HERBACEOUS AND ERICACEOUS COMMUNITIES IN THE HIGHLANDS OF SANTA CRUZ, THE GALAPAGOS ISLANDS[1]

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ABSTRACT

The herbaceous and ericaceous vegetation in the highlands of Santa Cruz was studied to find relations of plant communities to topographical relief. The vegetation was classified into six communities according to a scatter diagram of vegetation samples (relevés) processed by the reciprocal averaging method and according to the dominant species. The communities classified are *Paspalum conjugatum* community, *Pteridium aquilinum*/*Blechnum polypodioides* community, *Lycopodium clavatum* community, *Hypericum uliginosum* community, *Polypodium tridens* community, and *Pernettya howellii* community. Of the communities recognized, the *Paspalum conjugatum* community was found on moist, gentle slopes and flat sites. The *Pernettya howellii* community was established on southeast-facing, steep slopes at higher altitudes exposed directly to the southern trade winds. This habitat becomes wet or moistened by moisture-saturated southern winds on cloudy and foggy days, but dries up in extended dry periods. The *Polypodium tridens* community was found only on nearly exposed lava. The three other communities were intermediate between the *Paspalum* community and the *Pernettya* community in phytosociological and topographical relations.

The treeless vegetation in the highlands of Santa Cruz, the Galápagos Islands, was first reported by Howell (1942, 1957: photos 2a, 3a, and 3b). Bowman (1961) called this treeless highland the Upland Zone, while Wiggins & Porter (1971) described it as the Fern–Sedge Zone.

In this treeless highland, Itow & Weber (1974) studied fens and bogs, and van der Werff (1978) described Habenario-Trisetetum howellii as a new plant association and the community of *Sphagnum erythrocalyx* and *Elaphoglossum glosophyllum*. Hamann (1981) investigated broad-leaved herbaceous vegetation during his extensive vegetation studies and described a *Pteridium aquilinum–Jaegeria gracilis* community, a *Sphagnum cuspidatum* community, and a *Jaegeria crassa* community in the Santa Cruz highland.

The present study was carried out in the highlands of Santa Cruz in 1970 from the standpoint of phytosociology, to find out what plant communities have developed and how they are related to altitude, slope aspect, and steepness of slope. A part of the study has been published previously (Itow & Weber, 1974). The present paper describes herbaceous and ericaceous plant communities found in the same highlands.

STUDY AREA AND METHODS

There are basically four vegetation zones on Santa Cruz in terms of climate, ranging from Dry through Transition and Moist to Highland zones, of which the last is treeless. Since the

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southeastern trade winds, which bring moisture to the islands, prevail during most of the year, the north side of the island is drier, and the zones are deflected upward. The treeless vegetation ranges from 560 m altitude on the southern slope to the summit of Mt. Crocker (860 m), and from 670 m to the highest point on the northern side (Itow, 1971). (For an outline map, see Itow & Weber, 1974, fig. 2.)

The area was originally treeless (Howell, 1942, 1957) and is still so. Parts of the area have occasionally been grazed or burnt (Hamann, 1975; van der Werff, 1978).

In 1970, the weather was unusually dry from February through April, and the summit area was visible every day from the south coast of the island. The rain gauge located at the lower boundary of the treeless highland zone (ca. 620 m) received only 147 mm of precipitation in those three months of 1970, while it received 250–800 mm in the same months between 1968 and 1975 (Charles Darwin Research Station, 1968–1975).

In each of the vegetation stands studied, the altitude, slope direction, and steepness of slope were recorded by readings of a pocket altimeter and a hand compass, respectively. Other conditions recognizable in the stand were also recorded.

Vegetation sampling followed Braun-Blanquet's relevé method, using 1–4-m^2 quadrats and adopting Braun-Blanquet's (1964) dominance classes (+, 1–5) and sociability classes. Voucher specimens were determined at Stanford University by Ira L. Wiggins and the author. One set of specimens is deposited in the California Academy of Sciences Herbarium, the other in the Nagasaki University Herbarium.

In Tables 1–5, the dominance and sociability classes of plants are presented together in the normal format (e.g., '4.3'), where the first digit is dominance class and the second is sociability class. The record "+" means the dominance class + and sociability class 1. Prominent bryophytes and lichens are listed in the tables under names given in the field.

The vegetation was classified roughly into three categories: fens and bogs accompanied by *Sphagnum* species, fern–sedge communities, and ericaceous communities. Vegetation samples (relevés) of herbaceous and ericaceous communities were processed with Hill's (1973) reciprocal averaging method (RA) to analyze phytosociological relations of plant communities. This method is effective in ordination of vegetation samples with little distortion and gives a scatter diagram (Gauch et al., 1977).

In compiling the tables of species composition, all the vegetation samples were grouped into communities according to the results obtained by the RA processing. In each of the community tables, the vegetation samples were arranged in order by the method given in Mueller-Dombois & Ellenberg (1974) to find subgroups in species composition within each of the classified communities (Tables 1–5).

