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# THE REPRODUCTIVE BIOLOGY OF *SOPHORA FERNANDEZIANA* (LEGUMINOSAE), A VULNERABLE ENDEMIC SPECIES FROM ISLA ROBINSON CRUSOE[1]

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*Sophora fernandeziana* is the only legume endemic to Isla Robinson Crusoe (Archipelago Juan Fernández, Chile); it is uncommon and becoming rare. Although its preservation status is listed as ''vulnerable,'' as with many species, little is known of its reproductive biology. Flowering phenology, floral morphology, nectar features, breeding system, and visitors were analyzed in two populations. Flowering is from late winter to early spring. Flowers last 6 d and have a number of ornithophilous features. A floral nectary begins to secrete highly concentrated nectar 48 h after flowers open. Nectar secretion increases as the flower ages but culminates in active nectar reabsorption as the flower senesces. Nectar production is negatively affected by nectar removal. Self-pollen germinates and tubes grow down the style. However, pollen tubes were only observed to enter the ovaries in open pollinated styles, suggesting the possibility of an ovarian self-incompatibility mechanism. Both sexes of the two hummingbird species that inhabit the island are regular visitors. Low fruit and seed set, low genetic diversity, and a shrinking number of populations all contribute to increased concern about the future of this species—and perhaps the hummingbirds that depend on it.

**Key words:** conservation biology; hummingbirds; island biology; nectar removal; nectar secretion; pollination biology; reproductive biology.

The small Juan Fernández archipelago in the Pacific Ocean is well known for the high level of endemism among the vascular plants (Marticorena et al., 1998). The archipelago basically consists of three islands, all of volcanic origin: Isla Robinson Crusoe (= Masatierra), located 667 km off the coast of continental Chile with an estimated age of 4 million years (my); Isla Alejandro Selkirk (= Masafuera), 181 km farther west and 1–2 my; and Isla Santa Clara, near Isla Robinson Crusoe at 5.8 my (Stuessy et al., 1984).

Unfortunately, more than 62% of the Juan Fernández flora is considered rare, and two species are already extinct (Stuessy et al., 1998). Endemic floras of oceanic islands are lost at higher rates than continental floras (Reid and Miller, 1989; Smith et al., 1993), because human disturbance of the fragile island habitats has taken place on a greater scale than in most continental systems (Loope et al., 1988; Mittermeier et al., 1999). Interestingly, in the Juan Fernández archipelago there were no permanent human settlements before the 16th century (Woodward, 1969); thus, disturbance has been occurring for less than 430 yr. However, its biota is particularly threatened by both anthropogenic and natural phenomena, including fire, erosion, vegetation cutting, grazing and predation by feral animals, and losses of habitat to aggressive introduced exotic weeds (Stuessy et al., 1998). There is increasing urgency for studying and preserving plant species (Carlquist, 1998; Raven, 1998), because island species are part of our biological heritage and are often key organisms for the study of plant evolution and speciation (Crawford and Stuessy, 1997; Baldwin et al., 1998).

Among endemics of the Juan Fernández archipelago there are only two legume species, both in the genus *Sophora* L. (subfam. Papilionoideae) from tribe Sophoreae, a tribe recently shown to be nonmonophyletic (Doyle et al., 2000). Both species belong to section *Edwardsia*, which is considered monophyletic and well differentiated from other *Sophora* (Peña and Cassels, 1996; Hurr et al., 1999; Peña et al., 2000). This section includes 17 island tree species of classical Antarctic-circumpolar distribution across the Pacific, south Atlantic, and Indian Oceans and southwest South America (Polhill, 1981; Peña et al., 2000; Heenan et al., 2001). Each of the two main islands of this archipelago supports one species: *S. fernandeziana* (Phil.) Skottsb. on Isla Robinson Crusoe and *S. masafuerana* (Phil.) Skottsb. on Isla Alejandro Selkirk.

The genus *Sophora* includes 45–50 species of worldwide distribution with its center of diversity in North America (Polhill, 1981; Sousa S. and Rudd, 1993; Peña et al., 2000). Peña et al. (2000) proposed that *Sophora* migrated from North America to South America and subsequently to the Pacific Ocean, suggesting *S. macrocarpa* J. E. Sm. from continental Chile as the likely ancestor of both Fernandezian species. An alternative hypothesis, provided by Hurr et al. (1999), suggests recent dispersal around the southern oceans through buoyant seeds from other non-*Edwardsia* species of the northwest Pacific.

*Sophora fernandeziana*—locally known as ''madera dura''—is a tree up to 10 m tall, with showy flowers and four-winged pods. Previous work on this species focused mainly on systematics (Skottsberg, 1922, 1953; Yakovlev, 1967; Tsoong and Ma, 1981), phylogeny (Peña and Cassels, 1996; Peña et al., 2000), chromosomes (Stiefkens et al., 2001), alkaloids (Hoeneisen et al., 1993), flavonoids (Ruiz et al., 1999), and allozyme diversity (Crawford et al., 2001).

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Little is known of its reproductive biology, other than scattered information on floral visitors, nectar presence (Skottsberg, 1928; Meza, 1988; Colwell, 1989; Bernardello et al., 2002) and pollen morphology (Peña et al., 1993). The same occurs for the genus as a whole: there are only limited data on floral ontogeny (Tucker, 1994), nectar (Haragsim and Macha, 1969; Clinch et al., 1972), pollen (Chung and Lee, 1990; Peña et al., 1993; Ferguson et al., 1994), breeding system (Arroyo, 1981), and floral visitors (Cockerell, 1902; McCann, 1952; Clinch et al., 1972; Godley, 1975; Arroyo, 1981).

As for endangered species in general (Holsinger, 1991; Anderson, 1995), understanding the reproductive biology of *S. fernandeziana* is critical to successful conservation efforts. Its present conservation status is ''vulnerable'' (Hilton-Taylor, 2000) mainly because of its restricted area on a small island, the few remaining known populations (approximately five; Crawford et al., 2001), and the small number of individuals left in the wild (between 50 and 100; T. F. Stuessy, Institüt für Botanik, Universität Wien, personal communication). In addition, Crawford et al. (2001) reported low allozyme genetic diversity at the species level.

In a recent expedition to Isla Robinson Crusoe, we studied the reproductive biology of *S. fernandeziana* addressing the following issues: (1) generalized floral features and the stages of floral development, (2) the pattern of nectar secretion and effects of removal on nectar production, (3) floral visitors and how pollination is accomplished, (4) the breeding system, seed and fruit set, and (5) consideration of these data for the assessment of reproductive strategies and implications for conservation.

## MATERIAL AND METHODS

Unfortunately, *S. fernandeziana* is rare and diminishing, thus, few plants are available for study. The specimens studied were seven trees in a natural population (Chile, Isla Robinson Crusoe, Vaquería, 350 m asl, 11 October 2000, Bernardello 880, CORD, CONN) and three trees planted in 1983 at the CONAF experimental garden, San Juan Bautista, from seeds harvested from the same natural population studied (Bernardello 890, CORD; Anderson 3064, CONN). Wild and cultivated specimens were used for observations of visitors and studies of floral morphology, anatomy, and development, nectar chemical composition, pollen/ovule ratio (P/O), and pollen viability, whereas the planted trees were used for experimental crosses, analyses of nectar secretion patterns and effects of nectar removal.

***Flower lifetime***—Randomly chosen flowers in the bud stage were tagged for identification and bagged using nylon net bags to exclude visitors. Flower longevity was determined from 15 flowers per tree by following their development until they wilted.

