Revista Chilena de Historia Natural
58: 9-17, 1985

Commentary

A mechanistic approach to the study of succession in the Chilean matorral

Un enfoque mecanicista para el estudio de la sucesión en el matorral chileno

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ABSTRACT

Plant succession was clasically conceived as a predictable series of stages that lead to a stable climax vegetation in accordance with the regional climate. This conception has been replaced in recent years by a more process-oriented, and population-based approach that takes into account the probabilistic nature of successional phenomena. Under this approach, individual replacement mechanisms leading to changes in species composition are the central focus of research. Several mechanisms of replacement may operate at one time, and the same mechanisms may act at different times in succession. Successional pathways are largely influenced by the nature of disturbance events, spatial and temporal environmental variation, and historical factors that affect invasion, establishment and replacement patterns.

In mediterranean shrublands of the world, natural fires are the major disturbance agent, initiating succession. In areas of California, France, Australia and South Africa, most woody species have regeneration mechanisms which respond directly to fire, so that the same species present before the fire, resprout, regrow or colonize after fire. Vegetation recovers in a period between 2 and 20 yr in most areas. Replacement of shrubs by trees is inhibited and does not occur unless fires are absent for a prolonged time.

In the sclerophyllous vegetation (matorral) of central Chile, disturbances are mostly related to human activities. Clearing of land for agriculture and livestock raising are the major forms of disturbance; fires are less important and also related to human impact. After abandonment, few early successional stages are possible because of the small number of shrub species which can act as pioneers. Pioneer shrubs serve as recruitment foci for several sclerophyllous species whose seeds are dispersed predominantly by birds. Establishment and growth of these species may be facilitated by the microclimate generated by pioneers. Replacement of early successional species can follow a number of pathways because seed input and seedling survival are probabilistic events.

Key words: Chile, matorral, mechanisms of succession, mediterranean climate, sclerophyllous vegetation.

RESUMEN

La sucesión vegetal fue concebida clásicamente como una serie predecible de estados que conducían a un clímax estable de acuerdo al clima regional. En los años recientes esta concepción de sucesión ha sido reemplazada por un enfoque basado en procesos que ocurren a nivel poblacional, y que toma en cuenta la naturaleza probabilística de los fenómenos sucesionales. De acuerdo a este enfoque, la investigación se centra en los mecanismos de reemplazo de individuos, los que conducen a cambios en la composición de especies. Durante una sucesión pueden operar varios mecanismos de reemplazo, ya sea simultáneamente o en diferentes tiempos. La naturaleza de las perturbaciones, la variación espacial y temporal de las condiciones locales y los factores históricos que afectan la invasión, el establecimiento y la conducta de las especies, influyen en gran medida en las vías sucesionales.

En las regiones de clima mediterráneo del mundo el fuego es el principal agente de perturbación iniciando la sucesión. La mayoría de las especies arbustivas en California, Francia, Australia y Sudáfrica tienen mecanismos de regeneración que responden directamente al fuego, de tal modo que las mismas especies dominantes antes del fuego rebrotan o recolonizan después de la perturbación. En la mayoría de las áreas, la vegetación se recupera en un período entre 2 y 20 años. El reemplazo de arbustos por árboles se produce sólo si no ocurren incendios por un tiempo prolongado y los arbustos entran en senescencia.

En la vegetación esclerófila (matorral) de Chile central, las perturbaciones son principalmente causadas por el hombre. Las perturbaciones más importantes son la apertura del matorral para generar áreas de cultivo y zonas de pastoreo; los incendios son menos importantes y también relacionados con la actividad humana. Los estados sucesionales tempranos, después del abandono de las tierras, son muy pocos, debido al pequeño número de especies arbustivas que pueden actuar como pioneras. Los arbustos pioneros sirven como focos de invasión para varias especies esclerófilas, cuyas semillas son dispersadas predominantemente por aves. El microclima bajo los arbustos pioneros puede facilitar el establecimiento de otras especies. El reemplazo de las especies dominantes en los primeros estados sucesionales puede seguir varias vías alternativas, porque la caída de semillas y la sobrevivencia de plántulas son eventos probabilísticos.

