

Zonation Pattern, Succession Process and Invasion by Aliens in Species-poor Insular Vegetation of the Galápagos Islands

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Abstract

The Galápagos Islands, located 1,000 km west of the South American coast on the equator in the easternmost Pacific, are of volcanic origin. The vascular plant flora is poor and disharmonic, comprising *ca.* 200 endemic taxa. The vegetation is altitudinally arranged, roughly related to the increase in precipitation, from the maritime and dry zones in the lowlands, through the transition and moist zones, to the treeless highland zone. The zonation is deflected upward in elevation on the leeward side of each island and on leeward islands, due to the rainshadow of the southeasterly trade winds which bring moisture to the islands. The treelessness of the highlands is attributed to the fluctuation of weather conditions between extreme dryness and extreme moisture saturation, to which no tree species adapted to such fluctuation has migrated and in which no endemic trees have evolved. Of the flora, an endemic genus *Scalesia* (Compositae) has attracted special attention. The genus consists of 15 heliophilous species, of which 12 are shrubs distributed in the dry lowlands and three are trees found in the moist zone. All the species are allopatric in distribution. *Scalesia pedunculata*, the largest tree of the genus, 12 m high and 15 cm in DBH, predominates in the moist zone of Santa Cruz Island. The canopy population of the dense forest is a cohort of the same age, and nearly all the trees die synchronously at maximum maturity, triggered by a large amount of El Niño rainfall or by extreme drought in La Niña years. Such a stand-level dieback resets the cohort generation, and then self-cyclic succession starts with no successors or shade-tolerant trees. The same was observed in an *S. cordata* forest on Sierra Negra Volcano of Isabela Island. Alien plants, introduced intentionally or accidentally to the islands, are spreading into semi-natural and natural areas as well as in disturbed habitats. Aliens have increased since the first half of the 19th century and now exceed 600 in number of species. Naturalized aliens include tree species that establish self-recruiting populations filling gaps in habitats and tree niches, since the flora is poor in tree species. El Niño rainfall creates favorable conditions for invasive aliens and accelerates their expansion to semi-natural and natural vegetation. Some of the endemic taxa are declining to endangered status due to invasion by alien plants and grazing by introduced animals like goats and donkeys. The vegetation is changing not only in agricultural and town areas but also in part of the Galápagos National Park despite its strict regulations for protection and conservation.

Key words: alien plants, ecological disharmony, endemism, floristic disharmony, habitat, invasiveness, niche, species richness, stand-level dieback, vegetation zonation.

1. Introduction

The Galápagos Islands lie in the easternmost equatorial Pacific, almost on the opposite side of the globe from Japan. The archipelago has been well known since Charles Darwin's books: *The Voyage of the Beagle* (Darwin, 1845) and *The Origin of Species* (Darwin, 1859). Since then the archipelago has attracted a number of biologists, who gave various nicknames to the archipelago, of which "Noah's Arc of the Pacific" (Eibl-Eibesfeldt, 1960) well indicates

the biological nature of the archipelago. I named it the "Cradle of Evolution Theory" (Itow, 1966a, 1983), after Darwin's description, "Hence, both in space and time, we seem to be brought somewhat near to great fact--that mystery of mysteries--the first appearance of new beings on this earth" (Darwin, 1845).

Animals well known as peculiar to the Galápagos Islands include a penguin, flightless cormorant, finches, gulls, land and marine iguanas, giant tortoises and many others. The tameness of those animals is also attractive to visitors from all over the world.

northward along the South American coast.

The Galápagos year can be divided into two seasons: a warm and rainy season from January to May and a cool “garúa” season from June to December (Fig. 2). In the rainy season of a normal year, the southeast trade winds are weak, the South Equatorial Current flows south of the archipelago, warmer water comes from the north, and precipitation occurs in the form of showers. The precipitation in this season accounts for more than two thirds of the annual rainfall, especially at low and middle elevations. In the “garúa”, or cool, season, the trade winds are strong, the cold South Equatorial Current surrounds the archipelago, and precipitation occurs in the form of drizzle, which is called “garúa” in the Galápagos. In this season, the high elevations of the windward islands are usually enveloped heavily by clouds and receive high amounts of precipitation. In El Niño years, which come every 3-6 years, with a major event every 15-20 years, the precipitation and temperature are higher throughout the year. Figure 2 shows the precipitation and temperatures during the 1982-1983 El Niño. In La Niña years, which usually follow El Niño years, the precipitation and temperatures are low. Figure 2 also gives data of the 1985 La Niña.

The descriptions of climate and weather given above are for Santa Cruz, which is a centrally located high-elevation island in the archipelago. The same is nearly true for southerly located, windward, high-elevation islands and volcanoes, like San Cristóbal, Floreana, and the volcanoes of Cerro Azul and Sierra Negra on Isabela Island, which the trade winds hit directly. The leeward islands and slopes, on the other hand, receive less precipitation. The vegetation zonation pattern shows the climatological differences between windward and leeward islands and slopes.

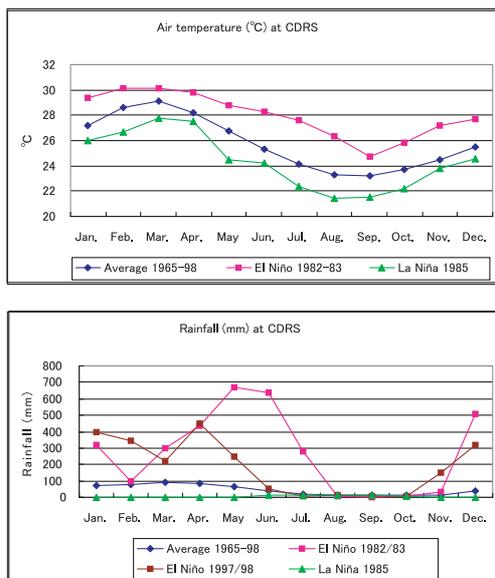


Fig. 2 Air temperature and precipitation patterns at Charles Darwin Research Station (CDRS), Academy Bay, on the south coast of the centrally located island of Santa Cruz. Figures show averages of normal years and anomalies in El Niño and La Niña years.

2.3 Floristic disharmony

Porter (1983) states that most of the Galápagos native flora is derived from Central and Tropical America and the rest from Andean, Caribbean or pantropical regions. He also estimates the number of original introductions, based on the morphology of seeds and fruits adaptive to natural agents of introduction such as birds, winds and oceanic drift. For example, plants bearing berries or drupes are thought to have been introduced by birds internally, wetland plants bearing minute seeds by birds externally, plants bearing minute seeds with parachutes or wings by air, and plants bearing salt-tolerant and buoyant seeds or fruits by oceanic currents. Based on this, the indigenous flowering plant flora (including endemics and non-endemics, excluding human-introduced species) has been derived from 306 introductions by means of natural agents, and the fern flora has been derived from 107 introductions, all by air except a waterfern by birds. Of the 306 natural introductions of flowering plants, 243 (or 79% of the total) were by birds internally in the digestive tract, or externally attached to feathers or webbed feet. Twenty-eight (9%) by wind, and 35 (11%) by oceanic drift. Nearly 80% of natural introductions were by birds, probably because birds carrying seeds from the continent would deliberately aim for other land, including islands, while seeds buoyant on air or sea currents have very little probability of arriving on small remote islands in the vast ocean.

In all cases, birds and winds carry only small seeds, and not large and heavy ones. Natural agents cannot carry all the flora of the source area, but only selected ones. This is the cause of floristic disharmony, or unbalanced constitution of the flora, of remote oceanic islands. The consequences can be seen in the fact that, among the Galápagos' indigenous flora, Agavaceae, Araceae, Cannaceae and Palmae are absent, Bromeliaceae, Hypoxidaceae, Iridaceae, Najadaceae, Ericaceae, Viscaceae, and Vitaceae are families represented by only one species, whereas families with unusually high percentages are small seeded Cyperaceae and Gramineae, externally bird-carried or air-born Compositae, internally bird-carried Boraginaceae, Cactaceae and Solanaceae. The exception is Leguminosae, which bears somewhat large seeds inside of capsules which float and are subject to oceanic drift. Floristic disharmony is one of the important characteristics of oceanic remote island biota. The endemism rate is 7% among the ferns and allied taxa, and 51% among the flowering plants.

2.4 Species poverty

Another aspect of disharmony is the poverty of tree and shrub species in the Galápagos Islands, as compared with continental areas. Tree species poverty can be shown by species diversity indices. The indices I used in my previous study (Itow, 1988) were Fisher's alpha index (Williams, 1947) and

Hurlbert's $S_{(n)}$ index (Hurlbert, 1971). The alpha index can be calculated by the formula

$$S = \alpha \ln(1 + N/\alpha),$$

where S is the total number of species and N is the total number of individuals found in the sampled community, and the alpha value indicates the theoretical number of species represented by single individuals in that biotic community. Larger values indicate that the community consists of a larger number of species.

Hurlbert's index can be calculated by the formula proposed recently by Morisita (1996),

$$S_{(100)} = \sum [1 - (1 - 100/N) x^i],$$

where x^i is the number of individuals in the i -th species, and N is the total number of individuals in the sampled community.

I used both the alpha and $S_{(100)}$ indices to compare the species-richness of trees and shrubs exceeding 3 cm diameter at breast height (DBH) between oceanic islands and continental areas (Itow, 1988). Since I have not collected any such data from continental rainforests, I cited data from Thailand and upper Amazonia. I also studied natural forests in Micronesia (oceanic islands), the Ryukyus (continental islands), the Bonins (Ogasawara) (oceanic islands) and Japan (continental islands). Table 1 compares the index values between continental habitats and oceanic island habitats. Figure 3 shows the

parallel relation of continental species-richness with climatic favorableness represented by Kira's warmth index (Kira, 1977). As seen in this graph, the Galápagos Archipelago is located in a subtropical climate, and the trees and shrubs in the oceanic Galápagos, Micronesia and Bonins are definitely poor in terms of saturation with tree species, nearly half the richness expected based on the climate, as compared with continental forests.

