Natural Interspecific Hybridization in *Gunnera* (Gunneraceae) of the Juan Fernandez Islands, Chile[1]

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ABSTRACT: Natural interspecific hybridization between *Gunnera bracteata* and *G. peltata* (Gunneraceae) in the Juan Fernandez Islands, Chile, is analyzed morphologically and chemically. Parental types from isolated populations were compared with parents and intermediates occurring together in Quebrada Villagra on Masatierra. Two transects were made in that area, one in a relatively undisturbed site, and another along a disturbed path. Hybrid indexes and distance diagrams were used to analyze morphological relationships, and leaf flavonoids revealed chemical affinities. Minor flavonoid divergence between parental species precluded detailed analysis of dynamics of hybridization. Morphological analysis revealed intermediacy in both transects, with intergradation back toward both parents. It is suggested that introgressive hybridization is occurring in Quebrada Villagra between these two wind-pollinated species, with more hybridization taking place in disturbed regions. Reduction in surface area and changes in the ecology of Masatierra during the past four million years may have brought the two species into closer contact and aided hybridization.

NATURAL HYBRIDIZATION IS A frequent phenomenon among flowering plants (Knobloch 1972, Grant 1981). Although hybrids and hybrid swarms have been detected in nature in many plant groups (Tanowitz and Adams 1986, Doyle and Doyle 1988, Grant and Wilken 1988, Tortosa 1988), the role of hybridization in plant evolution is still controversial (Levin 1979). Hybridization on one hand may be rejected as an evolutionarily important process because of low fitness and sterility of the hybrid derivatives. On the other hand, hybridization may be seen as an important process in the evolution of plant groups because it can be a source of recombination and therefore its importance can be as great as mutation and recombination (Grant 1981). A more realistic perspective is that hybridiza-

tion can have an evolutionarily significant effect if it is followed by establishment of advanced hybrid generations, with or without polyploidy, or by introgression (Grant 1981). Although the breakdown of isolating mechanisms is often the first factor in the appearance of natural interspecific hybrids, the environment determines whether these hybrids, advanced generation hybrids, or introgressants may become established successfully (Stebbins 1950). In a stable environment, hybrids are at a disadvantage with respect to parental populations because all niches are filled and no "hybrid" habitats exist where the hybrids can survive (Anderson 1948). Disturbance of the environment disrupts stable habitats, creating new open areas and new ecological niches that can be exploited by hybrid derivatives. In these new niches, hybrid individuals, with an enriched gene pool (Crins et al. 1988), have higher fitness than the parental populations and can compete successfully with them.

Oceanic islands, because of their recent origin, offer new habitats within a restricted geographical area. Hybridization might be favored in insular areas where segregates can exploit these new habitats and therefore con-

