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Rain forest vegetation of 'Eua Island, Kingdom of Tonga

DONALD R. DRAKE
Biology Department
Georgia Southern University
Landrum Box 8042
Statesboro, GA 30460, USA
Present address: School of Biological Sciences, Victoria University of Wellington, P. O. Box 600, Wellington, New Zealand

W. ARTHUR WHISTLER
TIMOTHY J. MOTLEY
Botany Department
University of Hawai'i
Honolulu, HI 96822, USA

CLYDE T. IMADA
Botany Department
Bernice P. Bishop Museum
P. O. Box 19000–A
Honolulu, HI 96817, USA

Abstract The indigenous vegetation of 'Eua Island, Tonga, is described and a species list presented. Quantitative data were collected from 40 forest plots in which all vascular plant species were recorded and the diameters of all stems ≥ 5 cm dbh were measured. Plot classification, based on basal area data, identified six forest types, two coastal and four inland, which reflect an elevational sequence from the coast to the island's summit (312 m a.s.l.). A polar ordination, based on basal area data, arranged plots from the four inland forest types in a sequence from low to high elevation along one ordination axis, and from more mature to less mature along a second axis. Species richness increased with elevation. Several additional, non-forest vegetation types, including fern- and grass-dominated vegetation of inland ridges and shrub-dominated vegetation of cliffs and rocky shores, were sampled semi-quantitatively and are also described.

Keywords 'Eua; Pacific Islands; rain forest; Tonga; flora; vegetation

INTRODUCTION

The Kingdom of Tonga consists of two parallel chains of islands that run roughly north and south, between 15–23° S latitude and 173–176° W longitude in the South Pacific Ocean (Fig. 1). The sparsely-inhabited western chain consists of relatively young, active, mainly andesitic volcanoes up to 1030 m a.s.l. The densely-inhabited eastern chain consists of older, raised limestone islands up to 312 m a.s.l.

To date, there have been few published descriptions of the vegetation of Tonga. Uhe (1974) and Sykes (1981) have described the vegetation of the volcanic islands of Niuafo'ou and Late, respectively. The coastal communities of several small islets in the Tongatapu (Stoddart 1975; Ellison 1990) and Ha'apai (Woodroffe 1983) groups have been described. Palmer (1988) surveyed the least disturbed relictual stand of inland forest on the limestone island of Tongatapu. Straatmans (1964) and Sykes (1978) have published brief, qualitative descriptions of the vegetation of 'Eua, which is Tonga's highest, oldest, and least disturbed large, limestone island. Whistler (1992) has reviewed the vegetation of Samoa and Tonga.

Although 'Eua has long been reputed to support the richest, most unique forest in Tonga (Sykes 1978), no detailed, quantitative description of 'Eua's forest vegetation has ever been published. The rapid rate of forest clearing on 'Eua has recently begun to threaten its remaining stands of indigenous forest (Allen 1990), increasing the need for such a description for scientific and conservation purposes. The purpose of this study was to describe the composition and distribution of the indigenous vegetation of

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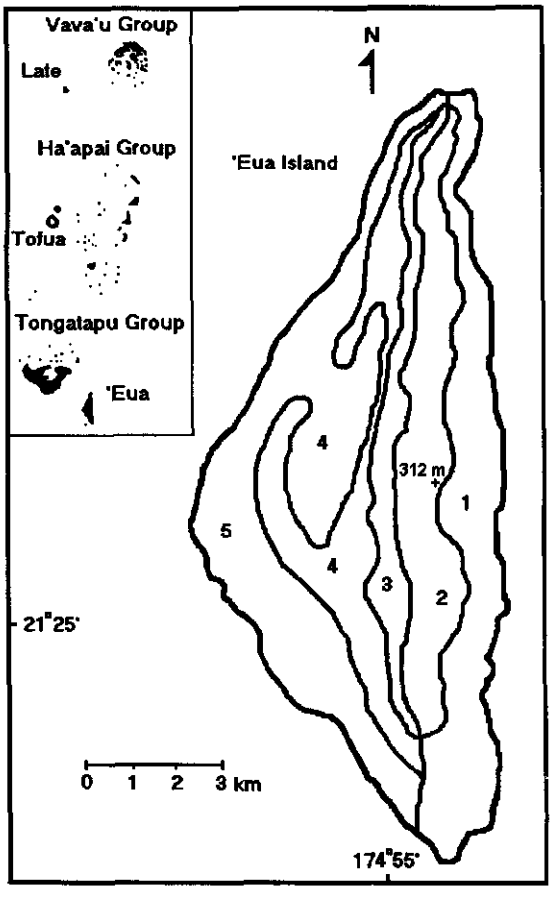

Fig. 1 Map of the major islands of Tonga and of the five physiographic provinces on 'Eua (after Hoffmeister 1932) : 1) the eastern terraces and coastal region, 2) the eastern ridge, 3) the dissected, western slope of the eastern ridge, 4) the western ridge and central valley, and 5) the western slope terraces and coastal region.