Palabras claves: Chile, clima mediterráneo, matorral, mecanismos de sucesión, vegetación esclerófila.

(Recibido el 2 de mayo de 1985. Aceptado el 27 de mayo de 1985.)

INTRODUCTION

Most classical studies of plant succession had as their main objectives the description and classification of seral stages in relation to a theoretical climatic climax for a region (Whittaker 1974). Underlying such studies was the Clementsian paradigm that considered succession as analogous to the development of an organism (Clements 1916). According to Clements, the development of the vegetation of a site followed a fixed and predictable series of stages that culminated in a stable plant community in equilibrium with its physical environment, the climax. Although this view was challenged by several plant ecologists who were contemporary with Clements (e.g., Gleason 1917, 1926, Cooper 1926, Tansley 1935), and later, was contested on empirical grounds by Cain (1947), Egler (1947), Mason (1947), and Whittaker (1951, 1953), Clements' ideas dominated the literature on succession for many years (Drury & Nisbet 1973, Simberloff 1980).

The rigidity of the Clementsian formalization of succession and the emphasis on the description of seral and climax stages and their connecting pathways, rested interest to the examination of the various mechanisms, acting at the population level, which are responsible for the vegetational change. Not until recently have plant ecologists taken a more process-oriented, and population-based approach to the study of succession (Horn 1975, Werner 1976, Bazzaz 1979, Peet & Christensen 1980, Pickett 1982). Presently, an alternative view, according to which vegetational change is a variable and often unpredictable process influenced by several different mechanisms has gained wide acceptance (Connel & Slatyer 1977, Miles 1979, Simberloff 1980, Horn 1981).

Studies of plant succession in central Chile are few (Schlegel 1966, Olivares & Gastó 1971, Gastó 1980), and a descriptive, classificatory approach has largely prevailed. We know very little about how an open patch in the Chilean sclerophyllous vegetation (matorral) is recolonized, how long successional changes take, or whether any directional change is likely. This paper has three main objectives: (1) To introduce a mechanistic framework that can provide insight into successional process in general, (2) to review what is known about succession in natural systems related to the matorral, such as other sclerophyllous woodlands of the world, and (3) to discuss some of the possible mechanisms of succession operating in the matorral of central Chile.

A MECHANISTIC FRAMEWORK

Succession can be defined as a temporal process of replacement of individuals of one species by another, or temporal changes in the performances (measured by variations in cover or biomass) of the individuals that form a patch of vegetation. Successional mechanisms should therefore explain how individuals, and hence species, yield or acquire space. In a classic paper, Connell & Slatyer (1977) summarized and proposed three mechanisms of succession as alternative and testable hypotheses. According to these authors, succession can follow either of three alternative courses: (1) Early successional species (pioneers) prepare the site for invasion and establishment of the next group of species; (2) pioneers monopolize the space and prevent the invasion of other species until their disappearance opens the site to new invaders, and (3) both pioneers and late successional species are present at the onset, and subsequent changes result from differences in growth rates and life spans of the species. Mechanism (1), termed "facilitation", is the only admitted mechanism in Clements' successional theory and is also discussed by Egler (1954) as the model of relay floristics. Mechanism (2), termed "inhibition", stresses the role of initial floristic composition (Egler 1954) in affecting subsequent changes. Mechanism (3), also called "tolerance", has as an implicit assumption the lack of significant interactions among the species.