***Floral morphology and anatomy***—Flowers ($n = 5$ per tree) were fixed in 70% ethanol, dehydrated in an ethyl alcohol-xylol series, and embedded in Paramat (BDH Laboratory Supplies, Poole, UK). Serial cross- and longitudinal sections were cut at 12 μm, mounted serially, stained with safranin-fast green-hematoxylin, and observed with a compound microscope. To localize stomata or starch grains, nectary tissue was cleared with NaOH (10% aqueous solution), washed with acetic acid : water (1 : 3), spread on a slide, and stained with an aqueous $I_2$-IK solution. Drawings were made using a camera lucida attachment on a stereomicroscope. Photomicrographs were taken on a Zeiss Axiophot microscope (Zeiss, Jena, Germany). using Kodak T-max film, 100 ASA (Kodak, Rochester, New York, USA).

***Nectar***—Due to the huge number of available flowers per tree, nectar extraction on the same tree is unlikely to introduce any bias in our results. Samples were extracted with capillary glass tubes without removing the flowers from the plant and taking special care to prevent damage to the nectaries. The presence of nectar was also checked in buds. Two variables were measured immediately after the extraction: volume (in microliters) using graduated micropipettes, and sugar concentration (percentage of sucrose, mass/total mass) with a pocket refractometer. The amount of sugar produced was expressed in milligrams following Kearns and Inouye (1993). Additional nectar drops were placed on Whatman #1 chromatography paper and dried rapidly. These samples were used subsequently to detect amino acids, lipids, phenols, alkaloids, and reducing acids after Baker and Baker (1975). Sugars were separated by paper chromatography on Whatman #3 chromatography paper with n-butanol : glacial acetic acid : water (3 : 1 : 1, volume/volume) as a solvent (Grant and Beggs, 1989). Dried chromatograms were treated with aniline phthalate to visualize sugars.

The nectar secretion pattern was determined using 13 bagged sets of 5–7 randomly assigned flowers. Data were taken once for each set, allowing the nectar to accumulate until the measurement. Measurements were performed at 0700 and 1900 hours each day, covering the entire flower lifetime. Nectar secretion rate (NSR) per hour was calculated dividing the amount of sugar (in milligrams) produced by the number of hours between the measurements (in milligrams per hour). Nectar reabsorption rate (NRR) per hour was calculated by dividing the amount of sugar (in milligrams) reabsorbed by the number of hours of the time period considered (in milligrams per hour).

Effects of removal on total nectar production were assessed using 12 bagged sets of 5–7 flowers each, on the same trees used for nectar secretion. Nectar was removed and measured from the same flower repeatedly, at 0700 and 1900 hours, throughout the flower lifetime. Sets were subjected to a different number of nectar removals: set 1 = removed 12 times, starting at flower opening; set 2 = removed 11 times, starting 12 h after flower opening; set 3 = removed 10 times, starting 24 h after flower opening; and so on, until reaching set 12 = removed once, at the end of the nectar secretion, having allowed nectar to accumulate until the measurement. To accurately compare the results, the set not involved within the reabsorption period was used as the control.

***Floral visitors***—The 10 trees of both populations studied were observed for a total period of about 30 h. Periods of observation ranged from 10 min to 1 h and were mostly done during daylight hours (0700–1000 hours, 1200–1400 hours, and 1800–2000 hours). Two nocturnal observations of 30 min each were made as well.

***The P/O ratio and pollen viability***—Buds examined for P/O ratios (15 per tree) were near anthesis, i.e., pollen was mature, but anthers had not dehisced. Pollen quantity was estimated using Anderson and Symon's (1989) modification of Lloyd's (1965) technique. With the aid of a dissecting microscope, all ovules were counted. Pollen viability was estimated as the percentage stainability of 100 grains from each of 15 flowers (five per tree) using aniline blue in lactophenol (Hauser and Morrison, 1964).

***Experimental crosses***—Branches with unopened flowers were tagged and bagged with nylon net bags to exclude visitors. Two days later, after the flowers had opened (stages 3–4, Fig. 1), autogamous hand crosses were performed by applying self-pollen from recently opened anthers (using the anthers themselves as pollen applicators) to stigmata. Pollinated flowers ($n = 45$, 15 from each of three trees) were collected and fixed in 70% ethanol 24, 36, and 48 h after pollination for analysis of pollen tube growth. Additional tagged and bagged sets were used to check for autonomous self-pollination and untreated, unbagged flowers for natural pollination; these flowers were collected 5 d after anthesis ($n = 45$, 15 from each tree). Gynoecia were softened with 8 mol/L NaOH for 1 h at 60°C in a water bath, rinsed, and stained in aniline blue 0.1 $NK_3PO_4$ for 2 h (Martin, 1959). Then, they were dissected from the flower on glass slides and flattened. The distance of pollen tubes growth was measured under an epifluorescence microscope.

***Fruit and seed set***—These variables were indirectly estimated by counting the total number of flowers on 30 flowering branches (50 cm long, 10 per

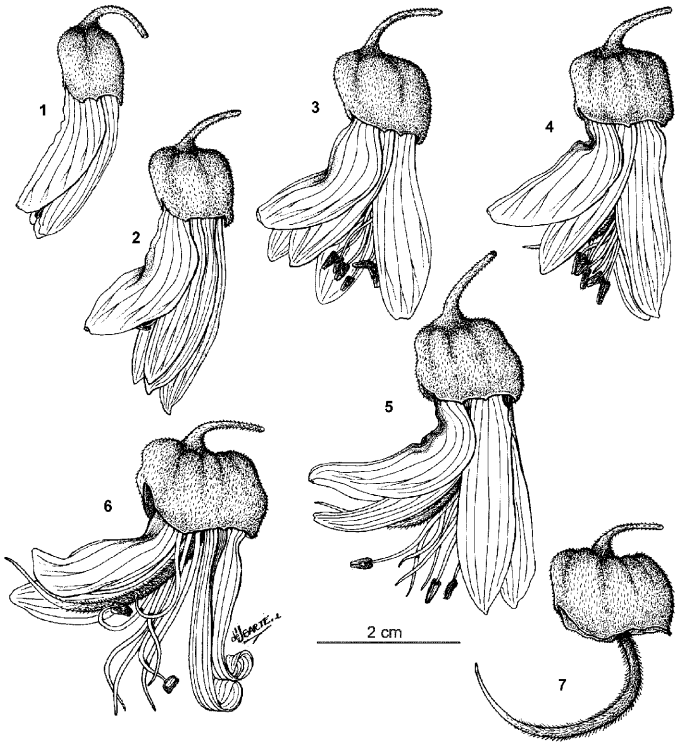


Fig. 1. Flower stages of *Sophora fernandeziana* as described in the text.

tree) and the total number of fruits on 30 fruiting branches of similar length (10 per tree). All seeds per fruit were counted.

***Statistical analyses***—Tests were performed using methods described in Sokal and Rohlf (1995). All distributions were tested for randomness of nominal data (Runs test), homogeneity of variance (Levene test), and departures from normality (Kolmogorov-Smirnov test for goodness of fit). The effects of nectar removal on total nectar sugar production was compared using one-way analysis of variance (ANOVA). Sets subjected to nectar removal were compared with control sets with *t* tests.