'Eua. A summary of the preliminary analysis of the data (Drake et al. 1990) was supplied to the Tongan Government and was used as a basis for establishing a national park on 'Eua in 1992.

STUDY AREA

Geology and soils

'Eua is a high island, roughly 81 km^2 in area, whose surface rises gradually from the west coast as a series of distinct terraces, to a high eastern ridge with a maximum elevation of 312 m a.s.l. (Hoffmeister 1932; Bryan et al. 1972; Wilde & Hewitt 1983) (Fig. 1). East of the ridge, a series of steep cliffs, interrupted by narrow terraces, leads to the coast. Much of the terraced relief is the result of periodic, geologic uplifting of the island. Hoffmeister (1932) mapped five physiographic provinces on 'Eua: 1) the eastern terraces and coastal region, 2) the eastern ridge, 3) the dissected, western slope of the eastern ridge, 4) the western ridge and central valley, and 5) the western slope terraces and coastal region.

Although most of its surface is covered by limestone, 'Eua is unique among Tonga's limestone islands in that its core consists of volcanic rocks, and these form exposed outcrops along the eastern ridge and eastern cliffs (Hoffmeister 1932; Bryan et al. 1972). Overlying the core, and forming additional outcrops along the eastern ridge and its margins, is a layer of Eocene foraminiferal and algal limestones. Overlying the Eocene limestones on the eastern ridge and its western slopes are Miocene submarine tuffs and tuffaceous limestone. Late Tertiary coral reef limestone comprises the bulk of the western ridge and central valley, and forms minor terraces along both coasts. Quaternary andesitic tephra forms a layer up to 2 m thick over most of the island, except in steep areas where it has been removed by erosion.

Most soils are derived from the young andesitic tephra with or without additional volcanic alluvium from older tephras (Wilde & Hewitt 1983). Deeply-weathered soils from the tuffs comprising the core are found where the core forms outcrops along the eastern ridge. Volcanic and calcareous parent materials combine to form colluvial soils on steep slopes and at the bases of cliffs. Elsewhere, calcareous materials are not involved in soil formation, except as unconsolidated sand along the coasts. Development of distinct soil horizons decreases, and evidence of continual soil development due to downslope movement increases, with increasing steepness of slope. The majority of 'Eua's soils are alfisols and mollisols, with inceptisols on the steep ($\geq 30°$) slopes and entisols (coralline sands) along some coasts (Wilde & Hewitt 1983).

Climate

'Eua lies within the south-east tradewind zone, and winds blow from the easterly quadrant 65–75% of the time. Mean annual rainfall is approximately 2700 mm, of which roughly ⅔ falls during the wet season of November to April (Thompson 1986). There is little seasonal variation in temperature. Sykes (1978) has remarked that the microclimate near the summit ridge appears cooler and moister than that at lower elevations.

METHODS

Data collection

In June and July 1990, forest vegetation was sampled in forty 600 m^2 plots (mainly 20 × 30 m), each located in a stand of forest representative of that found in the surrounding area. Stands that had obviously been disturbed by humans were avoided. For each plot, the precise location (on topographic map and aerial photo), elevation, aspect, slope, substrate (bare sand, limestone, volcanic soil), and canopy height were determined and all vascular plant species were recorded. A species list is presented in Appendix I. For all trees, diameters of all stems ≥ 5 cm diameter at breast height (dbh) were measured. For individuals < 5 cm dbh, as well as shrubs, herbs, epiphytes, and lianas, a Braun-Blanquet semi-quantitative estimate of cover was made for each species in each of several strata: shrub (c. 1–3(–5) m), ground cover (≤ 1.0 m), epiphyte, and liana (Mueller-Dombois & Ellenberg 1974). Braun-Blanquet, semi-quantitative cover estimates were also made in seven 600 m^2 plots in non-forest vegetation. Detailed notes on species distribution and forest composition were also compiled for sites not sampled quantitatively. Most of the plots were located in the most extensive tracts of undisturbed forest along the eastern coast and terraces, the eastern ridge, and the steep ravines of the western slope of the eastern ridge. A few additional plots were located in smaller, disjunct stands of indigenous vegetation scattered throughout the island.

