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Population Structure, Stand-level Dieback and Recovery of *Scalesia pedunculata* Forest in the Galapagos Islands

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Introduction

Scalesia pedunculata is a fast growing, short-lived tree of the Asteraceae, which forms dense, monospecific stands in the humid forest zone at middle elevations on Isla Santa Cruz of the Galapagos Islands (Bowman, 1961, Itow, 1965; Wiggins and Porter, 1971). The species apparently evolved from a herbaceous ancestor.

Between 1935 and 1940 *Scalesia pedunculata* underwent mass mortality according to observations recorded by a long-term local resident (Kastdalen, 1982). The forest thinned down to only a few scattered remnants until the flowering, coincident with a dry period during the early 1940s, and the forest area became densely restocked with seedlings of the same species.

The first named author of the present paper has been interested in the ecology and behavior of the species and carried out investigations of the size distribution of *Scalesia pedunculata* populations on his visit to the Galapagos in 1970, 1978 and 1981. The data he gathered showed that each stand of the forest consists of one or a few even-aged cohorts without any young generations, but the data were not published (a part of which are appearing in the present paper). Based on his field studies he noted some ecological characteristics of *S. pedunculata* such as (1) its pioneering behavior, (2) the species-poor constitution of the forest, (3) the absence of young tree generations in the stands, (4) the synchronized collapse of canopy tree populations at a post-mature life-stage, and (5) a self-cyclic or build-up-and-collapse succession (Itow, 1978, 1983: Original in Japanese). Hamann (1979) also reported on the pioneering behavior of the species and the cyclic replacement of the forest.

The 1982-1983 El Niño brought extremely high rainfall to the Galapagos Islands (Robalino, 1985), and mature populations of *S. pedunculata* died then and afterwards (Hamann, 1985; Lawesson, 1987). The present paper focuses on the population structure of *S. pedunculata* before the 1982-83 El Niño and its change afterwards, and further on a comparison of stand-level dieback phenomena with other Pacific island forests.

The study area is Los Gemeros, a nearly level terrain at an altitude of ca. 560 m, on Isla Santa Cruz. Quadrats of various sizes were used in the 1978 and 1981 field work, and sampling of selected

stands was done in 1987 together with the co-author.

Results

Figure 1 gives size distributions of four stands, all comprised of single species populations of *Scalesiapedunculata*. Population A1, sampled in a 10 m x 3 m quadrat, became established in 1974/75 on an abandoned right-of-way along a newly constructed road. At the time of sampling in 1978, the stand consisted of a young cohort, three to four years of age. This population had disappeared in 1981. It was a typical cohort and looked like the stand on Fig.2A, which was photographed nearby in 1978. Population A2 (sampled in a 10 m x 20 m quadrat, also in 1978) was a nearly mature stand coexisting on a nearby area. The population mode in terms of circumference was at 24 to 26 cm, and the size distribution was strongly skewed to the left. Population B was randomly sampled from the same area as A2 but three years later in 1981. The circumference mode had shifted to 34 to 36 cm and the whole population size range was now comprised of bigger trees. Figure 2B is a photograph of this mature population B taken in 1981. A noteworthy feature in the A2 and B populations was the total absence of young regeneration. This was so in spite of the presence of mature flowering trees.

In 1987, four years after the 1982/83 E1 Nino year, the forest on the same area had taken on a totally different appearance (Fig. 2C). There were only a few scattered old trees left standing and the ground was densely occupied by a new generation of *S. pedunculata*. At this time, sampling was done at three stands, that is, for 8 to 10 young individuals at each stand and for 11 mature individuals encountered there (Fig. 2C and Table 1). The mature cohort was a remnant of population B, a large part of which had undergone stand-level dieback following the E1 Nino year. The mature and remnant trees appeared to be the parent generation of the young generation.

