

## **Breeding systems in a temperate mediterranean-type climate montane sclerophyllous forest in central Chile**

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ARROYO, M. T. K. & USLAR, P., 1993. **Breeding systems in a temperate mediterranean-type climate montane sclerophyllous forest in central Chile.** The frequency of dioecy in the predominantly biotically-pollinated native flora of a temperate montane sclerophyllous forest in central Chile, 33°S, is determined. Experimental crosses and other tests were performed on a taxonomically diverse set of annual herbs, perennial herbs and woody species to detect genetic self-incompatibility, spontaneous selfing capacity and obligate agamospermy.

The overall frequency of dioecy in the community is 9%. Dioecy is unequally represented among life-forms, increasing in frequency with greater longevity: 0% in annual herbs; 2% in perennial herbs; 17% in shrubs; 57% in trees. Thirty-eight percent of 37 hermaphrodite species proved to be genetically self-incompatible. Self-incompatibility, like dioecy, increases in frequency with longevity: 0% in annual herbs; 50% in perennial herbs; 80% in shrubs. The self-compatible species showed a wide range of breeding habits from facultative outcrossing to strong autogamy. However, in most self-compatible species hand self-pollination increased fruit and seed set over spontaneous selfing. Obligate agamospermy was not detected among hermaphrodite species. Absolute and relative fecundity were strongly correlated with the degree of compatibility. However, reduced fecundity in obligate outbreeding species could not be unequivocally attributed to pollinator limitation.

For equivalent life-forms, the montane sclerophyllous forest exhibits proportionately more obligate outbreeding species than some tropical forests and other temperate communities. The strong tendency for obligate outcrossing in the Chilean community is seen as a result of interplay between life-history constraints and the intense abiotic and biotic pressures that are characteristic of the mediterranean-type climate community.

**ADDITIONAL KEY WORDS:**—Autogamy – dioecy – life-history constraints – pollinator limitation – self-incompatibility.

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## INTRODUCTION

Few plants communities have been surveyed for breeding systems. Existent studies are often biased in terms of life-form representation (e.g. Bawa, 1974; Ruiz & Arroyo, 1978; Bawa, Perry & Beach, 1985; Bullock, 1985). Several surveys of plant sexual systems across all life-forms have been undertaken (e.g. Bullock, 1985). However, such studies are of limited value in as far as assessing the relative overall importance of obligate outbreeding mechanisms in a community are concerned.

The breeding systems of temperate woody communities have been particularly neglected. Most community-oriented breeding system research for woody communities has been carried out in the tropics (Bawa, 1974; Bawa & Opler, 1975; Ruiz & Arroyo, 1978; Chan, 1981; Sobrevila & Arroyo, 1982; Tanner, 1982; Bawa *et al.*, 1985; Bullock, 1985; Ha *et al.*, 1988; Hernández & Carreon, 1987; Kress & Beach, 1989), with only isolated and incomplete studies in temperate forests and woodlands (Barrett & Helenurm, 1987). Yet temperate woody communities should be of interest. It is often claimed that tropical forests house large numbers of outcrossing species (e.g. Bullock, 1985). While modally true, to date, the possibility that temperate woody communities *contain proportionately more outcrossing species* than tropical forests cannot be legitimately excluded. Indeed Arroyo & Squeo (1990) recently showed that abiotically harsh, pollinator-depauperate Patagonian alpine communities contain very high frequencies of outbreeding species when particular life-forms are considered. Fox (1985) demonstrated a latitudinal increase in dioecy in North America. If this trend is paralleled by an increase in genetic self-incompatibility, high levels of obligate outbreeding could be expected at northern temperate latitudes. Temperate forests in particular might prove to contain high proportions of outcrossing species.

We have undertaken studies on native woody and herbaceous species in montane sclerophyllous forest in the mediterranean-type climate zone in central Chile. Montane sclerophyllous forest is an open, evergreen association characterized by a wide spectrum of life-forms (annuals to trees), and small, sclerophyllous trees. Such forest (or woodland as it is often referred to in view of its open nature) is found altitudinally above typical lowland mediterranean matorral vegetation to the upper limit for trees. It occurs over an altitudinal range of 1600–2400 m in the Cordillera de los Andes between 30°–35°S and from 700 to 1200 m in the Cordillera de la Costa at 33°S. It develops under a semi-arid mediterranean-type climate (di Castri & Hajek, 1976) with a long dry season of 8–9 months and a winter precipitation regime with occasional, but non-permanent snow. In montane sclerophyllous woodland, biotic pollination mechanisms predominate in the tree, shrub and herbaceous layers (Thrower & Bradbury, 1977; Uslar, 1982). Flowering occurs from September to May, with an evident peak in November–December.

In this paper we (a) provide data on the incidence of sexual dimorphism in the tree, shrub, perennial herb and annual herb life-forms of the above-mentioned community, (b) through controlled pollinations conducted under field conditions determine the compatibility status and selfing capacity for woody and herbaceous species, and (c) compare the absolute and relative fecundity of hermaphrodite species according to compatibility level.

## STUDY SITE

Montane sclerophyllous woodland along the Quebrada del Lunes on a 30° north-west facing slope between 1600 and 1800 m elevation, Santuario de la Naturaleza, Yerba Loca, Región Metropolitana, Chile, 33°20'S, 70°20'W was chosen for study. Annual precipitation at San José de Maipo, 1060 m elevation, 50 km to the south of the study site is 623 mm (di Castri & Hajek, 1976). The estimated mean annual temperature, based on Farellones, 2500 m (Arroyo, Armesto & Villagrán, 1981) near the study site, and a lapse rate of 0.6°C/100 m, is around 14°C.

At its upper altitudinal limit the site contains a fairly pure stand of *Kageneckia angustifolia* which eventually intergrades into mixed woodland lower down containing *K. oblonga* R. & P., *Lithrea caustica* (Mol.) H. & A., *Maytenus boaria* Mol., *Aristolelia chilensis* (Mol.) Stunz, and in fairly small quantities, *Quillaja saponaria* Mol. and *Escallonia myrtoidea* Bert. ex DC. *Kageneckia angustifolia*, *K. oblonga*, *L. caustica* and *Q. saponaria* are strong stump sprouters, a condition that also occurs in other mediterranean-type climate woody species (Herrera, 1987).