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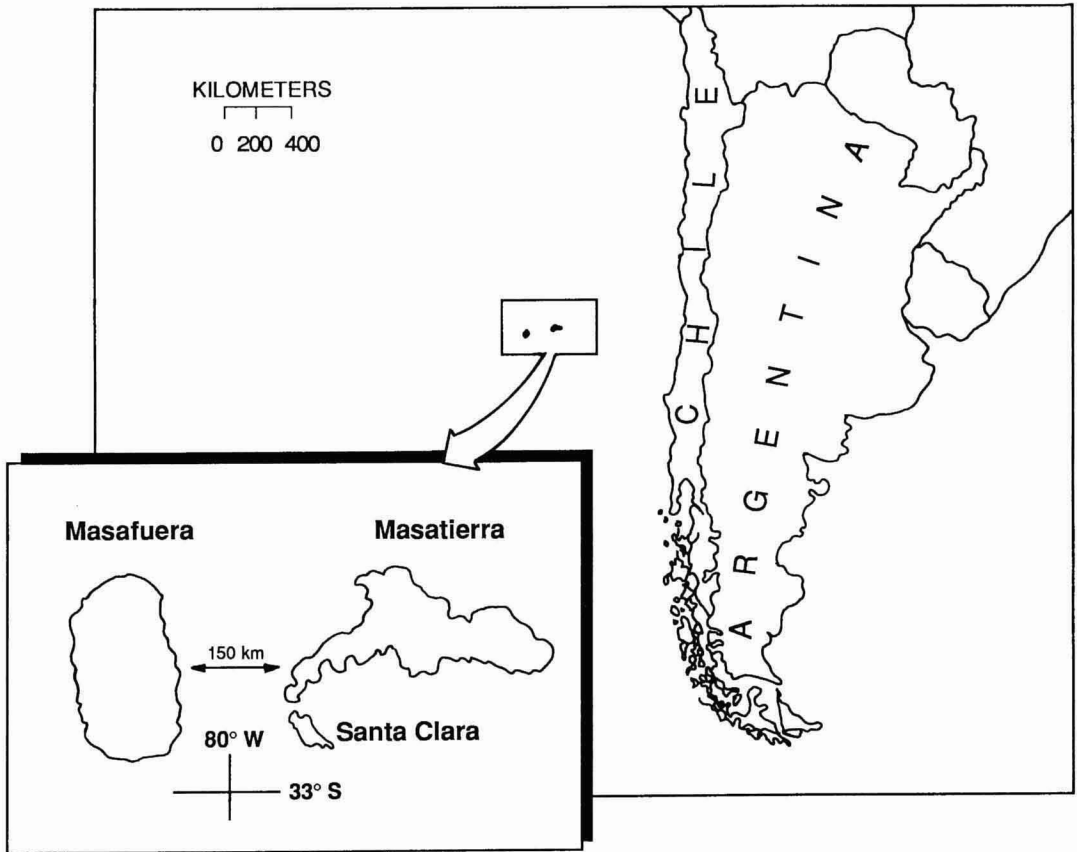
FIGURE 1. Map showing the location of the Juan Fernandez Archipelago in southern South America.

tribute to the evolutionary success of the group. Speciation on islands apparently has been accompanied by little genetic divergence at enzyme loci (Helenurm and Ganders 1985, Lowrey and Crawford 1985, Witter and Carr 1988), and congeneric species are usually highly interfertile (Gillett and Lim 1970, Ganders and Nagata 1984, Lowrey and Crawford 1985, Carr and Kyhos 1981, 1986). Hence the potential for natural interspecific hybridization in floras of oceanic islands is great.

One set of oceanic islands, the Juan Fernandez Archipelago (Figure 1), is a small group of three islands (Masatierra, Masafuera, and Santa Clara), located at 33° S latitude and 580 km west of the coast of Chile. Although its geographical position is not as dramatically isolated as that of the Hawaiian Archipelago, the angiosperm flora does show a 69% endemism at the specific level (Skottsberg 1956).

The most conspicuous example of natural interspecific hybridization in the Juan Fernandez Archipelago occurs in *Gunnera* (Gunneraceae). This genus is represented by three endemic species: *G. bracteata* Steud. ex. J. Benn., *G. masafuerae* Skottsb., and *G. peltata* Phil. All three species belong to subgenus *Panke* (Schindler, 1905), which is the largest group in the genus, with ca. 45 species distributed in South America and Hawaii (Schindler 1905, St. John 1946, Biloni 1959, Mora-Osejo 1978, 1984, Gomez 1983). *Gunnera peltata* is endemic to Masatierra, where it grows from 350 to 500 m. *Gunnera bracteata* is endemic to the same island, but is found at slightly higher elevations, from 400 m to the highest ridges at 600 m. *Gunnera masafuerae* is found on the

younger island (Masafuera), where it grows from 100 m to 1400 m along streams and on the walls of canyons. Skottsberg (1922) commented on a highly variable population of *Gunnera* growing in Quebrada Villagra on Masatierra. He hypothesized that intermediacy was due to hybridization between *G. bracteata* and *G. peltata* but did not investigate the situation further.

There are other reports of hybridization in *Gunnera*. Beutzenberg and Hair (1962) mentioned a possible hybrid swarm between two species growing in New Zealand. Palkovic (1978) suggested hybridization between *G. insignis* and *G. talamancana* in a disturbed area in Costa Rica, and Mora-Osejo (1984) mentioned hybrids between three sympatric species of *Gunnera* in Colombia (*G. atropurpurea*, *G. brephogea*, and *G. pilosa*).