Results

Figure 1 shows the scatter diagram of the vegetation samples (except *Polypodium tridens*-dominated stands on account of their extreme positions). Based on their positions on the scatter diagram and based on the dominant species, the 97 vegetation samples, including those dominated by *Polypodium tridens*, were classified into six different communities. They are *Paspalum conjugatum* community (Table 1), *Pteridium aquilinum/Blechnum polypodioides* community (Table 2), *Lycopodium clavatum* community (Table 3), *Hypericum uliginosum* community (Table 4), *Polypodium tridens* community (Table 4), and *Pernettya howellii* community (Table 5). Based on my field experiences in the highlands, the *x*-axis of the scatter diagram (Fig. 1) can be interpreted as representing a wet-to-dry gradient, but the *y*-axis is difficult to interpret. Figure 2 gives the distributions of the recognized communities in relation to altitude, slope directions, and slope steepness in degrees.

TABLE 1. *Paspalum conjugatum* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13
Altitude (m)	650	720	650	690	690	710	690	720	790	680	630	680	680
Slope aspect	NW	SW	—	—	—	—	—	—	NNW	—	—	—	—
Slope (degrees)	25	30	—	—	—	—	—	—	10	—	—	—	—
Numbers of species	15	14	16	12	10	12	10	12	12	6	6	5	3
CHARACTERISTIC SPECIES													
Paspalum conjugatum	5.4	5.4	5.4	1.2	2.2	5.4	5.5	5.4	5.4	5.5	4.4	5.5	5.5
DIFFERENTIAL SPECIES													
Vigna luteola	2.2	.	+.2	+	1.2	+	1.2	2.2	1.2	2.2	.	.	.
Commelina diffusa	.	+	+	+	+.2	2.3	+	+	1.1	2.2	.	.	.
Borreria laevis	3.3	2.2	+.2	3.4	3.3	+	.	+	.	.	.	.	.
Tournefortia rufo-sericea	1.2	2.2	+.2	.	.	.	.	.	.	.	.	.	.
Acnistus ellipticus	(+)	(+)	1.2	.	.	.	.	.	.	.	.	.	.
Panicum glutinosum	2.2	2.2	+.2	.	.	.	.	.	.	.	.	.	.
Justicia galapagana	+.2	(+)	.	.	.	.	.	.	.	.	.	.	.
Psychotria rufipes	.	(+)	1.2	.	.	.	.	.	.	.	.	.	.
Ctenitis pleiosoros	.	+	(+)	.	.	.	.	.	.	.	.	.	.
Hypolepis hostilis	.	+	+	.	.	.	.	.	.	.	.	.	.
COMPANIONS													
Pteridium aquilinum	1.2	2.2	1.2	+	1.2	.	.	3.3	+.2	1.2	2.2	1.1	.
Nephrolepis cordifolia	+.2	.	.	.	.	1.2	1.2	+	+.2	.	.	2.2	2.2
Polygonum opelousanum	.	.	+	5.4	4.4	1.2	.	.	+	1.2	+	.	.
Thelypteris pilosula	+.2	.	.	.	.	+.2	.	.	+.2	+.2	.	+.2	.
Drymaria cordata	.	.	.	+.2	1.2	.	.	+	+	.	.	.	.
Centella asiatica	.	.	.	2.3	3.3	4.4	2.3	.	.	.	.	.	.
Cyperus sp.	.	.	.	+.2	+	+	+	.	.	.	.	.	.
Blechnum occidentale	1.2	(+)	.	.	.	+	.	.	.	.	.	.	.
Alternanthera halimifolia	(+)	.	+.2	.	.	.	.	1.2	.	.	.	.	.
Hyptis rhomboidea	+.2	.	.	.	.	.	.	+.2	.	.	.	.	.
Scleria pterota	.	2.2	.	+.2	.	.	.	.	.	.	.	.	.
Hibiscus diversifolius	.	2.2	.	.	.	.	.	.	.	.	3.3	.	.
Jaegeria gracilis	.	.	1.2	.	.	.	.	+.2	.	.	.	.	.
Scleria hirtella	.	.	.	.	+.2	.	.	.	.	.	2.3	.	.
Panicum dichotomiflorum	.	.	.	.	.	1.2	1.2	.	.	.	.	.	.
Rhynchospora rugosa	.	.	.	.	.	.	2.2	.	.	.	2.3	.	.

Other companions. In stand number 1: *Pilea baurii* +.2, Pteridophyte sp. +; in number 3: *Cissampelos pareira* 1.1, *Zanthoxylum fagara* +.2; in number 4: *Polygonum hydropiperoides* +.2, *Thelypteris* sp. +.2; in number 6: *Oxalis* sp. +; in number 7: *Stenotaphrum secundatum* 1.2, *Eleocharis* sp. +.2; in number 8: *Cyperus grandifolius* +.2, *Phyllanthus caroliniensis* +.2, *Ichnanthus nemorosus* +.2; in number 9: *Drymaria monticola* +.2, *Paspalum galapageium* +.2, *Dichondra repens* (+); in number 12: *Eleocharis* sp. +; in number 13: *Ludwigia leptocarpa* 2.3.