## RESULTS

***Phenology***—*Sophora fernandeziana* blooms once a year from late winter to early spring (September–October). Its phenology corresponds to the annual frequency class of Newstrom et al. (1994), with only one annual cycle or flowering episode of an intermediate duration (approximately 2 mo). Fruits develop slowly; they are fully mature and still hanging from the tree in the next flowering season, when they are ready to disperse by gravity.

***Floral features***—Inflorescence axes, and consequently the flowers, are typically pendulous or subpendulous (Figs. 1, 2A). Flowers are showy, golden yellow, odorless, open diurnally, and last for 6 d. They are borne in reduced panicles with 2–12 flowers (Fig. 2A) or rarely singly. There is usually a maximum of three open flowers per inflorescence at the same time. Flowers are zygomorphic with a bowl-shaped, pubescent, fleshy, and obliquely truncated calyx with five small teeth. The corolla has a standard that does not reflex; this petal has a well-formed claw. The lower petals are more or less undifferentiated (i.e., wings and keel are quite similar in length). Wings have abaxial hidden sculpturing on the basal part. Both fertile whorls are exserted: the androecium with 10 free stamens and a stipitate, pubescent ovary with a glabrous style and a moist, small, capitate stigma. There $10 \pm 0.6$ ovules per flower (mean $\pm 1$ SE), whereas amount of pollen reaches a mean of $273\,080 \pm 48\,400$ pollen grains; the P/O ratio is 27 069.

We partitioned floral ontogeny into seven stages, as illustrated in Fig. 1: (1) ca. 3 cm pre-anthesal bud ready to open with bright yellow corolla, standard almost completely folded, and wings and keel separating slightly at the tip of the flower; fertile whorls are included and stamens are about at the level of the stigma (time: 0 h); (2) anthesis initiated, standard beginning to unfold from its base, keel and wings clearly distinct (time: 24 h); (3) open flower of ca. 4 cm long with standard more spread and fertile parts exserted (time: 48 h); (4) flower similar to the previous stage, but with the standard more perpendicular to the keel and fertile whorls more exserted with


Fig. 2. Inflorescences and infructescences of *Sophora fernandeziana*. (A) An inflorescence. Scale bar = 2 cm. (B) A fruiting branch. Scale bar = 4 cm.

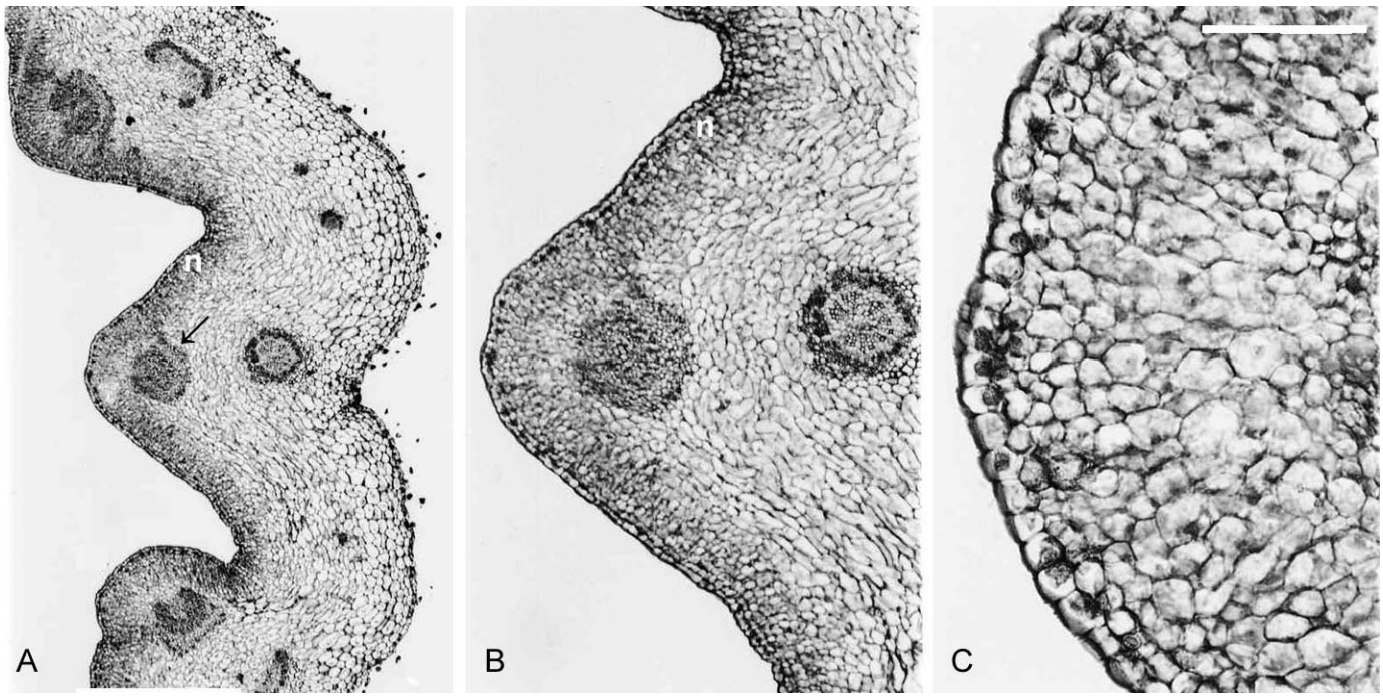


Fig. 3. Optical microscope photomicrographs showing nectary structure in *Sophora fernandeziana*. (A) Flower partial transection; n = nectary, arrow points to a vascular bundle Scale bar = 0.7 mm. (B) Detail of (A). Scale bar = 320 μm. (C) Detail of (B), showing the nectary tissue. Scale bar = 170 μm.

the pistil longer than the stamens (time: 72 h); (5) fully open flower, with standard entirely spread and completely perpendicular to the keel, some anthers may fall, leaving just the filaments, the color of the petals changes to dark yellow or light orange (time: 96 h); (6) flower beginning to fade, petals turn orange, most anthers fall, and filaments curl, whereas the calyx broadens (time: 120 h); (7) all petals and stamens fall, leaving only the calyx and pistil (time: 144 h).

***Nectary***—A structural floral nectary is located in the receptacle between the stamens and the ovary. It is disc-shaped and measures ca. 2 mm lateral, having several protuberances that increase the secretory surface (Fig. 3). Anatomically, it is composed of 10–12 layers of nectaripherous tissue, the cells bear druses, and it is supplied by vascular bundles with phloem and xylem (Fig. 3A–C). Stomata are found uniformly distributed in the epidermis of the nectary.

***Nectar***—Flowers produce nectar with a mean nectar concentration of 52%. Nectar concentration was consistent between the two populations sampled. All nectar samples had amino acids in a concentration of 195 μmol/L (i.e., three on the histidine scale) (Baker and Baker, 1975). Phenols, reducing acids, alkaloids, and lipids were not found. The three main nectar sugars (fructose, glucose, and sucrose) were always detected, but relative percentages could not be calculated.

Data on the nectar secretion pattern throughout the flower life span are plotted in Fig. 4. Nectar is first secreted when flowers are approximately 3 d old (after 48 h; Fig. 4). When nectar secretion starts, the volume and mass of sugar increase slowly until flowers are ca. 84 h old (NSR = 0.104 mg/h); then, both the volume and mass of sugar increase rapidly (NSR = 0.83 mg/h) until they reach maximum production around the fifth day (120 h) after anthesis (Fig. 4A, C). Nectar concentration behaves differently. It increases rapidly as soon as secretion starts and until flowers are about 72 h old. After this, the concentration remains relatively constant (Fig. 4B). At the end of the flower lifetime, there is an active nectar reabsorption period just after the peak of production (Fig. 4C) with a NRR = −0.32 mg/h.

