

## Phytogeography and Ecology of *Scalesia* (Compositae) Endemic to the Galápagos Islands<sup>1</sup>

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**ABSTRACT:** *Scalesia* (Compositae), a genus endemic to the Galápagos Islands, consists of 12 shrubby species distributed in the lowland dry zone and three tree species found in the mid-elevation moist zone. They are completely allopatric in distribution. All the species have herbaceous traits: fast growth, soft wood, large pith at the center of trunk, and flowering within 1 yr after germination (in greenhouse). The tree species *Scalesia pedunculata* Hook. f. is shade-intolerant and heliophilous, and predominates as a monoculture in the moist zone of the four larger high-elevation islands. In ecological succession, it functions as pioneer, successor, and climax canopy plant. Even at climax or maturity of this monodominant forest, the canopy is not accompanied by young generations beneath owing to its shade-intolerance. The canopy population of postmature forest dies back nearly synchronously. A new generation then develops to build new forest. The progression from germination to maturity, and further to senescence and die back, is a self-cyclic succession, without change of dominant species. Over much of its range, *S. pedunculata* is endangered by the effects of past agricultural exploitation or heavy browsing by free-ranging goats, pigs, and donkeys; however, the population on the north side of Isla Santa Cruz has been preserved in good condition in the Galápagos National Park.

THE GALÁPAGOS ISLANDS are located on the equator in the eastern Pacific, about 1000 km west of the South American coast. The archipelago is well known as a showcase of organic evolution. The flora shows a high endemism rate of 51% in flowering plants (Porter 1979). It contains seven endemic genera, of which *Scalesia* (Compositae) is one of the most important taxa, with 15 species and two subspecies, the largest number of species among the endemic genera. All species are woody; 12 are shrubs, 1–2 m high, distributed in dry woodlands, and three are trees, 3 to >10 m high, found in the mid-elevation moist zone. The *Scalesia* species are important members of the Galápagos vegetation.

Taxonomically, Stewart (1911) treated the 17 species and subspecies in his monograph of the Galápagos flora. Howell (1941) added

a new species. Eliasson (1974, 1975) published a comprehensive treatment of the genus, and recent nomenclature follows his systematic arrangement, though Cronquist (in Wiggins and Porter 1971) treated the same taxa in a different way. Recently, Hamann and Wium-Andersen (1986) described a new species.

My experience with and concern about the genus began in 1964, when I joined the International Galápagos Expedition, organized jointly by the University of California, Berkeley, and the California Academy of Sciences. Since then, I visited the islands in 1970, 1978, 1981, 1986, 1987, and 1991. My major concern was the vegetation ecology of the archipelago, in particular the distribution and ecology of *Scalesia* species in the field. Parts of my studies on the vegetation and *Scalesia* have appeared previously (Itow 1965, 1971, 1988, 1990, 1992, Itow and Weber 1974, Itow and Mueller-Dombois 1988).

In this paper, I focus on the distribution and ecology of *Scalesia*, describing pre-

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viously unpublished data and observations and citing literature to supplement my earlier articles and to draw a comprehensive picture of the genus. Taxonomic treatment follows Eliasson (1974) and Hamann and Wium-Andersen (1986).

#### ENVIRONMENTAL SETTING

##### *Physical Environment*

The Galápagos Islands are of volcanic origin, created over the Galápagos Hot Spot in the Nazca Plate (Hey 1977). Because the plate moves toward the southeast, easterly located islands are volcanologically older than westerly located ones, and the oldest lava is 3–5 million years old (Bailey 1976, Cox 1983). The highest peak is Volcán Wolf, the northwesternmost volcano of the archipelago, 1707 m above sea level. Volcanic ejecta in the archipelago are basaltic lava, scoria, pumice, and ash, either old or new, and these are the principal substrates that support plant life.

The rainfall pattern is another important factor affecting the plant life. Because the archipelago lies in the southeast trade wind zone, the climate and weather are strongly influenced by the moisture-bearing trade winds and the topography of the islands. In general, southeasterly located islands, particularly their windward sides, receive much more rainfall than northwesterly located islands and their leeward sides. A good windward/leeward example can be seen on Isla Santa Cruz, which is a centrally located island rising to an elevation of 864 m above sea level. The rainfall on this island ranges from 372 mm at the south coast, through 1070 mm at 200 m altitude, to 1845 mm at 620 m altitude on the southern side; low-elevation Isla Baltra, located next to the north coast of Santa Cruz, receives only 76 mm (Itow 1992).

For the southerly located high-elevation islands, San Cristóbal (715 m above sea level) and Floreana (640 m), records of annual rainfall (Charles Darwin Research Station, unpublished data) give ca. 400 mm for the

west coast of San Cristóbal and ca. 1600 mm at 300 m altitude, and ca. 250 mm for the west coast of Floreana and ca. 800 mm at 300 m altitude. Judging from those records and vegetation zones of those islands, rainfall pattern must be similar to that on Santa Cruz. The rainfall pattern must be similar for the southern side of Volcán Azul and Volcán Sierra Negra of Isabela because of the similarity of their vegetation zones.

The southeast trade winds unload moisture on the southerly located high-elevation islands, especially on their windward sides. Therefore, northerly located leeward islands and volcanoes receive lesser amounts of rain and are drier than the southerly located islands. Low-elevation islands are always dry, regardless of their location, because the trade winds are intercepted only slightly by the low topography.

##### *Vegetation Zonation*

There are basically four vegetation zones. They range from the dry zone, through the transition and moist zones, to the highland zone (Stewart 1911, 1915, Bowman 1961, Itow 1965, 1971, 1990, 1992, Wiggins and Porter 1971, Itow and Weber 1974, van der Werff 1978, 1979, 1980, Hamann 1979, 1981). The dry zone on an island is much wider on the leeward north side (Fosberg 1967, Itow 1971, 1992) and on northerly located islands than the other zones (Stewart 1911, 1915), reflecting the above-mentioned rainfall pattern.