Connell & Slatyer's (1977) paper sets a significant benchmark, by changing the view of succession as a rigid series of stages leading to climax, and stimulating an experimental approach to study vegetational changes (see Hils & Vankat 1982, Del Moral 1983, Houssard *et al.* 1980, Turner 1983, Harris *et al.* 1984, Armesto & Pickett, unpubl. MS.). Connell & Slatyer's work has been criticized, however, because (1) the three mechanisms proposed as alternative hypotheses can operate simultaneously in a given sere (Quinn & Dunham 1983, Breitburg 1985), and (2) additional mechanisms and pathways of succession there exist which are not considered by these authors (Pickett, Collins & Armesto, unpublished MS). All successions can be described in terms of the following processes (Clements 1916, MacMahon 1981): (1) Nudation, which is the opening of a site to invasion, (2) migration, i.e., the arrival of organisms at the open site, (3) ecesis i.e., the establishment of organisms in the site, (4) competition, i.e., the interactions among organisms at the site, and (5) reaction, i.e., the modification of site conditions by the organisms. These five processes encompass the entire range of causes of succession. Within this general framework, Connell & Slatyer's (1977) mechanisms account for processes (4) and (5). Little attention was devoted by these authors to causes of disturbance, which may be determining the course of succession in many systems (White 1979, Miles 1979, Vogl 1980), or to migration, that is the relation between succession and distance to propagule sources, availability of dispersal agents, availability of residual propagules, and isolation of the successional patch. With regard to pathways of succession, i.e., the series of stages or species replacement patterns that characterize a sere (Pickett *et al.*, unpubl. MS), Connell & Slatyer's (1977) mechanisms are implicitly linked to linear pathways, thus neglecting the variety of pathways observed in nature (see Horn 1981).

In summary, we propose to focus on specific mechanisms that could be responsible for the transitions associated with each stage in a successional pathway. This approach should admit that (1) multiple mechanisms may operate in one succession (at one or different times), (2) one succession can follow many alternative pathways, depending on the nature of the disturbance (severity, frequency and timing), and (3) historical and environmental factors influence invasion, establishment and performance of the species.

SUCCESSION IN MEDITERRANEAN-TYPE SHRUBLANDS (EXCLUSIVE OF CHILE)

Successional change in mediterranean climate areas of the world is generally associated with recovery from fire (e.g., Hanes 1971, Noble *et al.* 1980, Trabaud & Lepart 1980, Kruger 1983). Characteristics of the disturbance event thus have an overriding influence on succession in these communities, whereas species replacement mechanisms are less important. Species of mature stages can act as colonizers of burnt areas (see below), and hence they can "replace themselves". This regeneration process is known as autosuccession (Hanes 1971).

Fire-induced changes in sclerophyllous woodlands have been documented for the California chaparral (Hanes 1971), for maquis and garrigue formations in the Mediterranean Basin (Le Houerou 1974, Trabaud & Lepart 1980), for mallee heathlands in southern Australia (Noble *et al.* 1981, Gill *et al.* 1981), and for South African fynbos (Kruger 1977, 1983). A most striking characteristic of post-fire succession is the rapid recovery of the original vegetation. In the fynbos, 70-90% of the canopy cover redevelops in 2 yr, in the Australian heath canopy closes to 100% in 10 yr, in maquis and garrigue the same change takes 5 yr, and in the California chaparral between 10-20 yr (Kruger 1983). Furthermore, burnt stands tend to retain their floristic identity and woody species richness, despite some fluctuations after successive fires (Russell & Parsons 1978, Trabaud & Lepart 1980).

Rapid recovery is due to the ability of most plant species in mature stands to resist fire damage, to resprout directly from rootstocks, or to have fire-induced seed dispersal and germination mechanisms (Zedler 1981, Kruger 1983). Serotiny, that is, the retention of viable seed inside a protective organ on the plant, is frequent in shrub species from Australia and South Africa. Seeds are shed and germinate only after fire (Gill 1981, Kruger 1983). Most California shrubs maintain large seed banks in the soil and germination is fire-induced (Hanes 1971, Zedler 1981). Resprouting is another common response to fire which is related to the presence of lignotubers and epicormic growth (Noble 1982). As a consequence of these features of most dominant shrubs, regeneration takes place without any preparation of the site by pioneers. Accordingly, facilitation is not a mechanisms of post-fire succession.