In interpreting ecologically the poverty of tree species on oceanic islands, key concepts are 'habitat' and 'niche.' Habitat means the particular type, or site, of environmental conditions integrated by all factors affecting plant life. The vegetation zones are habitat types in the present study. Niche means the particular status or role of a species in a biotic community. In the present paper, tree, shrub, liana (climbing plant), and herb or grass are plant life-forms corresponding to broad plant niches. The poverty of tree species on oceanic islands implicitly suggests the vacancy of the tree niche in some habitats. This is an ecological aspect of floristic disharmony that should be noted as 'ecological disharmony' to understand the vegetation and ecosystem characteristics of oceanic islands. It will be discussed in detail in the sections on gradient analysis, succession process and invasion by aliens.

Table 1 Comparison of diversity values of natural forest communities as averages and ranges between mainlands and oceanic islands in the subtropical and tropical climates of East Asia, the Pacific and South America. (After Itow, 1988)

	Mainlands and Continental islands		Oceanic islands	
Subtropical				
	Ryukyus		Bonins	
WI		190 - 217		182 - 205
Alpha	11.6	(8.0-16.4)	4.15	(2.4-6.5)
$S_{(100)}$	26.0	(21.0-32.2)	13.2	(9.0-17.3)
Tropical				
	Thailand		Micronesia	
WI		244		210 - 260
Alpha	28.0	(26.2-30.0)	3.4	(1.8-4.9)
$S_{(100)}$	43.0	(41.5-44.4)	11.7	(8.5-15.0)
Equatorial South America				
	Amazonian upstream		Galápagos	
WI		c. 240		200 - 208
Alpha	26.5	(22.6-42.6)	2.1	(0.8-4.4)
$S_{(100)}$	40.5	(37.2-42.6)	7.8	(4.0-13.9)

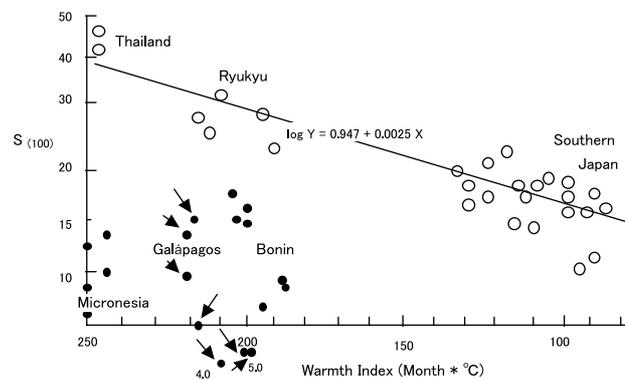


Fig. 3 A regression of species diversity values with the climatic favorableness as represented by Kira's warmth index in continental areas, showing the gaps in values of oceanic islands from the continent. (after Itow, 1988) Arrows indicate values of Galápagos forests. For indices, see text.

3. Patterns in Vegetation Zonation

3.1 Rainshadows

One purpose of my vegetation studies in the Galápagos Islands was to find patterns in space and time, as well as to describe unknown plant communities. I adopted the gradient analysis (Whittaker, 1967) as a method of detecting spatial patterns, and used elevation as the first gradient axis. Fieldwork on uninhabited islands was hard because of bushes and lava fields that were difficult to traverse. In some cases, I observed vegetation and landscapes from the boat, and studied carefully the records made by previous visitors. The vegetation zones I recognized ranged from the maritime zone along the coastline, through the dry zone, transition zone, and moist zone at middle elevations, to the highland zone. Figure 4 is a schematic illustration of vegetation zonation in an east-west cross-section of the archipelago from the easterly located windward island of San Cristóbal, through Santa Fé, and the centrally located Santa Cruz and Pinzón, to the leeward volcano of Alcedo and westernmost Fernandina, along the line of volcanologically old to new volcanoes.

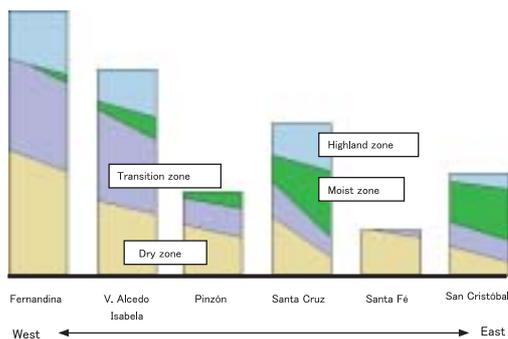


Fig. 4 Schema of vegetation zonation from the volcanologically old, meteorologically windward island of San Cristóbal, through three centrally located islands, to the new and leeward volcano of Alcedo, Isabela Island, and Fernandina.

The vegetation zones, excepting the maritime zone, are deflected upward in elevation on the leeward islands, and the same is true on the leeward north side of individual islands. As described before in the Meteorological section, the southeast trade winds bring moisture to the islands, and clouds develop better and precipitation occurs more heavily on the windward side. The upward deflection of the zones is due to rainshadows of the trade wind (Itows, 1971, 1975, 1992).

Zone boundaries can be identified by changes in zone characteristics, which are given below briefly, but are obscure in some cases where interrupted by recent lava flows.

3.2 Characteristics of the vegetation zones

Maritime zone (Fig. 5a):

Coasts along the shoreline are characterized by

salt-spray resistant vegetation. There are three main habitat types in the maritime zone. They are sand beach, lava coast, and mangrove. (Hereafter asterisks show species endemic to the Galápagos Islands.) Major plants on the beaches are *Amaranthus sclerantoides**, *Sporobolus virginicus*, *Tiquilia darwini**, *T. galapagoa**, and *Ipomoea pes-caprae*. Shrubs on dune crests are *Cryptocarpus pyriformis*, *Vallesia glabra*, *Nolana galapagensis** and *Scaevola plumieri*. Plants common on lava coasts are *Sesuvium edmonstonei** or *S. portulacastrum* in the first belt and *C. pyriformis* in the second. Mangroves of four species, *Rhizophora mangle*, *Avicenia germinans*, *Laguncularia racemosa* and *Conocarpus erecta*, are found on either lava or mud substrate in calm coves and inlets.

Dry zone (Figs. 5b & 5c):

The vegetation is decidedly xerophytic, consisting of white-barked trees and shrubs such as *Bursera graveolens* (most common), *Croton scouleri** (narrow-leaved varieties), *Piscidia carthagenensis*, *Castela galapageia**, *Cordia lutea*, *Tournefortia pubescens** and *Lantana peduncularis**. Some of them are drought-deciduous. Gigantic plants of *Opuntia* species* and *Jasminocereus thouarsii** are prominent in some areas. The other plants restricted to the dry zone are thorny Leguminosae trees and shrubs such as *Acacia* species, *Prosopis juliflora* and *Parkinsonia aculeata*. Of the endemic genus *Scalesia* (Compositae), shrubby species are restricted to the dry zone. The absence of terrestrial and epiphytic ferns is one of the characteristics of the dry zone vegetation, except in cracks in lava. The coloration of the vegetated dry-zone landscape is white to gray due to the white-barked trees and shrubs. The surface of the substrate is nearly completely covered by unweathered lava blocks with little accumulation of organic material in which plants can root.

Transition zone (Fig. 5d):

This zone is literally transitional from xerophytic to mesophytic. The surface of the substrate consists of lava blocks and weathered soil. *Bursera graveolens* trees reach a good size, up to 10 m high. The undergrowth of the forest is denser than in the dry zone. Ferns begin to appear in the ground layer of the forest and on tree trunks as epiphytes. One of the prominent characteristics is abundant growth of filamentous lichens such as *Ramalina* and *Usnea* species. On Santa Cruz, upper parts of the transition zone support sporadic growth of *Scalesia pedunculata** trees, which predominate in the lower half of the moist zone of this island.

Moist zone (Figs. 5e, 5f & 5g):

The mesophytic moist-zone vegetation is characterized by abundant growth of shrubs, herbs and terrestrial ferns in the forest and by green and brown bryophytes that festoon tree branches. On the islands of San Cristóbal and Santa Cruz, the moist zone can be subdivided into three sub-zones, *Scalesia pedun-*

*culata** forest (Fig. 5e), *Zanthoxylum fagara* forest, and *Miconia robinsoniana** scrub (Fig. 5g). On islands other than San Cristóbal and Santa Cruz, the *Miconia* scrub is absent. On the western islands, *Scalesia cordata** forest occupies the lower part of the moist zone on two southern volcanoes of Cerro Azul and Sierra Negra in Isabela, and *Scalesia microcephala** (Fig. 5f) on three volcanoes of Alcedo, Darwin and Wolf in the northern half of Isabela and on Fernandina. On those volcanoes and islands, the moist-zone vegetation is low in term of tree height, and sparse in terrestrial herbs and ferns and in epiphytic bryophytes. The sparse vegetation on those northwestern volcanoes is apparently due to volcanologically young substrates as a result of the closeness to the Galápagos hotspots and reduced precipitation in the rainshadows of the southeast trade winds.

