

CLONAL REPRODUCTION AND SUCCESSION: THE CASE OF *Baccharis linearis* IN THE
CHILEAN MATORRAL

Ramiro O. Bustamante

Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile,
Casilla 653, Santiago, Chile.

RESUMEN

La reproducción clonal es un atributo de historia de vida que puede permitir la dominancia de las especies que la poseen durante algunas fases de la sucesión secundaria. La prolongada dominancia documentada para *Baccharis linearis* en las zonas abiertas del matorral, puede ser explicada aludiendo a este mecanismo de reproducción. Se presentan datos que indican que las plántulas clonales de *B. linearis* presentan una mayor sobrevivencia en comparación a las plántulas sexuales de esta misma especie y a otras especies del matorral. Este modelo permite postular que el modelo de inhibición puede ser más adecuado que el de facilitación para entender la sucesión secundaria en el matorral centro-chileno.

ABSTRACT

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Clonal reproduction is a life history trait that allows a dominance of plants during some stages of succession. In this paper I show evidences which suggest that the frequently documented long-term dominance of *Baccharis linearis* in cleared zones of the Chilean matorral may be explained by clonal reproduction. Additionally, other evidences show that clonal seedlings of this species survive better than seedlings of other species. Therefore, I suggest that the inhibition model is more appropriate than the facilitation model to explain secondary succession in the Chilean matorral.

INTRODUCTION

Theoretical models suggest that clonal reproduction in plants (*sensu* Abrahamson 1980) may be an adaptive feature during colonization of secondary successional sites following disturbance (Walker & Chapin 1987) or during late successional stages where competition seems to be important (Abrahamson 1980). These models predict long-term dominance of a clonal species once established (Armesto & Pickett 1986, Tappeiner *et al.* 1991). Advantages of clonal reproduction in plants may be explained by: (i) photosynthates and nutrient translocation from adults to clonal offspring, thus increasing their survival and growth (Callaghan 1984, Evans 1988, Tissue & Nobel 1988, Alpert

1991) and (ii) rapid spread by modular growth (Smith & Palmer 1976), allowing pre-emption of space before other species, depending on sexual reproduction alone, may become established (Abrahamson 1980, Harper 1985, Sebens & Thorne 1985, Rubins 1988).

Baccharis linearis (Compositae), is a wind-dispersed pioneer species, that colonizes cleared zones of the Chilean matorral (Armesto & Pickett 1985). Tolerance to xeric conditions, a prolific seed production, wide dissemination by wind, and small and narrow leaves well defended against herbivores, presumably enable *B. linearis* to successfully colonize cleared zones (Armesto & Pickett 1985). Previous studies suggest that *B. linearis* tends to persist as the dominant species in these

habitats for a long time, thus arresting the development of a more diverse and sclerophyllous vegetation (Fuentes *et al.* 1986). However, this long-term monopolization of space in the matorral remains unaccounted for.

In this paper, I present empirical evidences of clonal reproduction in *Baccharis linearis*. In addition I demonstrate that clonal seedlings of *B. linearis* have higher survival probabilities than sexual seedlings of the same and/or other shrub species. Then, I discuss the facilitation model (*sensu* Connell & Slatyer 1977) proposed for secondary succession in the Chilean matorral (Armesto & Pickett 1985). I advance the hypothesis that clonal reproduction accounts for the persistence and dominance of *B. linearis* in cleared zones of the matorral thus suggesting that the inhibition model (*sensu* Connell & Slatyer 1977) may be more appropriate to understand secondary succession.

MATERIAL AND METHODS

Study sites.

The study sites are located in the mediterranean Chilean matorral (semi-arid shrubland, Rundel 1981). This region is characterized by warm dry summers (December to March) and cool wet winters (July to September). The annual precipitation averages 350 mm and the average temperature varies between 13° C and 22° C. Studies were carried out during 1988 and from Spring 1990 to Summer 1991 in vegetation patches dominated by *B. linearis* at two localities: El Pangue (Coastal range 33° 18' S; 71° 11' W) and San Carlos de Apoquindo (Andean range 33° 23' S; 70° 31' W).