Prolonged absence of fire in these ecological systems leads generally to stagnation, i.e., vegetational change becomes extremely slow (MacMahon 1981, Kruger 1983). This effect can be the result of inhibition of growth of tree seedlings by the dominant shrubs, through sequestering of nutrients or allelopathy (Kruger 1983). In other cases, long-term stability can simply be the result of limited seed dispersal, high longevity of the dominants (Vasek 1980), and the sporadic nature of seedling establishment episodes in mediterranean-type regions (Zedler 1981). In the first situation, the inhibition model of Connell & Slatyer (1977) may apply to those systems in the absence of fire (Debusche *et al.* 1980, Kruger 1983). In the second case, the tolerance mechanism seems to be supported. A slow process of replacement of shrubs by trees has been shown for certain areas of the California chaparral (Patric & Hanes 1966), and mediterranean-type communities in France (Debusche *et al.* 1980), Australia (Del Moral *et al.* 1978), and South Africa (Van Wilgen 1981). This change is attributed to senescense of the dominant shrubs and their inability to regenerate in the absence of fire (Kruger 1983). The mechanisms responsible for the replacement of shrubs remain unexplored.

In conclusion, in mediterranean-type shrublands (exclusive of Chile; see below), vegetation changes after disturbance by natural fires are the result of resprouting or recolonization by the same species that are present before the fire. Only when fires are prevented by local environmental conditions (e.g., sheltered ravines) or human activity, the fire-resistant community may be replaced by a different one. This pathway and the possible mechanisms involved are illustrated in a simple model in Fig. 1.

SUCCESSION IN THE CHILEAN MATORRAL

Plant community dynamics in the Chilean matorral differs fundamentally from the mediterranean climate regions discussed above. The most important difference is that fire has not had the profound evolutionary and historical impact it has had in other sclerophyllous shrublands (Mooney 1977, Cody & Mooney 1978, Armesto & Gutiérrez 1978). As a consequence, most shrub species of old-growth stands of matorral lack the capacity to recolonize immediately after disturbance; in other words they do not have any disturbance-dependent regeneration mechanisms. Thus, a different set of species (the pioneers) colonize open areas. Disturbance differs in nature and degree of impact on the vegetation of central Chile. Nowadays, man-related effects are responsible for a great majority of the modifications to the landscape that initiate succession. Fires are not the most frequent disturbance, and when they occur, they are the result of human activity. Other more important human-induced disturbances are wood-cutting, and the opening of land for agriculture and livestock raising (Bahre 1979).

Successional trends after disturbance by man have not yet been documented for any area of the Chilean matorral. In addition, even old-growth stands are likely to have suffered from some degree of human disturbance in the past. Consequently, it is not always easy to differentiate successional stands from older vegetation. We will focus here on successional pathways observed in post-agricultural and abandoned pasture lands, located below 400 m in the Coastal Range and the Central Depression between the Andean and Coastal Ranges, where most observations and data collecting by one of us (JA) have been made. The complete understanding of succession requires both the elucidation of patterns of community change through time and the determination of mechanism of turnover. We postulate that early successional stages are those dominated by

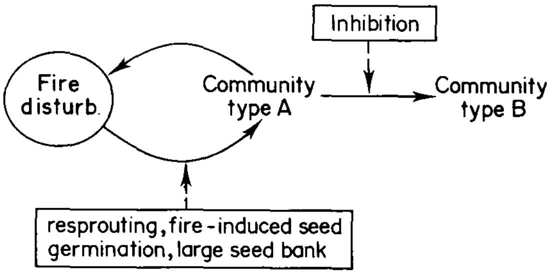

Fig. 1: A simplified model of plant succession in mediterranean-type shrublands where fire is a major disturbance factor. Communities are defined by their dominant shrub or tree species which are different in each mediterranean area. In general, community type A is dominated by fire-resistant shrubs, whereas community type B is dominated by tree species.

