

## Stand-level dieback and regeneration of forests in the Galápagos Islands

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### Abstract

Stand-level dieback and regeneration of forests in Galápagos are discussed, and related to natural- and man-made disturbances. The dieback of *Scalesia pedunculata* (Asteraceae) in Galápagos seems to follow the etiology and patterns seen in other pacific island groups. The currently large and synchronized cohorts of this early-successional species, found on Santa Cruz Island, may be explained by severe disturbances such as the natural el Niño phenomenon and human caused fires. It is suggested, that slow-growing species such as *Zanthoxylum fagara*, *Psidium galapageium* and *Acnistus ellipticus* have been suppressed by frequent fires in the highlands of Santa Cruz. The population dynamics of *Scalesia pedunculata* are suggested to follow a cyclus of 10–20 years duration, caused by senescence in the *Scalesia* stand, and promoted by extreme stress. Stand-level dieback is also reported from *Scalesia cordata*, *Erythrina velutina* and *Miconia robinsoniana*.

### Introduction

The succession and dynamics of vegetation in the Galápagos Islands have been reported on in a number of publications (e.g. de Vries & Tupiza in press; Eliasson 1984; Hamann 1979, 1981, 1985; Nowak *et al.* in press). However, there is little evidence on natural stand-level dieback and regeneration of large populations of species in Galápagos. Kastdalen (1982) mentioned the rapid dynamics of the endemic composite tree *Scalesia pedunculata* in the highlands of Santa Cruz as a naturally occurring successional event. He found almost complete dieback of the *Scalesia* trees in extremely wet years. In subsequent dry years regeneration was noticed. An important contribution to understanding the population dynamics of *Scalesia pedunculata* was given by

Hamann (1979). He found a very high initial mortality, and a growth rate like in pioneer trees. Most of the studied individuals died within 10 years of the germination, but a few seed-producing trees remained alive. *Scalesia* appeared to maintain dominance as a persistent monolayer tree, always being in the juvenile stage. Hamann suggested, that the life history of *Scalesia pedunculata* is that of an early successional species, with a rapid turnover. Eliasson (1984) described communities of *S. pedunculata* on Santa Cruz as climax forest. Van der Werff (1978) found that the *Scalesia* forests on Santa Cruz showed several characteristics traditionally found in secondary forest, such as rapid growth, soft wood, and heliophilous germination. However, he found no indications of this forest being secondary, and suggested that its appearance was because of lack of late-

successional tree species, which are found in continental forest systems.

During the extremely wet 'Niño' years of 1982–1983 (Hamann 1985) massive stand-level dieback of several square kilometers were observed in the *Scalesia pedunculata* forests on four of the Galápagos Islands. Dieback was reported also in the *Miconia robinsoniana* shrub vegetation on Santa Cruz between December 1984 and November 1985, (de Vries manuscr, Adersen, pers. comm.) presumably caused by severe drought following the Niño period. Similar cases of extensive stand-level dieback were observed in other types of vegetation (Nowak *et al.* in press; de Vries & Tupiza in press) involving *Scalesia cordata* and *Erythrina velutina*. Thorough knowledge of population dynamics is important to understand this phenomenon (Mueller-Dombois 1983, 1987).

The purpose of this paper is to review stand-level dieback and in particular the development of *Scalesia* forests in Galápagos. Preliminary results from a study on dynamics and succession in the *Scalesia* forests of Santa Cruz are included.