PASPALUM CONJUGATUM COMMUNITY

The *Paspalum conjugatum* community (Table 1) was found on gentle slopes and flat sites mostly at lower elevations in the treeless highland (Fig. 2A). In 1970, the habitat was scarcely dried, not even in long-lasting dry periods without rainfall and fogdrip. The vegetation was approximately one meter high. *Pteridium aquilinum* often co-dominated in rather less moist habitat. Major companions in the *Paspalum conjugatum* community are *Nephrolepis cordifolia, Polygonum opelousanum, Thelypteris pilosula,* and *Centella asiatica* (Table 1).

The community can be divided into two types. The one was distinguished by the presence of *Vigna luteola* and *Commelina diffusa* (Stands 1–10 in Table 1), and the other by their absence

TABLE 2. *Pteridium aquilinum/Blechnum polypodioides* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13
Altitude (m)	750	725	690	685	685	700	730	680	560	800	730	640	755
Slope aspect	SE	ESE	NW	SSE	ESE	S	SSE	SE	NNE	SE	NW	SSE	—
Slope (degrees)	20	15	30	25	20	30	10	30	2	30	5	10	5
Numbers of species	10	11	11	9	10	15	11	12	7	7	9	10	8
DOMINANT SPECIES													
Pteridium aquilinum	4.4	4.3	5.4	1.1	2.2	2.2	+.2	1.2	3.3	1.2	4.4	3.2	3.3
Blechnum polypodioides	3.2	5.4	3.3	5.4	5.4	3.4	5.5	5.5	2.2	5.5	2.3	4.4	2.3
DIFFERENTIAL SPECIES													
Vigna luteola	2.2	2.2	.	1.1	+	1.2	.	+	.	.	3.3	1.2	4.4
Conyza bonariensis	.	1.1	+	+	+	+	+	.	.	.	.	.	.
Pityrogramma calomelanos	.	(+)	.	.	.	1.2	1.2	.	(+)	+.2	.	3.4	.
Jaegeria gracilis	.	.	+.2	.	.	.	2.2	.	1.2	+	1.2	.	3.4
Thelypteris pilosula	.	+.2	.	+.2	+	.	.	+	.	+	+.2	+.2	.
Borreria laevis	+	+	.	.	.	.	.	.	.	.	+.2	.	.
COMPANIONS													
Phyllanthus caroliniensis	2.2	1.2	+	1.1	+	2.2	.	2.2	.	+	+	+	+
Hypericum uliginosum	.	.	+	+	1.1	+.2	3.3	1.2	+.2	+.2	.	.	.
Panicum dichotomiflorum	.	.	.	.	.	2.2	.	+.2	.	.	.	.	.
Commelina diffusa	1.2	+.2	.	.	.	.	.	+	.	.	.	.	.
Gramineae sp.	.	.	.	+.2	1.2	.	.	.	.	.	.	.	.
Pilea baurii	.	.	+	.	.	.	.	.	.	.	.	.	.
Cyperus grandifolius	3.3	1.2	.	.	1.2	1.2	.	.	.	.	.	.	.
Hyptis rhomboidea	+	.	.	.	.	+.2	+.2	.	.	.	.	.	+
Centella asiatica	.	(+)	.	.	.	4.4	.	2.3	.	.	.	.	.
Nephrolepis cordifolia	.	.	.	.	.	.	.	1.2	.	.	.	+	.
Paspalum conjugatum	.	.	.	.	.	.	.	.	3.2	.	1.2	.	1.2
Mecardonia dianthera	.	.	+.2	+.2	.	.	+.2	.	.	.	.	.	.
Blechnum occidentale	.	.	+	.	.	.	.	.	.	.	.	.	.
Polygonum opelousanum	+.2	.	.	.	.	+	.	.	.	.	.	.	1.2
Drymaria monticola	+	.	.	.	.	+.2	.	.	.	.	.	.	.
Ophioglossum reticulatum	.	.	.	.	+	.	.	.	+	.	.	.	.
Drymaria cordata	.	.	.	.	.	.	+.2	.	.	.	.	.	.
Thelypteris sp.	.	.	.	.	.	.	+.2	+.2	.	.	.	.	.
(Brown hepatics)	.	.	.	.	.	.	.	.	.	.	.	.	.
Justicia galapagana	.	.	.	.	.	+	.	.	.	.	.	.	.
Paspalum sp.	.	.	.	.	.	.	.	+.2	.	.	.	.	.
Cladonia spp.	.	.	.	.	.	.	.	.	.	.	.	.	.

Other companions. In stand number 3: *Paspalum galapageium* var. *minoratum* +.2, Pteridophyte sp. +; in number 6: *Solanum nodiflorum* +; in number 7: *Marchantia* sp. 3.3; in number 11: *Cyperus virens* subsp. *drummondii* +; in number 12: *Ipomoea* sp. 1.2, *Miconia robinsoniana* +.2, *Asplenium serra* +; in number 14: *Psidium guajava* 3.2, *Pilea* sp. +; in number 18: *Lycopodium reflexum* +; in number 19: *Dichondra repens* 3.3; in number 23: *Rhynchospora rugosa* 2.2.