The moist zone vegetation has been heavily

disturbed by man on the southerly located inhabited islands of San Cristóbal, Floreana and Santa Cruz and the windward volcano Sierra Negra of Isabela. The central parts of these islands and the volcano have been disturbed and converted to farmland and pastures. Nowadays *Scalesia pedunculata* forests are restricted to only the north side of Santa Cruz and are found very sparsely on San Cristóbal, Floreana and Santiago. *Scalesia cordata* forests are also nearly gone from the Sierra Negra Volcano of Isabela.

Highland zone (Fig. 5h):

The present zone is characterized by treeless vegetation, and has been called by different names such as the grassy zone (Stewart, 1911), mountain zone (Svenson, 1935), upland zone (Bowman, 1961), fern-sedge zone (Wiggins & Porter, 1971), evergreen fern meadow or pampa (Werff, 1979), and broad-leaved herb vegetation, meadow or pampa (Hamann, 1981).



Fig. 5 Vegetation of different zones. a: Maritime vegetation on sand beach, Rábida. Top-left is sparse forest of *Bursera graveolens*. b: Dry zone landscape as seen from Isla Eden on the northwest side of Santa Cruz. c: Dry zone vegetation on lava field at Villamil, Isabela. d: *Bursera graveolens* forest in the transition zone on Santa Cruz. e: Dense forest of *Scalesia pedunculata* at Los Gemelos, Santa Cruz. Top-left is the transition zone to the dry zone on the north side of the island. f: Sparse forest of *Scalesia microcephala* at a middle elevation on the east side of Alcedo, Isabela. g: *Miconia robinsoniana* scrub at Cerro Media Luna, Santa Cruz. Photo taken in 1991 when *Cinchona pubescens* (green trees) had already invaded sporadically. h: Treeless highland vegetation at Cerro Crocker, the highest point of Santa Cruz. The brake at center is an endemic tree-fern, *Cyathea weatherbyana*.

As these names suggest, major plant species of the present zone are ferns, grasses, sedges and herbs. Trees are absent and shrubs are restricted to leeward slopes and depressions, while the endemic tree fern, *Cyathea weatherbyana**, is prominent in some areas.

There are several types of plant communities in the Santa Cruz highlands, which will be described later in detail. The highland treeless vegetation of other islands is also varied in types and species composition..

3.3 Reason for highland treelessness

As to the reason for the treelessness, there have been two hypotheses. One attributes the treelessness to the greater wind velocity and decreased precipitation (Stewart, 1911: p.286; Bowman, 1961: p.18; Wiggins & Porter, 1971: p.27). The other takes an opposite view, which is that the high air humidity blocks evapotranspiration and mineral uptake by plants (Werff, 1978: p.31). Both views are individually partly true to weather conditions of the highlands, since the dry phase appears infrequently during the warm rainy season, especially so in La Niña years, and the wet phase appears frequently in the garúa season.

The rainfall patterns in the Galápagos vary greatly within and between seasons and months (Grant, 1986). The highlands become infrequently completely dry for weeks and months owing to strong dry winds, particularly during the La Niña warm season, while they become very wet during the garúa season due to heavy drizzle and fogs which last for weeks and months without a break.

My hypothesis on the treelessness is as below. There are tree species that adapt to dry conditions, like desert plants, and there are tree species that adapt to wet conditions, like wetland plants. The dry extremes, even once in many years, will kill trees adapted

to wet or moist habitats, and the wet extremes kill those adapted to dry conditions. In the Galápagos Islands, however, no tree species adapted, or resistant, to both extremely dry and extremely wet conditions has migrated to or evolved in this oceanic archipelago. I proposed this hypothesis at the Galápagos Botany Workshop in 1987, which is cited in p. 595 of Vegetation of the Tropical Pacific Islands (Mueller-Dombois & Fosberg, 1998). Unfortunately, my hypothesis has been verified by the vigorous invasion of the Santa Cruz treeless highlands by the tree *Cinchona pubescens* in the 1990s. (For details, see the Alien chapter of the present paper.)

3.4 Detailed gradient analysis of Santa Cruz vegetation

Fieldwork on Santa Cruz has revealed the rainshadow effects on vegetation zonation in detail (Itow, 1971, 1975). In 1964 and 1970, the *Zanthoxylum fagara* natural forest still kept its physiognomic feature, a brownish appearance due to brown liverworts, *Frullania* festooning the tree branches, but it had already lost its natural conditions due to animal grazing and agricultural exploitation.

On the leeward north side of the same island, on the other hand, the zones are largely deflected upward in terms of the zonation, and, on the north side, *Zanthoxylum* forest and *Miconia* scrub are absent while the *Scalesia* forest is directly contiguous to the treeless highlands (Fig. 6). The gradient analysis of vegetation gives us not only the zonation pattern but also the distribution ranges of individual plant species in relation to elevation and substrate conditions, on both the windward and leeward sides of the island (Fig. 6).

In 1970 and 1978 when I conducted most of my fieldwork, the natural vegetation on Santa Cruz was

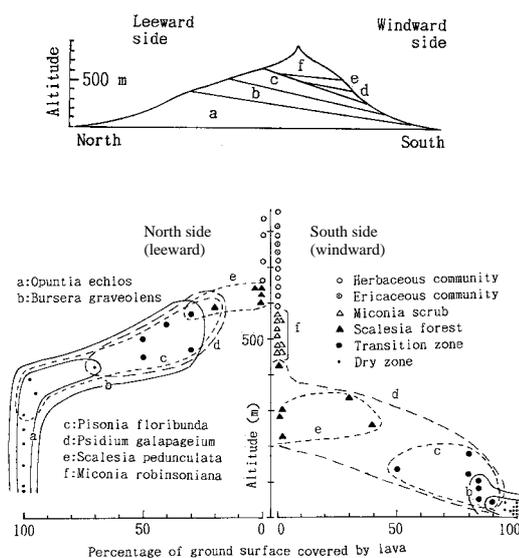


Fig. 6 (Above) Zonation pattern of vegetation on Isla Santa Cruz. The rainshadow effect can be seen in the upward deflection of zonation on the leeward northside of the island. (Below) Gradient analysis of vegetation in relation to elevation and substrates as represented by the coverage of lava on the ground surface, showing distributions of selected plant species and individual plant communities. (After Itow, 1992)

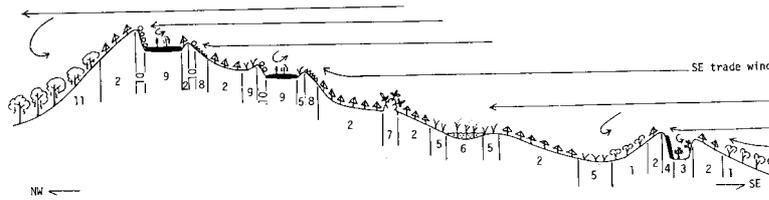


Fig. 7 Transect of the Santa Cruz highland, showing the distributions of eleven types of plant communities, including fens and bogs. 1. *Miconia robinsoniana* scrub, 2. *Pteridium aquilinum* / *Blechnum polypodioides* community, 3. *Cyathea weatherbyana* stand, 4. vertical bog, 5. *Paspalum conjugatum* community, 6. fen, 7. *Polypodium tridens* community, 8. *Lycopodium clavatum* community, 9. raised bog, 10. *Pernettya howellii* community, 11. *Scalesia pedunculata* forest. (After Itow, 1990)

undamaged or little disturbed on both the south and north sides of the island, excepting the *Scalesia* forest and *Zanthoxylum* forest in the moist zone. The same was true of the highland zone, which supported six types of plant communities. Each of them was dominated individually by *Paspalum conjugatum*, *Pteridium aquilinum*-*Blechnum polypodioides*, *Lycopodium clavatum*, *Hypericum uliginosum*, *Polypodium tridens**, and *Pernettya howellii** (Itow, 1990). The order of the above descriptions is roughly parallel from moist to dry habitats in the highlands (Fig. 7). In addition, there were three types of *Sphagnum*-dominated vegetation. They were fens dominated by *S. cuspidatum* var. *serrulatum*, raised bogs dominated by *S. erythrocalix* and vertical bogs (Fig. 8) dominated by the same bog moss (Itow & Weber, 1974). All the highland plant communities listed above were treeless, but many of them have been changed gradually since the 1990s due to the invasion by an alien tree, *Cinchona pubescens*.

The gradient analysis also detects a pattern of tree species richness along the elevation gradient. Both of the diversity indices I adopted, Fisher's alpha and Hurlburt's $S_{(n)}$, tell us how many species can be found in the community. Figure 9 shows the change in index values for woody plants with trunks larger 3 cm

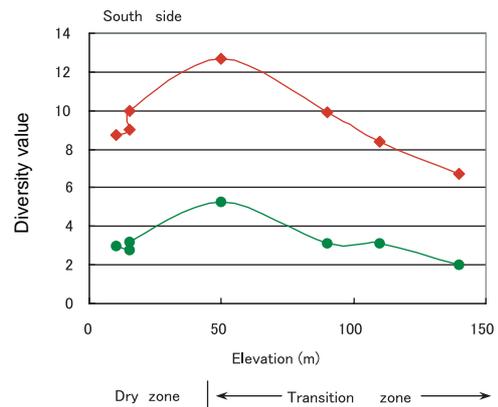
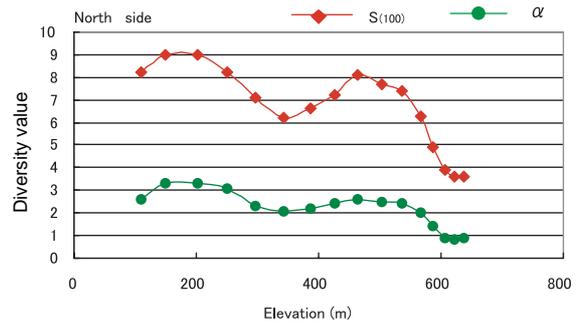


Fig. 9 Trends in woody species richness along the elevation gradient on the north and south sides of Santa Cruz. Note higher values in the transition zone, showing a mixture of dry zone and moist zone species, and low values in the *Scalesia* forest.