The emergent tree strata gives way to a discontinuous shrub layer with *Schinus molanus* (Phil.) Engler, *Podanthus mitique* Lindl., *Solanum ligustrinum* Lodd, *Ribes polyanthes* Phil., and *Berberis* sp. A second group of shrubs more commonly found in the subalpine (Arroyo, Armesto & Villagrán, 1981) (e.g. *Mulinum spinosum* (Cav.) Pers. and *Viviania marifolia* Cav.) occupy rocky outcrops within the woodland.

In the spring, following the winter rains, a rich herbaceous understory composed of annuals, showy-flowered geophytes and perennial herbs associated with a pollinating fauna composed of semi-social and solitary bees, hummingbirds, flies and beetles (Uslar, 1982) appears in the inter-tree spaces. Common annuals in the montane forest are *Homalocarpus dichotomus* (Poepp. ex DC.) Math & Const., *Chaetanthera moenchoides* Less, *Calandrinia compressa* Schrad. ex DC., *Pectocarya dimorpha* (Johnst.) Johnst., *Viola* affin. *frigida* Phil. and *Calycera sessiliflora* Phil. Abundant geophytes in the woodland are *Alstroemeria ligtu* L. subsp. *simsii* (Sprengel) Bayer, *A. pallida* Graham, *Leucocoryne ixiooides* (Hook.) Lindley, and *Hippeastrum bicolor* (R. & P.) Baker.

The total native vascular flora on the study site comprises 109 species, belonging to 48 families and 83 genera. *Ephedra andina* Poepp. ex C. A. Mey., a small, prostrate shrub, is the only gymnosperm.

## METHODS

All native species were examined in the field for sex expression, using supplemental bibliographic information where necessary. Species were classed as dioecious, androdioecious, gynodioecious and non-sexually dimorphic. The non-sexually dimorphic category, thus includes true hermaphrodites, monoecious, andromonoecious, gynomonoecious, heterostylous and polygamous species.

Controlled pollinations and other tests were carried out in 47 hermaphrodite species, representing 48% of the total for the community, in order to determine compatibility status, spontaneous selfing capacity and presence of obligate agamospermy. Species were chosen to reflect the life-form spectrum and taxonomic diversity of the community. However, handling possibilities over the

relatively short flowering period and the presence of sufficient individuals of a species in the area for the tests to be performed also influenced species selection.

Self-incompatibility was assessed by comparing the relative seed set per flower for hand self- and cross-pollination (Bawa, 1974; Ruiz & Arroyo, 1978). Unopened flower buds on several individuals of each species in the field were bagged just before anthesis. Over a series of independent visits, one group of open flowers on each of a number of the bagged individuals was self-pollinated using pollen from the same flower or from other open flowers in the bags. A second group of flowers was cross-pollinated with pollen from other individuals in the population.

A third group of previously bagged flowers was labelled without further treatment (untreated) to assess capacity for spontaneous self-pollination. A fourth group of the bagged flowers was emasculated to assess the possibility of obligate agamospermy. The last test was not performed for Asteraceae and some very small flowered species in other families because of technical difficulties of manipulating the flowers. Following each treatment, all flowers were rebagged until a week or so after the final test was performed. Treatments were scored for fruit and seed set as the fruits matured. To avoid the confounding effects of fruit abortion (see Bawa & Webb, 1984), we were very careful to assess fruit set at an equivalent stage of development in each species. In a limited number of cases, seed counts could not be made for all fruits because of predation or premature dehiscence.

For species where both hand self-pollination and hand-cross were obtained, a continuously varying self-incompatibility index (ISI) (Ruiz & Arroyo, 1978) was calculated. We considered all species in which less than 20% seed set per flower was obtained under hand self-pollination in comparison with hand cross-pollination as self-incompatible (Bawa, 1974; Ruiz & Arroyo, 1978; Sobrevila & Arroyo, 1982; Arroyo & Squeo, 1990).

We were unable to complete the full series of tests in a number of species. Species for which the cross-pollination data are lacking but which produced more than 20% fruit set and abundant seed per fruit by hand self-pollination were considered self-compatible. However, those un-cross-pollinated species which produced less than 20% fruit set by self-pollination were considered inconclusive, as the possibility that low fruit set by self-pollination resulted from the bagging conditions could not be excluded.

Absolute fecundity (open fruit and seed production) and relative fecundity (fruit and seed production per flower in open- versus hand-cross pollinated flowers) were assessed in order to determine whether fecundity is affected by compatibility level. For absolute open-pollination fruit set, flowers on marked inflorescences or individual marked flowers on a number of branches of a plant were recorded for several individuals. For relative fecundity, we used the same cross-pollination data used as a control in the self-incompatibility tests. Percent fruit set was arcsine transformed for statistical procedures.

## RESULTS

### *Sexual dimorphism*

The frequency of dioecy in the total native flora is 9.2% (Table 1). The dioecious species are *Baccharis* sp. (Asteraceae), *Ephedra andina* (Ephedraceae),

TABLE 1. Incidence of dioecy in the native flora of a montane sclerophyllous forest in Central Chile. Also shown is the percentage contribution of each life-form in the total flora

Life-form	No. spp. (%)	Dioecy	
		N%	%
Trees	7 (6.42%)	4	57.14
Shrubs*	30 (27.52%)	5	16.67
Perennial herbs†	51 (46.79%)	1	1.96
Annual herbs	21 (19.27%)	0	0
All life-forms	109	10	9.17

\*Includes one columnar cactus.

†Includes suffrutices and one cactus species.  $P = 0.0004$  for herbaceous vs woody species (Fisher's Exact test).

*Kageneckia angustifolia* (Rosaceae), *K. oblonga* (Rosaceae), *Lithrea caustica* (Anacardiaceae), *Maytenus boaria* (Celastraceae), *Mulinum spinosum* (Umbelliferae), *Podanthus mitique* (Compositae), *Schinus montanus* (Anacardiaceae), *Valeriana stricta* (Valerianaceae). The ten sexually dimorphic species belong to seven families and nine genera. Four dioecious species are dominant or common species in the woodland (*Kageneckia angustifolia*, *K. oblonga*, *Schinus montanus*, *Valeriana stricta*), and three of the four strong stump sprouters (*K. angustifolia*, *K. oblonga* and *Lithrea caustica*) in the woodland are dioecious. *Aristolelia chilensis* was seen to have male to morphologically hermaphrodite and female plants. More work is needed to ascertain the functional breeding system of this species.

The frequency of dioecy increases across life-form, from 0% in annual herbs to 2.0% in perennial herbs, 16.7% in shrubs and finally 57.1% in trees (Table 1). Considering shrubs and trees together, dioecy characterizes 24.3% of all woody species. In contrast, 1.4% of the herbaceous flora exhibits dioecy. The one dioecious herbaceous species (*Valeriana stricta*) is suffruticose.