(Stands 11–13). The former was found in sheltered sites that were free or nearly so from direct southern winds, where shrubs like *Tournefortia rufo-sericea, Acnistus ellipticus, Psychotria rufipes,* and ferns like *Ctenitis pleiosoros* and *Hypolepis hostilis* were seen.

The first type corresponds closely to van der Werff's (1978) "atypical" community of his table 10, and to Hamann's (1981) *Jaegeria crassa* community (Site 15), although there are some differences in species composition.

14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
680	580	580	620	680	630	730	66	660	690	780	780	670	810	685	720	680	670	680	670
SSE	S		WSW	SE	NNW	—	NNW	NNW	NW	SE	SE	SE	—	NW	NW	—	NW	NW	NE
30	5	5	5	25	15	—	30	30	25	30	30	30	—	20	30	—	25	25	30
12	11	9	12	10	8	4	5	4	9	7	7	6	5	4	5	3	3	3	2
2.2	3.2	4.4	4.4	5.5	5.4	2.2	3.4	4.4	3.3	2.2	4.4	2.2	3.3	3.3	4.4	4.4	3.3	4.3	3.4
3.4	5.4	2.3	4.4	3.3	2.2	5.5	5.5	5.5	4.4	2.3	3.3	5.4	2.3	5.5	2.3	5.5	5.5	5.5	5.5
.	+.2	1.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	+	+	+	1.1	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
+.2	+.2	.	+.2	.	+.2	.	.	.	+.2	.	.	.	.	.	.	.	.	.	.
1.2	1.2	2.2	.	.	2.2	.	.	.	.	.	.	2.2	.	.	.	.	.	.	.
.	+.2	+.2	+.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	+	+.2	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+	.	.	.	.	.	+	+.2	+.2	1.2	1.2	1.2	2.2	+.2	.	.	.	.	.	.
.	.	.	.	.	.	2.2	.	.	+.2	2.2	2.2	1.2	.	+.2	.	.	.	.	.
.	.	.	.	.	.	.	+	+	+.2	.	.	.	4.4	.	2.3	.	.	.	.
.	+	+.2	.	2.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	2.2	.	.	.	.	+	.	.	+	+	.
+.2	+	+	.	1.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.	.	.
3.4	.	.	.	.	.	.	.	.	3.3	.	.	.	.	.	.	.	.	.	.
1.2	.	.	.	.	.	.	.	.	.	2.2	2.2	.	.	.	.	.	.	.	.
.	.	.	2.2	.	.	.	.	.	.	.	.	.	.	.	2.3	.	.	.	.
.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	1.2	.	+.2	+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
.	.	.	(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
+.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1.2	.	.	.
.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
2.2	.	.	.	.	.	.	.	.	.	1.2	+.2	.	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4.4	.	.	.	.
.	.	.	.	.	.	.	.	.	.	.	.	+.2	.	.	.	.	.	.	.
.	.	.	.	.	.	.	.	.	.	2.2	3.3	.	.	.	.	.	.	.	.

PTERIDIUM AQUILINUM/BLECHNUM POLYPODIOIDES COMMUNITY

The *Pteridium aquilinum/Blechnum polypodioides* community (Table 2) occupied the largest area of the highland slopes. It was widely distributed on the south- and north-facing slopes (Fig. 2B). The vegetation was low on south-facing slopes, one meter high on north-facing slopes. *Paspalum conjugatum* was rare here; *Phyllanthus caroliniensis* and *Hypericum uliginosum* were frequent.

The community is divided into two types. One is characterized by the presence of *Vigna luteola, Conyza bonariensis, Pityrogramma calomelanos, Jaegeria gracilis*, and *Thelypteris pilosula*