In the dry zone, *Bursera graveolens* (HBK.) Trian. & Planch. is most prevalent over the archipelago. There are many white-barked trees such as *Acacia* species, *Cordia* species, *Croton scouleri* Hook. f., *Piscidia carthagensis* Jacq., *Prosopis juliflora* (Sw.) DC, and *Tournefortia* species. Giant cacti, *Opuntia* and *Jasminocereus*, are prominent on some islands (Islas Santa Fé and Plaza [see Figure 8], the southern sides of Isla Santa Cruz, and Volcán Sierra Negra of Isabela). Shrubby species of *Scaevola* are found among those plants in the dry zone. Transition-zone vegetation is truly transitional between xerophytic and mesophytic. Major substrates in

the dry and transition zones are volcanic ejecta, almost unweathered because of low rainfall.

In the moist zone, the ejecta are well weathered, and the soils are deep and fertile. Abundant growth of terrestrial ferns and epiphytic bryophytes and ferns indicates that the atmospheric moisture and precipitation regimes are high enough to support lush plant life here. Prominent in the moist zone are trees of *Scalesia*, *Psidium galapageium* Hook. f., and *Zanthoxylum fagara* (L.) Sarg., and shrubs of *Acnistus ellipticus* Hook. f., *Psychotria rufipes* Hook. f., and *Tournefortia rufo-sericea* Hook. f. In the highland zone,

treeless vegetation prevails. (For details on Santa Cruz, see Itow 1990 and 1992.)

#### BIOGEOGRAPHY OF *Scalesia* SPECIES

There are 15 species, four subspecies, and two varieties in the genus *Scalesia* (Table 1). Based on my botanical explorations in seven visits to all islands and volcanoes (except remote northernmost Islas Darwin and Wolf, and Volcán Wolf of Isabela) and of all species but one (*S. atractyloides* Arnott), together with previous studies (Wiggins and Porter 1971, Elliason 1974, 1975, Hamann

TABLE 1  
DISTRIBUTION OF *Scalesia* SPECIES ON INDIVIDUAL ISLANDS AND VOLCANOES OF THE GALÁPAGOS

TAXA	ISLAND AND VOLCANO <sup>a</sup>																
	SC	FL	SF	SZ	BL	ED	ST	BA	PZ	az	ng	al	dw	wf	FE	PT	WL
Tree taxa																	
<i>pedunculata</i>	X	X	—	X	—	—	X	—	—	—	—	—	—	—	—	—	—
<i>cordata</i>	—	—	—	—	—	—	—	—	—	X	X	—	—	—	—	—	—
<i>microcephala</i>																	
var. <i>microcephala</i>	—	—	—	—	—	—	—	—	—	—	—	X	X	—	X	—	—
var. <i>cordifolia</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	X	—	—	—
Shrub taxa																	
<i>incisa</i>	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>divisa</i>	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>gordilloi</i>	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>villosa</i>	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>affinis</i>																	
subsp. <i>affinis</i>	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
subsp. <i>brachyloba</i>	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—
subsp. <i>gummifera</i>	—	—	—	—	—	—	—	—	—	X	X	X	X	X	X	—	—
<i>helleri</i>																	
subsp. <i>helleri</i>	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—	—
subsp. <i>santacruziana</i>	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>retroflexa</i>	—	—	—	X	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>crockeri</i>	—	—	—	X	X	—	—	—	—	—	—	—	—	—	—	—	—
<i>aspera</i>	—	—	—	X	—	X	—	—	—	—	—	—	—	—	—	—	—
<i>stewartii</i>	—	—	—	—	—	—	X	X	—	—	—	—	—	—	—	—	—
<i>atractyloides</i>																	
var. <i>atractyloides</i>	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—
var. <i>darwinii</i>	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—	—	—
<i>baurii</i>																	
subsp. <i>baurii</i>	—	—	—	—	—	—	—	—	X	—	—	—	—	—	—	—	—
subsp. <i>hopkinsii</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	X	X
Number of taxa	4	3	1	6	1	1	4	1	1	2	2	2	2	2	2	1	1

<sup>a</sup> SC, San Cristóbal; FL, Floreana; SF, Santa Fé; SZ, Santa Cruz; BL, Baltra (off NE coast of SZ); ED, Eden (off NW coast of SZ); ST, Santiago; BA, Bartolome (off E coast of ST); PZ, Pinzon; FE, Fernandina; PT, Pinta; WL, Wolf. Volcanoes of Isabela: az, Azul; ng, Sierra Negra; al, Alcedo; dw, Darwin; wf, Wolf.

and Wium-Andersen 1986), all the species are nearly completely allopatric in distribution, with a wide distance between their individual ranges in the archipelago (Figure 1). Intermediate forms, or hybrids, rarely have been found within the individual ranges concerned (cf. Figure 8, sites A and B).

Figures 1 and 2 show the distribution of *Scalesia* species on individual islands. Islas Santa Cruz and San Cristóbal, which are among the larger and geologically older islands, located centrally and easterly in the archipelago, respectively, and whose elevations reach the moist zone, harbor six and