#### Self-incompatibility

Conclusive results were obtained for 37 hermaphrodite species (Table 2). We also considered it important to report inconclusive results (Appendix 1). When breeding system is based only on self-pollination results, as was the case for some of the species studied by us, total results could *underestimate* the true frequency of self-incompatibility in a community in that a negative result for self-pollination is not considered sufficient in itself to conclude self-incompatibility.

Emasculatation produced no strong evidence for obligate apomixis among hermaphrodites species in the woodland (Table 2). A single fruit containing one seed among nine flowers emasculated on seven plants of *Relbunium hypocarpium* is probably a result of pollen contamination.

Fourteen hermaphrodite species (37.8%) were found to be self-incompatible and 23 (62.2%) self-compatible (Tables 2, 3). Four additional species (*Tweedia brevipes*, *Mutisia ilicifolia*, *Adesmia* sp. and *Ribes polyanthes*; Appendix 1) are potentially self-incompatible. Thus, the true frequency of self-incompatibility in

TABLE 2. Results of controlled pollinations and other tests performed on native species in the montane sclerophyllous forest, central Chile. Open = flowers observed for open-pollination; untreated = bagged flowers observed for spontaneous self-pollination; self = controlled hand self-pollinated flowers; cross = controlled hand cross-pollinated flowers; emasculated = controlled emasculated flowers observed for agamospermic fruit and seed set; NC = not counted; ISI = Self-incompatibility index; SI = self-incompatible; SC = self-compatible

Species	Test	Flowers (plants)	Fruit set	% Fruit set	Total seed	Average seed/fruit	Average seed/flower	Breeding system (ISI)
<b>Amaryllidaceae</b>								
<i>Astromeria ligta</i> L. subsp. <i>simsii</i> (Sprengel) Bayer Perennial herb	Open Untreated Selfed Crossed Emasculated	365(26) 56(15) 38(14) 17(6) 32(14)	177 14 15 16 0	48.49 25.00 39.47 94.12 0	1091(62) <sup>2</sup> 91(10) 131(13) 322(15) 0	17.60 9.10 10.08 21.47 —	8.53 2.28 3.98 20.20 —	SI (0.197)
<i>Astromeria pallida</i> Graham Perennial herb	Open Untreated Selfed Crossed Emasculated	148(23) 89(22) 49(20) 12(7) 27(18)	96 16 20 11 0	64.87 17.98 40.82 91.67 0	214(23) 95(13) 152(17) 106 —	9.30 7.31 8.94 9.64 —	6.04 1.31 3.65 8.83 —	SC (0.413)
<i>Hippeastrum bicolor</i> (R. & P.) Baker Perennial herb	Open Untreated Selfed Crossed Emasculated	185(30) 52(12) 24(10) 44(16) 27(12)	58 0 0 37 0	31.35 0 0 84.09 0	2713 — — 1730 —	46.78 — — 46.76 —	14.67 — — 39.32 —	SI (0)
<b>Asteraceae</b>								
<i>Chaetanthera moenchoides</i> Less Annual herb	Open Untreated	761(11) 292(8)	629 217	82.65 74.32	629 217	1.00 1.00	0.83 0.74	SC
<i>Haplophragma paucidentatus</i> Phil. Shrub	Open Untreated	665(7) 365(5)	577 303	86.77 83.01	577 305	1.00 1.00	0.87 0.83	SC
<i>Leucheria congesta</i> (D. Don) Phil. Annual herb	Open Untreated	655(10) 370(7)	589 332	89.92 89.72	589 332	1.00 1.00	0.90 0.90	SC
<i>Madia sativa</i> Mol. Annual herb	Open Untreated	437(10) 399(10)	430 389	98.40 97.49	430 389	1.00 1.00	0.98 0.97	SC
<i>Senecio coronopodiophyllus</i> Phil. Suffruticose	Open Untreated	521(10) 367(6)	516 359	99.04 97.82	516 359	1.00 1.00	0.99 0.98	SC

<p> <b>Berberidaceae</b>  <i>Berberis</i> sp.            Shrub         </p>	<p>           154(9)            62(7)            37(7)            0            10(4)            21(7)         </p>	<p>           8            0            0            7            0         </p>	<p>           5.20            0            0            70.00            0         </p>	<p>           28            —            —            24            —         </p>	<p>           3.50            —            —            3.43            —         </p>	<p>           0.18            —            —            2.40            —         </p>	<p>           SI            (0)         </p>
<p> <b>Bignoniaceae</b>  <i>Escrocarpus scaber</i> R. &amp; P.            Suffrutice         </p>	<p>           175(12)            98(10)            44(10)            39(11)            39(10)         </p>	<p>           65            6            15            31            0         </p>	<p>           37.14            6.12            34.09            79.48            0         </p>	<p>           13119(56)            976            1545(8)            6378(26)         </p>	<p>           234.27            162.67            193.13            245.31            —         </p>	<p>           87.01            9.96            65.83            194.99            —         </p>	<p>           SC            (0.338)         </p>
<p> <b>Boraginaceae</b>  <i>Pectocarya dimorpha</i> (Johnst.)            Johnst.            Annual herb         </p>	<p>           87(45)            51(24)            52(38)         </p>	<p>           84            46            50         </p>	<p>           96.55            90.20            96.15         </p>	<p>           262            142            154         </p>	<p>           3.12            3.09            3.08         </p>	<p>           3.01            2.78            2.96         </p>	<p>           SC         </p>
<p> <i>Plagiobothrys tinctorius</i> (R. &amp; P.)            A. Gray            Annual herb         </p>	<p>           55(19)            50(25)            45(30)         </p>	<p>           53            49            45         </p>	<p>           96.36            98.00            100.00         </p>	<p>           134            123            120         </p>	<p>           2.53            2.51            2.67         </p>	<p>           2.44            2.46            2.67         </p>	<p>           SC         </p>
<p> <b>Calyceae</b>  <i>Calyceca sessiliflora</i> Phil.            Annual herb         </p>	<p>           150(7)            117(7)            55(5)         </p>	<p>           130            85            46         </p>	<p>           86.67            72.65            83.64         </p>	<p>           130            85            46         </p>	<p>           1.00            1.00            1.00         </p>	<p>           0.87            0.73            0.84         </p>	<p>           SC         </p>
<p> <b>Geraniaceae</b>  <i>Geranium berterianum</i> Colla ex Savi            Perennial herb         </p>	<p>           52(10)            83(12)            40(11)            28(12)            35(10)         </p>	<p>           46            72            36            25            0         </p>	<p>           88.46            86.74            90.00            89.28            0         </p>	<p>           203            299            159            124            —         </p>	<p>           4.41            4.15            4.42            4.96            —         </p>	<p>           3.90            3.60            3.98            4.43            —         </p>	<p>           SC            (0.898)         </p>
<p> <b>Iridaceae</b>  <i>Siyirichium arenarium</i> Poepp.            Perennial herb         </p>	<p>           253(21)            64(28)            29(19)            28(12)            21(20)         </p>	<p>           107            0            2            25            0         </p>	<p>           42.29            0            6.90            89.29            0         </p>	<p>           842(93)            —            0            224            —         </p>	<p>           9.05            —            0            8.96            —         </p>	<p>           3.83            —            0.00            8.00            —         </p>	<p>           SI            (0)         </p>