Fig. 8 Vertical bog formation on wind-exposed wall of parasite volcano.

DBH along the elevation. The arid and transition zone plant communities consist of seven to ten woody species, while the moist zone *Scalesia* forest consists of only three to five species. The forest canopy is predominantly composed of *Scalesia pedunculata*, a tree to like Compositae, 12 m high and 15 cm in DBH on average. The forest is definitely poor in tree and shrub species.

4. Ecology of Endemic Genus *Scalesia*

My special interest has gradually become focused on the endemic genus *Scalesia* (Compositae) since my early field studies in 1964 and subsequent ones in

1970, because I frequently encountered different *Scalesia* species in the dry and moist zones on nearly all the islands I visited. Different species of shrubby *Scalesia* are found in the dry zones on different islands, and different tree species in the moist zones on different islands. I thought that no vegetation study in the Galápagos would be complete without ecological studies of this genus.

4.1 Patterns in speciation and distribution

There are 15 species, four subspecies and six varieties, of which three species and one variety are trees and 12 species four subspecies and five varieties are shrubs (Eliasson, 1970; Hamann & Wium-Andersen, 1986). Ono (1967, 1971) first studied the chromosomes of the genus and revealed 68 chromosomes in somatic cells for all of the six species he studied. Eliasson (1970, 1974) confirmed the same results in nine taxa he studied. Ono (1967, 1971) and Eliasson (1974) suggested *Helianthus*, *Thitonia* or *Viguiera* as the closest relatives of *Scalesia*, although Schilling *et al.* (1994) showed the close affinity of *Scalesia* to the genus *Pappobolus*, an Andean endemic, based on a study of chlorophyll DNA. Apparently, *Scalesia* species have evolved from an ancestral herbaceous plant to 12 shrubby species and three tree species. All the species are allopatric in the present-day distribution. Hereafter I treat the five main volcanoes of Isabela as different individual islands, because they originated as separate islands which were then connected to neighboring volcanoes by low and vast lava fields.

To understand speciation pattern in this genus, I accepted two assumptions. The first is biogeographic, that larger islands are able to harbour more species, as MacArthur & Wilson (1967) predicted and verified. The second is related to the time available for speciation, that is, older islands have more years for speciation and therefore support more species than younger islands. Reflecting a combination of these two assumptions, older and larger islands actually do

harbour more species than newer and smaller islands (Fig. 10). High-elevation islands support a tree species in their moist zones, while low-elevation, small islands, volcanologically either new or old, harbour only one shrub species in their dry lowlands. Large but young islands harbour one shrub species and one tree species in their dry and moist zones, respectively, whereas large and old islands harbour a few to several shrub species in their dry zones and one tree species in their moist zones.

All the shrub species, excepting *Scalesia baurii* subsp. *baurii*, which is restricted to Pinzón, are distributed in the dry lowlands, while three of the tree species are found in the moist zones on middle- and high-elevation volcanoes and islands. I have collected specimens of all shrub species but one, *S. atractyloides*, from their habitats, all of which are outcrops of lava or unweathered substrates scattered among sparse forest of *Bursera graveolens* or similar sparse vegetation in the dry zone. The habitat is apparently strongly heliophilous.

Of the three tree species, *Scalesia microcephala* forests are sparse in density and 3-5 m high in the middle elevations of Fernandina and the volcanoes Wolf, Darwin and Alcedo of northern Isabela (cf. Fig. 5f). *Scalesia cordata* forests are dense and 8-10 m high in the middle elevations of Sierra Negra and Cerro Azul, southern Isabela. The *Scalesia pedunculata* forest is dense and 8-12 m high in the moist zones of Santiago, Santa Cruz, Floreana, and San Cristóbal.

I also collected ripe seeds of *Scalesia* in 1970 for Ono's (1971) chromosomal study of five species, some of which I sowed in a greenhouse in Japan. The seedlings grew fast to one meter and flowered six months after germination. In *S. pedunculata*, the largest tree species in the genus, the trunk reaches 12 m in height and 15 cm in DBH, with annual rings up to 0.5-1.0 cm thick. The wood of this species is soft with a large pith at the center (Fig. 11). Fast growth, flowering in the germination year and large

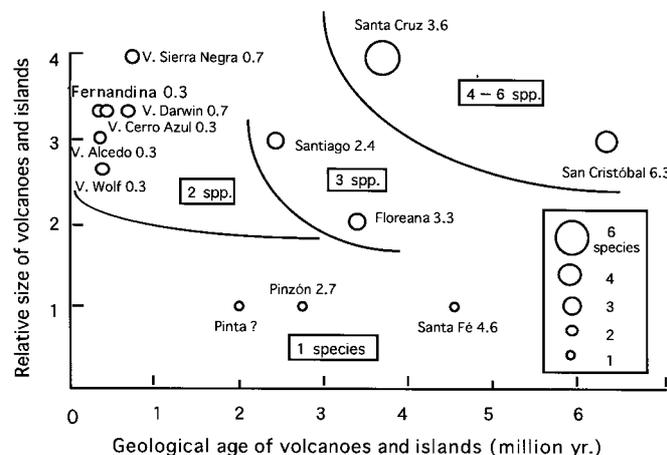


Fig. 10 Relationship of the number of *Scalesia* species with the relative age and size of volcanoes and islands. Numerals affixed to volcano and island names are their maximum geological ages cited from Geist (1996).



Fig. 11 *Scalesia pedunculata* trunk. Note the large pith at center and width of annual rings.

pith are apparently herbaceous traits of the plant. Hamann (1979) suggested its life span may be 15-20 years.

In the remote past in a geological sense, the moist habitat and tree niche were nearly vacant in the Galápagos. Tree *Scalesia* species have evolved from a herbaceous ancestor, filling the vacancies in both moist habitat and the tree niche. The present *Scalesia* forest is low in species richness in Whittaker's (1972) sense, ranging $S_{(100)} = 3-5$ (Itow, 1988, 1992).

Of the three tree *Scalesias*, *S. pedunculata* is distributed in the most fertile habitat of the southerly to centrally located high-elevation islands of San Cristóbal, Floreana, Santa Cruz, and Santiago. The natural forests of this species have been nearly extirpated from San Cristóbal and Floreana, due to early settlement and exploitation since the 19th century, and from Santiago due to heavy grazing and browsing by feral goats for a century. Fortunately the natural forest of this species has remained on the north side of Santa Cruz until now.



Fig. 12 (a) Mature forest of *Scalesia pedunculata* at Los Gemelos, Santa Cruz in 1981, two years prior to the 1982-1983 stand-level dieback. (b) Young generation at the same area in 1986, one year after the new cohort germinated in 1985.

4.2 Succession process of *Scalesia pedunculata* forest

There was a dense forest of *S. pedunculata* in the Los Gemelos area at a middle elevation ca. 550 m above sea level on Santa Cruz, when I visited there in 1970 and 1978 (Fig. 12a). Since then I have recorded the diameter of trunks of selected *S. pedunculata* trees (not density in quadrat) in 1978, 1981, 1987, 1991, 1995, 1998 and 2002 (Fig. 13). The 1982-1983 El Niño event brought a large amount of rainfall, 10 times that of a normal year, and nearly all the *Scalesia* trees died synchronously. This was a good example of stand-level dieback of forest (Mueller-Dombois, 1988, 1992). New cohorts germinated in 1985 and produced 100% ground coverage (Fig. 12b). As seen in those pictures, other trees associated with *S. pedunculata* were quite sparse, and only of *Zanthoxylum fagara* and *Psidium galapageium*. The stand is nearly purely dominated by *S. pedunculata*, with no shade-tolerant tree species. As the species is heliophilous, the seeds germinate only when mature trees fall down and sunny habitat is created. Thus the succession is collapse-and-recruiting, or self-cyclic (Itow & Mueller-Dombois, 1988; Itow,

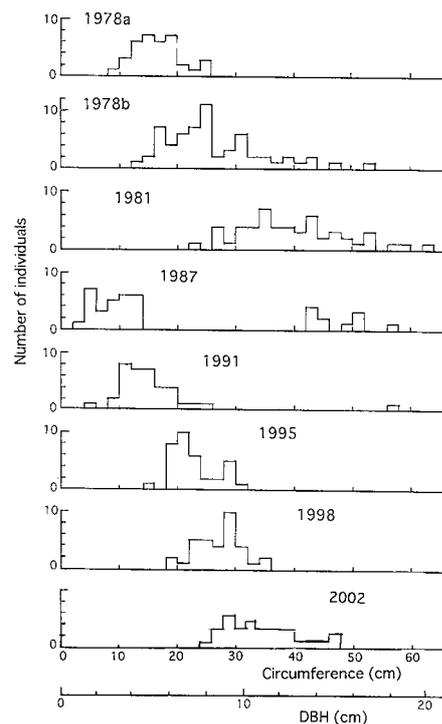


Fig. 13 Change in size distribution of *Scalesia pedunculata* at the Los Gemelos area of Santa Cruz. The 1978a population (top) was a four-year old generation established on abandoned soils. The 1978b and 1981 populations were approaching the mature stage. In 1982-1983, a heavy El Niño occurred, and the old generation died back synchronously. The 1987 population consisted of a few old trees and many of the new generation. The figures of 1978a-1991 are reproduced from Itow and Mueller-Dombois (1988) and Itow (1995). New measurements made in 1995, 1998 and 2002 are added.