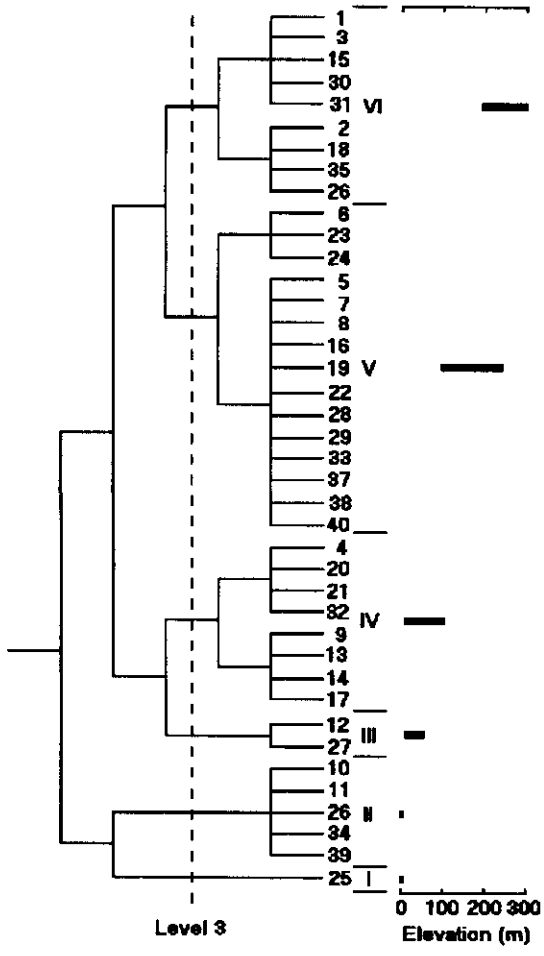

Fig. 2 Dendrogram derived from two-way indicator species analysis (TWINSPAN) classification of 40 forest plots, using relative basal area of tree species. Roman numerals represent the following vegetation types: I. *Excoecaria-Tournefortia* coastal forest, II. *Hernandia-Terminalia* coastal forest, III. *Maniltoa-Pleiogynium* lowland rain forest, IV. *Myristica* lowland rain forest, V. *Calophyllum* mixed upland rain forest, VI. *Calophyllum-Garcinia* upland rain forest. The elevational range over which each type occurs is indicated at the right.

Data analysis

Relative basal area data for the 86 tree species recorded in the 40 plots that were sampled quantitatively were analysed using two-way indicator species analysis (TWINSPAN, Hill 1979) to identify species associations. Relative basal area data for 35 inland forest plots were also analysed using a Bray-Curtis polar ordination (ORDIFLEX, Gauch 1979) to identify gradients in species composition. The five coastal forest plots on coralline sands and raised limestone benches were excluded from the ordination because their dissimilarity to the 35 inland plots resulted in poor separation among the inland plots. End points of the first axis were the two plots that were most dissimilar to each other; end points of the second axis were the two remaining plots that were most dissimilar to each other and had first axis scores between 40 and 60.

RESULTS

TWINSPAN identified six ecologically interpretable groups of plots at the third level of classification, with the three largest groups being divided into three additional subtypes at the fourth level (Fig. 2). One plot (no. 34), containing a large, outlying coastal tree, was misclassified by TWINSPAN and, in the community descriptions below, is grouped based on its

position in the ordination. In general, TWINSPAN ordered the plots into groups reflecting a topographic sequence from the coast to the summit ridge. Characteristics of the six community types and their variants are outlined below. In the following descriptions, species within a given stratum are listed in order of decreasing relative basal area (trees) or Braun-Blanquet cover values (smaller species). For the dominant species, mean relative basal area (rba) and maximum dbh are given in parentheses (% rba, diam. cm).

I. *Excoecaria-Tournefortia* coastal forest is found at elevations < 5 m a.s.l. on raised limestone substrates that lack sand or soil. It exists in small, disjunct patches that combine to form a narrow band along the coast, though they rarely extend more than 20 m inland. There is often no beach along the seaward margin of these forest patches, and therefore exposure to waves and salt spray, particularly during storms, must be great. Species richness is low.

Excoecaria agallocha (48%, 69 cm) and *Tournefortia argentea* (syn. *Argusia argentea*) (40%, 75 cm) dominate the canopy. Both are multi-stemmed trees that reach a height of 12 m. *Hibiscus tiliaceus*, another multi-stemmed tree, forms a somewhat lower middle stratum, which often includes *Neisosperma oppositifolium*, *Schleinitzia insularum*, and *Morinda citrifolia*. The shrub stratum contains scattered individuals of *Bikkia tetrandra*, *Wollastonia biflora*, *Clerodendrum inerme*, and *Scaevola sericea*, all of which are much more abundant in the strand vegetation (type VII) on the seaward margin of this forest. Terrestrial herbs, epiphytes, and lianas are rare.