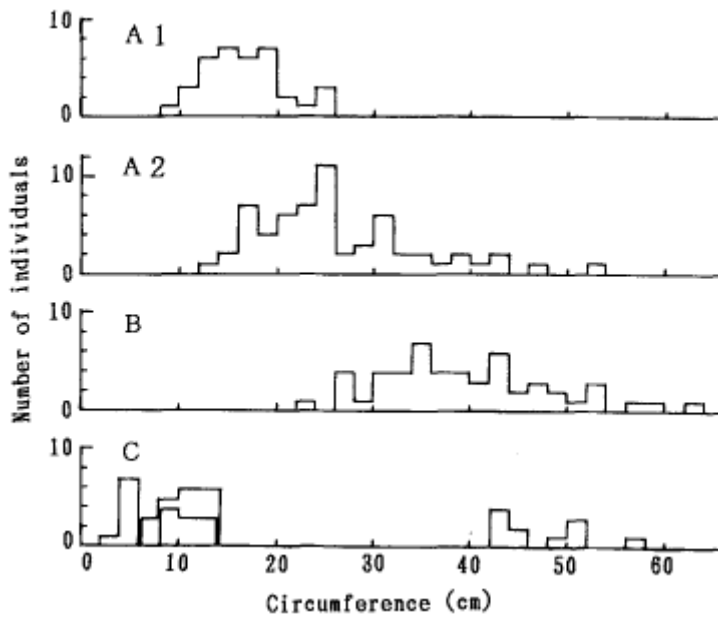


Fig. 1. Size distributions of *Scalesia pedunculata* (A) 1978, (B) 1981 and (C) 1987 populations at Los Gumeros on Isla Santa Cruz. A1. The 1978 four-year old population established on abandoned soils (Fig. 2A). A2. The 1978 population. The modal class of circumference is 24-26 cm. B. The 1981 population at the same area as at A2. The modal class is 34-36 cm (Fig. 2B). C. The 1987 population consisting of three young cohorts and old ones (Fig. 2C).

