native forests or *Eucaliptus* forests (Brooks et al. 2004). It can also be seen that this surface area is burnt by fires with a low daily spread rate. The analysis shows that the fires in the Valparaíso Region have mostly low spread rates (< 10 ha per day) and low and medium intensity.

In line with this, different studies on the sclerophyllous matorral of central Chile have shown that a significant proportion of the seed bank in the soil can remain viable after low and medium intensity fires, and also these fires can eventually stimulate seed germination in some species (Pauchard et al. 2008, Figueroa et al. 2009, Gómez-González & Cavieres 2009), which may explain the greater importance of seed bank survival in relation to seed dispersal for establishment of plants naturalized in burned areas (Gómez-González et al. 2011). On the other hand, high intensity fire has negative effects on the viability of this same seed bank (Gómez-González & Cavieres 2009).

Fire season

The CONAF (2008) fire record reveals that over the ten years of this study the surface area affected by fire increases substantially during the dry summer season (Fig. 7). The fire distribution pattern over the 1997 to 2007 period was significantly different for the different seasons of the year (Kruskal-Wallis, H = 36; 3 Gl; P < 0,001). In summer fires were recorded for each of the ten years, while in spring there were several years in which no fires were recorded (Fig. 7). Similarly, approximately 90 % of the surface area is burnt during summer, except during 1997 and 1999, when the fall and spring seasons contributed > 25 % of the year's fires (Fig. 7). The season of the fires has a direct effect on the dynamics and composition of the plant communities (Costa et al. 1992, Morgan et al. 2001). According to the dynamics of the easily germinated seed bank in the matorral of central Chile, which is mainly composed of naturalized exotic grasses (Figueroa et al. 2004a, 2004b), fires that may affect a higher percentage of the seeds stored in the soil are those which occur during summer, because during this season a higher

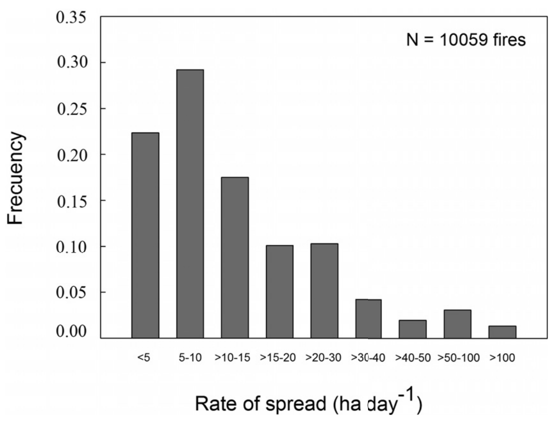

Fig. 6: Frequency distribution of fire spread rate (ha per day) recorded for 1997 to 2007 in the Region of Valparaíso, central Chile.

Distribución de frecuencias de la tasa de expansión de incendios (ha por día) registrados entre 1997 y 2007 en la región de Valparaíso, Chile central.

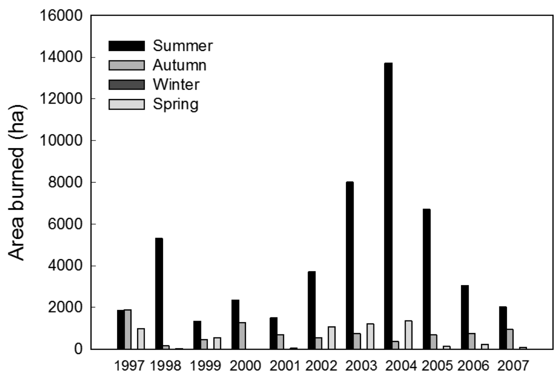

Fig. 7: Total area burned each year recorded for 1997 to 2007 in the Region of Valparaíso, central Chile.

Superficie total quemada en cada estación del año entre 1997 y 2007 en la región de Valparaíso, Chile central.

proportion of viable seeds is accumulated in the soil (Figueroa et al. 2004a).

Also, during summer and fall the amount of dead plant biomass on the soil surface is higher than at other times of the year, especially that which comes from the annual and perennial grasses that have lost aerial tissue during the season. The soil and vegetation conditions may determine, in part, the effect of the fires on the regeneration and the dynamics of the vegetation in the area and of the naturalized flora. Although they may eventually destroy a significant proportion of the viable seed bank, fires during summer also clear the surface of the soil of dried plant material and release organic compounds into the soil which were constituents of the tissues of the burnt plants. Both these effects would allow for faster germination of species with seeds that are activated by fire or at least tolerant to its presence (Figueroa et al. 2009), and they may subsequently facilitate the growth of seedlings on the affected surface (Fig. 3).