### Previous evidence of stand-level dieback in Galápagos

Published evidence of diebacks is very scanty. Kastdalen (1982) is probably the first to report on the dynamics of *Scalesia pedunculata* on Santa Cruz. He commented: 'during the first five or six years of our stay it seemed that *Scalesia pedunculata* was disappearing...there were only mature trees and no young ones were coming up to replace the old ones which were dying. Then in 1944 or 1945 there were prolonged droughts of about four months duration in each year...most of the underbrush died, and the damage was further increased by the wild cattle and donkeys. The succeeding garua season showed a simply fantastic recovery of the *Scalesia* forest. Where formerly there had been only scattered or single trees, there were now forests of young *Scalesias*'. Like Kastdalen, Hamann (1979, 1985) found that *Scalesia* could recover very rapidly under certain conditions, especially after prolonged droughts, or other disturbances. However, it was assumed, that

the presence of other tree species, like *Zanthoxylum* and *Pisonia* could slow down the regeneration process of a new cohort, as the ground was covered with more trees, shrubs and vines. At other places an almost pure *Scalesia* forest was found. Hamann concluded that *Scalesia* rarely becomes older than 15 yr.

### Disturbances in the highlands of Santa Cruz

The highlands of Santa Cruz have been influenced considerably for the last 50 yr. Man-made fires seem to have occurred frequently (Eckhardt 1972; de Roy pers. comm.). The precise locations of the fires are not known, but their extent may have been considerable in dry years. It has generally been assumed, that fires only affected the tree-less pampa vegetation of Santa Cruz. However, new data from Isabela (Nowak *et al.* in press) show that fire in humid *Scalesia* vegetation may occur after a drought. Photographic evidence for this is present in the files of the Charles Darwin Research Station (CDRS), with photographs from a fire in the most humid *Scalesia* forest on Santa Cruz. Kastdalen (1982) also reported how domestic cattle and donkeys ran wild since the 1930s and had a considerable effect on the vegetation.

Figure 1 shows the relation between the precipitation data from CDRS, completed with indications

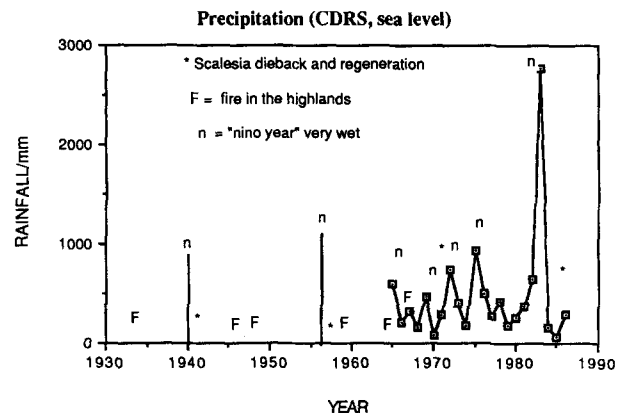


Fig. 1. Precipitation as measured at the Charles Darwin Research Station, Santa Cruz, sea-level, with indication of Niño years, reported fire in the highlands, and occurrence of *Scalesia pedunculata* dieback.

on wet years from Kastdalen (1982) and Naranjo (1985), information on major diebacks and confirmed fires in the highlands. Diebacks seem to have occurred in connection with extremely rainy years, and a recovery of new cohorts in subsequent dry years.

### Study area

Most of the Galápagos Islands are dominated by one or more typical shield volcanoes. The lowlands and northern slopes are largely covered with lava fields, whereas the southern slopes and the higher parts above 200 m generally receive more precipitation and therefore have better developed soil profiles.

The climate is determined by sea currents around the archipelago. The cool season occurs between July and December, due to predominance of cold water around the Archipelago. In December, warm water currents from Central America often start to dominate and sea-temperatures rise. This causes a more or less pronounced wet period. In some years an unusual upwarming of the surface waters occurs in the entire eastern equatorial Pacific, connected with a large scale oceanwide air-sea oscillation, called El Niño. (Perry 1984; Robinson & del Pino 1985). The average precipitation in the highlands is much higher than at the coast, but extreme drought or wetness may still occur there as well.