Clonal reproduction vs. sexual reproduction.

Seedlings of *B. linearis*, 15 cm or less in height, without signs of lignification, were counted in 20 quadrats of 0.5 x 0.5 m, per locality. I recognized two distinct microhabitats: under the canopy of adult shrubs of *B. linearis* and open spaces, and set up 10 quadrats per microhabitat. Within each quadrat, all young individuals were uprooted and their origin was recorded: (i) individuals that emerged from subterranean roots of established adults were classified as clonal seedlings and, (ii) individuals with an autonomous root system were classified as sexual seedlings. Tests of independence between reproductive mode, microhabitat,

and locality were performed by a three way contingency table (Sokal & Rohlf 1981).

Seedlings monitoring.

I monitored shrub seedlings at species level, by using 40 quadrats of 0.5 x 0.5 m, located at random, under the canopy of 20 adults of *B. linearis* in September 1990 (Spring) and in January 1991 (Summer). For the identification of sexual seedlings of *B. linearis*, I excavated to distinguish the root system of individuals. By the last date, I evaluated the proportion of survivorship for each shrub species by using the expression $lx = Nx / No$, where No is the number of individuals at time 0 (September 1990) and Nx is the number of individuals surviving at time X (January 1991). Mean proportion tests (Sokal & Rohlf 1981) were performed in order to compare seedling survival between species.

RESULTS

Clonal reproduction vs sexual reproduction.

At El Pangue and San Carlos de Apoquindo a large number of clonal seedlings relative to sexual seedlings were observed both under the canopy of adults and in open microhabitats (Table 1). Additionally, a global analysis shows that both clonal and sexual seedlings are significantly more abundant under the canopy of adults, than in open spaces (80.9% and 95.6% for clonal and sexual seedlings respectively, see Table 1). Moreover, clonal reproduction is independent of locality (contingency test, $p > 0,25$) and microhabitat (contingency test, $p > 0,10$) (Table 2). These results suggest that clonal reproduction is the most important reproductive mode of *B. linearis* in the Chilean matorral, irrespective of locality and microhabitat and offsprings tend to be concentrated under the canopy of adult plants.

Seedlings monitoring

Under the canopy of adults, I found five seedlings species, one pioneer species (*B. linearis*, clonal and sexual seedlings), one mid-successional species (*Muehlenbeckia hastulata*) and three late successional species (*Cryptocarya alba*, *Quillaja saponaria* and *Schinus sp.*). These species are vertebrate—seed dispersed (Armesto *et al.* 1987) except *B. linearis* and *Q. saponaria* which are wind-seed dispersed.

TABLE 1.

Percentage of clonal offsprings among the total of observed progeny under and between canopies of adult *B. linearis* in El Pangue and San Carlos de Apoquindo. In parenthesis total number of seedlings for each situation.

Study sites	Microhabitat		
	Under	Between	Total
El Pangue	94.2 (154)	97.0 (33)	94.7 (187)
San Carlos de Apoquindo	90.2 (122)	100.0 (28)	92.0 (150)
Total	92.4 (276)	98.4 (61)	93.5 (337)

TABLE 2.

Test of independence in a three-way contingency table (Sokal & Rohlf 1981) for reproductive mode of *B. linearis* in two localities: El Pangue and San Carlos de Apoquindo, and in two microhabitats: under and between adults shrubs.