1995; Fig. 14). The same was observed in a dense forest of *S. cordata* on Sierra Negra Volcano of Isabela Island (Lawesson, 1988). In the sparse forest of *Scalesias*, stand-level dieback does not occur but the population recruits with continuous generation under open canopy (Lawesson, 1988; Shimizu, 1997).

In 1997, the second heaviest recent El Niño occurred, but complete stand-level dieback did not occur in the Los Gemelos forest, because the stand was young and premature with an age of *ca.* 12 years after the 1985 cohort germination, while it occurred in a dense *Scalesia* forest at La Caseta around 200 m above sea level (Hamann, 2001), which is the low-elevation limit of *Scalesia* forests.

In the *S. pedunculata* forest at Los Gemelos immediately after the 1997 El Niño, the above-ground biomass was *ca.* 60 kg ha⁻¹, which is one-fourth to one-sixth that of the *Metrosideros polymorpha* forest in Hawaii. Mineral nutrients such as soluble potassium, and exchangeable calcium and magnesium are rich in the forest soils, almost 5.5 to 10 times those in the Hawaiian forest soils (Kitayama & Itow, 1999). The foliage of the canopy was nearly 100% in coverage and was thought to be approaching maturity, but stand-level dieback has not yet occurred as of 2002, when the forest was 17 years old. This is because the trees seem to be dying gradually, leaving gaps in the canopy and creating sunny spots on the forest floor where new seedlings appear. The forest may be recruited by continuous generation, as Shimizu (1997) predicted.

4.3 Hypothesis on stand-level dieback

The question on stand-level dieback is why the dieback occurs in dense monospecific cohort forests of *Scalesia pedunculata* and *S. cordata* but not in

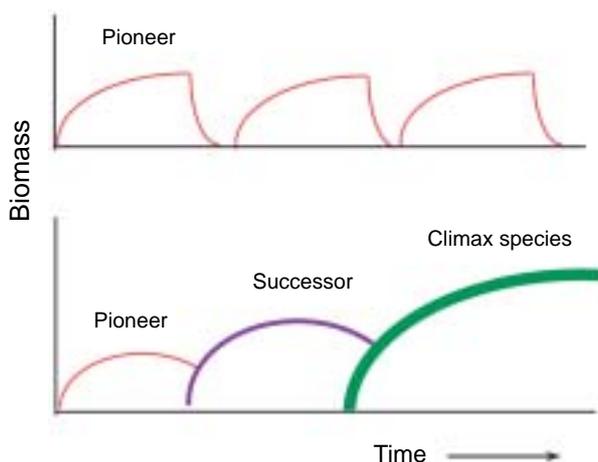


Fig. 14 A schematic illustration of (above) self-cyclic succession of heliophilous *Scalesia pedunculata* as represented by synchronous stand-level dieback and subsequent cohort regeneration, with a comparison to (below) normal succession with heliophilous pioneers, followed by successors, and finally shade-tolerant climax species, which is found in species-rich subtropical regions in the northern hemisphere.

sparse forests of the same species. A clue to this question seems to be in the growth habits of the species on the one hand, and the self-thinning process of the population on the other. Based on samplings and measurements made in 1998 at Santa Rosa, 350 m in elevation on the northwest side of Santa Cruz, Kitayama and Itow (1999) have revealed allometric relationships between the DBH and dry weight of wood and foliage in *S. pedunculata* as below:

$$W_w = 0.01540 (D^2)^{1.609059} \quad (r^2 = 0.99), \quad \text{and} \\ W_f = 0.01769 (D^2)^{0.77946} \quad (r^2 = 0.76),$$

where W_w and W_f are the dry biomass (kg) of wood and foliage, respectively, and D is the trunk diameter (cm) at breast height over bark. It should be noted that the growth rate in wood biomass is as large as twice the net biomass increment in foliage. This fact suggests that in every individual tree, the photosynthetic assimilation gain by the foliage may not provide enough energy to support the respiration loss in the wood and roots at a mature point, which seems to be the life span of the tree.

In 1970 at La Caseta, located at 200 m in elevation on the southwest side of Santa Cruz, there were 10 stands of different sizes (ages) of *S. pedunculata*. Within each of the stands, individuals were nearly the same size, and could be of a single-aged cohort. The average DBH was 1.4 cm in the youngest stand and 9.4 cm in the oldest stand. The population density per 100 m² was 325 in the youngest and 36 in the oldest stand. Figure 15 shows the self-thinning process of density in a series from young stands to older ones, as the forest develops.

Here the biomass of individual trees and that of the stand can be calculated, using the allometric equations given above. Figure 16a shows the increase in stand-based wood biomass in relation to forest development, in which the population density decreases and DBH increases. The stand-based foliage biomass (Fig. 16b), however, stays the same, or decreases a little, as the forest develops, although some irregularities are seen.

This fact predicts hypothetically that the stand-based assimilation gain by foliage may not provide enough energy to support the respiration loss in wood and roots at a mature stage of the forest's development, and that a synchronous dieback may occur in such an

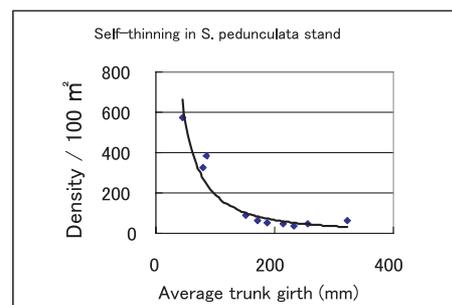


Fig. 15 Self-thinning of *Scalesia pedunculata* population density per 100 m² during forest development. Data from La Caseta collected in 1970.

even-sized cohort mature stand. Actually a synchronous stand-level dieback did occur in 1982-1983 (Fig. 13). The dieback plays an important role in setting back the population to a new cohort generation, creating a sunny habitat for seed germination of this heliophilous species. Each individual of the cohort grows again and will approach its senescent stage, thinning its population, unless the cohort encounters some disturbance like disease or insect attacks. Then the stand must die back again synchronously when an environmental anomaly like heavy rainfall or extreme drought acts as a trigger. Then again the dieback sets the population to a new, next cohort and a new succession starts. The whole series of ecological events is a self-cyclic succession or a buildup-collapse succession, which includes the phases of initial build-up of the new cohort, its growth, senescence, and dieback (Fig. 14).

Synchronous diebacks in *Scalesia* species will occur in dense and even-sized cohort mature populations, when they encounter environmental anomalies like heavy rainfall (Itow & Mueller-Dombois, 1988; Lawesson, 1988) or extreme drought (Kastdalen, 1982). In canopy-broken forests of the same species, as Shimizu (1997) described as continuous regeneration, the population recruits continuously with new seedlings that grow at sunny spots on the forest floor, and individual old trees die when they reach their maximum maturity, or when they are damaged by disease or insect attack.

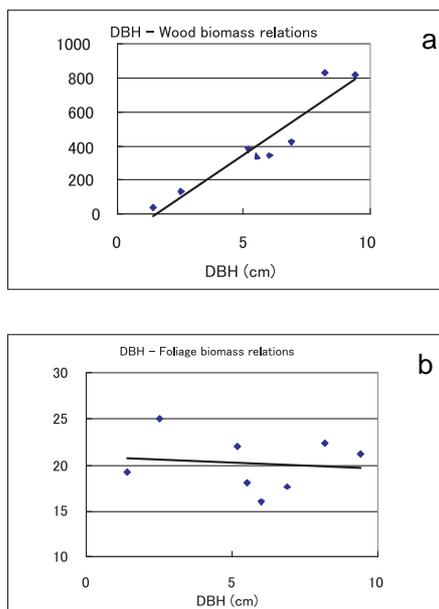


Fig. 16 Changes in (a) wood and (b) foliage biomass of the *Scalesia pedunculata* stand (100 m²) during forest development, adapted by the allometric equations given in the text.

5. Invasion of Island's Ecosystem by Alien Species

5.1 Background

Since the islands of the Galápagos Archipelago are of volcanic origin, and were originally free from any terrestrial life, all the plant species are aliens, in a sense, originally introduced from outside by natural agents such as winds, birds, and oceanic currents. Plants that were so introduced and established on the islands and plants evolved from those plants are named as indigenous, or native. The aliens or exotics treated in the present paper are plants that have been introduced intentionally by man or accidentally in relation to human activities.

Since introductions of alien plants, either intentional or accidental, are associated with human activities, a brief human history of the archipelago is needed here in order to understand the background of alien plants. Since the discovery of the islands in 1535, they were occasionally visited by buccaneers in the 17-18th and frequently by whalers in the 18-19th centuries. Man first settled there in the first half of the 19th century on the island of Floreana, and then at the turn of the century on the island of San Cristóbal and on the Sierra Negra Volcano of Isabela Island. Settlement on Santa Cruz began in the 1920s. Human habitations were restricted to areas on the coasts and at middle elevations where one or both of arable land and drinking water were available.

The archipelago was designated a National Park in 1959, and the Charles Darwin Research Station (CDRS) and the Galápagos National Park Service (GNPS) were inaugurated in 1964 and 1968, respectively. Up to that date, goats and donkeys had run wild on many of the uninhabited islands as well as on inhabited islands, and cows and horses also ran wild on the four inhabited islands. Since ecotourism started under strict regulation in the mid-1970s, plant and animal life and the unspoiled scenery of the volcanic archipelago attracted visitors from all over the world. The consequent inflow of man and cargo increased year by year. The human population has multiplied tenfold in half a century, from *ca.* 1,400 in 1950, via *ca.* 4,000 in 1974 and *ca.* 9,700 in 1990, to *ca.* 16,000 at the turn of the 21st century. Human habitation is still restricted to mid-elevation agricultural zones and the coastal towns of the four islands of San Cristóbal, Floreana, Santa Cruz, and Sierra Negra Volcano of Isabela. Galápagos National Park occupies 97% of the land surface, which is zoned into four categories with different protection regulations, which are the Maximum protection zone, Primitive zone, Special use zone and Visitors' zone (Galápagos National Park Service, 2000).