FIRE-ASSOCIATED SPREADING MECHANISMS IN NATURALIZED PLANTS

Fire-dependent resprouting

Many naturalized species restrict seedling establishment to the immediate postfire and thus have fire-dependent recruitment (Keeley 1998). Fire-dependent recruiters resprout from root masses after the most recent fire, although resprouting is thus not a specific evolutionary response to fire (Bradshaw et al. 2011). Resprouting occurs from dormant buds or lignotubers effectively protected by the soil. Fire frequency can have an impact on the relative dominance of sprouting and nonsprouting species (Parker & Kelly 1989). In California, Australia, the Mediterranean region, South Africa, and central Chile, phanerophytes, geophytes, and perennial grasses can be conspicuous following fire, because they are resprouters and generally obligate resprouters (Parker & Kelly 1989, Armesto et al. 1995, Arianoutsou 1998, Hoffmann et al. 1998). There are evidences that exotic species in central Chile are resprouters, and several after the fire (Table 2), highlighting species as *Cardaria draba* L., *Cirsium arvense* L., *Convolvulus arvensis* L., *Cynodon dactylon* (L.) Pers., *Cytisus scoparius* (L.) Link, *Rumex acetosella* L., *Ulex europaeus* L., and *Sorghum halapensis* (L.) Pers. (Bossard & Rejmanek 1994, Matthei 1995, Klimeš & Klimešová 1999, Bossuyt et al. 2007, Reyes et al. 2009), which are widely naturalized at different land use sites in the region (Teillier et al. 2010).

In general, resprouters have lower rates of seed production than do seeders (Bradshaw et al. 2011). Additionally, species that develop permanent seed banks due to dormancy in their seeds are generally nonresprouting (Baskin & Baskin 1998). Both types of post-fire regeneration (seed bank and resprouting) may be alternative mechanisms in environments subjected to frequent fire regimens (Pickett & McDonnell 1989, Bradshaw et al. 2011).

Fire-associated germination and emergence traits

The literature review suggests that a significant group of naturalized species in central Chile have traits associated directly with fire. Table 2 shows that a large number of species naturalized in central Chile need to have their seeds subjected to warm stratification (e.g., *Agrostemma githago* L., *Anthemis cotula* L., *Avena fatua* L., *Dianthus armeria* L., and others). Although this trait does not constitute direct adaptation to fire, the soil cleared of vegetation by incineration is subjected to higher temperatures during the day than soils under shade. Under these new environmental conditions seeds of plant species that require warm stratification can germinate (Vázquez-Yanes & Orozco-Segovia 1993).

In a plant community analyses in the central matorral of Chile, heat and smoke facilitated the emergence of few common exotic plants (e.g., *Erodium cicutarium* (L.) L'Hér. Ex Aiton, *Erodium moschatum* L., *Vulpia bromoides* (L.) S.F. Gray, and *Poa annua* L., although they represented 28 % of the exotic plant community reported (Figueroa et al. 2009). Other records and published data show a similar or lower representation of fire-associated naturalized plants, but in all cases those are the most abundant species in the community (e.g., *Anthriscus caucalis* M. Bieb., *Avena barbata* Pott ex Link) (Figueroa et al. 2009, Goméz-González et al. 2011, Figueroa & Cavieres unpublished data).

TABLE 2

Exotic species of central Chile with traits associated to regeneration in environments subjected to vegetation fire. WS = Seeds require warm stratification; ESH = Seedling emergency stimulated by heat; ESS = Seedling emergency stimulated by cold smoke; EISH = Seedling emergency inhibited by smoke and heat. GS = Germination stimulated by cold smoke; GHS = Germination stimulated by heat shock; GSF = Growth stimulated by fire; ESF = Establishment stimulated by fire; RRF = Resistant roots to fire; RSH = Resistant seeds to heat shock; RSSH = Resprouting stimulated by smoke and heat shock.

Especies exóticas de Chile central que presentan atributos relacionados a la regeneración en ambientes sometidos a incendios de la vegetación. WS = Las semillas requieren estratificación cálida; ESH = Emergencia de plántulas estimulada por calor; ESS = Emergencia de plántulas estimulada por humo frío; EISH = Emergencia de plántulas inhibida humo y calor; GS = Germinación estimulada por humo frío; GHS = Germinación estimulada por golpe de calor; GSF = Crecimiento estimulado por incendios; ESF = Establecimiento estimulado por incendio; RRF = Raíces resistentes a incendios; RSH = Semillas resistentes al golpe de calor; RSSH = Rebrote estimulado por humo y golpe de calor.