TABLE 3. *Lycopodium clavatum* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Altitude (m)	720	700	710	720	710	710	810	670	625	730	800	720	720	620	630	580	680	730	690
Slope aspect	SE	SE	SE	SE	SE	SE	SSE	SE	SSE	ESE	SE	SE	SE	SE	SSE	ENE	ESE	SE	SSE
Slope (degrees)	30	30	27	27	25	25	25	30	35	30	20	30	30	30	35	15	20	—	30
Numbers of species	9	12	9	7	9	8	12	8	11	9	11	7	4	6	9	8	8	6	11
CHARACTERISTIC SPECIES																			
Lycopodium clavatum	5.4	4.4	4.4	3.4	5.4	5.4	4.4	5.5	4.4	5.4	5.5	5.4	5.4	5.4	5.4	5.5	5.5	3.4	5.4
DIFFERENTIAL SPECIES																			
Hypericum uliginosum	+.2	.	1.2	2.2	+	+.2	3.3	1.2	+.2	1.2	+	.	.	.	.	.	.	.	.
Nephrolepis cordifolia	+	(+)	+.2	1.2	.	.	2.2	+.2	3.2	1.2	+	.	.	.	.	+.2	.	.	.
Polypodium tridens	1.2	1.2	1.2	2.2	(+)	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.
COMPANIONS																			
Pteridium aquilinum	1.2	3.3	2.2	2.3	1.1	1.1	1.1	.	1.1	2.2	1.2	1.2	2.2	1.2	1.1	1.1	1.1	1.1	2.1
Blechnum polypodioides	.	(+)	2.3	1.2	(+)	+.2	2.2	+.2	2.3	3.3	2.2	+.2	.	3.4	2.2	+.2	1.2	.	1.2
Phyllanthus caroliniensis	1.2	1.2	1.2	.	1.2	1.2	+.2	+	.	1.2	1.1	3.3	1.2	.	+	.	+	.	+
Vigna luteola	1.2	3.2	.	.	.	.	+	.	(+)	.	.	1.2	2.2	+.2	+. 2	+.2	.	.	.
(Brown hepatics)	.	.	3.3	.	3.3	4.4	.	.	.	1.2	+.2	.	.	.	.	.	.	4.4	2.2
Commelina diffusa	+	+.2	.	.	.	.	+.2	.	.	+	.	.	.	.	.	+.2	.	.	+.2
Thelypteris pilosula	.	.	.	.	.	.	.	+.2	+.2	.	.	.	.	+.2	+.2	+. 2	.	.	+.2
Pityrogramma calomelanos	.	.	.	.	.	.	.	+.2	(+)	.	+	.	.	.	.	.	1.2	.	.
Borreria laevis	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	(+)	+.2	.	.
Justicia galapagana	.	.	.	.	1.2	2.2	.	.	(+)	.	.	.	.	.	.	.	.	.	.
Lycopodium cernuum	.	.	.	.	1.2	.	1.2	.	.	(+)	.	.	.	.	.	.	.	.	.
Cyathea weatherbyana	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.	.	.	.	1.1	+
Miconia robinsoniana	.	.	.	.	.	.	.	.	1.2	.	.	.	.	1.2	+.2	.	.	.	.
Alternanthera halimifolia	(+)	.	.	.	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	.
Blechnum occidentale	.	(+)	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.
Panicum dichotomiflorum	.	.	1.2	1.2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Centella asiatica	.	.	.	.	.	.	2.3	.	.	.	.	.	.	.	.	.	.	.	3.3
Polypodium aureum	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Cyperus grandifolius	.	.	.	.	.	.	.	.	(+)	.	.	.	.	.	.	.	+	.	.
Asplenium serra	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1.1	.

Other companions. In stand number 2: *Cissampelos pareira* +.2, *Drymaria cordata* +; in number 7: *Peperomia* spp. +; in number 11: *Ophioglossum reticulatum* +, Gramineae sp. +; in number 15: *Polypodium* sp. +; in number 17: *Conyza bonariensis* +; in number 18: *Cladonia* sp. 2.3; in number 19: *Pilea baurii* +.2, *Hydrocotyle* sp. +.

TABLE 4. *Hypericum uliginosum* community and *Polypodium tridens* community.

Stand number	1	2	3	4	5	6	7	8	9	10
Altitude (m)	670	670	670	660	570	580	670	690	760	760
Slope asepct	SSE	SSE	SSE	—	—	—	—	—	—	—
Slope (degrees)	30	3	2	—	—	—	—	—	—	—
Numbers of species	8	4	4	5	6	3	5	3	3	4
DOMINANT AND CHARACTERISTIC SPECIES										
Hypericum uliginosum	4.3	3.3	4.4	3.3	+.2	2.2	1.2	2.2	3.2	3.2
Polypodium tridens	.	.	.	.	3.3	4.3	5.4	2.3	3.3	3.3
(Brown hepatics)	.	.	.	.	2.2	.	+	2.2	.	2.2
COMPANIONS										
Cladonia spp.	1.2	2.3	.	.	.	2.2	+	.	.	.
Stenotaphrum secundatum	.	.	2.2	2.2	.	.	.	.	1.2	2.2
Jaegeria gracilis	.	1.2	2.3	2.2	.	.	.	.	.	.
Rhynchospora rugosa	.	.	2.3	1.2	.	.	.	.	.	.
Pteridium aquilinum	.	.	.	.	1.2	.	1.2	.	.	.

Other companions. In stand number 1: *Conyza bonariensis* +, *Blechnum polypodioides* 1.2, *Phyllanthus caroliniensis* +.2, *Hypoxis decumbens* 2.2, *Histiopteris incisa* +, *Dicranopteris flexuosa* +; in number 2: *Paspalum* sp. 2.2; in number 4: *Setaria geniculata* 2.2; *Pityrogramma calomelanos* 1.2, *Cladina* spp. 2.2.

(Stands 1–19 in Table 2), and the other by their absence (Stands 20–33), although there are exceptions. The first type closely resembles Hamann's (1981) *Pteridium aquilinum-Jaegeria gracilis* community (Site 19).

LYCOPODIUM CLAVATUM COMMUNITY

The *Lycopodium clavatum* community (Table 3) was distributed mostly on south-facing slopes in low and middle altitudes of the highland (Fig. 2C). The slopes are directly exposed to southern winds and sometimes dried by them, as in the dry period February–April 1970, but moistened by moisture-saturated winds on foggy and rainy days. The habitat fluctuates between dry and wet extremes.