The removal of nectar affects sugar production ($F_{12, 401} = 28.39$, $P < 0.0001$; Table 1). Set 10 was used as the control because it was not involved within the reabsorption period. All sets subjected to removal produced less sugar than the control (Fig. 5). Sets 1–4, in which flowers were subjected to 12, 11, 10, and nine removals, respectively, had a very marked reduction in sugar production, whereas the remaining flower sets, subjected to 8–4 removals, have a progressive increase in nectar production as the number of removals decreased, but none ever reached the sugar amount produced by the control set (Fig. 5).

***Breeding system***—Pollen viability is high (97%). Autonomous self-pollination treatments indicate that self-pollen grains are able to reach the stigma. In addition, both autogamous treatments (autonomous and manual) yielded pollen tubes down the style, although in neither case did pollen tubes reach the ovules. On the other hand, open-pollinated flowers had pollen tubes reaching the apical ovule after 120 h after flower opening.

***Visitors***—Both sexes of the two hummingbird species that inhabit Isla Robinson Crusoe (*Sephanoides fernandensis*, endemic, and *S. sephaniodes*, native) have been observed as regular visitors in the study sites. Hummingbirds can be observed throughout the day at blooming trees, aggressively defending the trees. Given that each tree has a large number of simul-

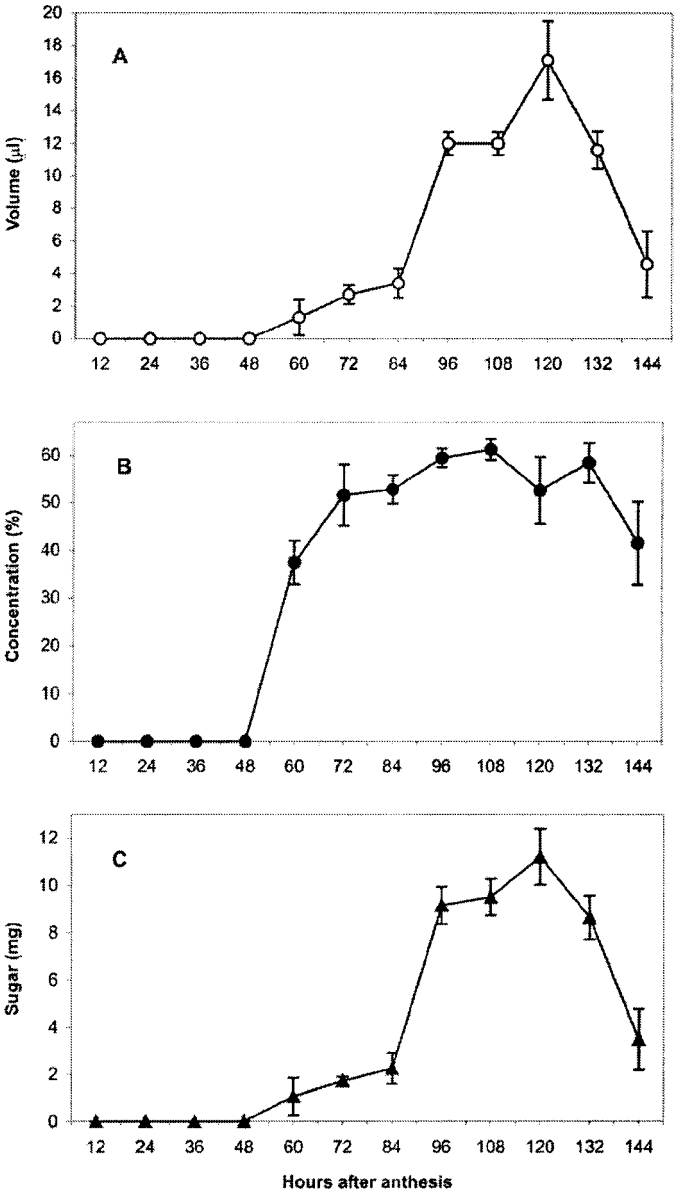


Fig. 4. (A) Nectar volume, (B) nectar concentration, and (C) amount of sugar throughout the flower lifetime of *Sophora fernandeziana*. See Material and Methods for sample sizes.

taneously open flowers, hummingbirds take nectar from several flowers of an individual tree before going to another one.

On the cultivated specimens, introduced Argentine ants (*Linepithema humile*, Formicidae) were observed visiting the flowers and taking nectar, and an introduced curculionid species (*Naupactus xanthographus*, Entiminae) was detected actively eating flowers.

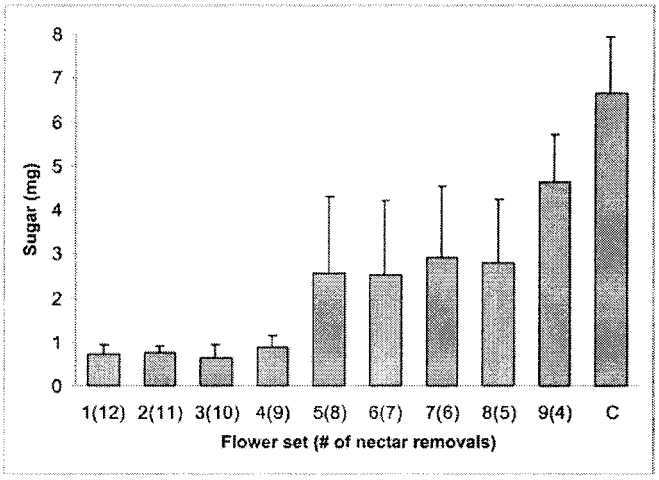


Fig. 5. Histogram of nectar sugar production in flower sets of *Sophora fernandeziana* subjected to periodic removals and control. Values are the means + SD. C = Control. See Material and Methods for sample sizes.

***Fruit and seed production***—Pods are typically four-winged, dry, coriaceous to subligneous, brown, and ultimately dehiscent (Fig. 2B). The natural fruit set is low. Flowering branches average 91 ± 41 flowers ($n$ = 30, 10 per tree, range 25–169), and fruiting branches average 7.4 ± 4.40 fruits ($n$ = 30, 10 per tree, range 1–16). Thus, the indirectly estimated fruit production is about 8%. Seeds are dark brown, dry, and hard. The number of seeds per fruit ranges from 1 to 4 ($x$ = 2.0 ± 0.8; $n$ = 70), i.e., 20% of the ovules became seeds.