During an expedition to the Juan Fernandez Islands in 1984 we critically reexamined the highly morphologically variable population of *Gunnera* in Quebrada Villagra that was mentioned by Skottsberg (1922). This variable population is of considerable importance because if it is the result of hybridization, it would be the most conspicuous example of interspecific hybridization in the entire flora of the archipelago. The objectives of this paper, therefore, are to (1) use morphological and flavonoid data to clarify whether hybridization does occur between *G. bracteata* and *G. peltata*; (2) understand the nature and dynamics of this hybridization; and (3) evaluate its evolutionary importance.

MATERIALS AND METHODS

Sampling

Plant material and data were collected during expeditions to the Juan Fernandez Archipelago organized by the Departments of Botany of The Ohio State University (OS) and Universidad de Concepcion (CONC), Chile, during January–February 1980, 1984, and 1990. Vouchers of the parental species are on deposit at OS, with duplicates at CONC. Specimens of the hybrid individual samples are at OS only.

Ninety-four individual plants of *G. bracteata* and *G. peltata* and intermediates were analyzed from eight populations (Figure 2). Seven specimens of *G. peltata* are from three isolated pure populations: (1) a population in Plazoleta del Yunque (*Stuessy et al. 6616A*); (2) a population in Quebrada El Pangal (*Stuessy et al.6314*); and (3) a population in a ravine from Cordon Chifladores down toward Puerto Frances (*Stuessy et al. 6671*). Four specimens of *G. bracteata* are from four isolated populations: (1) Valle Colonial (*Stuessy and Sanders 5001H*); (2) Cerro Damajuana (*Stuessy and Sanders 5104*); (3) Corrales de Molina (*Stuessy, Crawford and Wiens 11306*); and (4) Cerro Agudo (*Stuessy and Garcia 11661*). Eighty-three morphologically variable individuals are from an intermediate population in Quebrada Villagra. Two transects were set in that locality (Figure 2). Transect 1 (24 individuals; *Stuessy et al. 6494*) ran from the bottom of the ravine up through the forest from 430 m to 575 m. This habitat has remained almost unchanged and represents a relatively undisturbed environment. Transect 2 (59 individuals; *Stuessy et al 6481*) followed the trail up from the ravine at 145 m to Selkirk's Lookout at 555 m and represents the disturbed habitat. Sampling was nonrandom because an attempt was made to cover variation seen. The largest leaf from each plant was chosen for morphological analysis. Samples for flavonoid analysis were taken at the same time from the same leaf. Four to six scales (modified leaves that cover the apical meristem) were chosen for detailed study.

Morphological Characters

Fifteen characters that best discriminated the two parental species were analyzed both in the field and in herbarium material (Table 1). Only vegetative characters were utilized because no plant was in flower and only a small proportion of individuals had fruits. Each datum represents the mean value of three or four individual measurements. Biological data such as chromosome numbers and pollen fertility would have been helpful in understanding the dynamics of hybridization