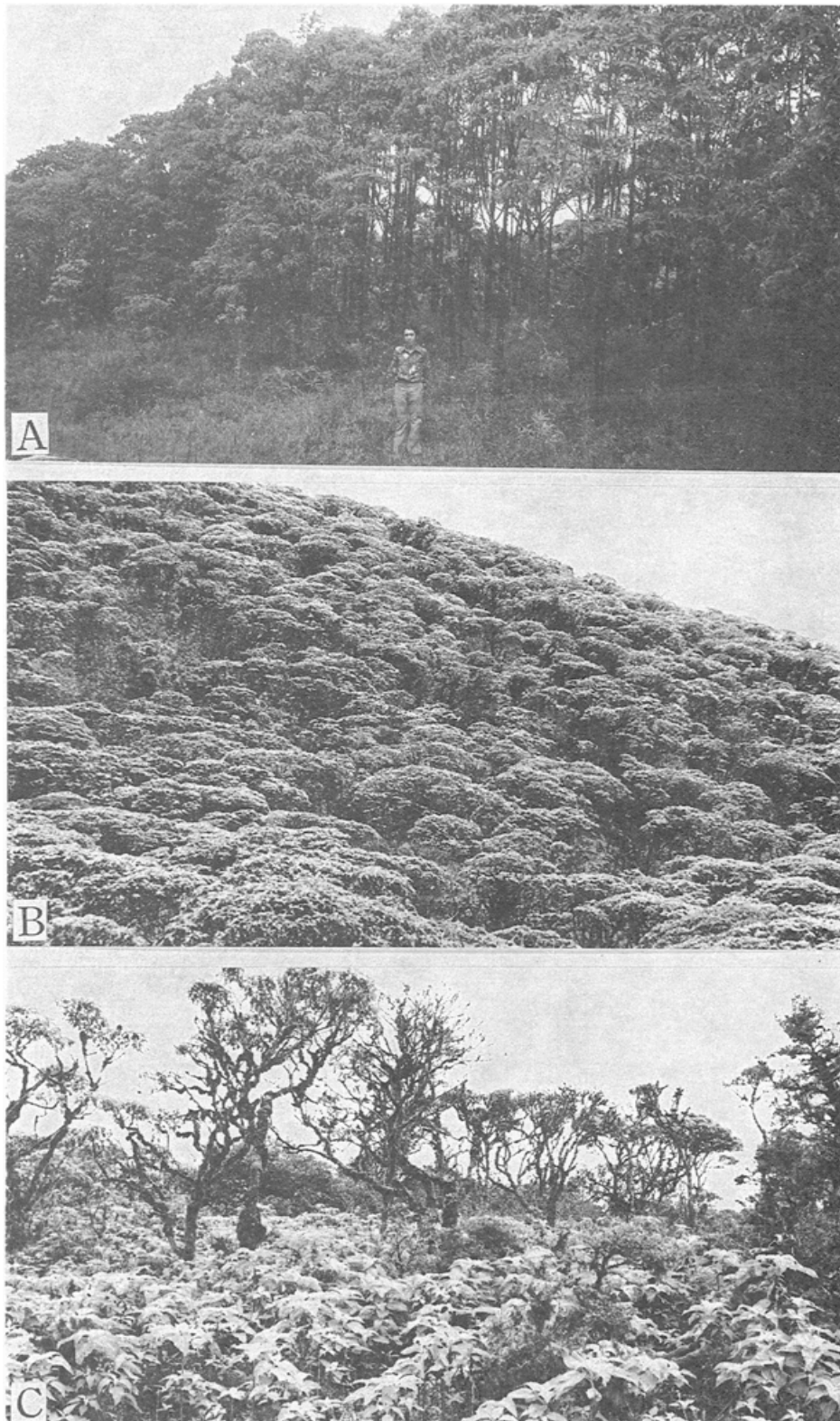


Fig. 2. A: A four-year old cohort of *S. pedunculata* established on a cleared strip along a road completed in 1975 (Photo taken in 1978). B: A mature stand of *S. pedunculata* at Los Gemeros (Photo taken in 1981). C: Remnant trees left after stand-level dieback during the 1982-83 E1 Nino and recovering cohort (Photo taken in 1987).

Table 1. Measurements of *Scalesia pedunculata* cohorts at Los Gemeros in 1987. Figures in parentheses are averages.

Circumference (cm)	Height (m)	Circumference (cm)	Height (m)
Young cohort a (<i>n</i> = 8)		Young cohort c (<i>n</i> = 10)	
4.4	1.2	8.0	3.2
2.2	2.0	10.5	4.0
5.8	1.8	10.0	4.0
5.0	2.1	10.0	4.2
4.4	2.0	14.0	4.5
5.3	1.9	11.7	4.0
5.1	1.9	13.0	4.5
5.5	1.9	11.3	4.0
(4.7)	(1.9)	9.5	3.5
Young cohort b (<i>n</i> = 10)		Old living cohort (<i>n</i> = 11)	
13.0	2.5	45.0	6.0
7.5	2.4	43.0	5.5
11.5	2.5	45.0	6.5
11.3	2.3	43.5	4.5
10.5	2.6	44.5	5.5
7.3	2.0	49.5	7.0
12.0	2.1	43.0	8.0
6.7	1.9	51.0	8.0
9.8	2.4	51.0	8.0
14.0	2.6	57.0	10.0
(10.4)	(2.3)	51.4	5.0
		(47.6)	(6.7)

Discussion

The *Scalesia pedunculata* forest occupies a humid tropical landscape in a climatic setting not unlike that of multi-species tropical lowland rainforests on the continents. These continental forests are known to turn over or cycle in form of gap dynamics, whereby single tree-fall gaps appear to be the norm. In contrast, the *Scalesia* forest turns over in the form of mass mortality or stand-level dieback.

The same phenomenon has been observed and studied in other Pacific island forests, for example in New Zealand's *Nothofagus* forests (Wardle and Allen, 1983; Ogden, 1988), Hawaii's *Metrosideros* forests (Mueller-Dombois, 1983, 1987a; Jacobi et al., 1988), in the montane *Nothofagus pullei* forests of Papua New Guinea (Ash, 1982; Arentz, 1983, 1988) and in subalpine *Abies* forests of Japan (Kohyama and Fujita, 1981; Kohyama, 1988). However, natural dieback is not restricted to Pacific islands. It also occurs in the Adirondak Mountains of Upstate New York (Sprugel, 1976; Sprugel and Bormann, 1981), and a smaller area mosaic pattern has been observed in remnants of European virgin forests (Mueller-Dombois, 1987b).