5.2 Increase in alien plants

In the study of introduced plants, the first step is distinguishing alien species from indigenous ones.

This step is easy for intentionally introduced plants such as ornamentals, fruits and crops cultivated in gardens and farmlands, and also for those plants useful for man even if they are spreading in natural and semi-natural habitats. It is not so easy, however, to distinguish accidentally introduced herbs and grasses from indigenous species of natural introduction by winds, birds, and oceanic drifts. For this step, I largely followed categories in Porter (1983) and Lawesson *et al.* (1987), where plants are classified as endemic, non-endemic native, introduced, and cultivated or garden escapes. They treated the last two categories as alien species, but their evaluation was not always the same for some particular herbs and graminoids. For example, one author put species *X* (e.g. *Desmodium glabrum*) in the introduced category but the other in the native category. In the present study, I classified such species into the alien category, and therefore, the number of alien species became larger than the enumeration in either Porter (1983) or Lawesson *et al.* (1987).

The second step is to trace back to the earlier lists to grasp of the increase in aliens, enumerating the alien species as defined above in each of the past collection lists. For this step, I treated the alien species that were listed in an earlier list, as present in the later lists even if they were not listed under any categories in the latter. This is because the lists earlier than Porter (1983) were different in focus; one listed cultivated plants, the others did not. Thus the number of alien species increases cumulatively from the early days to the present, adding new records of aliens.

The first collections of aliens were made by Charles Darwin during the 35 days of his stay in 1835 (Hooker, 1847). He collected 209 species, of which 14 are supposed as aliens in the present definition. A few botanical explorations followed, and immediately after the turn of the century, the California Academy of Sciences carried out a year-long scientific expedition in 1905-1906, in which 100 alien species were listed (Stewart, 1911). A few more investiga-

tions followed, until the CDRS was launched in 1964. Since then the CDRS's botanists have conducted extensive and intensive investigations by themselves, and have supported field work by visiting scientists. The 1987 checklist of the flora (Lawesson *et al.*, 1987) enumerated 255 introduced and cultivated species (310 in my count being based on the present definition as above). In the course of the present study, I counted ferns, monocotyledons and dicotyledons separately. Until 1990, no ferns had been listed as introduced; monocots and dicots occupied about 20%-80%, respectively, of the total alien species in each of the lists studied. Figure 17 shows the increase in those aliens during a little more than a century and half since Darwin's biological explorations. Recent enumerations of total numbers after 1990 are cited from the CDRS's botanists, Jaramillo (1999) and Tye (2001b).

The increase in alien plants is apparently dependent on two factors: real increase due to genuine new introductions, and amounts and focus of field research. At present, the CDRS's botanists enumerate *ca.* 600 species (Tye, 2001b), which includes three introduced fern species (Tye, Personal communication, 2002). The alien species listed are not spread evenly over the islands but are largely confined to agricultural and urban areas. Relatively few alien species have invaded the National Park area but some of these are now widespread even on uninhabited islands (Tye, Personal communication, 2002).

5.3 Habitats and niches for aliens

Hereafter the present chapter focuses on alien plants that spread and recruit by their own dispersal and reproductive abilities in natural, semi-natural and man-altered habitats, irrespective of introduction purposes, means and processes, but excludes plants that were intentionally introduced and are so far still only found in cultivation in agricultural and town areas. Examples of the latter are ornamentals (e.g. China rose, *Hibiscus rosa-sinensis* L.) and crop plants (e.g. sweet potato, *Ipomoea batatas* Lam.).

The conceptual frame to understand invasion of insular ecosystems by aliens should consist of the habitat and niche for individual species. In the present study, the habitat can be conceived along two axes. One is the altitudinal zonation from maritime and dry zones, through the transition and moist zones, to the highland zone. This gradient runs parallel with the altitudinal increase in annual precipitation, though its monthly distribution in the different zones differs somewhat. The other is the degradation axis, which ranges from natural, through semi-natural, to disturbed or man-altered. 'Natural' means truly natural conditions that support vegetation composed of endemic and indigenous non-endemic plant species. Individual vegetation zones support natural plant communities, as described in the previous chapters. 'Disturbed' or 'man-altered' indicates habitats that

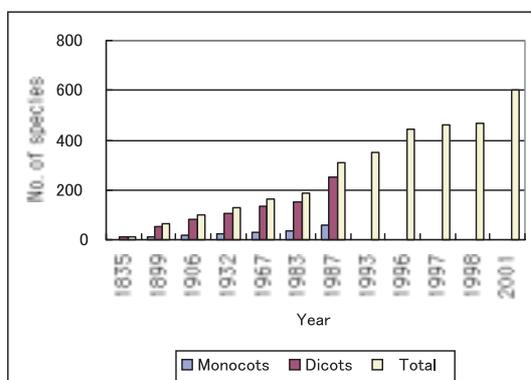


Fig. 17 Increase of alien plant species during the century and a half since Darwin's collections. Counts after 1990 are only the total numbers cited. For definition of aliens and methodology of count, see text.

have been completely destroyed by man and then used for human life. Examples are agricultural areas like crop lands and pastures, heavily trampled trails, parklands in residential areas, gardens, and so forth. 'Semi-natural' indicates, for example, forests from which timber trees have been extracted in the past, habitats that were cleared once in forested areas and now support plant communities established after such light disturbance. Forest-edge communities are another good example of the 'semi-natural' category.

The concept 'niche' in the present study means the status or place of a species within a plant community. Trees, shrubs, lianas (climbing plants), and herbs or grasses are plant life-forms corresponding to niches. In each of the life-forms, pioneer, successor and climax species are niches in a series of plant succession. An introduced plant species can be conceived as occupying a habitat range and a niche. For example, *Persea americana*, one of the invasive tree species, occupies a moist habitat and tree niche in the Galápagos; *Passiflora edulis* occupies a moist habitat and a liana niche.

The susceptibility of habitat to aliens depends in part on the species poverty of the area (Cronk & Fuller, 1995), which implies vacancy of niches. As discussed in the previous chapters of the present paper, the flora of oceanic islands is poor and disharmonic in an ecological sense, and, therefore, insular vegetation is susceptible to aliens in its vacant habitats and vacant niches. Good examples in the Galápagos are the moist fertile habitat with deep soils and the tree niche in it, where tree species of *Scalesia* have evolved from an herbaceous ancestor to fill the habitat and niche, and where invasive trees like *Cinchona pubescens* and *Cedrela odorata* are invading, filling gaps in a moist habitat and a tree niche. The same is true of species-poor vegetation on other oceanic islands (Brockie *et al.*, 1988). *Myrica faya* is invading species-poor vegetation of the Hawaiian volcanoes (Brockie *et al.*, 1988; Vitousek, 1989); *Pinus luchuensis*, *Casuarina equisetifolia* and *Bischofia javanica* are invading species-poor natural forests of

the Bonin (Ogasawara) Islands, Japan (Okutomi *et al.*, 1985; Shimizu & Tabata, 1985; Shimizu, 1988). The same is true again of liana in the moist habitats of the Galápagos, where *Passiflora colinvauxii* has evolved and is climbing over trunks and branches of *Scalesia pedunculata* trees. This liana is the sole species in this niche, where an invasive alien liana of *Passiflora edulis* is spreading and replacing endemic *P. colinvauxii*, filling gaps that are still vacant in this fertile habitat.

5.4 Invasiveness and invasive species

In order to understand invasiveness of aliens, it is important to understand their ecology. Invasiveness is related to traits such as seed morphology, seed dispersibility, seed dormancy, shade tolerance, drought tolerance, and others. There have been few studies of these aspects of Galápagos aliens up to now, but a study on *Rubus niveus*, one of the worst invaders, revealed traits relating to invasiveness such as phenological patterns, size of seed bank, viability of seeds in the seed bank, and germination patterns that lead to high invasiveness of the species (Landazuri, Personal communication, 2002). Articles referring to introduced plants are also informative regarding invasiveness of individual aliens (cf. Brockie *et al.*, 1988; Hamann, 1984, 1991; Jaramillo, 1999; Loope *et al.*, 1988; MacDonald *et al.*, 1988; Shimizu, 1997; Soria *et al.*, 2002). Table 2 indicates the invasiveness of several selected aliens, which are somewhat subjectively evaluated, from my own observations and descriptions in the above cited literature, into three ranks of high (+++), medium (++), and low (+) for each of the traits and characteristics.

The present section hereafter describes some of the worst invaders in the Galápagos.

***Cinchona pubescens* Vahl.** (Rubiaceae), or quinine tree, is one of the worst invasive tree species in the Galápagos. A farmer first planted this invasive tree on one property in 1946, and naturalized plants were found in the Santa Cruz highlands in 1971 (Hamann, 1984). The present species bears a

Table 2 Invasiveness of selected six aliens evaluated with their traits and characteristics, with a comparison to three endemics.