TABLE 2.—*contd.*

Species	Test	Flowers (plants)	Fruit set	% Fruit set	Total seed	Average seed/ fruit	Average seed/ flower	Breeding system (SI)
<i>Sisyrinchium philippii</i> Klatt Perennial herb	Open	93(2)	42	45.16	297	7.07	3.19	SC
	Untreated	39(9)	1	2.56	2	2.00	0.05	(0.313)
	Selfed	17(10)	4	23.53	19	4.75	1.12	
	Crossed	24(11)	19	79.17	86	4.53	3.58	
	Emasculated	25(10)	0	0	—	—	—	
Labiatae <i>Stachys albicaulis</i> Lindl. Perennial herb	Open	279(19)	230	82.44	605	2.63	2.17	SC
	Untreated	98(13)	54	55.10	238	4.41	2.43	(0.827)
	Selfed	35(9)	30	85.71	82	2.73	2.34	
	Crossed	42(7)	42	100.00	119	2.83	2.83	
	Emasculated	21(9)	0	0	—	—	—	
Liliaceae <i>Leucocoryne ixionides</i> (Hook.) Lindl. Perennial herb	Open	59(15)	33	55.93	602	18.24	10.20	SI
	Untreated	28(18)	2	7.14	5	2.50	0.18	(0.056)
	Selfed	24(16)	4	16.67	21	5.25	0.88	
	Crossed	25(8)	23	92.00	390	16.96	15.60	
	Emasculated	23(16)	0	0	—	—	—	
Loasaceae <i>Loasa heterophylla</i> (H. & A.) Gilg Perennial herb	Open	59(11)	40	67.80	223	5.58	3.78	SI
	Untreated	21(5)	0	0	—	—	—	(0.029)
	Selfed	14(5)	2	14.29	2	1.00	0.14	
	Crossed	9(5)	8	88.89	43	5.38	4.78	
	Emasculated	9(5)	0	0	—	—	—	
Malvaceae <i>Cristaria dissecta</i> H. & A. Annual herb	Open	73(19)	64	87.67	395	6.17	5.41	SC
	Untreated	56(18)	47	83.93	267	5.68	4.77	(0.831)
	Selfed	35(19)	31	88.57	191	6.16	5.46	
	Crossed	14(10)	14	100.00	92	6.57	6.56	
	Emasculated	16(10)	0	0	—	—	—	
Oxalidaceae <i>Oxalis carmosa</i> Mol. Perennial herb	Open	40(13)	37	92.50	1328(14)	94.86	87.74	SC
	Untreated	95(14)	81	85.26	3784(54)	70.07	59.75	
	Selfed	19(8)	18	94.74	1318(16)	82.38	78.04	
	Emasculated	12(5)	0	0	—	—	—	



Papilionaceae										
<i>Adesmia montana</i> Phil.										
Perennial herb										
Open	212(13)	136	64.15	247	2.21	1.42	SI (0.183)	2.21	1.42	
Untreated	78(17)	13	16.67	22	1.69	0.28		1.69	0.28	
Selfed	51(11)	20	39.21	28	1.40	0.55		1.40	0.55	
Crossed	3(1)	3	100.00	9	3.00	3.00		3.00	3.00	
Emasculated	21(9)	0	0	—	—	—		—	—	
<i>Adesmia mucronata</i> H. & A.										
Annual herb										
Open	118(10)	74	62.71	177	2.39	1.50	SC (0.289)	2.39	1.50	
Untreated	64(12)	28	43.75	60	2.14	0.94		2.14	0.94	
Selfed	16(9)	7	43.75	15	2.14	0.94		2.14	0.94	
Crossed	4(2)	4	100.00	13	3.25	3.25		3.25	3.25	
Emasculated	23(8)	0	0	—	—	—		—	—	
Polygalaceae										
<i>Momina angustifolia</i> DC.										
Perennial herb										
Open	174(14)	82	47.13	82	1.00	0.47	SI (0)	1.00	0.47	
Untreated	52(13)	0	0	—	—	—		—	—	
Selfed	45(13)	0	0	—	—	—		—	—	
Crossed	15(12)	11	73.33	11	1.00	0.73		1.00	0.73	
Emasculated	32(13)	0	0	—	—	—		—	—	
Portulacaceae										
<i>Calandrinia compressa</i> Schrad. ex DC.										
Annual herb										
Open	48(12)	47	97.92	539(37)	14.57	14.26	SC	14.57	14.26	
Untreated	28(8)	27	96.43	311	11.52	11.11		11.52	11.11	
Selfed	22(9)	22	100.00	237(20)	11.85	11.85		11.85	11.85	
Emasculated	6(5)	0	0	—	—	—		—	—	
Open	109(13)	102	93.58	9782(69)	141.77	132.66		SC (0.698)	141.77	132.66
Untreated	42(12)	33	78.57	2381(22)	108.23	85.04	108.23		85.04	
Selfed	17(9)	13	76.47	1678	129.08	98.71	129.08		98.71	
Crossed	13(8)	13	100.00	1698(12)	141.50	141.50	141.50		141.50	
Emasculated	27(10)	0	0	—	—	—	—		—	
<i>Calandrinia prostrata</i> Phil. ex DC.										
Annual herb										
Open	49(8)	49	100.00	419(48)	8.73	8.73	SC (0.992)	8.73	8.73	
Untreated	45(12)	44	97.78	379	8.61	8.42		8.61	8.42	
Selfed	14(4)	14	100.00	118	8.43	8.43		8.43	8.43	
Crossed	4(2)	4	100.00	34	8.50	8.50		8.50	8.50	
Emasculated	3(3)	0	0	—	—	—		—	—	
Rhamnaceae										
<i>Taquetia quinquenervia</i> (Gill. & Hook.) Johnston.										
Shrub										
Open	672(15)	328	48.80	328	1.00	0.49	SI (0.169)	1.00	0.49	
Untreated	497(14)	19(48) <sup>3</sup>	3.82	11(11)	1.00	0.04		1.00	0.04	
Selfed	65(10)	9	13.85	7(7)	1.00	0.14		1.00	0.14	
Crossed	12(7)	10	83.33	10	1.00	0.83		1.00	0.83	
Emasculated	50(10)	0	0	—	—	—		—	—	