Species	Family	Traits	References
Agrostemma githago	Caryophyllaceae	WS	Baskin & Baskin (1998)
Aira caryophyllea	Poaceae	ESF	Gómez-González et al. (2011)
Anthemis cotula	Asteraceae	WS	Baskin & Baskin (1998)
Anthriscus caucalis	Apiaceae	ESH (137 °C)	Gómez-González & Cavieres (2009)
Anthriscus caucalis	Apiaceae	ESS	Cavieres & Figueroa (unpublished data)
Aphanes arvensis	Rosaceae	EISH	Cavieres & Figueroa (unpublished data)
Avena barbata	Poaceae	ESS	Cavieres & Figueroa (unpublished data)
Avena fatua	Poaceae	WS	Baskin & Baskin (1998)
Avena sterilis	Poaceae	GS (5 m)/GHS (5 m; 80 °C)	Reyes &Trabaud (2009)
Bromus scoparius	Poaceae	GSF	Contreras (2009)
Bromus secalinus	Poaceae	WS	Baskin & Baskin (1998)
Bromus tectorum	Poaceae	WS	Baskin & Baskin (1998)
Bromus tectorum	Poaceae	GHS	Blank & Young (1998)
Bromus tectorum	Poaceae	GSF	Blank et al. (1994)
Capsella bursa-pastoris	Brassicaceae	WS	Baskin & Baskin (1989)
Cardaria draba	Brassicaceae	RRF	CNAP (2000)
Cyperus rotundus	Cyperaceae	WS	Baskin & Baskin (1998)
Cytisus striatus	Fabaceae	GHS (5-10 m; 80 °C) (5-10 m; 110 °C)	Rivas et al. (2006)
Cytisus scoparius	Fabaceae	GHS (10 m; 80 °C) (5 m; 110 °C)	Rivas et al. (2006)
Cirsium vulgare	Asteraceae	ESH (high intensity)	Laterra et al. (2006)
Dactylis glomerata	Poaceae	GHS (20 min)	Pérez-Fernández & Rodríguez-Echeverría (2003)
Dianthus armeria	Caryophyllaceae	WS	Baskin & Baskin (1998)
Erodium cicutarium	Fabaceae	EISH	Figueroa et al. (2009)
Erodium moschatum	Fabaceae	ESH (10 min; 100 °C)	Figueroa et al. (2009)
Galium aparine	Rubiaceae	WS	Baskin & Baskin (1998)
Galium aparine	Rubiaceae	WS	Grime et al. (1981)
Hordeum marinum	Poaceae	ESH (100 °C)	Gómez-González & Cavieres (2009)
Lamium amplexicaule	Lamiaceae	WS	Baskin & Baskin (1981)
Lapsana communis	Asteraceae	WS	Baskin & Baskin (1998)
Lolium multiflorum	Poaceae	WS	Young et al. (1975)

TABLE 2. Continuación

Species	Family	Traits	References
Lofgia gallica	Asteraceae	ESH (35 °C)	Gómez-González & Cavieres (2009)
Onopordum acanthium	Asteraceae	GHS (2 m; 100 °C)	Qaderi & Cavers (2003)
Oryza sativa	Poaceae	WS	Cohn & Hughes (1981)
Poa annua	Poaceae	WS	Standifer & Wilson (1988)
Poa annua	Poaceae	ESS	Figueroa et al. (2009)
Portulaca oleracea	Portulacaceae	WS	Baskin & Baskin (1988)
Raphanus raphanistrum	Brassicaceae	WS	Baskin & Baskin (1998)
Raphanus raphanistrum	Brassicaceae	RSH (500 °C)	Walsh & Newman (2007)
Robinia pseudoacacia	Fabaceae	WS	Masaka & Yamada (2009)
Rumex acetosella	Polygonaceae	WS	Grime et al. (1981)
Rumex crispus	Polygonaceae	WS	Baskin & Baskin (1985)
Sisymbrium officinale	Brassicaceae	WS	Baskin & Baskin (1998)
Stellaria media	Caryophyllaceae	WS	Baskin & Baskin (1998)
Spartium junceum	Fabaceae	GHS (5-10 min; 80-110 °C)/GS (5-15 min)	Hanley (2009) Reyes & Trabaud (2009)
Trifolium pratense	Fabaceae	ESH (137 °C/100 °C)	Gómez-González & Cavieres (2009)
Ulex europaeus	Fabaceae	GHS (110 °C)	Hanley (2009)
Ulex europaeus	Fabaceae	RSSH	Reyes et al. (2009)
Vulpia bromoides	Poaceae	ESH (10 min; 100 °C)/ EISH	Figueroa et al. (2009)
Vulpia myuros	Poaceae	ESH (35 °C)	Gómez-González & Cavieres (2009)