There are only a few common tree species in the highlands (Table 1). Some could be called biological or heliophilous nomads (Hallé *et al.* 1978) or weed trees (*Scalesia* spp., *Trema micrantha*, *Solanum erianthum*), while others are slow-growing and shade-tolerant sciaphilous species (Hallé *et al.* 1978) of late successional stages, (*Psidium galapageium*, *Zanthoxylum fagara*, *Acnistus ellipticus*). The fast growing pioneer trees are favoured by disturbances and will soon become dominant in the vegetation. As a stand of a pioneer species dies from senescence, slow growing shade-tolerant species may emerge, unless the area again is subject to external disturbance or extreme stress. Such successional relations have been studied in an area on the rim of volcano Fernandina, which was subject to a tephra eruption in 1968 (Hendrix & Smith 1986). *Scalesia microcephala* and *Sola-*

*num erianthum* rapidly colonized the area, whereas *Zanthoxylum fagara* invaded very slowly. A similar pattern has been observed in a large area on Isabela which burnt in 1985 (Nowak *et al.* in press).

### Methods

Populations of *Scalesia pedunculata* were studied in two permanent quadrats in homogeneous vegetation on Santa Cruz Island. The quadrat size was 10 × 10 m. One quadrat was established close to Cerro Crocker, at its northern slope, 700 m a.s.l., another in the Caseta area at 170 m a.s.l. (established by T. de Vries). All *Scalesia* individuals were marked with metal tags and monitored from 1985 to 1987, measuring height and DBH. Data on structure and composition of the plant communities were collected as well.

### Results and discussion

Before the dieback the *Scalesia* population included almost a pure stand of old trees, presumably in a stable phase. Small seedlings or saplings were rare or absent (Eliasson 1984). As shown by Eliasson (1984), the competition among these adult trees of sufficient vigour was so strong, that newly opened tree-fall patches quickly regenerated through self-replacement by meristem growth (but not by seeds) and thereby were covered by the neighboring crowns.

Table 1. Common tree species in natural highland forests in Galápagos, and their characteristics. (Arborescent shrubs not included).

Species	Type of growth	Type of wood	Importance
<i>Scalesia cordata</i>	rapid	soft	locally dominant
<i>S. pedunculata</i>	rapid	soft	very dominant
<i>S. microcephala</i>	unknown	soft	not dominant
<i>Zanthoxylum fagara</i>	slow	hard	locally dominant
<i>Psidium galapageium</i>	slow	hard	locally dominant
<i>Trema micrantha</i>	rapid	soft	dominant
<i>Acnistus ellipticus</i>	slow	unknown	not dominant
<i>Solanum erianthum</i>	rapid	soft	locally dominant

This would happen provided the disturbance was only small, and the forest in a vigorous state. However, in December 1980–January 1981, when a large area was cleared, *Scalesia* achenes rapidly germinated as a consequence of the increased light. This represented a rejuvenation phase, as no meristem growth was involved but only the intrastructural seed reserve. This may be seen in the data from before the Niño period. Densities of tall trees in the Caseta quadrat were 52, 121, 43 and 38 trees per 100 sq. m, in 1970, 1972, 1975 and 1977, respectively (Hamann 1979). The last record before the Niño phenomenon is from March 1982, where 17 trees were still alive in one quadrat (Hamann 1985). These latter died before August 1983, except four of which two were dying. The remaining two old trees stayed alive through the Niño rain.

In 1985 a remarkable rejuvenation of *Scalesia* was observed. Estimates in the Caseta quadrat show 5500 saplings per 100 sq. m. In Table 2, the appearance of the 1985 cohort is expressed by the height classes encountered in the Caseta quadrat. Similar figures are shown in Table 3 for the Mount Crocker area. *Scalesia pedunculata* is clearly divided into an old cohort and the new one. Mortality in the initial

Table 2. Appearance of the 1985 cohort of *Scalesia pedunculata* on Santa Cruz as shown by numbers of saplings and old trees in the Caseta quadrat.