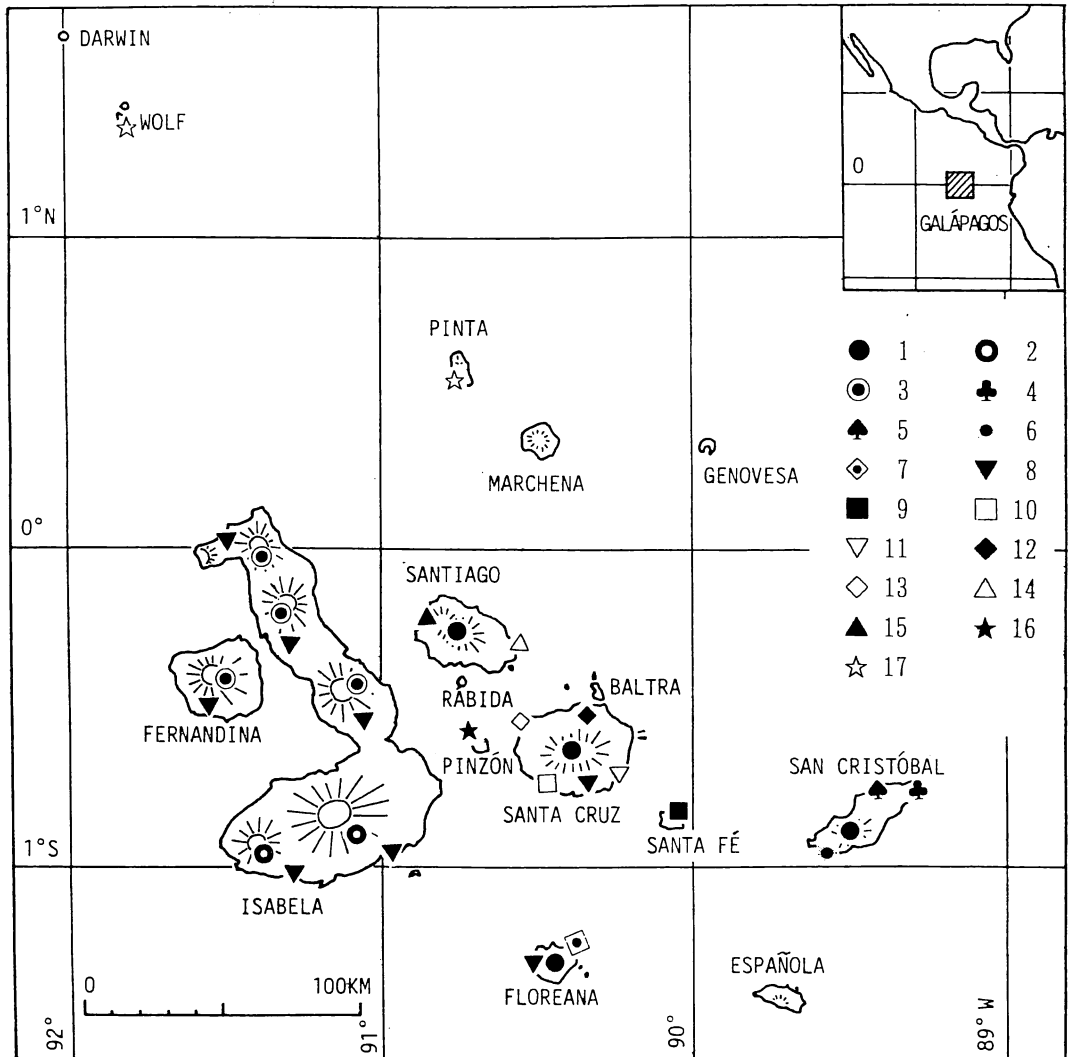


FIGURE 1. Map of the Galápagos Islands, Ecuador, showing the distribution of 15 species and two subspecies of *Scalesia* (Compositae). 1–3: Tree species distributed in the moist zone; 4–17: shrub species distributed in the dry zone. 1, *Scalesia pedunculata*; 2, *S. cordata*; 3, *S. microcephala* (one variety included); 4, *S. incisa*; 5, *S. divisa*; 6, *S. gordiloi*; 7, *S. villosa*; 8, *S. affinis* (two subspecies included); 9, *S. helleri* subsp. *helleri*; 10, *S. helleri* subsp. *santacruziana*; 11, *S. retroflexa*; 12, *S. crockeri*; 13, *S. aspera*; 14, *S. stewartii*; 15, *S. atractyloides* (one variety included); 16, *S. baurii* subsp. *baurii*; 17, *S. baurii* subsp. *hopkinsii*.

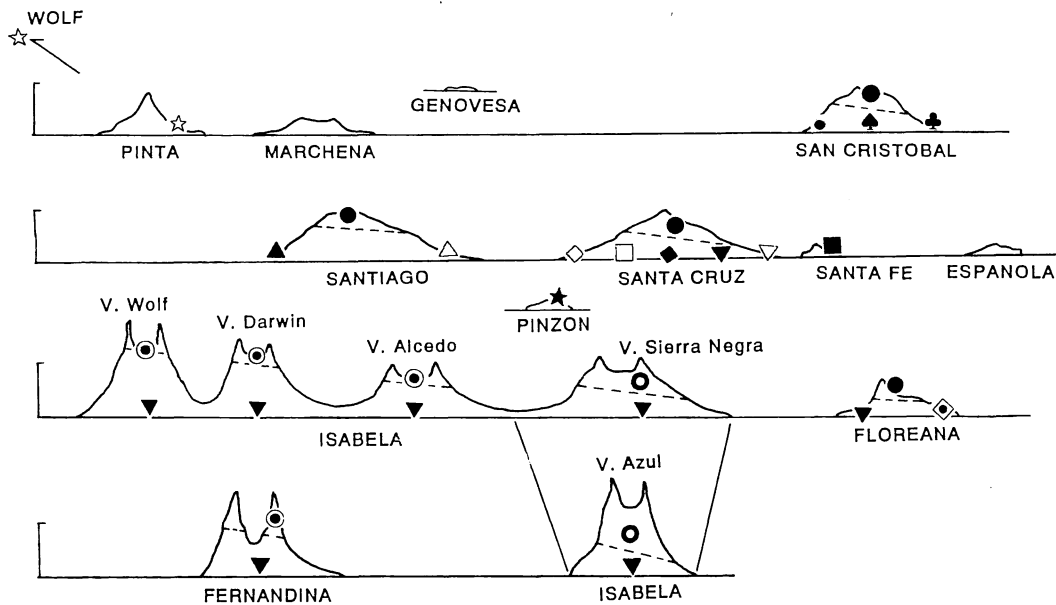


FIGURE 2. Schematic NW-SE profile of the Galápagos Islands, showing the distribution of the 17 taxa of *Scalesia*. Broken lines indicate approximate altitudes of the lower level of the moist zone. Species symbols are the same as in Figure 1.

four species, respectively. One of them is the tree *Scalesia pedunculata* Hook. f. found in the moist zone, and the others are shrubs in the dry zone. The shrubs on Santa Cruz are *S. affinis* subsp. *brachyloba* Harling, *S. aspera* Andersson, *S. crockeri* Howell, *S. helleri* subsp. *santacruziana* Harling, and *S. retroflexa* Hemsley, and those on San Cristóbal are *S. divisa* Andersson, *S. gordilloi* Hamann & Wium-Andersen, and *S. incisa* Hook. f.