Heat, smoke, and their combinations are important keys to germination of seeds that are sensitive to fire (Gill 1981, Keeley 1991, 1995, Enright et al. 1997, Lloyd et al., 2000, Read et al. 2000, Enright & Kintrup 2001, Hill & French 2003, Clarke & French 2005, Thomas et al. 2007). There is documentation on naturalized species in central Chile (see Table 2) which have seeds that are triggered to germinate when subjected to thermal shock (e.g., *Cytisus striatus* (J. Hill) Rothm., *Cytisus scoparius* (L.) Link, *Onopordum acanthium* L., and others) or triggered when the seeds are exposed to the smoke from the burning vegetation (e.g., *Avena sterilis* L., *Dactylis glomerata* L., *Spartium junceum* L., and others). Similarly, a small group of naturalized plants have been detected whose seedlings emerge when triggered by exposure of the soil to the smoke from the burning of woody vegetation (*A. caucalis*, *A. barbata*, *P. annua*; see Table 2).

With regard to the mechanisms directly involved in the responses described above, thermal shock may break the seed coat, some chemical compound that inhibits germination may be destroyed, or it may have an effect similar to the corrosive action of sulfuric acid on the seed coat (Baskin & Baskin 1998). With respect to those mechanisms associated with smoke, compounds present in the smoke derived from the cellulose in the plants have been described, which may cause seed germination (Flematti et al. 2004).

Fire tolerance in naturalized plants

There is evidence of the development of tolerance to the effects of fire on seed germination and the emergence of naturalized species in central Chile (Figueroa et al. 2009, Gómez-González et al. 2008, Figueroa & Cavieres unpublished data). For example, in a study of the matorral from the coastal range in central Chile, the emergence of seedlings of 75 % of herbaceous plants, from which 60 % are naturalized, is indifferent to exposure to 100 ºC for a period of 5 min (Figueroa et al. 2009). In this last community, 70 % of the naturalized species are indifferent to heat and smoke. Similarly, tolerance to the effects of fire in > 80 % of naturalized plants was also found in studies carried out in a pre-mountain matorral in central Chile (Gómez-González & Cavieres 2009, Figueroa & Cavieres unpublished data).

With regard to this phenomenon it has been suggested that tolerance to perturbation by fire may contribute to the invasive ability of naturalized plants of European origin in continents where fire is natural or intentional (Keeley 1995). Tolerance to frequent perturbation by fire may have been a trait selected by an important proportion of European flora in its original habitat, giving the species a strong colonizing ability in sites frequently affected by farming perturbations (Di Castri 1989).

Although plants do not require fire or burning to be able to regenerate, the presence of traits that confer tolerance to heat can be sufficient to give an advantage to those species that are impeded from regenerating due to the effects of fire.

Annual species that are tolerant to fire normally rapidly colonize the substrate made available after a fire (e.g., *Bromus* spp, *Cardamine hirsuta* L., *Trifolium glomeratum* L., *Raphanus raphanistrum* L.) This has been documented on different continents where the same Eurasian species have been introduced and are dominant among the naturalized flora, including central Chile (Montenegro et al. 1991, Trabaud 1991, D'Antonio & Vitousek 1992, Arroyo et al. 2000, Valbuena & Trabaud 2001).

Positive feedback

With regard to the replacement of native by exotic plants, in central Chile the literature suggests the existence of positive feedback between regeneration of exotic species and fire frequency (Pauchard et al. 2008). This mechanism suggests that fires promote the reproduction of highly inflammable exotic species, and that the continuous regeneration of these species increases fire frequency. In central Chile, Pauchard et al. (2008) described this mechanism for the shrub *Teline monspessulana* (L.) K. Koch. There is also evidence in species of Eurasian origin which increase the frequency of fires in the grasslands in the west of North America, and these same species are naturalized and common in central Chile (e.g., *Arundo donax* L., *Bromus madritensis* L., *Bromus tectorum* L., *Schismus barbatus* (L.) Thell., and *E. cicutarium*) (Dukes & Mooney 2004).