Un modelo de la sucesión vegetal en áreas de tipo mediterráneo donde el fuego es el principal agente de perturbación. Las comunidades son definidas por sus especies dominantes, árboles o arbustos, las que son diferentes en cada área. En general, la comunidad A está dominada por arbustos resistentes al fuego, mientras que la comunidad B está dominada por especies arbóreas.

shrubs with specific features of pioneers. We recognize as pioneer shrubs those species that share all of the following characteristics: (1) they usually form monospecific or low diversity stands; (2) they are widespread in the areas defined above; (3) they are capable of tolerating xeric conditions that characterize open sites (Del Pozo, unpublished data); and (4) they have profuse seed production and wide dissemination. This analysis leaves only a small group of shrub species as the most likely candidates for acting as pioneers in the matorral (Table 1). We will now look at the mechanisms of colonization of disturbed areas by these species, and describe possible mechanisms by which they could be replaced by other sclerophyllous shrubs.

Acacia caven is a semideciduous shrub, broadly distributed in central Chile, where it is usually found in monospecific stands (Gutiérrez & Fuentes 1979, Gutiérrez & Armesto 1981a). It grows on all gentle slopes and plains where the original sclerophyllous woodland has been cleared and grazing by livestock is a severe and chronic disturbance (Fuentes & Hajek 1979). Colonization by this species is likely to occur along with the introduction of cattle, because it has been shown (Gutiérrez & Armesto 1981b) that pods of *Acacia* are eaten by cattle and horses which are the main dispersers of its seeds. Seedling survival in open areas is favored by their drought resistance (Aljaro *et al.* 1972) and their thorny habit that protects them from being eaten by cattle. It appears that if cattle are not removed completely from the area, stands dominated by *Acacia caven* do not develop into other types of vegetation (Fuentes & Hajek 1979).

On the other hand, abandoned agricultural land which is not severely grazed is generally invaded by one or more species of Compositae shrubs (Table 1), belonging to the genera *Baccharis* and *Gutierrezia.* These species have wind-dispersed seeds that quickly reach open areas and germinate in large numbers (Gutiérrez & Armesto 1977). Plants have small linear leaves and are presumably highly resistant to drought. They seem to be well defended against herbivores because of the presence of glandular trichomes in their leaves (Aljaro *et al.* 1984) and the probable presence of

TABLE 1

Common matorral shrubs and trees associated with different successional stages and their mode of dissemination based on dispersal syndromes

Arboles y arbustos comunes en el matorral y su asociación con distintos estados sucesionales. Modos de dispersión basados en síndromes

SPECIES	DISPERSAL AGENT (S)
Pioneers	
Acacia caven (Leguminosae)	livestock
Gutierrezia paniculata (Compositae)	wind
Bacharis spp. (Compositae)	wind
Mid-successional	
Muehlenbeckia hastulata (Polygonaceae)	birds
Lithraea caustica (Anacardiaceae)	birds, mammals
Late-successional*	
Quillaja saponaria (Rosaceae)	wind
Maytenus boaria (Celastraceae)	birds
Peumus boldus (Monimiaceae)	birds
Schinus latifolius (Anacardiaceae)	birds
Cryptocarya alba (Lauraceae)	birds, mammals?
Myrceugenella chequen (Myrtaceae)	birds
Myrceugenia obtusa (Myrtaceae)	birds
Beilschmiedia miersii (Lauraceae)	mammals

* The order reflects the approximate position of the species along a gradient from xeric to mesic.

compounds with anti-herbivore properties in their tissues (Mabry & Gill 1979).