In contrast, the two larger westerly islands, Isabela and Fernandina, contain only few species. On Isabela they include two tree species, *Scalesia cordata* Stewart in the southern moist zone and *S. microcephala* Robinson in the northern higher zone, and shrub species *S. affinis* subsp. *gummifera* (Hook. f.) Harling throughout the dry zone. On Fernandina there are only two species, the tree *S. microcephala* and the shrub *S. affinis* subsp. *gummifera*, where they occur likewise as members of the moist and dry zones, respectively (See Figure 1 and Figure 2 [profile]).

Low-elevation small islands, which are

covered only by dry-zone vegetation, support one *Scalesia* species only. These small islands include Wolf with *S. baurii* subsp. *hopkinsii* (Robinson & Greenman) Eliasson, Pinta with the same species, Pinzón with *S. baurii* subsp. *baurii* Robinson & Greenman, and Santa Fé with *S. helleri* Robinson subsp. *helleri*. Isla Floreana, an old but medium-sized island whose elevation reaches the moist zone, harbors two shrub species, *S. affinis* subsp. *affinis* Hook. f. and *S. villosa* Stewart, and one tree species, *S. pedunculata*. Isla Santiago, a relatively new but large island with a moist zone, supports two shrub species, *S. attractyloides* Hook. f. and *S. stewartii* Riley, and one tree species, *S. pedunculata*. *Scalesia* is absent on Islas Española, Rábida, Genovesa, Marchena, and Darwin.

The above-mentioned species and distribution patterns of *Scalesia* can be summarized as follows: (1) all the species are allopatric in distribution; (2) older and larger islands harbor more species than newer and smaller islands (Figure 3); (3) high-elevation islands support tree species in their moist

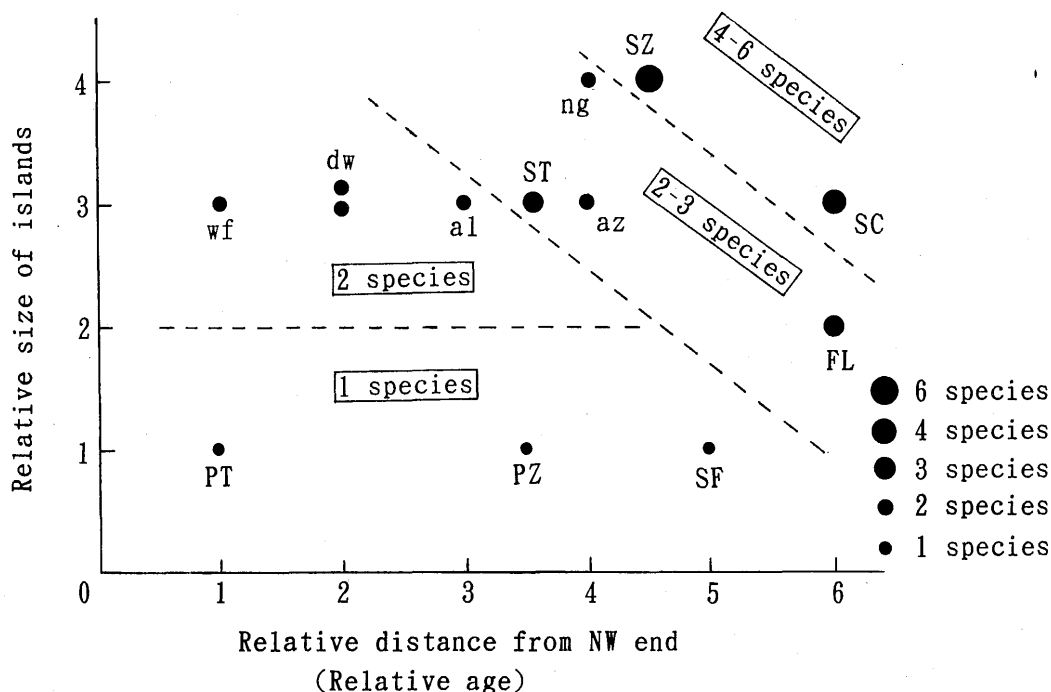


FIGURE 3. Relationship of number of *Scaesia* species with relative age and size of islands. Relative age is presented by relative distance from the youngest island, located at the NW end of the archipelago (see Figure 1). Note that older (southeasterly located) and larger islands harbor more species of *Scaesia*. Island designations as in Table 1.

zones; and (4) low-elevation islands, geologically either new or old, harbor only one shrub species.

Of the shrub species distributed in the dry zone, several species have been ranked as endangered (E) or vulnerable (V) in conservation status (Lawesson 1990). They are *Scaesia atractyloides* (E) on Santiago, *S. stewartii* (V) on Santiago and Bartolome (off the east coast of Santiago), *S. retroflexa* (E) and *S. helleri* subsp. *santacruziana* (E) on Santa Cruz, and *S. gordilloi* (V) on San Cristóbal. Based on my field studies in 1986, 1987, and 1991, the following populations on individual islands should be ranked in the V category: *S. affinis* subsp. *affinis* on Floreana and *S. affinis* subsp. *brachyloba* on Santa Cruz, and *S. pedunculata* on San Cristóbal and Santiago. Major threats are heavy browsing by introduced feral goats in the dry zone; and in the moist zone, past agricultural exploitation by settlers on San Cristóbal and free-ranging donkeys and pigs on Santiago.