Facilitation

The other mechanism described in the literature suggests that naturalized grasses are facilitated by fire. Recurrent fires caused by humans have allowed naturalized grasses to spread, as well as a few colonizing short-life native woody species (Segura et al. 1998, Figueroa et al. 2009). On the other hand, long-life native woody species, frequent in the late succession of the matorral, may be inhibited by vegetation fires (Segura et al. 1998, Gómez-González et al. 2008). Because of this, depending on their biogeographic origin and life history, two responses in plants to the fires in central Chile are observed: recurrent fires are favoring fast replacement of native woody and perennial herbaceous species for a low-diversity covering of colonizing woody species (*Acacia*), and a diverse covering of annual species which are naturalized (Altieri & Rodríguez 1974, Avila et al. 1981, Villaseñor & Sáiz 1993, Figueroa et al. 2004a, Gómez-González & Cavieres 2009). The facilitation mechanism would mainly be associated with the recurrent liberation of resources in the soil, greater available light, and available sites to be colonized, promoting a fire regimen (Sax 2002).

CONCLUSIONS

In the world, naturalized plants are frequently associated with fire. During the last century, vegetation in central Chile suffered dramatic changes due to, among other factors, the intensive use of fire. Similarly, in this revision we show that among the mechanisms that allow the spread of naturalized plants in the sclerophyllous forests and scrublands of central Chile may be those that are associated to perturbation by fire: life-history traits, tolerance, facilitation, and positive feedback. Hence, in central Chile fire increases the abundance and richness of naturalized species in detriment of native species.

In Fig. 8 we propose a conceptual model which represents the dispersal assisted by humans of exotic species and the spread of naturalized species under the effect of fire regimens, which helps explain the composition and structure of the matorral of central Chile in an early successional state. However, research is still required on the impact of the current composition of the vegetation on the variation of the human imposed fire regimen in central Chile (Brooks et al. 2004).

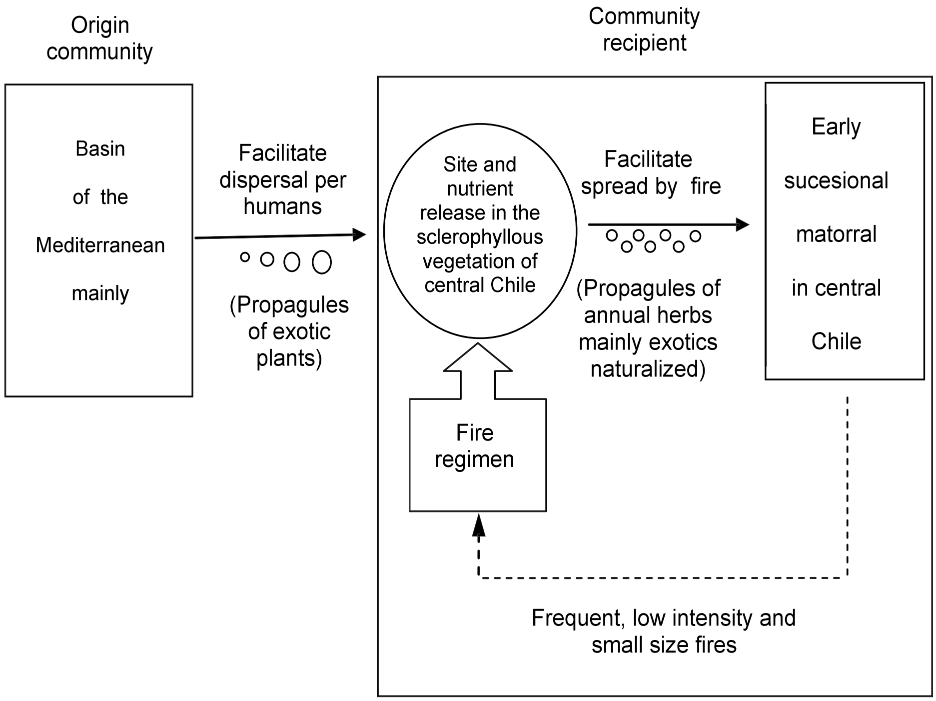

Fig. 8: Representation of the dispersal and spreading process facilitated by human activity and fire regimen, respectively, in exotic plants of Mediterranean origin in the matorral of central Chile.

Representación del proceso de dispersión y expansión facilitada por humanos y por el régimen de fuego, respectivamente, en plantas exóticas de origen mediterráneo en el matorral de Chile central.

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