## DISCUSSION

***Flower features***—Tribe Sophoreae stands out among the Papilionoideae as the least specialized tribe; however, within it, the genus *Sophora* is considered as one of the more specialized elements (Polhill, 1981; Tucker, 1994). Section *Edwardsia* is distinctive because its members have adaptations for bird pollination, e.g., larger flower size, yellow petals, nearly equal petal size and shape, long exserted stamens, and lack of typical papilionoid corolla structure (Polhill, 1981; Tucker, 1994). In addition to these floral traits, *S. fernandeziana* has other ornithophilous characteristics, such as diurnal anthesis, pendant flower position, large separation of nectar reservoir from stigma and anthers, and odorless flowers (cf. Faegri and van der Pijl, 1979). In a paper on pollen morphology in relation to pollinators in Papilionoideae, Ferguson and Skvarla (1982) included some palynological characters for bird-pollinated taxa: complex exine stratification and verrucate

TABLE 1. Nectar volume (in microliters), concentration (percentage mass/total mass), and mass of sugar (in milligrams) produced in *Sophora fernandeziana* in sets when nectar is experimentally removed (all sets combined) and controls. Values are means ± SD, $t$ = $t$ test values, and $n$ = number of flowers.

| | Volume | | | | Concentration | | | | Mass | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment | Mean ± 1 SD | $n$ | $t$ | $P$ | Mean ± 1 SD | $n$ | $t$ | $P$ | Mean ± 1 SD | $n$ | $t$ | $P$ |
| With removal | 3.85 ± 2.7 | 45 | 2.65 | 0.025 | 37.8 ± 16.8 | 45 | 4.60 | 0.002 | 2.24 ± 1.7 | 45 | 2.77 | 0.021 |
| Control | 10.2 ± 2.06 | 5 | | | 51.6 ± 5.3 | 5 | | | 6.65 ± 1.3 | 5 | | |

or coarsely reticulate ornamentation of the pollen surface. According to Peña et al. (1993), *S. fernandeziana* pollen has reticulate ornamentation with a heterobrochate reticulum, sculpturing compatible with the bird pollination syndrome.

The nectary type we observed in *S. fernandeziana* is characteristic of Papilionoideae (e.g., Waddle and Lersten, 1973; Fahn, 1979; Davis et al., 1988). The presence of stomata is a common feature of floral nectaries of legumes in general (Davis et al., 1988). Studies in *Vicia faba* have demonstrated that the main functions of stomata seem to be those of assisting nectar escape from the gland and, perhaps, enhancement of reabsorption of uncollected nectar (Davis and Gunning, 1993).

***Nectar***—Nectar is the most common reward for the archipelago flora as a whole (Skottsberg, 1928; Bernardello et al., 2000, 2002; Anderson et al., 2001b), including *S. fernandeziana*. Flowers of *S. fernandeziana* do not secrete nectar in bud stage nor on the first 2 d after flower opening. Individual flowers have a large variance in nectar content because nectar removal decreases production and nectar is also reabsorbed. Given that each tree bears many inflorescences throughout the flowering season and that each includes many flowers of different ages at all times, pollinators enjoy a constant nectar supply when dealing with *Sophora*. The amount of reward encountered by animals may affect pollinator behavior, which in turn determines pollen transport and deposition at least within the populations, and therefore the number of autogamous and xenogamous seeds produced (Zimmerman and Pyke, 1986).

Nectar concentration remains relatively constant throughout the flower lifetime, as has been observed in other South American legume species (Cocucci et al., 1992; Galetto et al., 2000). However, nectar volume and the amount of sugar progressively increase as the flower ages. Thus, one might predict an increase in pollination events and mating opportunities (either xenogamous or geitonogamous), during middle and late stages of the flower lifetime (vs. early stages), a conclusion that may also be inferred from morphological traits (see later).

A nectar reabsorption period takes place before the flower wilts. Nectar production obviously involves a cost to the plant in terms of growth and/or reproduction (Pyke, 1991), consequently, the decline in total nectar production following removal and nectar reabsorption in aging flowers would reduce this cost. Reabsorption of nectar allows the plant to reuse the source of carbon for alternative purposes such as developing seeds (Zimmerman, 1988; Burquez and Corbet, 1991), presumably with a consequent reproductive advantage.

Nectar removal strongly decreased nectar production, indicating that nectar secretion may be reduced or stopped after pollinator visits. This reduction in nectar investment also could benefit seed production (Heinrich, 1983). This mechanism also maximizes pollen transfer because hummingbirds would need to visit different flowers and thus perhaps different plants in order to satisfy their metabolic requirements (Feinsinger, 1978).

***Pollination and breeding system***—In oceanic islands pollinator faunas are generally small with many groups completely absent (Carlquist, 1974; Woodell, 1979; Barrett, 1998; McMullen, 1999). This trend was found in the Juan Fernández Islands as well, where floral visitors other than hummingbirds are rare or unknown (Skottsberg, 1928; Anderson et al., 2001; Bernardello et al., 2002). Thus, the wide extent of nectar rewards is a manifestation of the origin of this flora more than it is of its current pollination status (Bernardello et al., 2000; Bernardello et al., 2002). The fauna of the Juan Fernández archipelago is known partly because of the two hummingbird species: one of them is the only endemic known on oceanic islands (*Sephanoides fernandensis*); the other (*S. sephaniodes*) is also found south of the Atacama desert in Chile (Colwell, 1989; Roy et al., 1998). Both sexes of the two species have been recorded as regular visitors of 14 woody angiosperms, i.e., 9% of the flora (Bernardello et al., 2002), including *S. fernandeziana* (Brooke, 1987; Meza, 1988; Colwell, 1989; Bernardello et al., 2000, 2002; Anderson et al., 2001b).

Assuming that there is a coevolutionary relationship between nectar features and type of pollinator, several authors have proposed that certain nectar volumes and concentrations attract different pollinator guilds (e.g., Baker, 1975; Pyke and Waser, 1981; Cruden et al., 1983; Opler, 1983). In particular, hummingbird flowers often bear large amounts (ca. 10–16 μL) of dilute nectar (ca. 20% sugar) (e.g., Cruden et al., 1983; Opler, 1983; Tamm and Gass, 1986). Neither the mean nectar volume (8 μL) nor mean concentration (52%) in *S. fernandeziana* accord with these values. However, under laboratory conditions, hummingbirds given a choice of sugar solutions prefer the highest sugar concentration offered over an equal volume presentation (e.g., Hainsworth and Wolf, 1976; Stiles, 1976; Tamm and Gass, 1986; Mitchell and Paton, 1990). Bees could certainly use this reward as well, but the only bee on Isla Robinson Crusoe (*Lasioglossum fernandezis*; Engel, 2000), is a recent adventive (Anderson et al., 2001a) and is restricted to San Juan Bautista, the only permanent settlement. Even though the cultivated plants (in the CONAF experimental garden) of *S. fernandeziana* are within this range, these small bees were never observed taking *S. fernandeziana* nectar.

*Sophora* elsewhere includes both insect- and bird-pollinated species (Tucker, 1994). Among the pollinating birds are hummingbirds, honeycreepers, honeyeaters, and lorikeets (e.g., McCann, 1952; Clinch et al., 1972; Godley, 1975; Arroyo, 1981; Tucker, 1994). McCann (1952) indicated that the bird pollination of *S. tetraptera* in New Zealand is supplemented or replaced at times by insect pollination, both resulting in fruit set. Bernardello et al. (2002) suggested that the first *Sophora* colonists on the Juan Fernández archipelago would have already been ornithophilous and with the arrival of hummingbirds would have been able to maintain hummingbird pollination. This suggestion is supported by the existence of hummingbird-pollinated species closely related to *S. fernandeziana* in southern South America (Arroyo, 1981), the probable origin of this species (Peña et al., 2000).

Because fertilized flowers take more than a year to develop into fruits, experimental crosses to absolutely determine the breeding system of *S. fernandeziana* were not possible. Self-pollen is capable of germinating and growing in self-stigmas and styles, but self-pollen tubes were not observed penetrating the ovules. However, open-pollinated flowers showed pollen tubes entering the ovules. Under this scenario, ovarian self-incompatibility may be operating in this species, as previously found in several members of the family (Gibbs and Bianchi, 1999), but additional experimental data are needed.