#### HERBACEOUS TRAITS OF *Scaesia* SPECIES

Small shrub species (e.g., *S. villosa*, *S. stewartii*) grow up to 1 m high and 5 cm in diameter at the stem base, and large shrubs (e.g., *S. baurii*, *S. helleri*, *S. incisa*, and *S. gordilloi*) 2 m high and 10 cm across. Medium-sized tree species of *S. cordata* and *S. microcephala* are 3–5 m high and 10 cm in diameter at breast height (DBH); *S. pedunculata* is more than 10 m high and 15 cm DBH. The largest specimen I recorded for *S. pedunculata* was 29 cm DBH. Apparently the shrub species are Microphanerophytes and the tree species are Mesophanerophytes in the life-form categories of Mueller-Dombois and Ellenberg (1974).

Regardless of their shrub- or treelike stature, the growth of all species is fast. In *S. pedunculata*, for example, growth in height is 4–4.5 m in the first year and ca. 7 m in the second year after germination (Hamann 1979, Lawesson 1988). The wood is soft be-

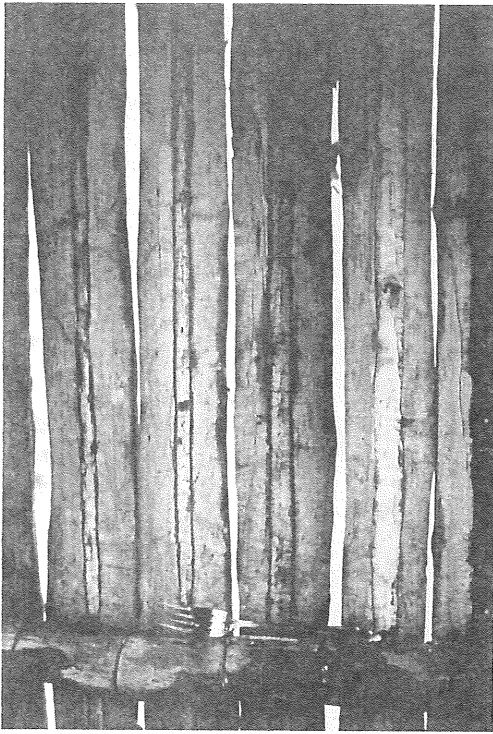


FIGURE 4. Cross section of tree trunk of *Scalesia pedunculata*, used as wall of farmer's house. For size, see the fork at bottom.

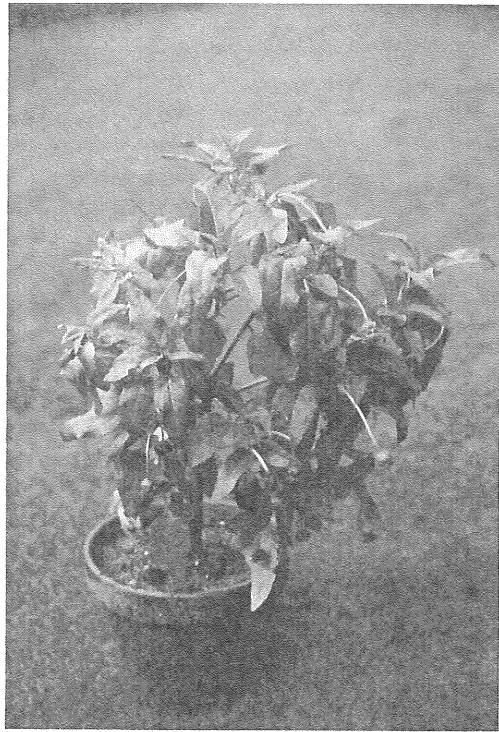


FIGURE 5. A specimen of *Scalesia gordilloi*, flowering in the greenhouse 5 months after germination.

cause of the rapid growth. A specimen of *S. pedunculata* trunk had an annual ring width of ca. 1 cm and a pith diameter of 1–2 cm (Figure 4). In 1971, upon returning from my second visit, I sowed seeds of some species collected in 1970 in my greenhouse. *S. incisa*, *S. microcephala*, and *S. gordilloi* (the last-named was treated as *S. divisa* at that time [Eliasson 1975] and later described as *S. gordilloi* [Hamann and Wium-Andersen 1986]) germinated within 10 days after sowing and flowered within half a year after germination (Figure 5). The same was found for *S. villosa* by Eliasson (1974). The above-mentioned characters, fast growth, soft wood, large pith of trunk, and flowering in the first year, are apparently herbaceous traits.

Ono (1967*a,b*, 1971) assumed a close relationship of the genus to *Tithonia* or *Viguiera* (Compositae), based on his chromosome counts ( $2n = 68$  in *S. affinis*, *S. baurii* subsp.

*baurii*, *S. incisa*, *S. microcephala*, and *S. pedunculata*). In contrast, Eliasson (1970, 1974) suggested a close affinity to *Helianthus* and *Viguiera* (Compositae) from the chromosome number ( $2n = 68$  in his additional counts for *S. aspera*, *S. atractyloides* var. *darwinii*, *S. divisa*, *S. helleri* subsp. *helleri*, and *S. villosa*), flower morphology, and wood anatomy. It is likely that *Scalesia* has evolved from an unknown herbaceous ancestor.