TABLE 2.- *contd.*

Species	Test	Flowers (plants)	Fruit set	% Fruit set	Total seed	Average seed/ fruit	Average seed/ flower	Breeding system (ISI)
Rubiaceae								
<i>Rebunium hypocarpium</i> (L.) Hemsl.	Open	31(7)	31	100.00	54	1.74	1.74	SC (0.880)
Perennial herb	Untreated	34(7)	33	97.06	56	1.70	1.65	
	Selcd	21(7)	21	100.00	37	1.76	1.76	
	Crosscd	3(3)	3	100.00	6	2.00	2.00	
	Emasculated	9(7)	1	11.11	1	1.00	0.11	
Scrophulariaceae								
<i>Calceolaria purpurata</i> Graham	Open	99(5)	29	29.29	2467(21)	111.48	34.41	SI (0.049)
Perennial herb	Untreated	25(5)	0	0	—	—	—	
	Selcd	15(4)	3	20.00	64	21.33	4.27	
	Crosscd	11(5)	9	81.81	959	106.56	87.81	
	Emasculated	17(5)	0	0	—	—	—	
<i>Calceolaria</i> sp. <sup>1</sup>	Open	235(15)	88	37.45	13928(54)	257.92	96.59	SI (0.183)
Perennial herb	Untreated	98(15)	9(15)	9.18	596(9)	66.22	6.08	
	Selcd	46(12)	7	15.22	NC	—	—	
	Crosscd	12(7)	10	83.33	2608(9)	289.78	241.48	
	Emasculated	53(14)	0	0	—	—	—	
Solanaceae								
<i>Salpiglossis sinuata</i> R. & P.	Open	212(25)	88	41.51	11195(66)	169.62	70.41	SI (0.119)
Perennial herb	Untreated	58(13)	5	8.62	484(4)	121.00	10.43	
	Selcd	30(10)	7	23.33	957	136.71	31.90	
	Crosscd	22(12)	22	100.00	5914	268.82	268.82	
	Emasculated	24(10)	0	0	—	—	—	

<i>Solanum ligustrinum</i> Lodd. Shrub	Open	109(12)	54	49.54	399	7.39	3.66	SI
	Untreated	100(12)	0	0	—	—	—	(0)
	Selfed	34(9)	0	0	—	—	—	
	Crossed	23(8)	21	91.30	148	7.05	6.44	
	Emasculated	41(12)	0	0	—	—	—	
Tropaeolaceae <i>Tropaeolum tricolor</i> Sweet Perennial herb	Open	77(8)	38	49.35	111	2.92	1.44	SC
	Untreated	33(8)	16	48.49	46	2.88	1.39	
	Selfed	39(8)	21	53.85	63	3.00	1.62	
	Crossed	10(6)	0	0	—	—	—	
	Emasculated	32(8)	0	0	—	—	—	
Umbelliferae <i>Homalocarpus dictyolomus</i> (Poepp. ex DC.) Math. et Const. Annual herb	Open	130(10)	83	63.85	136	1.64	1.05	SC
	Untreated	128(12)	53	41.41	83	1.57	0.65	
	Selfed	14(6)	8	57.14	13	1.63	0.93	
	Emasculated	13(8)	0	—	—	—	—	
	Open	104(17)	98	94.23	796	8.12	7.65	SC
Violaceae <i>Viola</i> sp. Annual herb	Untreated	39(12)	28	71.79	212	7.57	5.44	
	Selfed	16(7)	15	93.75	119	7.93	7.44	
	Open	75(11)	26	34.67	34(20)	1.70	0.60	SI
Vivianaceae <i>Viviania marifolia</i> Cav. Shrub	Untreated	42(10)	0	0	—	—	—	(0)
	Selfed	31(10)	0	0	—	—	—	
	Crossed	25(7)	16	64.00	27	1.69	1.08	
	Emasculated	19(10)	0	0	—	—	—	
	Open	19(10)	0	0	—	—	—	

<sup>1</sup>ISI based on fruit set data; <sup>2</sup>Indicates number of fruits counted of total obtained; <sup>3</sup>some 'fruits' with fully aborted seeds.

TABLE 3. Frequency of self-incompatibility in native hermaphrodite species according to life-form and in the total sample of species studied in the montane sclerophyllous forest in central Chile

Life-form	Total species	Self-compatible		Self-incompatible	
		N	%	N	%
Annual herbs (11 gen./8 fam.)	12	12	100.00	0	0.00
Perennial herbs* (16 gen./16 fam.)	20	10	50.00	10	50.00
Shrubs (5 gen./5 fam.)	5	1	20.00	4	80.00
Total sample	37	23	62.16	14	37.84

\*Includes suffrutices.  $P = 0.004$  for annual vs perennial herbs;  $P = 0.002$  for annual herbs vs shrubs;  $P = 0.341$  for perennial herbs vs shrubs.

the complete sample of species studied could be higher than we report. Eleven families and 13 genera were represented among the self-incompatible species and 16 and 21, respectively among the self-compatible taxa. Such taxonomic diversity among breeding system groups probably precludes any strong taxonomic bias among the results. Further support for this is seen in *Alstroemeria*, *Adesmia* and *Sisyrinchium* where both self-incompatible and self-compatible species are found in the same genus within the woodland.

Six self-incompatible species showed absolute self-incompatibility (*Hippeastrum bicolor*, *Berberis* sp., *Sisyrinchium arenarium*, *Monnina angustifolia*, *Solanum ligustrinum*, *Viviania marifolia*). Self-pollination stimulated some fruit development in *Sisyrinchium arenarium*, however such fruits were devoid of seed (Table 2). Three further species classed as self-incompatible (*Leucocoryne ixioides*, *Loasa heterophylla*, *Calceolaria purpurea*) produced only around 5% relative seed set by selfing. Thus 60% of the species classed as self-incompatible are highly so. The average ISI index for self-incompatible species was 0.073. Thus in general, the level of incompatibility in those species classed as self-incompatible is very high.