Height classes/m	Aug. 1985	Nov. 1985	Jan. 1986	Mar. 1986	June 1986	Oct. 1986	July 1987
0.5	5500	17	7	0	0	0	0
1	0	135	71	25	4	0	0
1.5	0	95	89	45	19	2	1
2	0	21	29	27	35	7	0
2.5	0	0	0	2	24	13	0
3	0	0	0	0	5	15	0
3.5	0	0	0	0	0	19	2
4	0	0	0	0	0	13	9
4.5	0	0	0	0	0	2	12
5	0	0	0	0	0	0	8
5.5	1	1	1	1	1	1	8
6	1	1	1	1	1	1	11
6.5	0	0	0	0	0	0	9
7	0	0	0	0	0	0	3
Number of trees	5502	270	198	101	89	73	63

Table 3. *Scalesia* regeneration Crocker 1985–1987.

Appearance of the 1985 cohort of *Scalesia pedunculata* on Santa Cruz, as shown by numbers of saplings and old trees in the 'Cerro Crocker' quadrat.

Height classes/m	Nov. 1985	Jan. 1986	Mar. 1986	June 1986	Oct. 1986	July 1987
0.5	24	13	5	3	0	0
1	40	54	24	4	2	0
1.5	4	22	43	31	3	0
2	0	5	33	26	17	0
2.5	0	0	5	26	19	2
3	0	0	1	18	15	4
3.5	0	0	0	2	23	12
4	0	0	0	0	3	11
4.5	0	0	0	0	0	16
5	0	0	0	0	0	15
5.5	0	0	0	0	0	1
12.5	3	3	3	3	2	2
Number of trees	71	97	114	113	84	63

phase is very large, which agrees with Hamann's observations. In the Caseta quadrat ca. 5500 new saplings came up, but only 61 of these were still alive in July 1987, which gives a mortality of 99%. The mortality in Mount Crocker was apparently lower, but here no counts of saplings were made.

During 1986 and 1987, no new saplings emerged. The growing *Scalesia* trees shaded out most other species, except for shade tolerant ferns and shrubs. Synchronized dieback and recovery of *Scalesia pedunculata* on Santa Cruz may be due to repeated fires and grazing by domestic animals. Relative dominance of *S. pedunculata* as compared to other tree species may be explained by such disturbances, which favour rapidly growing early successional heliophilous species, and disfavour slower growing fire-sensitive species. The stands of *Scalesia* may therefore have become more and more uniform due to repeated catastrophic events such as fires and severe browsing. Regarding the etiology of the nearly complete stand-level dieback, it is probably important, that before the Niño phenomenon 1982–1983 the *Scalesia* forest was an adult or old stand with large trees, forming a closed canopy (Hamann 1981; Eliasson 1984). The expected maximum life-span for *Scalesia pedunculata* in the Caseta area may be

around 10–15 yr (Hamann 1979). It is therefore probable that natural cohort senescence of the species was important for the dieback encountered, in the same manner as has been reported for forests on Hawaii and New Zealand (Mueller-Dombois 1987). Dieback could therefore be explained by assuming that the mature forests of *Scalesia* were reaching a state of reduced vigour or partial senescence, and hence they were highly susceptible to disturbance. Together with the extreme Niño conditions (strong winds, water saturated soil and high air-temperatures) the intrinsic characteristics of the *Scalesia* may have resulted in the dieback of large stands. As stated by Mueller-Dombois (1987), during the terminal phase of its cyclus, a cohort may break down, either suddenly or gradually. If the disturbance is small and patchy, a quick regeneration will occur and the cohort survives. If the disturbance is large this is not possible, and a seed-dependent rejuvenation is necessary. Environmental extremes may occur during the whole life-span of a cohort stand. As long as the cohort is in a normal state of vigour, it will survive such extremes. However, when a senescence stage is reached, a certain extreme, such as climatic stress, may act as a trigger for a general collapse of the cohort. With the expected life-span of *Scalesia pedunculata* cohorts as well as the climatic setting, it is probable that the combination of uniform cohorts, life-span and population structure will cause repeated stand level dieback, as indeed has been observed. It seems also probable that dieback is a cyclic event, with a rejuvenation phase, an adult phase and a senescent phase. If new disturbance occurs in the latter phase, a dieback phase will follow. If no disturbance occurs, the cyclus may continue with the formation of a more diverse forest, where slow-growing trees become more important. This proposed life history has been summarized in Table 4.