#### ECOLOGY OF *Scalesia pedunculata*

*Scalesia pedunculata* is found on the islands of San Cristóbal, Floreana, Santa Cruz, and Santiago. It is always associated with the moist zone. The zone begins and ends at different elevations on different islands. On Santa Cruz, the *Scalesia* forest ranges between 180 and 280 m altitude on the windward south side of the island and be-

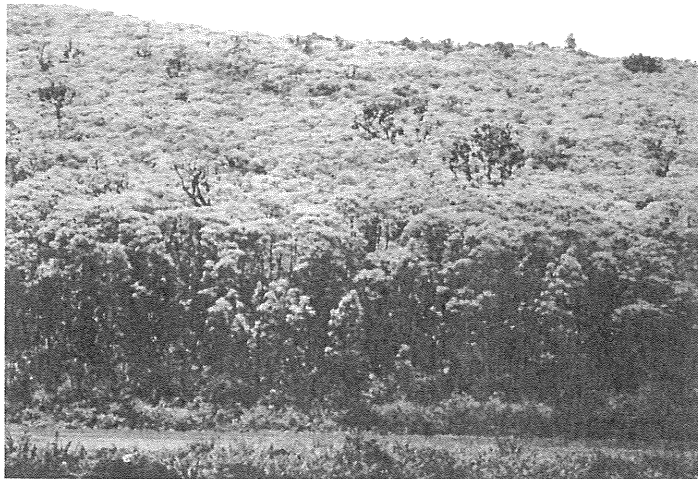
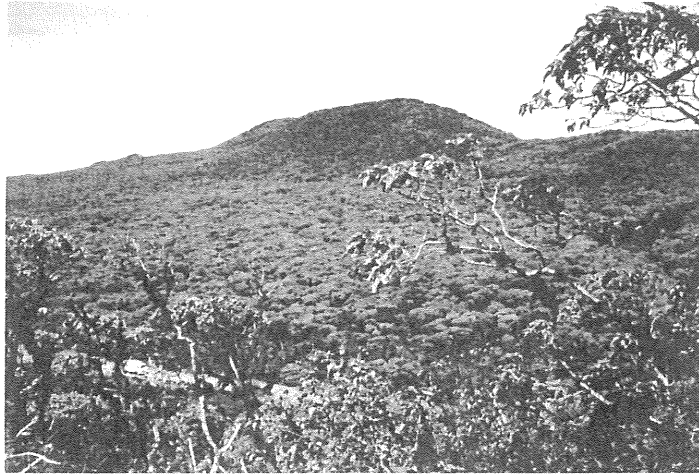


FIGURE 6. *Scalesia pedunculata* forest in Los Gemelos, Isla Santa Cruz. (Top) Mature forest in 1981. (Middle) Forest in 1987, consisting of a few remnant trees of the dieback old generation and a dense cohort of young trees established after stand-level dieback in the 1982–1983 El Niño year. (Bottom) Forest in 1991 at the same area. Old trees have decreased and the young cohort has become tall as compared with the 1987 forest.



tween 560 and 670 m altitude on the leeward north side (Itow 1971, 1992). The habitat of the moist zone is the most fertile in the archipelago, where the rainfall is high, volcanic ejecta are well weathered, and the soils are deep enough to support lush plant life (and present-day agricultural production).

In spite of the fertile soils found in the moist zone, however, few tree species immigrated into this habitat. The potential tree niche was apparently not occupied by any tree species. Instead, a herbaceous species of Compositae evolved here to a tree of normal size, namely *S. pedunculata*.

*S. pedunculata* shows the same herbaceous traits as given above for the genus as a whole. In addition, the life span of this tree species is estimated as about 15 yr at the most (Hamann 1979) in spite of a treelike appearance, attaining 20–25 cm DBH and more than 10 m height in maximal growth. It now occupies the tree layer of the island forest (or the tree niche) in this habitat of the archipelago.

Because of the rarity of other tree species adapted to the fertile habitat, *S. pedunculata* dominates the forest like a monoculture (Figure 6). Low values of diversity of shrubs and trees (DBH > 3.0 cm), as measured by Shannon's  $H' = 0.4\text{--}1.0$ , Fisher's  $\alpha = 0.6\text{--}1.1$ , and Itow's  $S(50) = 3.0\text{--}4.6$  (Itow 1988, 1992), are another documentation of the monospecific character of this forest.

As with the shrub species of the genus, *S. pedunculata* is also shade-intolerant and heliophilous (Itow 1983, Eliasson 1984, Itow and Mueller-Dombois 1988). It functions as a pioneer in ecological succession in the fertile moist zone (Figure 7: 1978a population). In the absence of shade-tolerant trees that would function as climax canopy species, *S. pedunculata* also assumes the role of successor that follows the pioneer in later stages in succession (Figure 7: 1978b and 1987 populations). Moreover, *S. pedunculata* dominates in a succession of life stages, with few trees of other species associated (Figure 6). (Itow and Mueller-Dombois 1988).

Because the tree is shade-intolerant, the seed does not germinate on the forest floor at any stage after canopy has developed, and seedlings and saplings cannot grow in the

shade under the canopy. The canopy trees approach their age limit at 15 yr. When they get old, if they encounter extreme conditions such as an extremely dry year as in the early 1940s (Kastdalen 1982) or an extremely wet year as in the 1982–1983 El Niño event (Hamann 1985, Itow and Mueller-Dombois 1988, Lawesson 1988), old trees occupying the canopy layer die synchronously. Almost immediately, a new cohort of seedlings develops under the dieback stand (Figure 6: middle; Figure 7: 1987 population). Thus, the age of the population becomes uniform or nearly so (Figure 6: bottom; Figure 7: 1991 population). In the absence of extreme conditions, the aging cohort population may also die nearly synchronously again. This phenomenon follows the cohort senescence theory (Mueller-Dombois 1983, 1986, Itow & Mueller-Dombois 1988). A similar dieback and reproduction pattern at the stand level applies to *S. cordata* on Isla Isabela (Lawesson 1988). Phenomena in other canopy species have been reported from Hawai'i (Mueller-Dombois 1987) and other Pacific islands (Mueller-Dombois 1988).

In the Galápagos Islands, extreme conditions, either dry or wet, repeated with intervals of several decades, must play an important role in setting back the population to the seedling generation or in starting a new succession with a new generation of shade-intolerant *S. pedunculata*. The whole series of ecological events is a self-cyclic succession or a buildup-collapse succession (Itow 1978, 1983 [both in Japanese]), which includes the phases of stand-level dieback and initial buildup. This self-cyclic succession is the consequence of the monodominance of the heliophilous tree *S. pedunculata* in the most fertile habitat in the absence of other canopy species in these isolated oceanic islands.