**** Transect 1, Quebrada Villagra (6494)
▪ ▪ ▪ Transect 2, Quebrada Villagra (6481)

G. peltata
● Plazoleta del Yunque (6616A)
◑ Quebrada El Pangal (6314)
◐ Puerto Frances (6671)

G. bracteata
■ Valle Colonial (5001H)
□ Cerro Damajuana (5104)
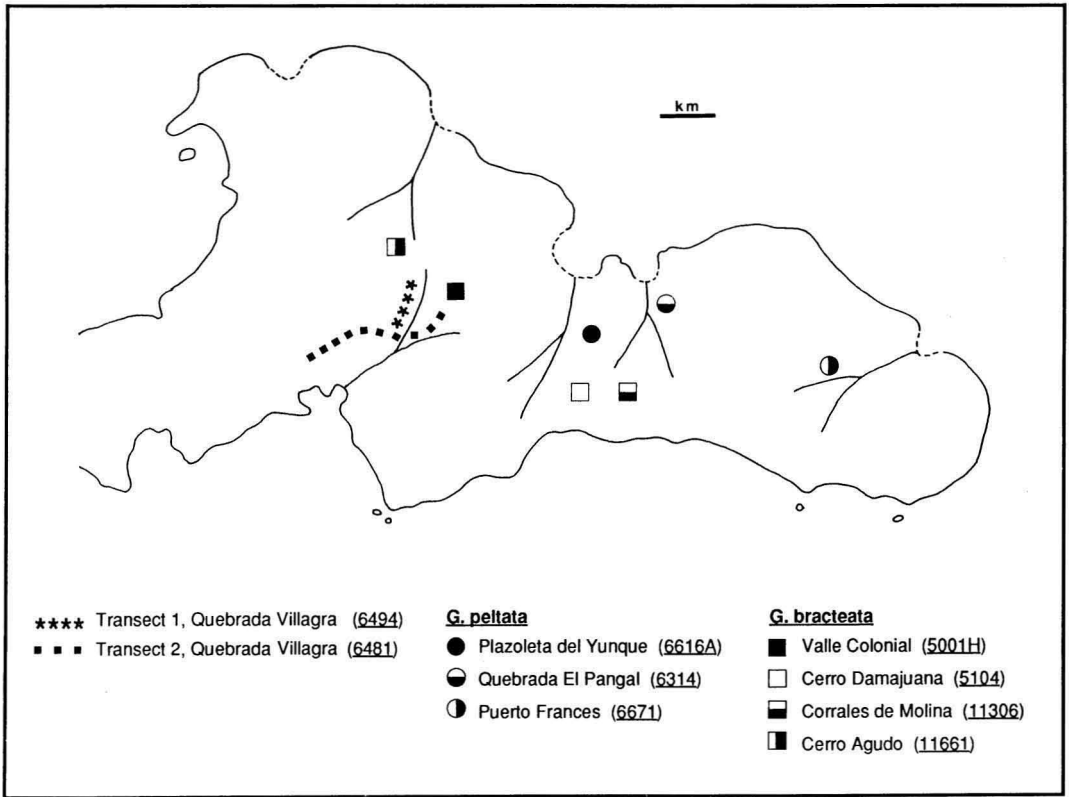▱ Corrales de Molina (11306)
▦ Cerro Agudo (11661)

FIGURE 2. Map of Masatierra showing the locations of pure populations of *Gunnera bracteata* and *G. peltata* and the intermediate zone with transects 1 and 2.

TABLE 1

CHARACTERS USED AND VALUES ASSIGNED TO CHARACTER STATES IN THE MORPHOLOGICAL HYBRID INDEX

	HYBRID INDEX VALUE		
CHARACTER	0	1	2
1. Leaf vestiture	glabrous	intermediate	hirsute
2. Leaf texture	smooth	intermediate	rugose
3. Murications	absent	few	many
4. Leaf (blade) length (cm)	16–37	38–59	60–81
5. Number of mucros on leaf margin (per 3 cm)	0–8	9–17	18–26
6. Height of tertiary teeth (cm)	0–0.6	0.7–1.3	1.4–2
7. Warts on primary veins (per 3 cm)	0–8	9–17	18–26
8. Scale length (cm)	1.5–10	11–20	21–30
9. Scale width (cm)	2.3–1.9	1.8–1.2	1.1–0.5
10. Lascinia length (cm)	0–0.9	1–7	8–15
11. Number of lascinia	absent	few	many
12. Petiole murications	absent	few	many
13. Slime on apical meristem	abundant	scarce	absent
14. Ligule color	green	green/red	red
15. Vein width (mm)	5–10	11–16	17–22

between *G. bracteata* and *G. peltata*, but because both species were in fruit at the time of sampling, it was impossible to collect floral buds and pollen.

Flavonoid Characters

Twenty-six individual plants were chosen for flavonoid studies. These correspond to seven plants of *G. bracteata* with hybrid index scores of 0–1, five individuals of *G. peltata* with hybrid index scores of 24–29, and 14 intermediates with hybrid index scores of 6–21.

Ground leaves were extracted with 85% and 50% aqueous methanol. The combined extracts were evaporated to dryness and taken up in aqueous methanol. The aqueous methanolic-soluble extracts were spotted near the bottom left-hand corner of 46 × 57 cm sheets of Whatman 3MM chromatographic paper and then developed in two dimensions with TBA (ter-butanol : acetic acid : water, 3 : 1 : 1) and 15% acetic acid. The chromatograms were examined over ultraviolet light following standard procedures (Mabry et al. 1970). Individual flavonoids were identified by UV spectral analysis, by hydrolysis in 0.1 N TFA (Wilkins and Bohm 1976), and by circular chromatography of sugars (Becker et al. 1977).