Open areas dominated by *Baccharis* and *Gutierrezia* can be invaded by *Muehlenbeckia hastulata,* a shrub species with fleshy, bird-dispersed fruits (J. Armesto, personal observation). Plants of this latter species are usually seen under the shade of shrubs of the other two species which may serve as recruitment foci (McDonnell & Stiles 1983, Fuentes *et al.* 1984). Another species which may invade early successional stands dominated by *Baccharis* or *Gutierrezia* is *Lithraea caustica,* especially when propagule sources are nearby (J. Armesto, unpubl. data). This species has a broad range of tolerance to soil moisture levels (Martínez & Armesto 1983) so that it can be found in open, xeric sites as well as in mesic ones. Seeds of *Lithraea* can be dispersed into open areas by birds and foxes (J. Armesto, personal observation). Establishment of seedlings can be facilitated by the protection of other shrubs (*Baccharis, Gutierrezia, Muehlenbeckia*), under which desiccation is reduced (Fuentes *et al.,* unpubl. MS, Del Pozo *et al.,* unpubl. data). Replacement of *Acacia, Baccharis* or *Gutierrezia* stands by *Muehlenbeckia* or *Lithraea* has been postulated by several authors (Gutiérrez & Armesto 1977, Fuentes & Gutiérrez 1981, Fuentes *et al.* 1984). While *Muehlenbeckia* seems to disappear as the early successional stages proceed, *Lithraea* tends to persist longer in the successional sequence because it is also found as a co-dominant in old-growth stands of matorral (Armesto *et al.* 1979).

The predominance of bird-dispersed seeds among sclerophyllous shrubs in the matorral (Table 1) suggests that colonization patterns are different from those seen in other mediterranean regions of the world where regeneration mechanisms are fire-adapted. A similar invasion pattern may occur, however, during the replacement of shrubs by trees in the absence of fire (see Debusche *et al.* 1982). In central Chile, pioneer shrubs which are able to colonize open sites serve as recruitment foci for bird-disseminated seeds (Fuentes *et al.* 1984, and unpubl. MS) and a large number of seedlings are found beneath the canopy of pioneer individuals (Table 2; see also Fuentes *et al.* 1984). Since the microclimate under bushes seems to enhance seedling survival in comparison to open areas (Fuentes *et al.,* unpubl. MS), facilitation (*sensu* Connell & Slatyer 1977) may be an important successional mechanism for the replacement of pioneers. Subsequent successional stages are difficult to predict because replacement patterns are largely a function of site conditions (e.g., soil moisture, nutrient levels, seed bank, distance to seed sources, etc.), availability of birds and fleshy fruits, and patterns of seed-

TABLE 2

Distribution of seedlings (less than 30 cm high) occurring in an open, successional area in Quebrada El Tigre, Zapallar (Armesto & Martínez, unpublished data). Seedlings were sampled in a 2 x 100 m transect.

Distribución de plántulas (menores de 30 cm) en un área sucesional en la Quebrada El Tigre, Zapallar (Armesto & Martínez, datos no publicados). Las plántulas fueron muestreadas en un transecto de 2 x 100 m.

SEEDLINGS	GROWING UNDER PIONEER SHRUBS		GROWING IN OPENINGS BETWEEN SHRUBS
	Lithraea caustica (N=4)	*Baccharis sp.* (N =4)	
Aristotelia chilensis	0	1	0
Cryptocarya alba	2	2	0
Maytenus boaria	39	19	0
Lithraea caustica	0	2	1
Myrceugenia obtusa	1	0	0
Peumus boldus	7	1	0
Schinus latifolius	0	1	0
TOTALS	49	26	1

ling mortality due to herbivory. All these factors vary widely in space and time. Accordingly, a mosaic structure can be expected for the matorral, where different types of communities are derived from early successional stands with a similar species composition (Fig. 2).