The dominant species was always *Lycopodium clavatum,* associated with *Pteridium aquilinum* and *Blechnum polypodioides.* Major companions in the community were *Phyllanthus caroliniensis, Vigna luteola,* and *Commelina diffusa.* Small patches of brown hepatics (Tables 2–5), probably *Jungermanniales* species, were frequently prominent in the *Lycopodium clavatum* community.

This community is subdivided into two types. One type (Stands 1–11 in Table 3) is characterized by *Hypericum uliginosum, Nephrolepis cordifolia,* and *Polypodium tridens,* and the other by their absence (Stands 12–19).

HYPERICUM ULIGINOSUM COMMUNITY

Figure 2D shows the distribution of the *Hypericum uliginosum* community on slopes at rather low altitudes. The community was some 30 cm tall and was found only on thin soils, which were dry on fine days.

POLYPODIUM TRIDENS COMMUNITY

The *Polypodium tridens* community (Stands 5–10 in Table 4) was found on thin soils accumulated on nearly exposed lava (Fig. 2E). Here again, *Hypericum uliginosum* was always found. The

TABLE 5. *Pernettya howellii* community.

Stand number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Altitude (m)	790	800	790	790	790	790	730	810	780	810	790	780	810	810	810	800	810	740	670	740	740	740
Slope aspect	SE	SSE	SE	SE	SE	SE	SE	SE	ESE	SE	SSE	ESE	SW	SSE	SSE	SE	NNE	SE	SE	SE	SE	SE
Slope (degrees)	30	35	35	35	35	30	30	27	35	27	35	35	45	30	27	27	20	30	80	30	30	30
Numbers of species	6	6	6	4	5	7	5	8	5	7	8	5	8	5	7	8	9	3	3	3	2	2
CHARACTERISTIC SPECIES																						
Pernettya howellii	5.5	3.3	4.4	5.4	4.4	5.5	5.5	5.4	5.4	5.4	5.5	5.4	5.4	5.5	5.4	4.4	5.4	5.5	5.5	5.5	5.5	5.5
DIFFERENTIAL SPECIES																						
Hypericum uliginosum	1.2	.	+	+	2.2	1.2	1.2	2.2	1.2	1.2	1.2	1.2	+	(+)	1.2	+.2	(+)	.	.	.	.	.
Pteridium aquilinum	1.1	+.2	.	.	.	+	1.1	+	+	1.2	.	1.2	+	1. 1	1.1	(+)	2.2	+	.	1.1	.	.
Nephrolepis cordifolia	.	.	2.3	+	2.2	+	.	+.2	.	1.2	.	.	.	2.3	2.2	.	1.2	.	+	.	.	.
Phyllanthus caroliniensis	+.2	2.2	+.2	.	.	.	.	+.2	.	2.2	1.2	.	1.2	.	1.2	(+)	+.2	.	.	.	.	.
(Brown hepatics)	2.2	.	.	.	1.2	2.2	2.2	.	.	.	1.2	.	+.2	.	.	.	+.2	.	.	.	.	.
COMPANIONS																						
Blechnum polypodioides	1.2	3.3	4.4	2.3	1.2	+.2	.	2.2	3.3	2.2	1.2	1.2	3.2	2.3	2.2	4.4	3.2	1.2	2.1	2.2	1.2	1.2
Commelina diffusa	.	.	.	.	.	.	.	1.2	.	.	.	.	.	.	1.2	+	+	.	.	.	.	.
Vigna luteola	.	.	.	.	.	.	.	.	+.2	+	.	.	.	.	.	.	+	.	.	.	.	.
Conyza bonariensis	.	+	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.
Histiopteris incisa	.	1.2	(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lycopodium reflexum	.	.	.	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Thelypteris pilosula	.	.	.	.	.	.	.	.	.	.	.	+	+.2	.	.	.	.	.	.	.	.	.

Other companions. In stand number 7: *Stenotaphrum secundatum* +.2; in number 8: *Cyathea weatherbyana* +.2; in number 11: *Pityrogramma calomelanos* +.2; in number 16: *Hyptis rhomboidea* +, *Panicum dichotomiflorum* +.2.

habitat was dry and, therefore, the number of component species was small (only 4.0 on average in this community).

PERNETTYA HOWELLII COMMUNITY

This ericaceous community (Table 5) was nearly exclusively distributed on southeast-facing windward slopes in high altitudes in the highlands (Fig. 2F). The largest tract of the community is 10 m wide and 30 m long on a south-facing, inside steep slope of a crater west of the highest point of Mt. Crocker. The habitat was extremely dry February–April, 1970. The *Pernettya howellii*