	Aliens						Endemics		
	1	2	3	4	5	6	7	8	9
	<i>Cinchona pubescens</i>	<i>Persea americana</i>	<i>Cedrela odorata</i>	<i>Psidium guajava</i>	<i>Rubus niveus</i> *	<i>Lantana camara</i>	<i>Scalesia pedunculata</i>	<i>Psidium galapageium</i>	<i>Lantana pedunculata</i>
Seed									
Productivity	+++	+	+++	+++	+++	++	++	++	+
Dispersibility	+++	+	+++	++	+++	+++	+	++	++
air		gravity	air	animal	bird	bird	gravity and air	bird	bird
Dormancy	+	+	?	+++	+++	+++	-	+++	+++
Germination									
in shade	++	+++	++	++	++	++	-	++	-
in light	+++	++	+++	+++	+++	+++	+++	++	+++
Seedling									
Shade tolerance	++	+++	+++	++	+++	+	-	++	-
Drought resistance	++	++	++	++	++	+++	+	-	+++
Sprouting after cutting	+++	+	++	+++	+++	+++	-	+	+
Age to maturity	+++	+	++	+++	+++	+++	+++	+	++
Total score	22	15	20	23	25	23	10	15	15

* Evaluation after Landazuri (pers. com. 2002); others are mine with comments by Tye (pers. com. 2002).

number of wind-dispersed seeds and has spread widely in the moist and highland zones of Santa Cruz. Since it favors moist habitats and resists dry conditions as well, the plants have invaded the highlands where the habitat fluctuates between extremely wet and extremely dry conditions and where the tree niche has been vacant from any indigenous tree species. The invasion is still restricted to Santa Cruz. Figure 18 illustrates its expansion in the originally treeless highlands.

Psidium guajava L. (Myrtaceae) or guava, is one of the worst invasive trees, originally planted in orchards and gardens for fruit. The fruit, *ca.* 5 cm in diameter, harbours many small seeds inside and feral introduced animals, like donkeys, cows, horses and goats, carry the seeds in their digestive tract and disperse them into semi-natural and natural vegetation. The plant favors moist habitats and has expanded in the moist zone of the four inhabited islands: San Cristóbal, Floreana, Santa Cruz and the Sierra Negra Volcano of Isabela. On the uninhabited island of Santiago, this species was also planted but has not yet spread. The plants on Sierra Negra Volcano were found abundantly in and around the agricultural area of Santo Tomás in 1970 when I visited first there, and have expanded since then into the originally treeless highlands, where cows and horses run wild, up to high elevations close to the caldera rim in 1998. Its sprouting ability after cutting and burning is strong (Macdonald *et al.*, 1988; Lawesson & Ortiz, 1990;



Fig. 18 Invasion of the treeless Santa Cruz highlands by aggressive *Cinchona pubescens*. Photos (from top down) taken in 1970, 1991 and 2001.

Shimizu, 1997). On Santa Cruz, *P. guajava* was infrequently found in the moist zone in 1964, but abundantly in pastures in the upper moist zone (which originally supported *Zanthoxylum* forest) to the highlands in 2000.

Syzygium jambos Alston, rose apple or jambos, is another invasive species of the same family. The species has invaded disturbed areas in the San Cristóbal moist zone, and forms nearly monospecific thickets there, although it is not yet as serious on other islands.

Cedrela odorata L. (Meliaceae), West Indian cedar, was originally planted as shade and for timber along trails and paths in the moist zone between Bellavista and Santa Rosa on the south side of Santa Cruz. The tree is 30 m high and 70 cm DBH, and the wood is hard and used for furniture. It produces wind-dispersed seeds and invades semi-natural and natural habitats as well as disturbed areas (Lawesson & Ortiz 1990; Soria *et al.*, 2002), in some cases, reaching distant regions north of the central mountain range of the island.

Persea americana Mill. (Lauraceae), avocado, is a fruit tree, originally planted around farmers' houses in the moist zone. It bears large fruits, 15 cm long and 10 cm across, having a large seed, 5 cm in diameter, inside. The seed is dispersed only by gravity but rolled by wild-running animals into nearby areas. Seedlings and saplings are highly shade-tolerant and establish well in colonies competing with other plants. Once established, the trees grow up to 30 m high and 70 cm in DBH, and persist many years, dispersing seeds around the mother trees and expanding their distribution range gradually. Groves of this species can be seen not only in populated agricultural areas but also in the abandoned agricultural area of Alemania, on the Sierra Negra Volcano of Isabela (Shimizu, 1997).

Rubus niveus Thunb. (Rosaceae) or blackberry, is a recently introduced and badly invasive shrub species. The plant is armed with prickles on arching stems that can grow to 4 m long. In my fieldwork on San Cristóbal, no plants were found in 1970 and 1978, and a few in forest-edge habitats in the transition zone in 1986. The first sighting of this species was made in 1983 on the same island (Lawesson & Ortiz, 1990). Thereafter it has expanded its range up to the highest part of the island, covering forest-edges and herbaceous vegetation. Originally the Galápagos flora was poor in shrub species adapted to open habitats like forest edges in the moist zone; apparently *Rubus niveus* fills this vacant shrub niche in the species-poor, ecologically disharmonic vegetation. It now is one of the commonest plants found along roads and paths and along forest-edges from the transition zone up to the highland zone of San Cristóbal. I do not know precisely the year of its introduction to Santa Cruz; no plants were seen in 1964, 1970, 1978 and 1986 but a few were found at Santa Rosa in 1991.

Since then the species has spread along roads and paths in the moist zone, and further into natural forests of *Scalesia pedunculata* at Los Gemelos along the road that crosses the island (Fig. 19). As described previously in Table 2, its invasiveness, as evaluated by such traits as seed production, dispersal, seed bank, dormancy, sprouting after cutting, etc., is very high (Landazuri, Personal communication, 2002). Recently Soria *et al.* (2002) reported naturalization of three other *Rubus* species, *R. glauca*, *R. adenotricos*, and *R. megalococcus* on Santa Cruz. Their invasiveness is unknown but probably high.

Passiflora edulis Sims (Passifloraceae), or passion fruit, is a perennial liana or creeping plant. A native species of this genus, *Passiflora foetida* var. *galapagensis* Killip, is a member of the dry zone vegetation. This is also a perennial liana, climbing trees and shrubs or creeping along open ground. *P. edulis* was originally introduced into farmers' settlements for its delicious fruits. It is adapted to a humid climate, and the fruit harbors many seeds that can be dispersed

through digestive tracts of animals. Its seedlings and saplings are shade-tolerant. Vines elongate 10 m or more, climbing trees and creeping along the ground. In the *Scalesia* forest zone, there is an endemic liana, *Passiflora colinvauxii* Wiggins, which has evolved from an ancestral *Passiflora* species, adapting to the moist fertile habitat and occupying a liana niche in the Santa Cruz moist zone. Invasive *P. edulis* is competing with and replacing this endemic in the *Scalesia* forest. Two other introduced species of the same genus, *P. ligularis* A. Juss. and *P. quadrangularis* L. are similar to *P. edulis* in their behavior (Lawesson & Ortiz, 1990).

Table 3 gives a list of the 15 worst invasive plants in the Galápagos, selected rather subjectively based on my own observations and experiences since my first visit in 1964 and thereafter. The list also describes species traits and characteristics that are thought to be related to invasiveness, as well as present situations of distribution and invasion.



Fig. 19 Ground vegetation of *Scalesia pedunculata* forests at Los Gemelos, invaded by aggressive *Rubus niveus* (above) and *Caesalpinia bonduc* (below). Photos taken in 2000 at Los Gemelos, Santa Cruz. The forest was free from those aliens in 1995.

Table 3 A list of fifteen worst invasive aliens in the Galápagos, with descriptions of present status.**TREES:***Cedrela odorata* L. (Meliaceae) (See text)*Cinchona pubescens* Vahl. (Rubiaceae) (See text)*Persea americana* L. (Lauraceae) (See text)*Psidium guajava* L. (Myrtaceae) (See text)*Syzygium jambos* (L.) Alston (Myrtaceae) (See text)*Syzygium malaccense* (L.) Merr. & Perry (Myrtaceae)

(Frequently established tree around houses and farmlands in the moist zone of San Cristobal, prominent due to its large tree size and red flowers)

SHRUBS:*Caesalpinia bonduc* (L.) Roxb. (Leguminosae)(Troublesome creeping shrub having strong prickles on stems; large seeds not so dispersive; covering densely cleared fields, sometimes invading into *Scalesia pedunculata* forest at Los Gemelos and El Chato, Santa Cruz. The present species covers the forest floor densely and prevents germination of *Scalesia* seeds)*Lantana camara* L. (Verbenaceae)(Originally introduced as ornamental, produces berries dispersed by birds, spread along paths and trails, sometimes into semi-natural and further natural vegetation, competing with endemic *L. pedunculularis* in the dry and transition zones.)*Ricinus communis* L. (Euphorbiaceae)

(Originally introduced for pharmaceutical or medicinal purposes, spreading along paths and trails and around houses in the transition to the moist zones, and invading natural vegetation in the arid zone.)

Rubus niveus Thunb. (Rosaceae) (See text.)**HERBS AND GRASSES:***Bryophyllum pinnatum* (Lam.) Oken (Crassulaceae)

(Originally introduced as ornamental; dispersed by minute seeds and vegetative reproduction from fallen leaves, spreading as ruderal along paths and trails in the transition and moist zones, and invading into natural forests, where it blankets the ground and replaces the natural herb layer.)

Pennisetum purpureum Schumach (Gramineae)

(Originally introduced as fodder plant; propagates by vigorous rhizome elongation as well as wind-born seeds; spreads along roads and trails, and invades semi-natural habitat along forest edges, but not deeply into natural forests.)

LIANAS:*Cucumis dipsaceus* C.G. Ehrenb. ex Spach. (Cucurbitaceae)

(Recently introduced vine; prominent due to its yellow fruits, many seeds inside, dispersed by birds, but distributed mainly along roads and paths in the dry to moist zones, occasionally into natural vegetation. A prominent weedy vine.)