#### *Scalesia pedunculata* POPULATIONS ON DIFFERENT ISLANDS

As stated before, *Scalesia pedunculata* occurs on Santa Cruz, San Cristóbal, Floreana, and Santiago. In the original vegetation of the moist zone on Santa Cruz, *S. pedunculata*

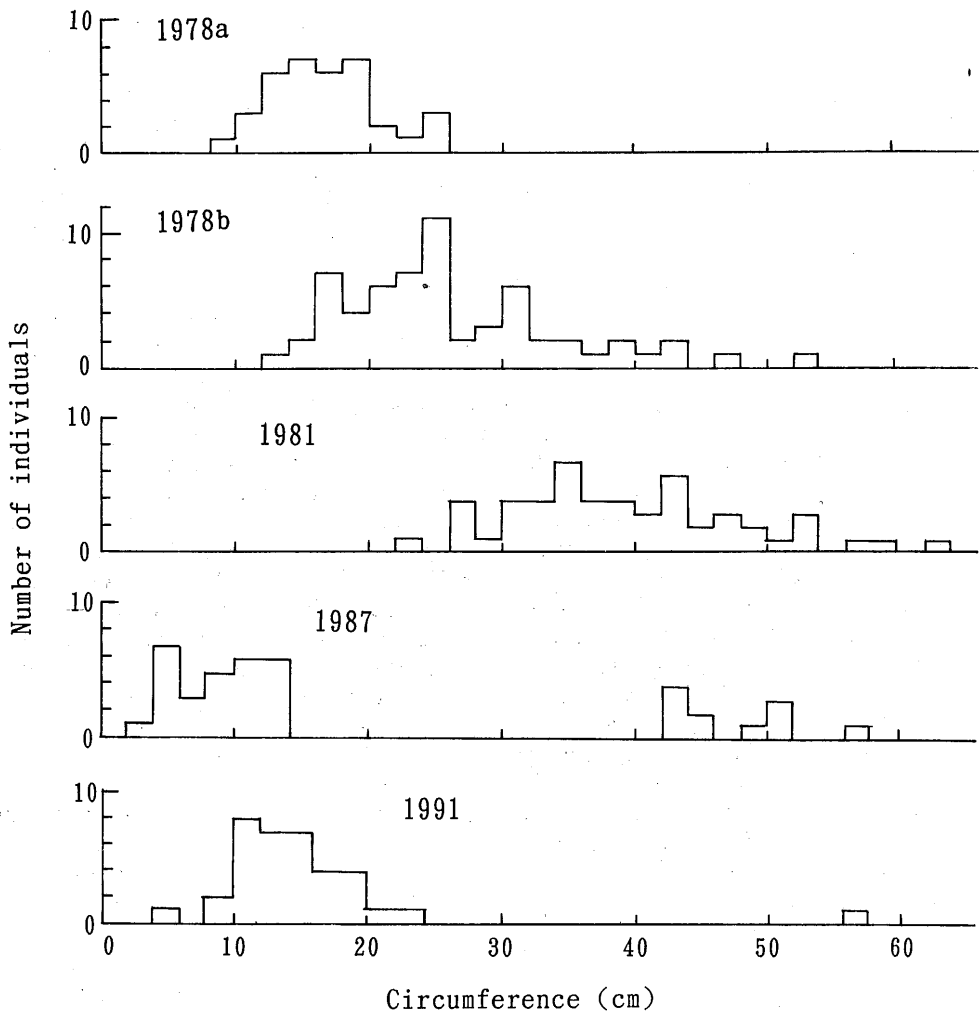


FIGURE 7. Changes in size distributions of *Scalesia pedunculata* at Los Gemelos, Santa Cruz. The 1978a population (top) was a 4-yr-old generation established on an abandoned field. The 1978b and 1981 populations were approaching the mature stage (cf. Figure 6, top). In 1982–1983, a heavy El Niño occurred, and the old generation died back synchronously. The 1987 population consisted of a few old trees and young regeneration (cf. Figure 6, middle). The 1991 population was mostly maturing trees (cf. Figure 6, bottom). Figures for 1978a–1987 are reproduced from Itow and Mueller-Dombois (1988) with permission of *Ecological Research*. New measurements made in 1991 (bottom) are added.

was distributed abundantly in the belt that surrounds the middle elevations around the island (Figure 8). During my 1964 field studies on Santa Cruz, there were good stands of *Scalesia* forest at Bella Vista, a village located at ca. 200 m altitude on the south side of the island. In 1970, only scattered trees were seen, and in the following years, the

species almost disappeared from the south side, because of expansion of agricultural exploitation caused by the increase of human settlers. Areas forested in the past are now changed to pasture, cultivated fields, banana and coffee plantations, or bushland of introduced *Psidium guajava* L. and *Persea americana* Mill. On the north side of Santa