With a large simultaneous floral display on individuals, as in this species, pollinators (particularly hummingbirds) may tend to spend more time among flowers of the same individual, a behavior yielding more geitonogamous than xenogamous

pollen transfer, thereby increasing selfing (Lloyd and Schoen, 1992).

Based on the P/O ratio categories proposed by Cruden (1977), *S. fernandeziana* would be obligately xenogamous. Nevertheless, the general pattern found in 25 endemic species from 17 families of the Juan Fernández Islands indicate that most of the cosexual species were found to be self-compatible and to promote selfing through geitonogamy (Anderson et al., 2001).

***Conservation biology***—It is clear that the vulnerable *S. fernandeziana* is prone to the direct and indirect effects of human activities and natural erosion and, within a short period of time, may become critically endangered or even extinct. As an example, the only two specimens found in the Damajuana hill population—at 430 m high along a steep cliff face—in our 1991, 1996, and 1997 field studies (Anderson 1616, CONN), had disappeared in 2000, thus reducing the already few wild populations. This unfortunate fate befell the congeneric *Sophora toromiro*, also belonging to sect. *Edwardsia*, endemic to Easter Island. Once it formed part of the natural vegetation on this island, but it is now extinct in the wild and only survives in cultivation in several botanical gardens of the world (Maunder et al., 2000). The significant corollary of the declining *S. fernandeziana* is the potential effect on the two hummingbird species, the ''signature vertebrates'' of the Juan Fernández, both of which may be imperiled by the decline of *S. fernandeziana*.

The possibility of having a self-incompatible breeding system, together with low fruit and seed set, low genetic diversity, and reduced population size are threats to the continued survival of this species. The ultimate fate of *S. fernandeziana* may depend on preserving the plant–hummingbird relationship including the web of organisms that affect both plant and pollinator, as suggested for the other hummingbird-pollinated species on these islands (Roy et al., 1999; Bernardello et al., 2002) and in general for endangered mutualisms (Kearns et al., 1998). Hummingbirds are pollen transfer agents promoting outcrossing as well as selfing, but reciprocally, *S. fernandeziana* is important for the birds nutrition because when it blooms, there are comparatively few nectar-bearing species available (Skottsberg, 1928).

Sufficient density of conspecifics is fundamental to maintain the level of inter-plant pollen transfer and of effective pollination visits (Kunin, 1997). Many invasives (e.g., *Rubus ulmifolius* Schott, Rosaceae) outcompete endemic species for habitat. If they produce abundant nectar and are visited by hummingbirds, the hummingbirds may be saved, but endemics like *Sophora* may be lost to insufficient visitation and pollination (Brooke, 1987; Colwell, 1989; Bernardello et al., 2000, 2002). Introduced animals are a problem in another context. They may reduce the hummingbird population mainly by eating their eggs (Colwell, 1989) or reduce the plant fruit set by eating flowers, as does the curculionid we observed. This insect species is a serious vineyard pest in Chile and Argentina (Ripa, 1983; Artigas, 1994). It was already known as introduced on Easter Island but not on the Juan Fernández archipelago. Unfortunately, given that it is a polyphagous species, the beetle must be consuming other endemic species on the island as well, and it should be eradicated immediately.

## LITERATURE CITED


ANDERSON, G. J. 1995. Systematics and reproductive biology. *In* P. C. Hoch and A. G. Stephenson [eds.], Experimental and molecular approaches to plant biosystematics, Monographs in systematic botany, vol. 53, 263–272. Missouri Botanical Garden, St. Louis, Missouri, USA.

ANDERSON, G. J., G. BERNARDELLO, AND M. S. ENGEL. 2001a. Conservation implications of a newly discovered bee species on Isla Robinson Crusoe, Chile. *Conservation Biology* 15: 803–805.

ANDERSON, G. J., G. BERNARDELLO, T. F. STUESSY, AND D. CRAWFORD. 2001b. Breeding systems and pollination of selected plants endemic to the Juan Fernandez Islands. *American Journal of Botany* 88: 220–233.

ANDERSON, G. J., AND D. E. SYMON. 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204–219.

ARROYO, M. T. K. 1981. Breeding systems and pollination biology in Leguminosae. *In* R. M. Polhill and P. H. Raven [eds.], Advances in legume systematics, part 2, 723–769. Royal Botanic Gardens, Kew, UK.

ARTIGAS, J. 1994. Entomología económica. Insectos de interés agrícola, forestal y veterinario. Ediciones Universidad de Concepción, vol. 2, Concepción, Chile.

BAKER, H. G. 1975. Sugar concentrations in nectars from hummingbird flowers. *Biotropica* 7: 37–41.

BAKER, H. G., AND I. BAKER. 1975. Studies of nectar-constitution and pollinator–plant coevolution. *In* L. E. Gilbert and P. H. Raven [eds.], Coevolution of animals and plants, 126–152. Columbia University Press, New York, New York, USA.

BALDWIN, B. G., D. J. CRAWFORD, J. F. ORTEGA, S. C. KIM, T. SANG, AND T. F. STUESSY. 1998. Molecular phylogenetic insights on the origin and evolution of oceanic island plants. *In* P. S. Soltis, D. E. Soltis and J. J. Doyle [eds.], Molecular systematics of plants II: DNA sequencing, 410–441. Kluwer Academic, New York, New York. USA.

BARRETT, S. C. H. 1998. The reproductive biology and genetics of island plants. *In* P. R. Grant [ed.], Evolution on islands, 18–34. Oxford University Press, Oxford, UK.

BERNARDELLO, G., G. J. ANDERSON, T. F. STUESSY, AND D. CRAWFORD. 2002. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernández Islands (Chile). *Botanical Review* 67: 255–308.

BERNARDELLO, G., L. GALETTO, AND G. J. ANDERSON. 2000. Floral nectary structure and nectar chemical composition of some species from Robinson Crusoe Island (Chile). *Canadian Journal of Botany* 78: 862–872.

BROOKE, M. DE L. 1987. The birds of the Juan Fernandez Islands, Chile. International Council for Bird Preservation Fauna and Flora Preservation Society, World Wildlife Fund, Cambridge, UK.

BURQUEZ, A., AND S. A. CORBET. 1991. Do flowers reabsorb nectar? *Functional Ecology* 5: 369–379.

CARLQUIST, S. 1974. Island biology. Columbia University Press, New York, New York, USA.

CARLQUIST, S. 1998. Shifting paradigms in island biology. *Aliso* 16: 85–88.

CHUNG, Y., AND S. LEE. 1990. A palynotaxonomic study of the *Sophora* group (Sophoreae, Papilionoideae, Leguminosae). *Korean Journal of Plant Taxonomy* 20: 257–282.

CLINCH, G. P., T. PALMER-JONES, AND J. W. FORSTER. 1972. Effect on honey bees of nectar from the yellow Kowhai (*Sophora macrophylla* Ait.). *New Zealand Journal of Agricultural Research* 15: 194–201.

COCKERELL, T. D. A. 1902. Flowers and insects in New Mexico. *American Naturalist* 36: 809–817.

COCUCCI, A. A., L. GALETTO, AND A. SÉRSIC. 1992. El síndrome floral de *Caesalpinia gilliesii* (Fabaceae-Caesalpinoideae). *Darwiniana* 31: 111–135.

COLWELL, R. K. 1989. Hummingbirds of the Juan Fernandez Islands: natural history, evolution and population status. *Ibis* 131: 548–566.