II. *Hernandia-Terminalia* coastal forest is found at elevations < 5 m a.s.l. on sand substrates. Although this forest is somewhat sheltered behind sand beaches and strand vegetation, it is presumably strongly influenced by salt spray, and occasionally by large storms such as cyclone 'Ofa, which had obviously disturbed the understory of many littoral forest sites in January 1990. Species richness is greater than in the *Excoecaria-Tournefortia* coastal forest.

The upper canopy is dominated by *Hernandia nymphaeifolia* (31%, 90 cm) and/or *Terminalia catappa* (25%, 122 cm). Other common, large (> 40 cm dbh) canopy trees include *Terminalia litoralis*, *Guettarda speciosa*, *Planchonella grayana*, *Schleinitzia insularum*, *Hibiscus tiliaceus*, *Myristica hypargyraea*, and *Pisonia grandis*; *Cocos nucifera* occurs in the canopy in places. The subcanopy is overwhelmingly dominated by *Neisosperma oppositifolium*, which can occasionally exceed 50 cm dbh, plus lesser amounts of *Cordia subcordata* (only on the northwest coast), and *Grewia crenata*. A lower stratum contains *Pandanus tectorius*, *Xylosma simulans*, *Cycas rumphii*, and *Vavaea amicorum*. The only common terrestrial herb is the fern *Phymatosorus grossus*, and epiphytes are rare. Lianas are sparse, the most common ones being *Epipremnum pinnatum*, *Hoya australis*, *Faradaya amicorum*, and *Jasminum didymum*.

III. *Maniltoa-Pleiogynium* lowland rain forest occurs only in the north-western quarter of the island along the western slope terraces and coastal region. This vegetation begins at the landward edge of the littoral forest, where sand or exposed limestone gives way to volcanic soils overlying limestone, and continues inland up to elevations of 60 m, on slopes ranging from 11–20°.

Here *Myristica hypargyraea* and *Neisosperma oppositifolium*, the dominant species of lowland rain forests over the rest of the island (see below), are completely absent. Instead, the dominant species are *Maniltoa grandiflora* (49%, 56 cm) and *Pleiogynium timoriense* (17%, 56 cm). Other large trees (> 35 cm dbh) include *Sapindus vitiensis* and *Aleurites moluccana*. The subcanopy contains *Chionanthus vitiensis*, *Xylosma simulans*, *Vavaea amicorum*, and *Diospyros samoensis*. A lower stratum contains *Cryptocarya hornei*, *Cycas rumphii*, *Memecylon vitiense*, *Micromelum minutum*, *Rhamnella vitiensis*, and the shrub *Graptophyllum insularum*. The most common terrestrial herb is *Asplenium polyodon*. Lianas comprise 29% of the species in the flora and are abundant, especially *Entada phaseoloides*, *Jasminum simplicifolium*, *Alyxia stellata*, *Jasminum didymum*, *Gynochtodes epiphytica*, and *Malaisia scandens*.

IV. *Myristica* lowland rain forest begins at the landward edge of the coastal forest, where sand or exposed limestone gives way to volcanic soils overlying limestone, and continues inland up to elevations of 110 m, on slopes ranging from 0–33° or more. It is found along the eastern slopes and terraces, western slope terraces, and coastal region, everywhere except in the north-western quarter of the island.

Myristica hypargyraea (53%, 97 cm) is the overwhelming dominant in this forest type, where no other species averages more than 13% rba. It is a

large tree, reaching a height of 25 m, and is usually present in all size classes. Occasional large (> 40 cm dbh) individuals of *Pleiogynium timoriense*, *Maniltoa grandiflora*, *Guettarda speciosa*, *Canarium harveyi*, *Diospyros samoensis*, *Planchonella grayana*, and *Calophyllum neo-ebudicum* are also scattered through this forest type. The subcanopy contains *Neisosperma oppositifolium* and *Xylosma simulans*. A lower stratum often includes *Diospyros samoensis*, *Hibiscus tiliaceus*, *Citronella samoensis*, *Cycas rumphii*, and the shrub *Macropiper puberulum*. Herbaceous species are uncommon, with little cover. *Asplenium australasicum* is occasionally present as an epiphyte. Lianas comprise 25% of the flora, the most abundant species being *Faradaya amicorum*, *Connarus* sp. nov., *Epipremnum pinnatum*, *Alyxia bracteolosa*, *Entada phaseoloides*, *Jasminum simplicifolium*, *Gynochtodes epiphytica*, and *Jasminum didymum*.