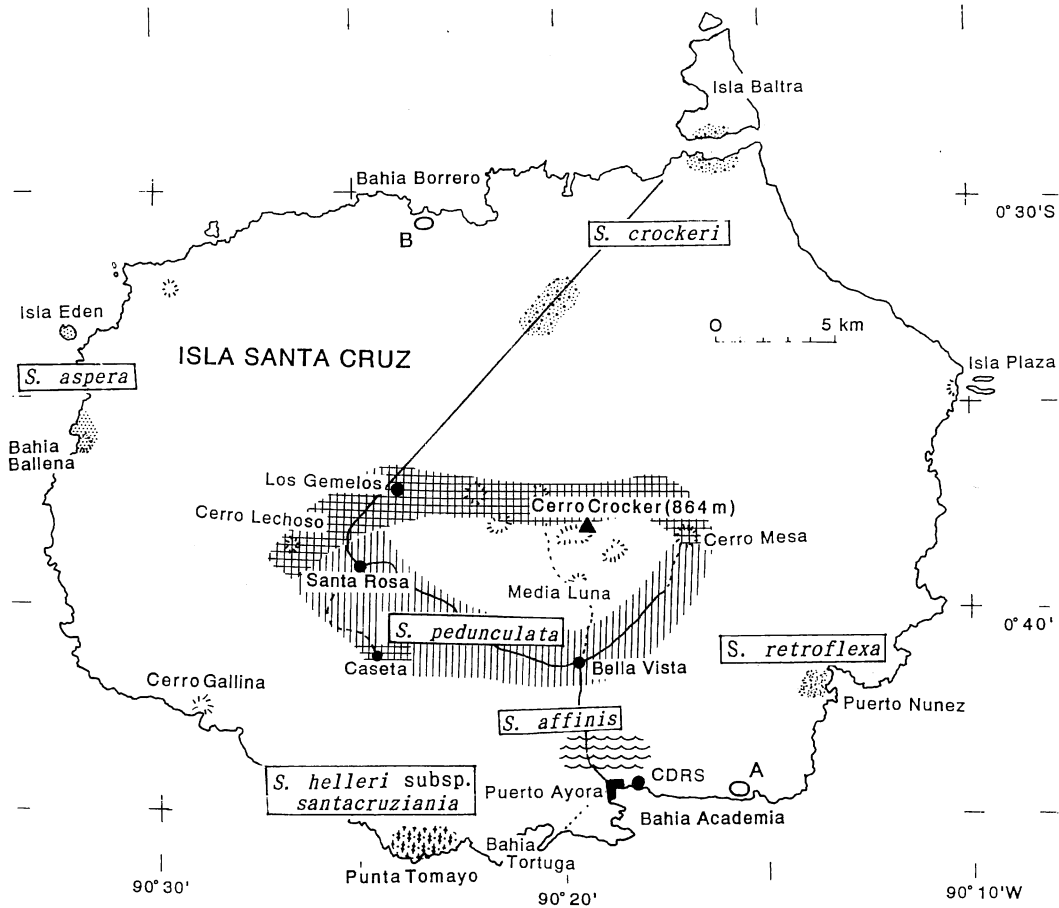


FIGURE 8. Map of Islas Santa Cruz and Baltra, showing the distribution of six *Scalesia* species, which I confirmed in my field studies, unless otherwise noted. Four species, *S. aspera*, *S. crockeri*, *S. helleri* subsp. *santacruziana*, and *S. retroflexa*, are restricted to the locations shown on the map. *S. affinis* was abundant in 1964 and 1970, but has recently become rare. The range of *S. pedunculata* on the southern side of Santa Cruz shows the assumed original distribution where, in 1964, a few forest stands were found; these have since disappeared. The range on the northern side (see Figure 6) is well preserved. Eliasson (1974, 1975) described the intermediate specimens of *S. affinis* and *S. retroflexa* from Point A on the south coast (where I collected a specimen) and intermediates of *S. crockeri* and *S. aspera* from Point B on the north coast of Santa Cruz.

Cruz primeval conditions as found in 1970 still prevailed in 1991, during which time our studies on *S. pedunculata* populations (Itow and Mueller-Dombois 1988) were conducted at Los Gemelos (i.e., before and after the 1982–1983 El Niño event [Figures 7 and 8]). This northern remnant of the belt is still one of the largest *S. pedunculata* forests in the Galápagos National Park.

Isla San Cristóbal is the easternmost is-

land where the four vegetation zones are well represented. People have exploited the fertile habitat since the second half of the nineteenth century (Gordillo 1990). During my 1964 visit to San Cristóbal, the fertile habitat, originally covered by *S. pedunculata* forest, was already under cultivation or covered by introduced, lush-growing *Psidium guajava* and *Eugenia jambos* L. In my 1986 field studies, only a few trees of *S. pedunculata*

were seen on a steep and inaccessible cliff along a watercourse on the south side of San Cristóbal. The *S. pedunculata* population on this island will probably survive in that restricted locality.

On Isla Floreana, major parts of the moist zone have been converted into pasture and agricultural cropland or to dense thickets of introduced *Psidium guajava* or *Lantana camara* L. since the nineteenth century. Fortunately, a part of the fertile area on the east flank of a hill, east of Black Beach, still supported a good stand of *S. pedunculata* in 1991. The population will survive if exploitation is stopped there.

On Isla Santiago, feral goats, pigs, and donkeys have been so numerous that the vegetation of the whole island has been seriously affected by heavy grazing and browsing. In 1970, when I traversed the island from the west coast to its summit area, a few trees of *S. pedunculata* were still present at an elevation of 710 m, together with mesophytic shrubs, such as *Croton scouleri* var. *grandifolius* Muell.-Arg., *Pisonia floribunda* Hook. f., *Psychotria rufipes*, and *Tournefortia rufosericea*. A small population of *S. pedunculata* survives there, because in the mid-1970s the Charles Darwin Research Station set up several enclosures to protect indigenous plants (Adersen 1990).

#### ACKNOWLEDGMENTS

I extend my sincere thanks to the directors of the Charles Darwin Research Station, David Snow in 1964, Roger Perry in 1970, Craig MacFarland and Hendrick Hoeck in 1978, Friedman Koester in 1981, Gunther Reck in 1986 and 1987, and Daniel Evans in 1991, for their support and encouragement of my studies. My thanks also go to the staff of the Station for assistance in logistics and fieldwork, and to the Galápagos National Park Service for permission for my field studies and plant collecting. Also I thank the following persons for their company and help in fieldwork: Daniel Weber and the late Robert Silberglied in 1970; Jacinto Gordillo in 1970 and 1978; Arnaldo Tupisa in 1978;

Joans E. Lawesson, J. Bosco Nowak, and Kunito Nehira in 1986; Dieter Mueller-Dombois in 1987; and Yuji Takatsuka in 1991. Last but not least, I cordially acknowledge the invitation by Kenneth Y. Kaneshiro to the U.S./Japan Joint Symposium, 1993, and constructive comments and advice given by D. Mueller-Dombois and Clifford W. Morden on an early draft of the manuscript.

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