After the 'Niño' years, the accumulated seed bank of *Scalesia pedunculata* quickly germinated. It was probably further promoted by the strong drought, which killed or mimimized much of the undergrowth. This agrees with Kastdalen's (1982) observations. A few trees of the old cohort survived the extreme conditions, and were still alive in 1987. This may be due to genetic variation within the cohort.

Table 4. Suggested model for *Scalesia pedunculata* forest dynamics on Santa Cruz, Galápagos. 1. Germination phase; 2. Rejuvenation phase, where *Scalesia* saplings grow from seedling to 5–10 m tall trees, depending on local environmental conditions; 3. First optimal (adult) phase, which is a steady state; 4. First senescence phase of the *Scalesia* population; 5. Partial break down of the cohort structure; 6. Second optimal phase, where a combination of new *Scalesia* trees and slow growing trees is formed; 7. Second senescence phase, where the second cohort of the species is further broken down, and replaced by other species.

Succession phase:	Duration (yr)	Dominant species:
1. Germination	1–2	Herbs & <i>Scalesia</i>
2. Rejuvenation	2–5	<i>Scalesia</i>
3. Adult	5–10	<i>Scalesia</i> & Shrubs
4. First <i>Scalesia</i> senescence	1–5	<i>Scalesia</i>
5. Partial rejuvenation and displacement	5–15	<i>Scalesia</i> , some other trees
6. Adult diverse forest	until disturbance	<i>Scalesia</i> , some other trees
7. Second <i>Scalesia</i> senescence	10–15	Various tree species

More likely, the former forest, although of uniform appearance, contained different cohorts, in different phases, viz. adult and senescent phases, differently susceptible to abiotic stress-factors.

General dieback of large stands of trees or shrubs is not restricted to *Scalesia pedunculata*. *S. cordata* in the Sierra Negra area died over large areas after the Niño, and rejuvenated in 1985. However, most of this new generation died during 1987 because of severe attacks from endemic insects, while surviving plants became covered by a dense growth of *Ipomoea triloba* and *I. alba*.

The uniformity of *Miconia robinsoniana* in the highlands of Santa Cruz may be explained in a similar way. Several fires have occurred in the area, the latest one in 1967. In 1974 *Miconia* was restricted to a small area around Media Luna and its vicinity, probably delimited by the 1967 fire. *Miconia* now covers a large area extending to Cerro Crocker. Young *Miconia* were severely affected by the Niño, with many individuals apparently dying during 1982–1983, while the old populations first survived

the Niño, but then started to die during 1985.

A related observation concerns the apparent uniformity of some of the lowland tree cohorts, notably of *Bursera graveolens* which is dominant in large areas of dry coastal steppe forest. A synchronized population structure and dynamic pattern, including large stand-level dieback is to be expected in such areas (Mueller-Dombois 1987). Stands of *Bursera graveolens*, *Piscidia carthagensis*, *Erythrina velutina* and *Parkinsonia aculeata* seem to be very uniform in large areas. According to Grant (pers. comm.) rejuvenation of *Erythrina* is extremely difficult, although this tree may produce seeds annually. Similar observations of stands with a few old trees of this species and no saplings, have been made by the present author.

A succession theory based on observations on Hawaiian *Metrosideros* forests (Mueller-Dombois 1983, 1987) explains temporally recurring dieback as a pattern and process sequence in primary succession, where large initial cohorts have been formed due to catastrophic events. Canopy dieback of these large cohorts during their senescent stage gives rise to successively smaller and more patchy cohorts at each dieback cycle. The canopy dieback of *Scalesia pedunculata* on Santa Cruz island seems to fit this theory, and the uniformity of the cohorts may be explained with repeated man-made catastrophes such as fires and 'El Niño' events.