The ISI index, calculated for ten of the 23 self-compatible species, fluctuated from 0.313 in *Sisyrinchium philippii* to 0.991 in *Calandrinia prostrata*, with a mean of 0.648. In that there are more highly self-compatible species than moderately self-compatible species (Table 2) among the 14 species that were judged as self-compatible on the basis of more than 20% fruit set without recourse to cross-pollination data, this figure underestimates the mean ISI for self-compatible species in the community. With few exceptions, thus the self-compatible species are strongly self-compatible.

Untreated fruit set in self-compatible species ranged from of 2.6% in *Sisyrinchium philippii* to 98% in *Plagiobothrys tinctorius* with a mean of 65.2% (Tables 2, 4). Thus, many of the self-compatible species show fairly strong selfing capacity. However mean % open fruit set was significantly higher than untreated fruit set, indicating that many of the self-compatible species must be visited by pollinators. The difference between untreated fruit set and open pollination fruit set is strong in *S. philippii* and *Alstroemeria pallida* (Table 2) with large, showy pink flowers that are amply visited by bees (Uslar, 1982; Arroyo, Primack & Armesto, 1982). *Stachys albicaulis*, *Calandrinia grandiflora*, *Adesmia mucronata*, *Homalocarpus dichotomus* and *Viola* affin. *frigida*, are also undoubtedly facultatively outcrossed to some large degree, a conclusion which is supported by

TABLE 4. Untreated, hand self-pollinated and open-pollinated fruit set in genetically self-compatible species in montane sclerophyllous forest in central Chile. The data are for the 18 species for which the three pollination treatments were performed (see Table 2)

Treatment	Percent fruit set		
	Mean	S.D.	Range
Untreated	65.21	31.90	2.56-98.00
Hand-selfed	75.68	26.02	25.53-100.00
Open-pollinated	79.97	20.53	37.14-100.00

$t_{34} = 7.964^{****}$  for untreated vs hand self-pollinated.

$t_{34} = 0.720$ ;  $P = 0.50$  for hand-selfed vs open-pollinated.

$t_{34} = 4.438^{****}$  for untreated vs open-pollinated.

field observations of insect visits in all cases except *Viola* affn. *frigida*. *Calandrinia compressa*, *C. prostrata*, *Calycera sessiliflora*, *Chaetanthera moenchioides*, *Cristaria dissecta*, *Geranium berterianum*, *Leucheria congesta*, *Pectocarya dimorpha*, *Relbunium hypocarpium* and *Senecio coronopodiphyllus* are species in which untreated fruit set was high and similar to open-pollination fruit set. Although all of these species are clearly potentially heavy selfers, insect visitation has been observed in *Geranium berterianum* and *Cristaria dissecta* and thus occasional outcrossing is probable.

Mean % fruit set in the untreated flowers was significantly lower than hand-self-pollinated fruit set (Table 4). Seed set per fruit was also generally lower in the untreated spontaneously selfed flowers in comparison with hand-selfed flowers ( $T_s = 19$ ;  $N = 18$ ;  $P < 0.001$ ; Wilcoxon signed ranks test for two groups). The latter implies that the majority of the self-compatible species, including those with relatively high selfing potential, receive insufficient pollen to attain maximum seed under selfing through spontaneous pollen deposition.

As was seen with sexual dimorphism, self-incompatibility increases across life-form. The 12 native annual herbs are all self-compatible. In contrast, 80% of the shrubs are self-incompatible. Perennial herbs were intermediate for frequency of self-incompatibility (50%). At a finer level, more of the self-compatible perennial herbs are adapted for facultative outcrossing than annuals. Also a strong trend for self-incompatibility is seen among geophytes (3 of 4 species). Each life-form category is taxonomically diverse for genus and family (Table 3). Thus it is unlikely that the correlation between life-form and breeding system seen in the forest is a taxonomic artefact.

The tendency towards stronger adaptation for outcrossing in perennial herbs in comparison with annual herbs at the community level is paralleled within some genera. Annual *Adesmia mucronata* is self-compatible, while *A. montana*, a perennial herb, is self-incompatible. In *Calandrinia*, the annuals *C. prostrata* and *C. compressa* are highly self-compatible and strongly adapted for autogamy. *Calandrinia grandiflora*, a perennial herb, in contrast, is only moderately self-compatible and facultatively outcrossed.

#### Fecundity

Open-pollination absolute fecundity varied greatly among the woodland species (Table 5). At one extreme, *Berberis* sp. with absolute self-incompatibility

TABLE 5. Fecundity of self-incompatible and self-compatible species in the montane sclerophyllous forest.  $F_o =$  open-pollination absolute fecundity;  $F_c =$  hand cross-pollination absolute fecundity\*

Breeding system	$F_o/F_c$														
	Percent fruit set						Seed per fruit								
	Open-pollination		Cross-pollination		Fruit set		Seed per fruit		Seed per flower						
<i>N</i>	$\bar{X}$	SD	<i>N</i>	$\bar{X}$	SD	<i>N</i>	$\bar{X}$	SD	<i>N</i>	$\bar{X}$	SD	<i>N</i>	$\bar{X}$	SD	
Self-compatible	23	82.45	18.93	10	93.96	8.66	10	0.80	0.19	10	0.99	0.22	10	0.78	0.19
Self-incompatible	14	43.33	15.61	14	85.39	10.64	14	0.50	0.17	14	0.95	0.13	14	0.48	0.18
		$t_{35} = 6.135****$		$t_{22} = 2.420*$		$t_{22} = 4.019****$		$t_{22} = 0.4730$ ; N.S.		$t_{22} = 3.939****$					

\**N* varies because all species were not cross-pollinated. \* =  $P < 0.05$ ; \*\*\*\* =  $P < 0.001$ .

set 5.2% fruit, while at the other such species as *Relbunium hypocarpium* and *Calandrinia prostrata* set 100% fruit (Table 2). Mean % open fruit set was significantly lower in the self-incompatible species (Table 5), where proportionately only about half as much fruit was produced in comparison with self-compatible species. Linear regressions of ISI on % fruit set ( $F = 59.341$ ;  $P < 0.001$ ),  $F_o/F_c$ , based on % fruit set ( $F = 44.645$ ;  $P < 0.001$ ) and  $F_o/F_c$ , based on seed/flower crossed ( $F = 24.097$ ;  $P < 0.001$ ) were all significant, confirming the above trend at a finer level.