Hypothesis (Ho)	df	G	P
a) Independence of reproduction x locality	1	1.43	> 0.25
b) Independence of reproduction x microhabitat	1	1.73	> 0.10
c) Independence of locality x microhabitat	1	0.06	> 0.50
d) Interaction between reproduction x locality x microhabitat	1	0.11	> 0.10
e) Independence between reproduction x locality x microhabitat	4	3.34	> 0.25

Clonal seedlings of *B. linearis* were the most dominant, both during Spring (46.7% of total seedlings) and Summer (66.6%) (Table 3). This dominance increased significantly between seasons (proportion test, $Z = 2.09$, $p < 0.05$). By other hand, 100% of the sexual seedlings of *B. linearis*, which were in lower proportion than clonal seedlings in Spring (10.4% of the total seedlings of *B. linearis*), died by dessication in Summer. Additionally, clonal seedlings of *B. linearis* survived to summer in higher proportion than *Q. saponaria* seedlings (proportion test, $Z = 4.58$, $p < 0.001$), *C. alba* seedlings (proportion test, $Z = 2.46$, $p < 0.01$), *Schinus* sp. seedlings (proportion test, $Z = 3.25$, $p < 0.01$) and *M. hastulata* seedlings (proportion test, $Z = 4.23$, $p < 0.001$). In summary, these results suggest that clonal seedlings of *B. linearis* are the only effective source of reproduction for this species, they are the most abundant seedlings and presumably the most efficient to surmount the limiting conditions (extreme drought) imposed during summer.

TABLE 3.

Seedling abundance (expressed as number of individuals / 10 m²) and proportion of survivorships (1x) of shrub species under the canopy of adults of *B. linearis* during September 1990 (Spring) and January 1991 (Summer), El Pangue, V Region. For *B. linearis*, C = clonal seedlings and S = sexual seedlings.

Species	Spring	Summer	1x
<i>Baccharis linearis</i> (C)	43	40	0.93
<i>Baccharis linearis</i> (S)	5	0	0.00
<i>Quillaja saponaria</i>	10	3	0.30
<i>Cryptocarya alba</i>	8	5	0.60
<i>Schinus</i> spp.	8	4	0.50
<i>Muehlenbeckia hastulata</i>	18	8	0.44
TOTAL	92	60	0.65

DISCUSSION

In the Chilean matorral, pioneer shrubs (i.e. *B. linearis*) serve as recruitment foci for bird-disseminated seeds and seedlings underneath the canopy of adults (Fuentes *et al.* 1984, Armesto & Pickett 1985, Fuentes *et al.* 1986). In this way, mid and late successional species should arrive and establish in cleared zones which progressively evolve to a more diverse vegetation (Armesto & Pickett 1985). Thus, the facilitation model (*sensu* Connell & Slatyer 1977) has been argued to explain secondary succession in the matorral (Armesto & Pickett 1985). The predominance of clonal reproduction in *B. linearis* and the higher survival of clonal seedlings documented in this study, suggest an alternative hypothesis. Clonal offspring of *B. linearis* assure their survival and growth under the canopy of adults by the translocation of photosynthates and nutrients from "parents" (Callaghan 1984, Walker & Chapin 1987, Tissue & Nobel 1988). Seedlings originated by seeds deposited by dispersers, are not able to surmount the environmental constraints under *B. linearis* adults (drought, herbivory, see Fuentes *et al.* 1986). This fact suggests that adults of this species are "bad nurses" for late-successional species. In addition, the rapid growth by clonal reproduction allows a site consolidation and/or a monopolization of space and resources (Harper 1985), which eventually prevents

the establishment of late successional species by competition. Thus, the inhibition model (*sensu* Connell & Slatyer 1977) may be more appropriate than the facilitation model to explain secondary succession of the Chilean matorral. In fact, prediction derived from the inhibition model, that is, "... pioneers persist undamaged and/or continue to regenerate vegetatively and exclude or suppress subsequent colonists" (Connell & Slatyer 1977), is supported by the vegetational pattern observed in the matorral.

Many natural communities are dominated by clonal plant species (Cain 1990). However, studies of clonal reproduction in the context of succession are scarce (see Armesto & Pickett 1986, Tappeiner *et al.* 1991). Further vegetation studies focusing on this reproductive mode are necessary in order to understand its role and importance on secondary succession.

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