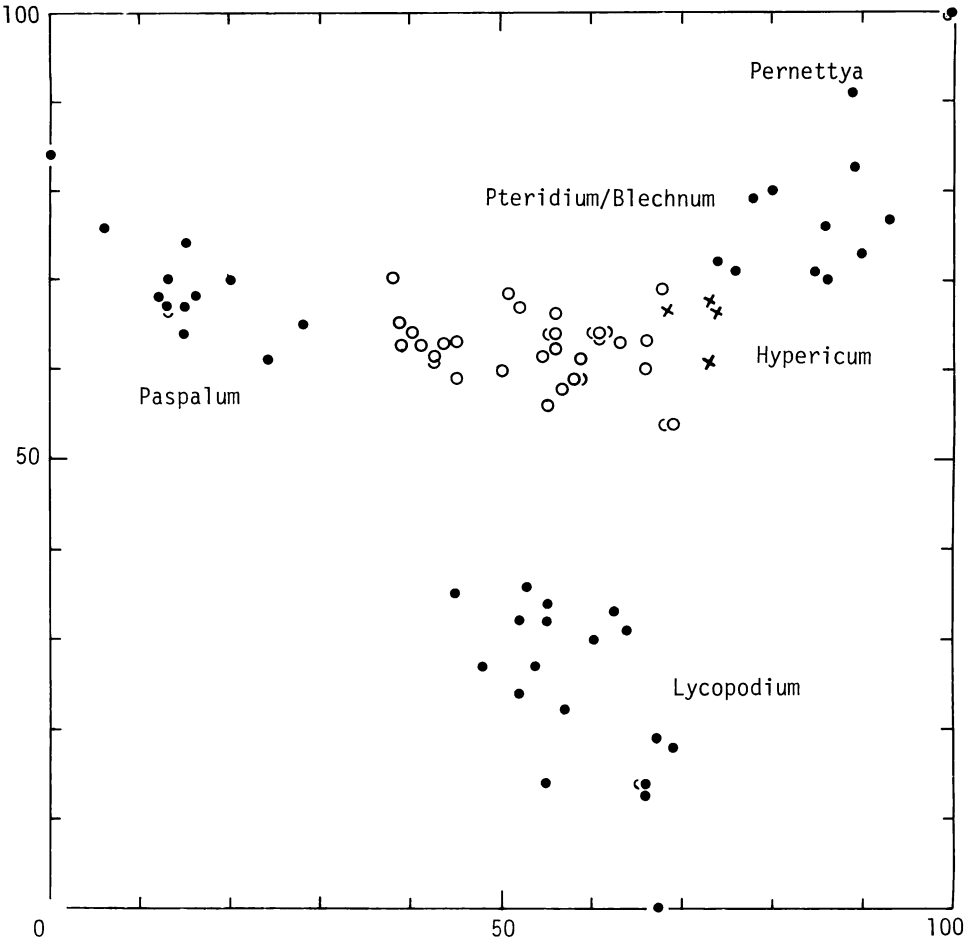

FIGURE 1. Scatter diagram of vegetation samples (excluding six *Polypodium tridens*-dominated stands), processed by reciprocal averaging.

community was about 30 cm high and consisted of a limited number of species (5.5 species on average). *Blechnum polypodioides* was an important companion in the community.

This community can be divided into two types. One is characterized by the presence of *Hypericum uliginosum, Pteridium aquilinum, Nephrolepis cordifolia, Phyllanthus caroliniensis,* and brown liverworts (probably *Jungermanniales* species as in the *Lycopodium* community) (Stands 1–17 in Table 5), and the other is distinguished by their absence (Stands 18–22), although there are three exceptional occurrences.

Van der Werff (1978) described a stand dominated by *Pernettya howellii,* which was found on a "wind-exposed slope." The area could be the same that I studied in 1970 (Stands 13–16 in Table 5), although the component species are fewer in the present study than in van der Werff's (1978). The difference must be due to the difference in quadrat sizes used and the extremely dry conditions in 1970; that year the *Pernettya howellii* community was the driest of the highland communities I studied. However, in 1978 and 1986, I revisited the locality and found that the community was humid by the southern winds, as van der Werff (1978) observed.