CRAWFORD, D., E. RUIZ, T. STUESSY, E. TEPE, P. AQUEVEQUE, F. GONZALEZ, R. JENSEN, G. J. ANDERSON, G. BERNARDELLO, M. BAEZA, U. SWENSON, AND M. SILVA O. 2001. Allozyme diversity in endemic flowering plant species of the Juan Fernandez Archipelago, Chile: ecological and historical factors with implications for conservation. *American Journal of Botany* 88: 2195–2203.

CRAWFORD, D. J., AND T. F. STUESSY. 1997. Plant speciation on oceanic islands. *In* K. Iwatsuki and P. H. Raven [eds.], Evolution and diversification of land plants, 249–267. Springer Verlag, Tokyo, Japan.

CRUDEN, R. W. 1977. Pollen–ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.

CRUDEN, R. W., S. M. HERMANN, AND S. PETERSON. 1983. Patterns of nectar production and plant–pollinator coevolution. *In* B. Bentley and T. S. Elias [eds.], The biology of nectaries, 80–125. Columbia University Press, New York, New York, USA.

DAVIS, A. R., AND B. E. S. GUNNING. 1993. The modified stomata of the floral nectary of *Vicia faba* L. 3. Physiological aspects, including comparison with foliar stomata. *Botanica Acta* 106: 241–253.

DAVIS, A. R., R. L. PETERSON, AND R. W. SHUEL. 1988. Vasculature and ultrastructure of the floral and stipular nectaries of *Vicia faba* (Leguminosae). *Canadian Journal of Botany* 66: 1435–1448.

DOYLE, J. J., J. A. CHAPPILL, C. D. BAILEY, AND T. KAJITA. 2000. Towards a comprehensive phylogeny of legumes: evidence from rbcL sequences and non-molecular data. *In* P. S. Herendeen and A. Bruneau [eds.], Advances in legume systematics, part 9, 1–20. Royal Botanic Gardens, Kew, UK.

ENGEL, M. S. 2000. A new *Lasioglossum* from the Juan Fernandez Islands (Hymenoptera: Halictidae). *Revista Chilena de Entomología* 27: 5–10.

FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd revised edition. Pergamon Press, Oxford, UK.

FAHN, A. 1979. Secretory tissues in plants. Academic Press, London, UK.

FEINSINGER, P. 1978. Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecological Monographs* 6: 105–128.

FERGUSON, I. K., B. D. SCHRIRE, AND R. SHEPPERSON. 1994. Pollen morphology of the tribe Sophoreae and relationships between subfamilies Caesalpinioideae and Papilionoideae. *In* I. K. Ferguson and S. Tucker [eds.], Advances in legume systematics 6: structural botany, 53–96. Royal Botanic Gardens, Kew, UK.

FERGUSON, I. K., AND J. J. SKVARLA. 1982. Pollen morphology in relation to pollinators in Papilionoideae (Leguminosae). *Botanical Journal of the Linnean Society* 84: 183–193.

GALETTO, L., G. BERNARDELLO, I. C. ISELE, J. VESPRINI, G. SPERONI, AND A. BERDUC. 2000. Reproductive biology of *Erythrina crista-galli* (Fabaceae). *Annals of the Missouri Botanical Garden* 87: 127–145.

GIBBS, P. E., AND M. B. BIANCHI. 1999. Does late-acting self-incompatibility (LSI) show family clustering? Two more species of Bignoniaceae with LSI: *Dolichandra cynanchoides* and *Tabebuia nodosa*. *Annals of Botany* 84: 449–457.

GODLEY, E. J. 1975. Kowhais. *New Zealand Nature Heritage* 5: 1804–1806.

GRANT, W. D., AND J. R. BEGGS. 1989. Carbohydrate analysis of beech honeydew. *New Zealand Journal of Zoology* 16: 283–288.

HAINSWORTH, F. R., AND L. L. WOLF. 1976. Nectar characteristics and food selection by hummingbirds. *Oikos* 25: 101–113.

HARAGSIM, O., AND J. MACHA. 1969. Sugar contained in Japanese sophora (*Sophora japonica*). *Sborník Ceskoslovenské Akademie Zemedelskych Ved. Rostllinna Vyroba* 15: 659–664.

HAUSER, E. J. P., AND J. P. MORRISON. 1964. The cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. *American Journal of Botany* 51: 748–752.

HEENAN, P. B., P. J. DE LANGE, AND A. D. WILTON. 2001. *Sophora* (Fabaceae) in New Zealand: taxonomy, distribution, and biogeography. *New Zealand Journal of Botany* 39: 17–53.

HEINRICH, B. 1983. Insect foraging energetics. *In* C. Jones and R. J. Little [eds.], Handbook of experimental pollination biology, 187–214. Van Nostrand Reinhold, New York, New York, USA.

HILTON-TAYLOR, C. 2000. IUCN red list of threatened species. IUCN, Gland, Switzerland.

HOENEISEN, M., M. SILVA, M. WINK, D. CRAWFORD, AND T. STUESSY. 1993. Alkaloids of *Sophora* of Juan Fernández Islands and related taxa. *Boletín de la Sociedad Chilena de Química* 38: 167–171.

HOLSINGER, K. E. 1991. Conservation of genetic diversity in rare and endangered plants. *In* E. C. Dudley [ed.], The unity of evolutionary biology, 626–633. Dioscorides Press, Portland, Oregon, USA.

HURR, K. A., P. J. LOCKHART, P. B. HEENAN, AND D. PENNY. 1999. Evidence for the recent dispersal of *Sophora* (Leguminosae) around the Southern oceans: molecular data. *Journal of Biogeography* 26: 565–577.

KEARNS, C. A., AND D. W. INOUYE. 1993. Techniques for pollination biologists. University Press of Colorado, Niwot, Colorado, USA.

KEARNS, C. A., D. W. INOUYE, AND N. M. WASER. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology and Systematics* 29: 83–112.

KUNIN, W. E. 1997. Population biology and rarity: on the complexity of density dependence in insect–plant interactions. *In* W. E. Kunin and K. J. Gaston [eds.], The biology of rarity, causes and consequences of rare-common differences, 150–173. Chapman & Hall, London, UK.

LLOYD, D. G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contributions of the Gray Herbarium of Harvard University* 195: 1–134.

LLOYD, D. G., AND D. J. SCHOEN. 1992. Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Science* 153: 358–369.

LOOPE, L. L., O. HAMMAN, AND C. P. STONE. 1988. Comparative conservation biology of oceanic archipelagos. *Bioscience* 38: 272–282.

MARTICORENA, C., T. F. STUESSY, AND C. M. BAEZA. 1998. Catalogue of the vascular flora of the Robinson Crusoe or Juan Fernández Islands, Chile. *Gayana Botánica* 55: 187–211.

MARTIN, F. W. 1959. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Technology* 34: 125–128.

MAUNDER, M., A. CULHAM, B. ALDEN, G. ZIZKA, C. ORLIAC, W. LOBIN, A. BORDEU, J. M. RAMIREZ, AND S. GLISSMANN-GOUGH. 2000. Conservation of the toromiro tree: case study in the management of a plant extinct in the wild. *Conservation Biology* 14: 1341–1350.

MCCANN, C. 1952. The Tui and its food plants. *Notornis* 1952: 6–14.

MCMULLEN, C. K. 1999. Flowering plants of the Galapagos. Cornell University Press, Ithaca, New York, USA.