The average fecundity remained essentially unaltered for self-compatible species but increased somewhat for self-incompatible species using  $F_o/F_c$  whether based on % fruit set or seed set per flower as a result of significantly lower hand cross-pollination fruit set (c. 10% lower) in the self-incompatible species (Table 5). However, the ratio of the number of seeds obtained per open- versus per hand-cross pollinated fruit was close to unity in both breeding system groups and did not differ significantly. Nevertheless, a strongly significant difference in fecundity remains between the two breeding systems groups using the relative measures (Table 5), suggesting that differential abortion is insufficient to explain the initial differences in absolute fecundity.

#### DISCUSSION

The temperate montane sclerophyllous forest, displays a broad range of breeding systems as a result of a strong correlation between breeding system and life-form. The life-form correlate, although well established for some taxonomic groups (e.g. Leguminosae: Arroyo, 1981), has only been clearly demonstrated previously for a few communities (e.g. Bullock, 1985 for sexual dimorphism; Arroyo & Squeo, 1990 for sexual dimorphism and self-incompatibility). In montane sclerophyllous woodland the self-compatible annuals cohabit with self-incompatible, self-compatible and even occasionally dioecious perennial herbs in the inter-tree spaces. In the woody strata self-incompatibility and dioecism predominate.

For given life-forms, the mediterranean-type climate forest appears to be richer in obligate outcrossing species than some tropical forests. In the tropics dioecy is represented in around one-quarter and rarely in as many as one-third of the tree species (Bawa, 1974; Bawa & Opler, 1975; Ruiz & Arroyo, 1978; Sobrevila & Arroyo, 1982; Tanner, 1982; Bawa *et al.*, 1985; Bullock, 1985). Dioecy among the montane sclerophyllous shrubs and herbs also exceeds that reported for equivalent life-forms in a tropical deciduous forest in Mexico (Bullock, 1985) and a montane cloud forest in Venezuela (Sobrevila & Arroyo, 1982).

The high frequency of self-incompatibility among shrubs in the Chilean community exceeds reports for the tropics (40–60%; Ruiz & Arroyo, 1978; Sobrevila; Arroyo, 1982). Interestingly there are relatively more self-incompatible shrubs in our woodland than there are in shrubs and trees combined (76%) and proportionately more absolute self-incompatible species among woody species classed as self-incompatible than in a tropical deciduous forest in Mexico (Bullock, 1985). Also, among shrubs in the sclerophyllous woodland the frequency of self-incompatibility approaches the maximum values reported for trees alone in tropical forests (86–89%; Bawa *et al.*, 1985; Ruiz & Arroyo, 1978).

In some montane tropical forests (Sobrevila & Arroyo, 1982; Tanner, 1982; Hernández & Carreon, 1987) there seem to be relatively fewer self-incompatible trees than there are shrubs in the Chilean woodland. Notwithstanding the limited data for the shrubs in the tropics, it seems then, that as was found for dioecy, self-incompatibility will also turn out to be better represented among the mediterranean-type climate community shrubs than in their tropical counterparts. The little data available for perennial herbs in tropical forests (Kress & Beach, 1989—11% self-incompatible) suggests that a parallel trend is likely to emerge for this life-form.

Although there seems to be more outbreeding in any given life-form in the Chilean mediterranean-type climate woodland in comparison with some tropical woody communities, it remains to be seen whether outcrossing mechanisms are more common considering total flora. The higher proportion of woody taxa in tropical forests might compensate for the seemingly lower life-form specific frequencies of obligate outbreeding.

The pollinator-depauperate and physically harsh cold-arid Patagonian alpine has proportionately more dioecious species considering equivalent life-forms than the mediterranean-type formation, but fewer self-incompatible species among hermaphrodites (Arroyo & Squeo, 1990). The latter difference is particularly notable for perennial herbs which in constituting a high proportion of the alpine flora weigh heavily on the final breeding system spectrum. Extrapolating from the life-form specific frequency of self-incompatibility for the samples of hermaphrodite species studied and the frequency of dioecy, the estimated frequency of xenogamous breeding systems in the Patagonian alpine varied from 27% in the lower alpine to 49% in the upper alpine (Arroyo & Squeo, 1990). In the sclerophyllous woodland the estimated level of obligate xenogamy is higher, reaching 53%. Thus, considering the entire communities, proportionately more species of the woodland seem to be adapted for obligate outbreeding than in the Patagonian alpine.

In British Columbia, Pojar (1974) reported frequencies of self-incompatibility in samples heavily weighted towards the perennial herb life-form of 25% in a salt marsh, 29% in a sphagnum bog and 44% in a sub-alpine meadow. Rathcke (1988) found self-compatibility in seven out of eight species of shrubs in a swamp in south-central Rhode Island, U.S.A. In the only other forest habitat studied to date in which experimental procedures are comparable with those used by us (a boreal forest in New Brunswick, Canada), Barrett & Helenurm (1987) reported self-incompatibility in 36% of 11 hermaphroditic insect-pollinated understorey perennial herbs. Thus, the Chilean sclerophyllous woodland seems to have more self-incompatible species than some North American communities for equivalent life-forms.

Little detailed information is available on breeding systems in other mediterranean-type climate woody communities. Dioecy is reported in 27% of the common woody mediterranean-type climate scrubland species in Spain (Herrera, 1987), a figure consistent with ours. Fruit set in bagged untreated hermaphrodites was low for the Spanish scrublands, indicating that most species are heavily dependent upon pollinators, as occurs in the Chilean community (Herrera, 1987). Moldenke (1979) reports self-incompatibility for many Californian woody chaparral species. However, in that experimental methods are not detailed, it is difficult to assess the Californian report in relation to ours.



Plant breeding systems are considered to be a manifestation of intrinsic life-history constraints (Ledig, 1986), abiotic and biotic selection (Charlesworth & Charlesworth, 1987; Arroyo & Squeo, 1990) and pollination conditions (Wyatt, 1983). In the breeding system literature, there has been a clear but questionable trend to consider the above-mentioned features as independent variables. Moreover, exaggerated weight has been given to pollination conditions (Wyatt, 1983). In an attempt to assess the combined effect of these variables, taking Ledig's (1986) argument into account that long-lived species accumulate larger mutation loads and are thus obliged to maintain obligate outcrossing, Arroyo & Squeo (1990) have argued that outcrossing should in general be strongly favoured in long-lived plant species independently of pollinator availability. This trend may be expressed as life-history constraints being hierarchically more important than pollinator availability in long-lived plant species. In contrast short-lived species should be able to respond to pollinator availability with ease and could lapse into self-compatibility even in pollinator-abundant conditions (Arroyo & Squeo, 1990). In pollinator depauperate conditions long-lived species are likely to adopt anemophily or apomixis over genetic self-compatibility. The same authors have argued that strong life-history related selection for outbreeding in long-lived species should be heightened in habitats where abiotic and biotic pressures determine low seedling recruitment and individual genotype quality becomes of paramount importance (cf. Charlesworth & Charlesworth, 1987).