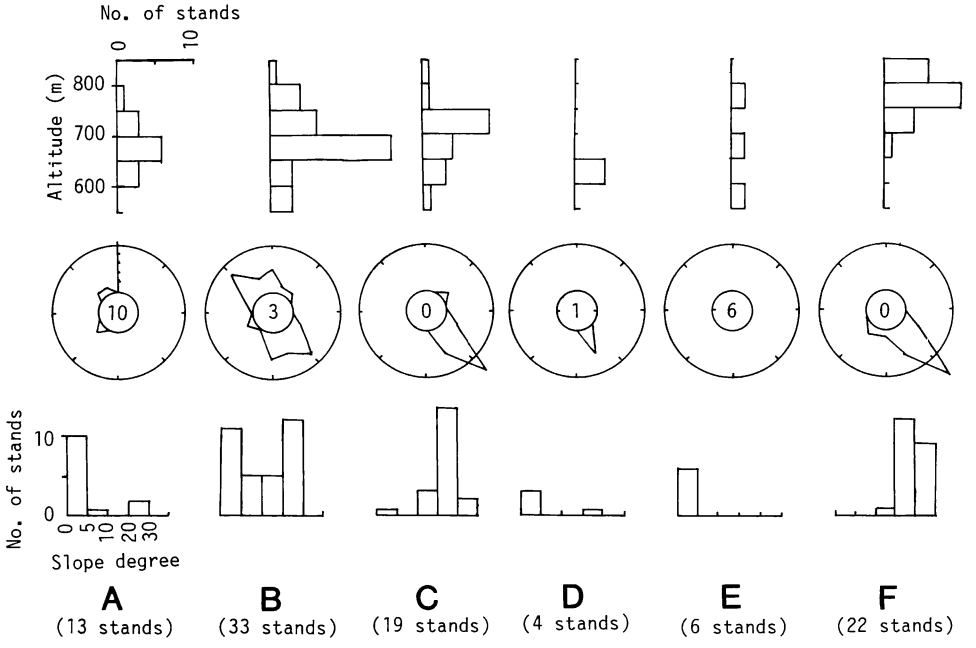

FIGURE 2. Distributions of the recognized communities in relation to altitude (top), slope direction (middle), and slope degree (bottom).—A. *Paspalum conjugatum* community.—B. *Pteridium aquilinum/Blechnum polypodioides* community.—C. *Lycopodium clavatum* community.—D. *Hypericum uliginosum* community.—E. *Polypodium tridens* community.—F. *Pernettya howellii* community. Numerals in the circles show numbers of relevés sampled from flat topography.

DISCUSSION

Figure 3 illustrates the distribution of the plant communities recognized in the summit area of Santa Cruz, including fens and bogs (described in Itow & Weber, 1974), *Miconia robinsoniana* scrub on the southern slope, and *Scalesia pedunculata* forest on the northern slope.

Van der Werff (1978) described Habenario-Trisetetum howellii from the highlands and listed as the character species *Habenaria monorrhiza, Centella asiatica, Mildella intramarginalis, Scleria hirtella, Setaria geniculata, Stenotaphrum secundatum,* and *Trisetum howellii.* Since the quadrat size used is larger in van der Werff's (1978) study than in mine, the number of species listed in a sample (relevé) is correspondingly higher. Despite this difference, the vegetation described in Tables 1–4 corresponds to van der Werff's Habenario-Trisetetum howellii. The most pronounced difference between them is the absence of *Habenaria monorrhiza, Mildella intramarginalis,* and *Trisetum howellii* in the communities described here. The first two species, however, were collected in the highlands in 1970 but did not occur in the sample sites. The third species was neither seen nor collected in 1970. Several sterile specimens of Gramineae, however, turned up in sample sites and were listed as Gramineae spp., as seen in Tables 2, 3, and 4. They might include *Trisetum howellii.* The three species mentioned were rarely seen in the highland vegetation in 1970, possibly due to the extreme dryness in that year.

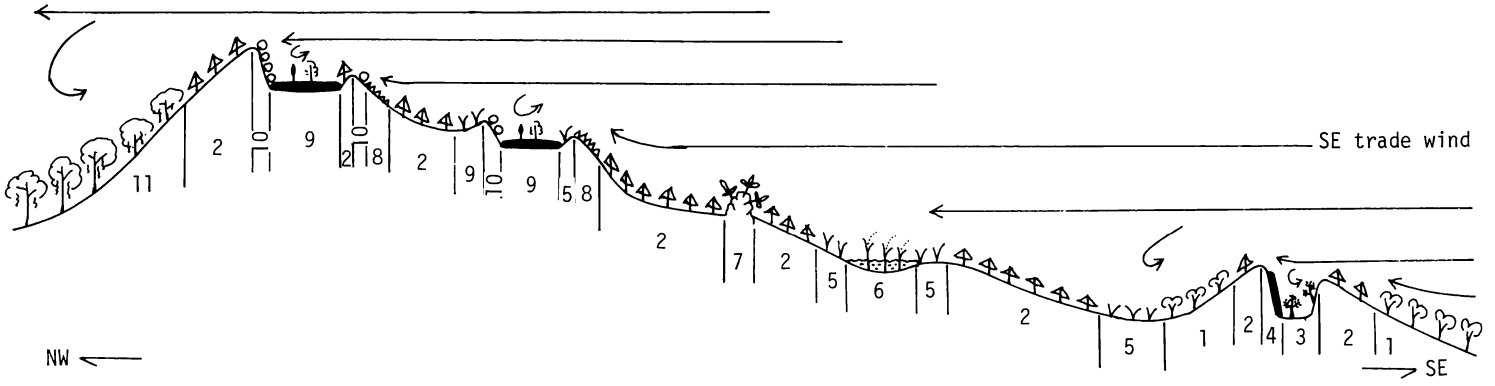

FIGURE 3. Community distribution in the Santa Cruz highland. 1, *Miconia robinsoniana* scrub. 2, *Pteridium aquilinum/Blechnum polypodioides* community. 3, *Cyathea weatherbyana* stand. 4, vertical bog. 5, *Paspalum conjugatum* community. 6, fen. 7, *Polypodium tridens* community. 8, *Lycopodium clavatum* community. 9, raised bog. 10, *Pernettya howellii* community. 11, *Scalesia pedunculata* forest.

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