It is here suggested that the occurrence of dieback and uniform cohorts of *Scalesia pedunculata* is a result of combined natural and man-made disturbances. As to the natural ones, the climatic setting forces the biotic environment to change constantly, as the climate is an unpredictable factor. One year may be extremely dry with desert conditions, whereas the subsequent year may show extremely wet conditions. This everlasting fluctuation in the physical conditions must cause some rather dramatic changes in the Galápagos plant and wildlife, including provoked stand-level dieback of whole populations of plants and also animals (Robinson & del Pino 1985).

The rapid dynamics of *Scalesia* also ensure, that the former tall forest, known from the highlands of Santa Cruz, will soon again appear, but then within another 10–20 years, a new stand level dieback is to be expected. It is of scientific and conservation in-

terest to continue long-term studies of the highland Galápagos forests. They may reveal whether the pure *Scalesia* forests are true natural forests, as stated by several authors, or, if left alone, will be displaced in part by other slow-growing species, leading to a more diverse forest.

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### References

- de Vries, T. & Tupiza, A. in press. The dynamics of six stands of *Scalesia cordata* in permanent plots in different habitats in Sierra Negra, Isabela, Galápagos. Monogr. Syst. Bot.
- Eckhardt, R. C. 1972. Introduced plants and animals in the Galápagos Islands. Bioscience 22: 585–598.
- Eliasson, U. 1984. Native climax forests. In: Perry, R. (ed.), Key environments. Galápagos, pp. 101–114. Pergamon Press, Oxford.
- Hallé, F., Oldeman, R. A. A. & Tomlinson, P. B. 1978. Tropical trees and forests. An architectural analysis. Springer Verlag, Berlin.
- Hamann, O. 1979. Dynamics of a stand of *Scalesia pedunculata* Hooker fil., Santa Cruz Island, Galápagos. J. Linn. Soc. Bot. 78: 67–84.
- Hamann, O. 1981. Plant communities of the Galápagos Islands. Dansk Bot. Ark., 34: 1–163.
- Hamann, O. 1985. The el Niño influence on the Galápagos vegetation. In: Robinson, G. & del Pino, E. M. (eds), The Niño in the Galápagos Islands: the 1982–1983 event: 299–330. Charles Darwin Foundation, Quito, Ecuador.
- Hendrix, L. B. & Smith, S. D. 1986. Post-eruption Revegetation of Isla Fernandina, Galápagos: II. Nat. Geogr. Res. 2(1): 6–16.
- Kastdalen, A. 1982. Changes in the biology of Santa Cruz Island between 1935 and 1965. Not. Galápagos 35: 7–12.
- Mueller-Dombois, D. 1983. Canopy dieback and successional

- processes in pacific forests. *Pacific Sci.* 37: 317–325.
- Mueller-Dombois, D. 1987. Natural dieback in forests. *Bioscience* 37: 575–583.
- Naranjo, P. 1985. El fenomeno el Niño y sus efectos en el clima del Ecuador. In: G. Robinson & E. M. del Pino (eds), *El Niño in the Galápagos Islands: The 1982–1983 Event*. Charles Darwin Foundation, Quito, Ecuador.
- Nowak, J. B., Lawesson, J. E., Adersen, H. & de Vries, T. in press. The post fire vegetation dynamics on southern Isabela, Galápagos Islands. *Monogr. Syst. Bot.*
- Perry, R. 1984 (ed.). *Key environments. Galápagos*. Pergamon Press, Oxford.
- Robinson, G. & del Pino, E. M. 1985 (eds). *El Niño in the Galápagos Islands: the 1982–1983 event*. Charles Darwin Foundation, Quito, Ecuador.
- van der Werff, H. H. 1978. *The vegetation of the Galápagos Islands*. Thesis Utrecht.