The aforementioned principles may be examined for montane sclerophyllous woodland. In Chilean sclerophyllous vegetation, seed germination is precarious due to uncertain rainfall events (an abiotic constraint) and tends to be concentrated in nurse sites under trees (Fuentes, Aviles & Segura, 1990). Substantial levels of herbivory have been reported (Montenegro, Jordan & Aljaro, 1980) (a biotic constraint). Many of the dominant woody species strongly adapted for outcrossing in the sclerophyllous woodland, although producing abundant seed are maintained primarily by sprouting as already mentioned, and must live many hundreds of years. The high genetic load expected in such long-lived woody species (Ledig, 1986), should reduce the probability of the survival of selfed genotypes resulting from spontaneous mutations for self-compatibility. The combined action of strong life-history constraints and the above-mentioned intense abiotic and biotic selection should produce exaggerated selection for outbreeding in the woody taxa in the sclerophyllous forest. Such selection apparently has been stronger than in some tropical forests, where trees probably live for shorter time spans, and where abiotic selective effects are perhaps less intense. The perennial and annual herbs of the woodland are subject to the same abiotic and biotic selective regime as the woody species. However, owing to their reduced longevity, selection for outcrossing should be relaxed in relation to the woody species. The strong abiotic selective regime in the woodland, nevertheless, again might explain why outcrossing seems to be more prominent in the perennial herbs of this community than in a tropical community.

A complete assessment of the selective factors determining breeding systems in any community requires evaluation of pollinator availability (cf. Wyatt, 1983). Average relative fecundity for self-incompatible species in the sclerophyllous forest, at face value, suggests that self-incompatible species receive insufficient

effective pollinator visits to realize their physiologically maximum fruit and seed set. Recently Zimmerman (1988) has pointed out that direct comparisons of open- and hand cross-pollination fruit set can lead to ambiguous conclusions concerning pollinator limitation unless the full set of flowers on the experimental inflorescences or plants are cross-pollinated. To the contrary, the plant may increase seed set in the experimental flowers (hand cross-pollinated) by reallocating resources from the unpollinated flowers to the experimental flowers. However, while such an effect was found in *Polemonium foliosissimum* (Zimmerman, 1988), it was essentially lacking in *Glechoma hederacea* (Widen & Widen, 1990), indicating that the response of different plant species might not be uniform. We were unable to hand-pollinate all flowers on the bagged inflorescences of herbaceous species because of logistic difficulties of attending each bagged experiment daily and obviously we did not attempt to pollinate all the flowers on shrubs. Thus without doubt, the Zimmerman (1988) effect could be affecting relative fecundity, particularly in the case of the large woody species. In that our data cannot critically assess pollinator-limitation, the question as to what degree pollinator availability has molded the breeding system spectrum in the Chilean sclerophyllous montane forest must remain open. Crucial for further comprehension of community breeding system spectra are comparisons of pollinator effectivity in tropical and temperate woody communities. Such studies might eventually show that some temperate communities receive more effective pollinator service than their tropical counterparts.

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## APPENDIX 1

Inconclusive results. See Table 2 for explanation of tests

Species	Test	Flowers (plants)	Fruit set	% Fruit set	Total seed	Average seed/ fruit	Average seed/ flower
<b>Asclepiadaceae</b>							
<i>Tweedia brevipes</i> (Phil.) Malme	Open	79(5)	5	6.33	NC	NC	NC
Perennial herb	Untreated	63(4)	0	0	—	—	—
	Selfed	7(3)	0	0	—	—	—
<b>Asteraceae</b>							
<i>Mutisia acerosa</i> Poepp. ex Less.	Open	186(5)	16	8.60	16	1.00	0.09
Shrub	Untreated	128(3)	0	0	—	—	—
	Open	163(13)	61	37.42	61	1.00	0.37
<i>Mutisia ilicifolia</i> Cav.	Untreated	128(3)	2	1.60	2	1.00	0.02
	Selfed	9(2)	0	0	—	—	—
<i>Mutisia rosea</i> Poepp. ex Less.	Open	201(11)	0	0	—	—	—
Suffrutesc	Untreated	187(9)	0	0	—	—	—
<b>Cactaceae</b>							
<i>Horridocactus</i> sp.	Open	44(8)	10	22.73	NC	NC	NC
Succulent	Untreated	116(16)	9	7.96	2137(4)	534.25	42.55
<b>Loasaceae</b>							
<i>Loasa sigmoidea</i> Urban & Gilg	Open	21(13)	14	66.67	444	31.71	21.14
Annual herb	Untreated	11(7)	1	9.09	39	39.00	3.54
	Crossed	9(6)	9	100.00	276	30.67	30.67
	Emasculated	9(5)	0	0	—	—	—
<b>Malesherbiaceae</b>							
<i>Malesherbia linearifolia</i> (Cav.) Pers.	Open	87(8)	28	32.18	395	14.11	4.54
Suffrutesc	Untreated	57(8)	8	14.04	55	6.88	0.97
<b>Papilionaceae</b>							
<i>Adesmia</i> sp.	Open	8(1)	2	25.00	7	3.50	0.88
Perennial herb.	Untreated	16(4)	0	0	—	—	—
	Selfed	10(4)	1	10.00	1	4.00	0.40
<b>Saxifragaceae</b>							
<i>Ribes polyanthes</i> Phil.	Open	358(9)	36	10.06	199	5.53	0.55
Shrub	Untreated	281(7)	14	4.98	74	5.28	0.26
	Selfed	97(6)	0	0	—	—	—
	Crossed	19(6)	0	0	—	—	—
<b>Scrophulariaceae</b>							
<i>Calceolaria thyrsoiflora</i> Graham	Open	165(11)	49	29.70	3622(28)	129.36	38.42
Shrub	Untreated	46(9)	7	15.22	93	13.29	2.02
	Selfed	45(9)	11	24.44	119	17.18	4.20
	Emasculated	42(9)	0	0	—	—	—