Data Analysis

The data were analyzed by hybrid index values (Anderson 1949) and distance diagrams (Wells 1980). The hybrid index is a method to show visually the population structure and the possible direction of gene flow. The hybrid index requires delimitation of the parental individuals. The characters used were transformed by vector transformation (Brochman 1987) into three classes (Table 1). Zero was defined as similar to *G. bracteata*, one as intermediate, and two as similar to *G. peltata*. The summed index scores ranged from zero to 29.

The distance diagram, a mutivariate approach with equal weight to all characters, also requires a priori recognition of the parental taxa. Two reference points, one for each parental taxon, were determined using all the characters employed in this study. Point A is the lowest reference point and corresponds to the minimum value of the characters for the taxon with the lowest mean. Point B, the highest reference point, is the maximum value of the characters for the taxon with the highest mean. The characters must be ranged between zero and one to give equal weight to the different scales of measurement (Gower 1971).

Morphology

The degree of morphological difference and nature of intermediacy between the two endemic species of *Gunnera* on Masatierra can be shown clearly by examining their scales (Figure 3), which are modified leaves that protect the terminal bud and enclosed apical meristem. In *G. peltata* these scales are red-crimson and deeply laciniate. In *G. bracteata* the scales are green, thin, entire, ovate, and covered by a gelatinous substance produced by cauline glands. The hybrid index more clearly reveals the overall morphological relationships between the two species and the intermediates. Individuals with scores between 22 and 29 represent *G. peltata*, and scores between 0 and 3 represent individuals of *G. bracteata* (Figure 4*A*). Hybrid indices of plants along transect 1 (situated on the northern slope of Quebrada Villagra) are shown in Figure 4*B*. The proportion of hybrid individuals in the undisturbed environment is very low, although some backcrosses to both parents may possibly exist. Figure 4*C* shows the population along transect 2 in the disturbed area. More individuals with hybrid scores between 4 and 21 are seen. Plants with hybrid indices near 15 are morphologically intermediate between the two parental species and most likely represent the central tendency of the F_1 generation. Individuals with hybrid indices of 17 to 21 may be variant F_1s or possibly backcrosses to *G. peltata*. Individuals with hybrid scores of 4 to 13 suggest that backcrosses to *G. bracteata* are also possible
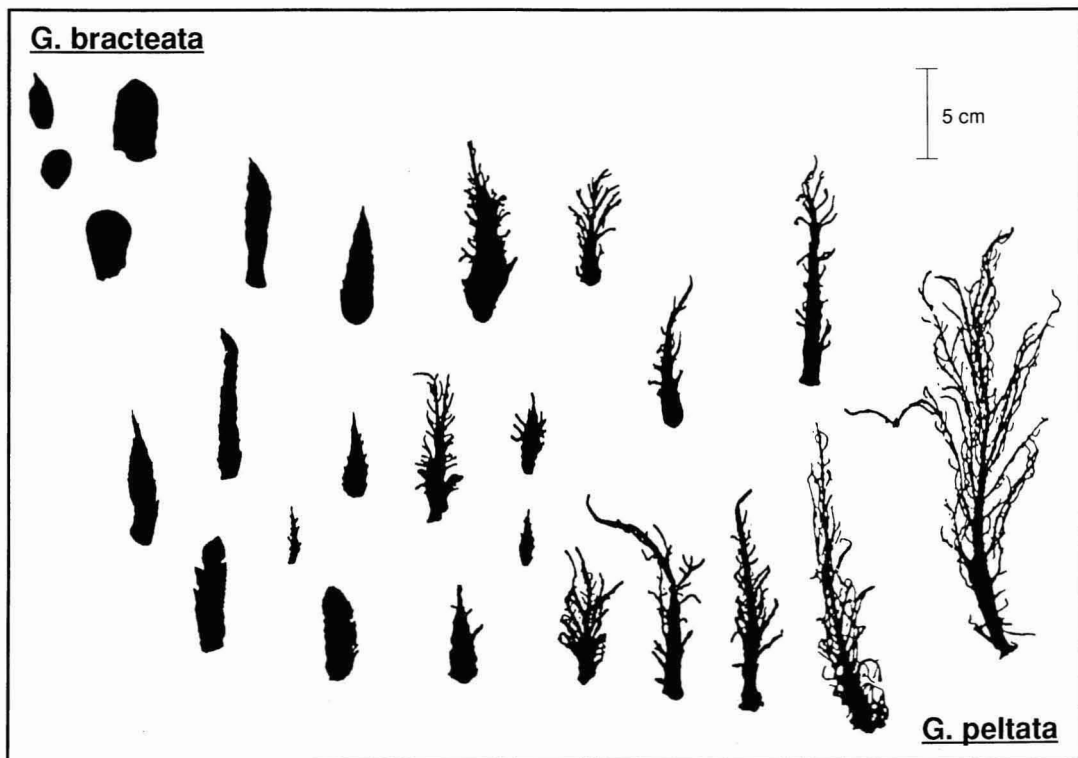
FIGURE 3. Scale silhouettes of the endemic species of *Gunnera* and intermediates on Masatierra. Typical *G. bracteata* forms are shown in the upper left corner, typical *G. peltata* in the lower right corner, and intermediate hybrid variations in between.