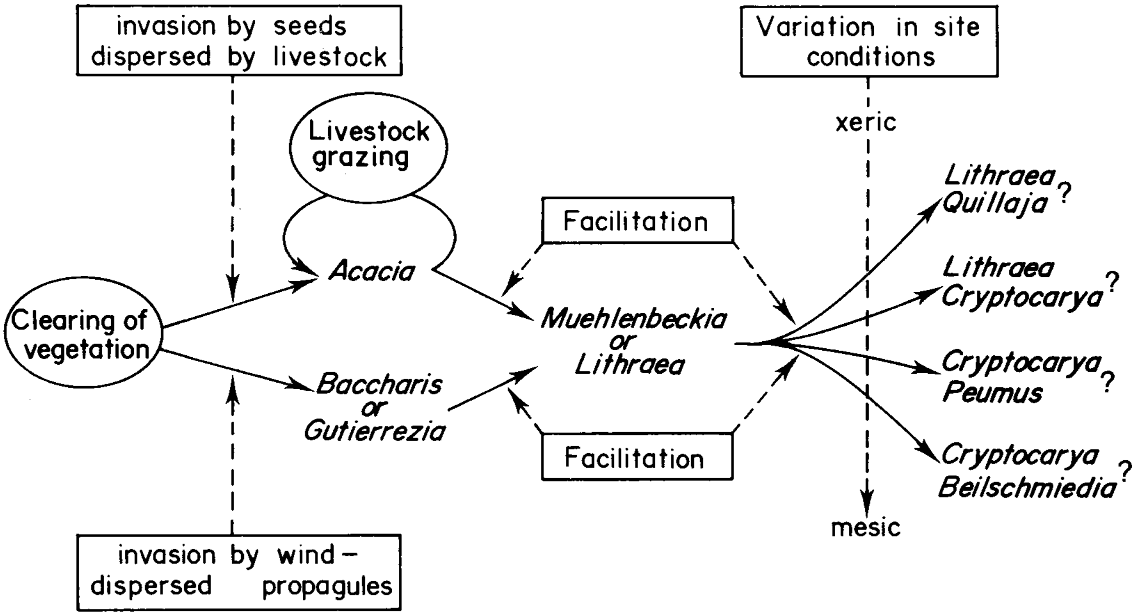

Fig. 2: A simplified model of plant succession in the Chilean matorral. Variation in site conditions reflects mainly variations in soil moisture, but it may also include variations in slope aspect, soil type, etc. Communities are defined by their dominant shrub or tree species. For complete species names see Table 1.

Un modelo simple de la sucesión vegetal en el matorral chileno. La variación en las condiciones del sitio refleja básicamente variación en la humedad del suelo, pero también podría considerar variaciones en la exposición, tipo de suelo, etc. Las comunidades están definidas por sus especies dominantes, árboles o arbustos. Los nombres completos de las especies se encuentran en la Tabla 1.

CONCLUSION

We have shown that studies focusing on mechanisms of succession, considered as a population process, are useful for identifying the causes of vegetational change and for predicting seral stages and possible successional pathways. Much research is still needed to understand succession in the matorral. By way of conclusion, we would like to suggest some basic questions that need to be addressed in future studies: (1) What determines the time span encompassed by different seral stages? (2) How do different site-specific factors influence the speed and direction of vegetational change? (3) How do different characteristics of the disturbance regime (i.e., size of open patch, severity and mode of disturbance, season and frequency of disturbance) affect early stages? (4) How do variations in fruit production and seedling establishment among years affect succession? The answers to these and other relevant questions should aid in the completion of the successional model for the Chilean matorral by refining the pathways sketched in Fig. 2, and combining them with the complete array of causes and interactions that drive the successional turnover.

ACKNOWLEDGMENTS

Partial funding for this work came from Projects N 2210-8515 of the Departamento de Investigación y Bibliotecas, Universidad de Chile, and INV-078-85 of the Dirección de Investigación, Academia Superior de Ciencias Pedagógicas de Santiago. Discussions with S. Collins, K. Dougherty, J.

Martínez, and C. Villagrán were important for clarifying many of the ideas presented here. The manuscript was greatly improved by the comments of E. Fuentes and F. Jaksic. Not all of their comments were accepted, however, and some points of disagreement are likely to remain. We are grateful to Cecilia Fernández Niemeyer for drawing the figures.

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