There are two aspects of forest dynamics worth further discussion. The first relates to the consequences of stand-level dieback, and the other to its causes.

Consequences of stand-level dieback

The data and earlier observations show that the collapse of monospecific *Scalesia* forest has been followed by reestablishment of the same species. Immediate reestablishment of canopy species is also observed in more diverse forests in small gaps, while large-area gaps in such multi-species forests usually result in the displacement of the original canopy species by successional species, often of the fast-growing type like *Sealesia pedunculata*. In the Hawaiian rainforest both patterns occur, "replacement dieback", where the canopy species *Metrosideros polymorpha* becomes reestablished and, "displacement dieback" where the canopy species becomes displaced by successional species. There are strong indications that replacement is not always by the same genetic type but instead by successional races of *M. polymorpha* (Stemmermann, 1983, 1986). Displacement dieback occurs naturally in the Hawaiian rainforest on nutritionally rich soils, where treeferns (*Cibotium* spp.) assume a dominant canopy role after *Metrosideros* dieback (Burton and Mueller-Dombois, 1984). *Metrosideros polymorpha* is a slow-growing tree species with a life span of at least 10 times that of *Scalesia pedunculata*. Anthropogenically influenced successional displacement also occurs and seems to be increasing where aggressive alien species invade (Jacobi et al., 1988). Such displacement appears to occur now also in some parts of the *Scalesia* forest area in the Galapagos Islands.

Causes of stand-level dieback

The recent *Sealesia* dieback may be said to have been caused by the 1982/83 El Niño, which brought unusually heavy rainfall to the Galapagos Islands, perhaps drowning the roots of the trees. However, the earlier dieback during the late 1930s, observed and recorded by Kastdalen (1982), was not associated with an El Niño.

A stand-level dieback can have an obvious single cause in some cases, such as a prolonged flooding of the root system, a fire, a volcanic explosion and a lava flow, a killer disease, or strong air pollution. Such catastrophic disturbances will kill a forest regardless of its species diversity and stand structure. However, many forest diebacks have no obvious causes. They include the Pacific island and mountain forest examples cited above and the *S. pedunculata* dieback.

An underlying common feature in most forests, in which stand-level dieback has no obvious single cause, is the low canopy species diversity and the simplified structure of the forest. The simplification refers to a cohort structure as found in plantation forests. In those artificial forests, cohorts in various age-states may display a checker-board pattern depending on the plantation system. Under natural conditions, cohorts form a spatially variable mosaic. In island and mountain forests with restricted habitats, not all life-stages may be coexisting side by side.

The demography of such forests may contain the important underlying cause of standlevel dieback, which refers to a cohort stand in a weak life-stage. This can happen when such a stand becomes

overstocked due to insufficient self-thinning during stand-development, or also, when a stand becomes established on a "wrong" site. In those cases, cohort stands can be forced into a state of "premature senescence".

Conclusions

In the introduction of this paper, synchronized collapse of canopy populations at a post mature life-stage was noted as one of the outstanding ecological characteristics of *S. pedunculata*. Thus, the Galapagos example follows the prediction of the "cohort senescence" theory as suggested for the *Metrosideros* rainforest dieback in Hawaii (Mueller-Dombois, 1983, 1985, 1987b). In this theory a frequently recurring environmental perturbation (a pulse-perturbation, not a catastrophic killer) becomes the dieback trigger for a stand that is already in a low vigor state due to its demographic history. A comprehensive theory of forest dynamics should predict not only the consequences of tree-fall gaps, but also those of stand-level dieback. Moreover, it must be equally concerned with the causes of tree mortality, which so far have received little attention by ecologists. Forest dieback, however, has now become an important ecological topic in industrial countries, where air pollution is presumed to be the major cause. The *Sealesia* dieback is another example of mass mortality due to natural causes. It further emphasizes the need of considering canopy species diversity and forest stand structure when trying to resolve the etiology of stand-level dieback and forest stability.

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