in the population. In transect 2, hybrid individuals make up 47% of the population, *G. bracteata* 31%, and *G. peltata* 22%. The distance diagrams gave the same basic results in the two transects and are therefore not shown here.

Flavonoids

A total of eight flavonoids was isolated from the 26 samples of *G. bracteata, G. peltata,* and intermediates. Five flavonoids were fully characterized, one partially identified as a flavone by R_f and UV spectral data, and two remain unknown. The flavonoids are as follows: (1) quercetin 3-0-xylosylglucoside, (2) quercetin 3-0-arabinoside, (3) quercetin 3-0-glucogalactoside, (4) quercetin 3-0-diglucoside, (5) isorhamnetin, (6) a flavone, and (7,8) two unknowns. *Gunnera peltata*

possesses all eight compounds. In *G. bracteata,* quercetin 3-0-glycoside (1) is absent. Infraspecific variation was detected in both species but is most pronounced in *G. bracteata* (flavonoids 4, 5, and 6 are variable). The hybrids show great variation in flavonoid content, especially compounds 1, 4, 5, and 6. Since the parental species differ in only one flavonoid (1), it was not possible to detect complementation of the flavonoid profile in the hybrids, nor to use these data for documenting the exact status of the hybrid individuals (i.e., whether F_1s, backcrosses, etc.).

DISCUSSION

Based on morphological characters, the *Gunnera* population in Quebrada Villagra
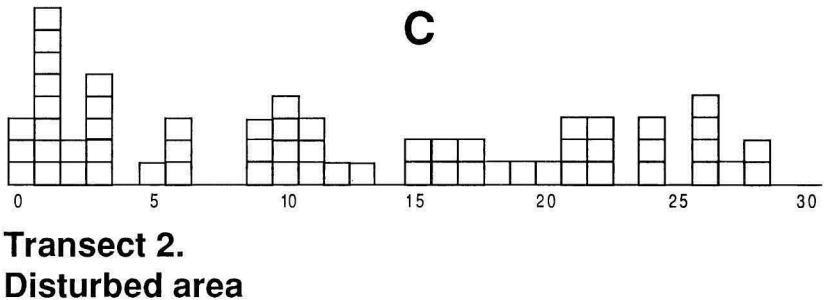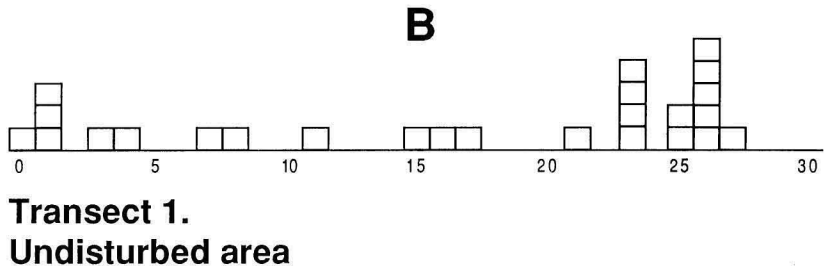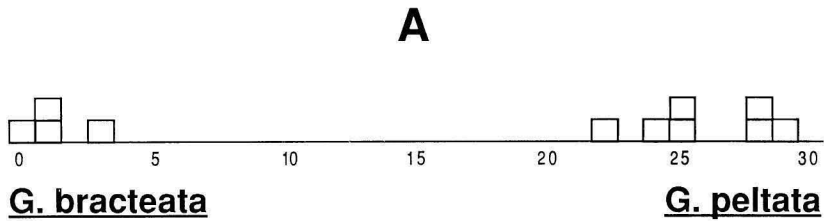
FIGURE 4. Frequency distribution of hybrid index of individuals (boxes) of *Gunnera* growing on Masatierra. Hybrid scale values are derived from the analysis of 15 morphological characters (Table 1). *A*, individuals of *G. peltata* growing in Quebrada El Pangal (*6314*), Plazoleta del Yunque (*6616A*), and Puerto Frances (*6671*); individuals of *G. bracteata* from Valle Colonial (*5001H*), Cerro Damajuana (*5104*), Corrales de Molina (*11306*), and Cerro Agudo (*11661*). *B*, population along the undisturbed north slope of Quebrada Villagra (transect 1, *6494*). *C*, population along disturbed trail in Quebrada Villagra (transect 2, *6481*).