Mormordica charantia L. (Cucurbitaceae)

(Widely spread in the dry and transition zones, prominent due to yellow flowers and red color of split fruit, seeds dispersed by birds. Invasive and prominent in the arid zone.)

Passiflora edulis Sims. (Passifloraceae) and two other species. (See text.)**5.5 Distribution chart**

The present-day distribution of aliens in the Galápagos depends on some other factors as well as the susceptibility of the habitat and invasiveness of the species. These factors include feral animals and rainfall in El Niño years. Herbivorous mammals like goats and donkeys destroy natural vegetation and create habitats susceptible to invasion by alien plants.

A small El Niño appears every three to six years in the Galápagos, bringing large amounts of precipitation. Since most of the alien plants in the Galápagos originate from moist or humid regions of the tropics and subtropics, and favor humid weather and climates, they can invade the mid-elevation moist zone that originally supported *Scalesia* forests. The moist zone is poor in tree species and therefore susceptible to moisture-favoring invaders. Heavy rains in El Niño years create moist habitats even in the transition and dry zones, where invasive aliens find favorable conditions that year and leave their seeds in the soil. Thus aliens originating in moist regions of the conti-

nent invade and spread into species-poor insular vegetation and habitats.

To understand the present-day distributions of aliens, time is another factor of importance. The time elapsed since the first introduction of a species allows its spread into agricultural and town areas, and further to natural habitats, depending on its invasiveness.

Figure 20 is a distribution chart that consists of two axes: vegetation zones on the Y ordinate and habitat degradation on the X abscissa. The chart shows the present-day distribution of individual aliens on Santa Cruz Island, integrating susceptibility of habitat, invasiveness of aliens and time elapsed.

6. Concluding and Prospective Remarks

Up to this chapter, the present paper does not refer to the threatened status of the Galápagos endemic flora. The matter is difficult for visitors to treat because a thorough search of the flora throughout the archipelago is needed. Lawesson *et al.* (1987) tried

first to evaluate each of the endemic and non-endemic native plant species in terms of the IUCN Red Data categories, based on their intensive botanical explorations of the archipelago. Adersen (1989) summarized 144 rare plants of individual islands, and suggested the threats to the rare plants to be erosion, fire, land use, introduced animals and introduced plants. Lawesson, former botanist of the Charles Darwin Research Station, summarized the status of 12 endemics and eight non-endemic natives as Endangered and 12 endemics and four non-endemic natives as Vulnerable (Lawesson, 1990). Tye, the present-day botanist at the CDRS, studied the matter by mapping individual endemic species distribution as well as conducting field investigations, and concluded that, of 195 of the endemic taxa, Three were extinct, 18 critically endangered, 30 endangered, 78 vulnerable, 16 near threatened, and 50 of least concern (Tye, 2001a). Major threats to endemic plants are feral grazing mammals like goats, donkeys and cows on several islands like San Cristóbal, Floreana, Santa Cruz, Santiago and Isabela, and aggressive alien plants, which disperse seeds, leave them in soils, compete with native species with their vigorous growth, and spread themselves in natural and semi-natural habitats. The protection and conservation of endemic plant species are one of the top priorities, which should be ranked in close relation to eradication and control of invasive alien plants, as well as of introduced animals.

The vegetation is an organized assemblage of component plant species. In Galápagos, it is still the object of ecological research and investigation from the habitat-related viewpoints of species constitution,

distribution patterns, succession series, and degradation processes due to invasion by aliens, and so forth. Up to now, the vegetation has been studied well on the inhabited islands of San Cristóbal, Floreana, Santa Cruz and Sierra Negra Volcano of Isabela, as reviewed in the previous chapters, while that of the uninhabited islands is less well-known regarding its patterns and processes, although Hamann (1981) described various plant communities of remote islands and volcanoes. Distributions of individual species, zonation patterns of vegetation and species composition of individual communities on individual islands and volcanoes are the major objects of vegetation ecology. The vegetation thus investigated and studied can be, and should be, mapped in documents of vegetation at particular ages (Itow, 1966b; Atkinson, 1990). If any of the islands, regions or areas had been thus mapped, the maps would, and will, give us an insight into vegetation changes of natural succession or man-induced deterioration.

Another important aspect in future vegetation studies is transect vegetation studies from the new-born western islands close to the Galápagos hotspot, through centrally located islands, to the volcanologically older eastern islands. Such transect studies will reveal the developmental process of ecosystems on volcanic islands over millions of years, as Kitayama (1996) and Kitayama *et al.* (1997) did in the Hawaiian volcanoes.

The wide-ranged surveys and investigations of vegetation as proposed above will reveal endangered vegetation types and communities. The *Zanthoxylum fagara* forest, originally present in the Santa Cruz upper moist zone prior to 1964 (Bowman, 1961), is

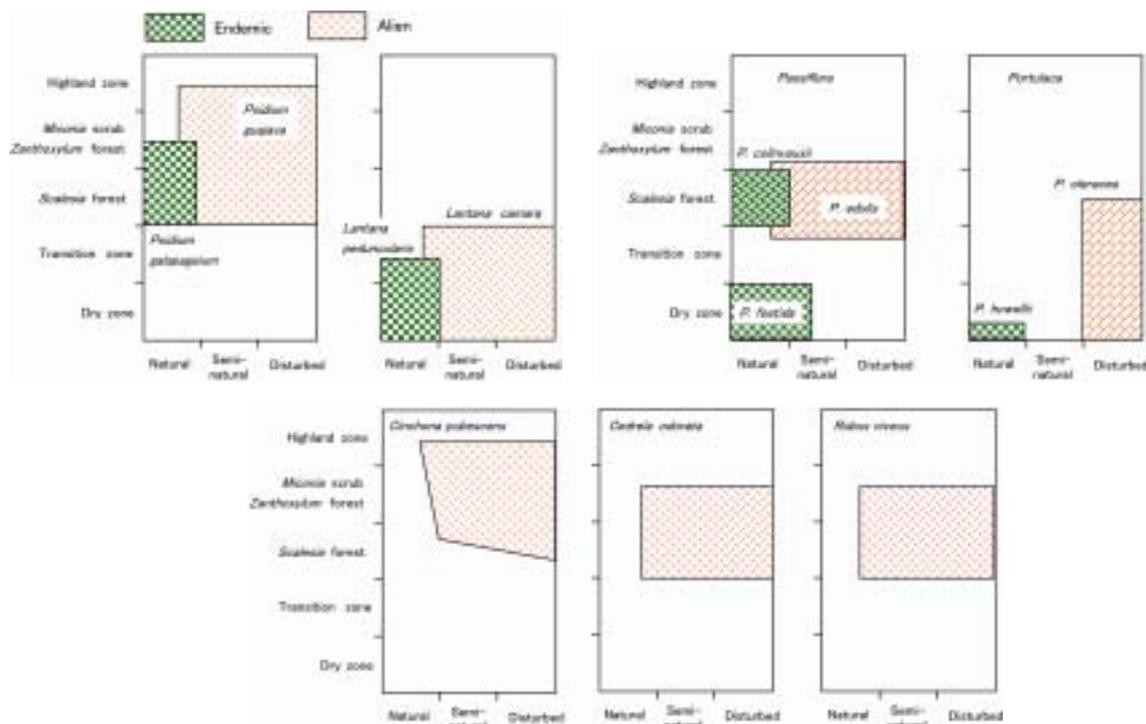


Fig. 20 Distribution charts of seven aliens on Santa Cruz, in relation to vegetation zones and habitat degradation. Five endemic counterparts, *Psidium galapageium*, *Lantana peduncularis*, *Passiflora colinvauxii* and *P. foetida* var. *galapagensis*, and *Portulaca howellii* (absent in Santa Cruz but present on nearby Isla Plaza), are given for comparison.

already gone (Werff, 1979), and fens and bogs (Itow & Weber 1974; Hamann, 1981), and other wetland communities and *Cyathea weatherbyana* thickets are endangered (Lawesson, 1990). The protection and conservation of particular endangered communities, and their restoration as well, should be a high priority, since endemic and non-endemic native species can be, and should be, preserved in their original ecosystems, which are really the stage of the organic evolution theater of the Galápagos where organisms have evolved and are evolving.

Acknowledgements

During the course of my vegetation studies on remote islands and uninhabited areas since my second visit in 1970 when my studies started, I owe in earnest thanks for much logistic support to the Charles Darwin Research Station. The Galápagos National Park Service (GNPS) permitted me to perform collecting work and export the collected material. On field trips, many people were my companions, without whom I would not have conducted my field-work well. They include Tjitte de Vries, Daniel Weber, the late Robert Silverglied, and Jacinto Gordillo in 1970; J. Gordillo and the late Arnaldo Tupiza in 1978; Jonas E. Lawesson, J. Bosco Nowak and Kunito Nehira in 1986; Dieter Mueller-Dombois in 1987; Ondina Landazuri in 1995; Kanehiro Kitayama in 1998; and Alan Tye, Mark Gardener, Patricia Jaramillo, Heinke Jaeger, Yasuhiko Miya, Kazumi Matsuoka, Iván Aldaz, O. Landazuri and J. Gordillo since 1998 up to 2002. The late Dr. Ira L. Wiggins, Stanford University, kindly identified specimens I collected on my field trips in 1964 and 1970, and permitted me access to sheets that had already been approved for publication in Wiggins & Porter's (1971) *Flora of the Galápagos Islands*. A. Tye and K. Kitayama gave me valuable suggestions and comments on my studies and on a part of the draft of the present paper. To those people and organizations, I send my sincere thanks.

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