MEZA H., J. 1988. Conservación del picaflor de Juan Fernández, Informe anual. CONAF, V Región, Valparaíso, Chile.

MITCHELL, R. J., AND D. C. PATON. 1990. Effects of nectar volume and concentration on sugar intake rates of Australian honeyeaters (Meliphagidae). *Oecologia* 83: 238–246.

MITTERMEIER, R. A., N. MYERS, AND C. GOETSCH MITTERMEIER. 1999. Hotspots, earth's biologically richest and most endangered terrestrial ecoregions. Cemex, Mexico City, Mexico.

NEWSTROM, L. E., G. W. FRANKIE, AND H. G. BAKER. 1994. A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica* 26: 141–159.

OPLER, P. 1983. Nectar production in a tropical ecosystem. *In* B. Bentley and T. S. Elias [eds.], The biology of nectaries, 30–79. Columbia University Press, New York, New York, USA.

PEÑA, R. C., AND B. K. CASSELS. 1996. Phylogenetic relationships between Chilean *Sophora* species (Papilionaceae). *Biochemical Ecology and Systematics* 24: 725–733.

PEÑA, R. C., L. ITURRIAGA, G. MONTENEGRO, AND B. K. CASSELS. 2000. Phylogenetic and biogeographic aspects of *Sophora* Sect. *Edwardsia* (Papilionaceae). *Pacific Science* 54: 159–167.

PEÑA, R. C., L. ITURRIAGA, A. M. MUJICA, AND G. MONTENEGRO. 1993. Análisis micromorfológico de polen de *Sophora* (Papilionaceae). Hipótesis filogenética sobre el origen de la sección *Edwardsia*. *Gayana Botánica* 50: 57–65.

POLHILL, R. M. 1981. Sophoreae Sprengel (1818). *In* R. M. Polhill and P. H. Raven [eds.], Advances in legume systematics, part 1, 213–230. Royal Botanic Gardens, Kew, UK.

PYKE, G. H. 1991. What does it cost a plant to produce floral nectar? *Nature* 350: 58–59.

PYKE, G. H., AND N. M. WASER. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica* 13: 260–270.

RAVEN, P. H. 1998. Plant conservation in a changing world. *Aliso* 16: 121–126.

REID, W. V., AND K. R. MILLER. 1989. Extinction: how serious a threat? *In* W. V. Reid and K. R. Miller [eds.], Keeping options alive: the scientific basis for conserving biodiversity, 31–56. World Resources Institute, Washington, D.C., USA.

RIPA, S. R. 1983. El burrito de los frutales y vides *Naupactus xanthographus*. Biología y control. *Boletín de Divulgación del INIA (Chile)* 98: 1–29.

ROY, M. S., J. C. TORRES-MURA, AND F. HERTEL. 1998. Evolution and history of hummingbirds (Aves: Trochilidae) from the Juan Fernandez Islands, Chile. *Ibis* 140: 265–273.

ROY, M. S., J. C. TORRES-MURA, F. HERTEL, M. LEMUS, AND R. SPONER. 1999. Conservation of the Juan Fernandez firecrown and its island habitat. *Oryx* 33: 223–232.

RUIZ, E., C. DONOSO, F. GONZALEZ, J. BECERRA, C. MARTICORENA, AND M. SILVA O. 1999. Phenetic relationships between Juan Fernández and continental Chilean species of *Sophora* (Fabaceae) based on flavonoids. *Boletín de la Sociedad Chilena de Química* 44: 351–356.

SKOTTSBERG, C. 1922. The phanerogams of the Juan Fernandez islands. *In*

C. Skottsberg [ed.], The natural history of the Juan Fernandez and Easter Islands, vol. 2, Botany, 97–240. Almqvist and Wiskell, Uppsala, Sweden.

SKOTTSBERG, C. 1928. Pollinationsbiologie und Samenverbreitung auf den Juan Fernandez Inseln. *In* C. Skottsberg [ed.], The natural history of the Juan Fernandez and Easter Islands, vol. 2, Botany, 503–547. Almqvist and Wiskell, Uppsala, Sweden.

SKOTTSBERG, C. 1953. A supplement to the pteridophytes and phanerogams of Juan Fernandez and Easter Island. *In* C. Skottsberg [ed.], The natural history of the Juan Fernandez and Easter Islands, vol. 2, Botany, 763–792. Almqvist and Wiskell, Uppsala, Sweden.

SMITH, F. D. M., R. M. MAY, R. PELLEW, T. H. JOHNSON, AND K. R. WALTER. 1993. How much do we know about the current extinction rate? *Trends in Ecology and Evolution* 8: 375–378.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. W. H. Freeman, San Francisco, California, USA.

SOUSA, S. M., AND V. RUDD. 1993. Revisión del género *Styphnolobium* (Leguminosae). *Annals of the Missouri Botanical Garden* 80: 270–283.

STIEFKENS, L., G. BERNARDELLO, AND G. J. ANDERSON. 2001. The somatic chromosomes of *Sophora fernandeziana* (Fabaceae), an endemic tree from Robinson Crusoe Island. *Pacific Science* 55: 71–75.

STILES, F. G. 1976. Taste preferences, color preferences, and flower choice in hummingbirds. *Condor* 78: 10–26.

STUESSY, T. F., K. A. FOLAND, J. F. SUTTER, R. W. SANDERS, AND M. SILVA O. 1984. Botanical and geological significance of potassium-argon dates from the Juan Fernandez Islands. *Science* 225: 49–51.

STUESSY, T. F., U. SWENSON, D. J. CRAWFORD, G. J. ANDERSON, AND M. SILVA O. 1998. Plant conservation in the Juan Fernandez archipelago, Chile. *Aliso* 16: 89–101.

TAMM, S., AND C. L. GASS. 1986. Energy intake rates and nectar concentration preferences by hummingbirds. *Oecologia* 70: 20–23.

TSOONG, P. C., AND C. Y. MA. 1981. A study on the genus *Sophora* Linn. (new taxa). *Acta Phytotaxonomica Cínica* 19: 1–22, 143–167.

TUCKER, S. C. 1994. Floral ontogeny in Sophoreae (Leguminosae: Papilionoideae): II. *Sophora* sensu lato (Sophora group). *American Journal of Botany* 81: 368–380.

WADDLE, R. M., AND N. L. LERSTEN. 1973. Morphology of discoid floral nectaries in Leguminosae, especially Tribe Phaseoleae (Papilionoideae). *Phytomorphology* 23: 152–161.

WOODELL, S. R. J. 1979. The role of unspecialized pollinators in the reproductive success of Aldabran plants. *Philosophical Transactions of the Royal Society of London, Series B* 286: 99–108.

WOODWARD, R. L. 1969. Robinson Crusoe Island: a history of the Juan Fernandez Islands. University of North Carolina Press, Chapel Hill, North Carolina, USA.

YAKOVLEV, G. P. 1967. A new system for the genus *Sophora*, and its phylogeny. *Trudy Leningradskogo Khimiko-Farmacevticheskogo Instituta* 17: 50–77 (in Russian).

ZIMMERMAN, M. 1988. Nectar production, flowering phenology and strategies for pollination. *In* J. Lovett-Doust and L. Lovett-Doust [eds.], Plant reproductive ecology, 157–178. Oxford University Press, New York, New York, USA.

ZIMMERMAN, M., AND G. H. PYKE. 1986. Reproduction in *Polemonium*: patterns and implication of floral nectar production and standing crops. *American Journal of Botany* 73: 1405–1415.