of the Juan Fernandez Islands consists of *G. bracteata* growing in relative abundance toward the highest part of the ridges, *G. peltata* growing at 400–540 m (being most abundant around 450 m), and variable individuals occurring between 250 and 555 m.

The individuals of *Gunnera* growing in Quebrada Villagra were studied in two transects. In transect 1 (Figure 5*A*), located on the north slope of Quebrada Villagra, there is no clear zonation of the two parental species, although in general *G. peltata* is more abundant in the lower portion of the transect and *G. bracteata* in the higher part. Hybrid individuals are present along with the parents, but their percentage is relatively lower when compared with hybrids growing along transect 2 in disturbed areas along the trail (Figure 5*B*).
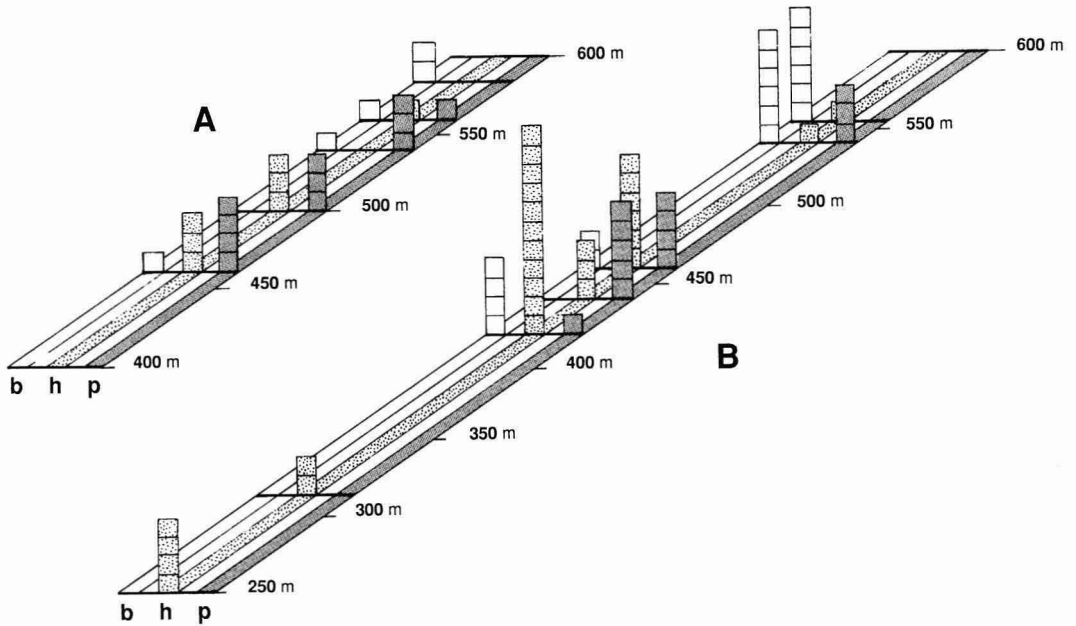
FIGURE 5. Comparison of occurrence of individuals of *Gunnera* in two transects in Quebrada Villagra on Masatierra. b = *G. bracteata* (clear); p = *G. peltata* (shaded); h = hybrid individuals (stippled). Squares represent number of individual plants growing at that elevation. *A*, transect 1, undisturbed. *B*, transect 2, disturbed.

In transect 2, *G. peltata* is absent both at the top of the transect (555 m) and lower than 420 m. The hybrids are found near the highest part of transect 2, and they are equally abundant between 420 and 460 m. *Gunnera bracteata*, although relatively abundant in the highest part of transect 2, also grows intermixed with hybrids and *G. peltata* in places where disturbance of the environment has opened the habitat and it is drier and more exposed. Below 310 m hybrids are abundant. That part of the transect is characterized by landslides due to the construction of a wider road.

The variable population of *Gunnera* growing in Quebrada Villagra meets several criteria of hybridity (Gottlieb 1972). It is morphologically variable, occurs in a disturbed and ecologically intermediate habitat, and is found in a zone of sympatry of the parental taxa. The variable hybrid population of *Gunnera* is known only from Quebrada Villagra and nowhere else in Masatierra. Here the environment has been profoundly disturbed by human intervention and by introduced

animals such as goats and domestic livestock. The construction of the trail in the upper part, and a road in the lower part of Quebrada Villagra, has contributed to the erosion of the soil and to the creation of more hybrid environments and open habitats. Hybridization of the habitat (Anderson 1948), brought about by disturbance of the environment, has created a series of new and different ecological niches. In the lower part of Quebrada Villagra disturbance has created open habitats where the hybrids have survived, probably because of relaxation of interspecific competition and stabilizing selection (Grant 1981). *Gunnera* is a perennial herb with rhizomes, which no doubt contributes to the maintenance of hybrids by asexual reproduction. To this we can add that *Gunnera* is a colonizing species in open habitats and poor soils, a characteristic facilitated by its symbiosis with nitrogen-fixing blue-green algae of the genus *Nostoc* (Towata 1985).

Isolation occurs over a small geographical area on islands. This original geographical

isolation probably has been reduced in *Gunnera* during the geological history of Masatierra, because of the reduction in size of the island (Sanders et al. 1987). Populations of *G. bracteata* and *G. peltata* now occur close enough together to allow overlapping in their distribution. In *Gunnera* protandry and wind-pollinated flowers promote outcrossing (Mora-Osejo 1984, Lowrey and Robinson 1988). Hybridization between the two species of *Gunnera* has been facilitated by the apparent lack of reproductive isolation plus the breeding system. Lack of reproductive isolation is not unique for the endemic species of *Gunnera*; some cases of interspecific hybridization have been reported between pairs of closely related species of *Gunnera* growing on the continent (Palkovic 1978, Mora-Osejo 1984).

All data suggest that the variable population growing in Quebrada Villagra is the result of introgressive hybridization with backcrossing to both parental species but more frequently to *G. peltata*. A factor that contributes to the complex pattern seen in Quebrada Villagra is that *Gunnera* is a perennial herb, and therefore, there are probably some F_1 generation plants intermixed with the introgressants.

We propose the following hypothesis for the evolution of introgressive hybridization in *Gunnera* on Masatierra. *Gunnera bracteata* and *G. peltata* evolved from some common ancestor that arrived in the islands no longer than 4.5 million years ago (Stuessy et al. 1984). The hypothetical ancestor must have been a propagule from *G. tinctoria*, the closest relative in southern South America (Pacheco, Stuessy, Crawford, and Silva, in prep.), or perhaps a common ancestor of *G. tinctoria* and the endemics on the islands. Availability of empty niches and geographical isolation promoted speciation in *Gunnera*. As a result, *G. bracteata* may have speciated into higher elevations (3000 m is estimated for Masatierra during early colonization [Sanders et al. 1987]). Increased aridity and elevation were factors that may have favored smaller and leathery leaves adapted for dry conditions. *Gunnera peltata*, on the other hand, speciated into middle elevations where rainfall and humidity

were high. These conditions are similar to habitats in which *Gunnera* now grows on the mainland. As discussed by Sanders et al. (1987), Masatierra has probably been reduced in size by erosion and submergence, a common trend during geological histories of oceanic islands. This reduction in size, together with changing climates, has brought the two species of *Gunnera* into contact, resulting in a zone of secondary intergradation. Hybridization probably occurred occasionally because of recent divergence and lack of reproductive isolation, but the hybrids had low chance of survival in a stable environment. Once the environment was disturbed because of human intervention, a series of hybridized habitats was created where the hybrids and backcrossed individuals were favored and survived. The result is seen in this variable population in Quebrada Villagra.

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