In places (plots 9, 14), this forest type appears to be in a state of recovery from some past disturbance; here the leading dominant is *Dendrocnide harveyi* (57%, 112 cm). *Dendrocnide harveyi* saplings do not occur in the understory beneath a closed canopy of mature trees. *Myristica hypargyraea* is codominant in the upper stratum and abundant in the lower strata.

V. *Calophyllum* mixed upland rain forest occurs on volcanic soils overlying the limestone of the upper eastern terraces, the western slope of the eastern ridge, and upper portions of the ridge and ravine system of the central valley, at elevations of 100–180(–240) m, on slopes of 2–45°. The tree strata are quite rich here, and no one species comprises, on average, more than 12% of the relative basal area in this forest. Of the 15 plots classified into this type, eight different species were the leading dominant in at least one plot, and no one species was the leading dominant in more than three plots.

The most consistently abundant large tree is *Calophyllum neo-ebudicum* (11%, 91 cm); it is present in all plots, reaches a height of 35 m, and is typically represented in all size classes. *Dysoxylum tongense* (12%, 171 cm) is the most common co-dominant, and is present in 80 % of the plots. Other common canopy species (> 50 cm dbh) are *Elattostachys falcata*, *Canarium harveyi*, *Myristica hypargyraea*, *Alphitonia zizyphoides*, *Maniltoa grandiflora*, *Neonauclea forsteri*, *Semecarpus vitiensis*, *Litsea mellifera*, and *Dysoxylum forsteri*. The subcanopy contains large amounts of *Diospyros samoensis*, *Cryptocarya hornei*, *Garcinia myrtifolia*, and *Citronella samoensis*. The lower stratum includes *Vavaea amicorum*, *Cryptocarya turbinata*, *Hedycarya dorstenioides*, and *Psychotria carnea*, and large amounts of the shrub *Macropiper puberulum*. The herb layer is well-developed, and is dominated by the ferns *Tectaria dissecta*, *Christella parasitica*, *Pteris comans*, and *Arachnoides aristata*; the ground orchid *Corymborkis veratrifolia* is also common. *Asplenium australasicum* is occasionally present as an epiphyte. Lianas comprise 23% of the flora and are extremely abundant, especially *Entada phaseoloides*, *Alyxia bracteolosa*, *Embelia vaupelii*, *Jasminum simplicifolium*, *Connarus* sp. nov., *Epipremnum pinnatum*, *Melodinus vitiensis*, *Jasminum didymum*, and *Gynochtodes epiphytica*.

In places, this forest type appears to be in a state of recovery from some past disturbance, and here the leading dominants are either *Dendrocnide harveyi* (55%, 95 cm) with *Bischofia javanica* (24%, 56 cm) (plots 7 and 8), or *Rhus taitensis* alone (65%, 99 cm) (plots 6, 23, and 24). Where present, these species combine to form ≥ 65% of the relative basal area, though they are absent from all smaller size classes, which are instead dominated by the other tree species common to the *Calophyllum* mixed forest.

VI. *Calophyllum-Garcinia* upland rain forest occurs on volcanic soils overlying limestone, at elevations of 190–300 m, on slopes of 5–40°. It is found upslope of the *Calophyllum* mixed forest and reaches its greatest development mainly on the steep slopes near the summit of the eastern ridge.

Here, in contrast to the *Calophyllum* mixed forest below, the upper canopy is more strongly and consistently dominated by *Calophyllum neo-ebudicum* (27%, 76 cm), which is typically represented in all size classes. Other common large (> 40 cm dbh) trees include *Neonauclea forsteri*, *Homalium whitmeeanum*, *Canarium harveyi*, *Podocarpus pallidus*, *Dysoxylum tongense*, *Elaeocarpus graeffei*, *Hernandia moerenhoutiana*, *Myristica hypargyraea*, and *Rhus taitensis*. The subcanopy is almost completely dominated by *Garcinia myrtifolia* (15%, 32 cm), which can occur at densities of more than 50 trees per plot; it is consistently represented in all size classes. The lower stratum contains *Vavaea amicorum* and the shrubs *Macropiper puberulum*, *Ixora calcicola*, *Cordyline fruticosa*, and *Phaleria glabra*. The herbaceous layer is well-developed and the most common elements are the ferns *Arachnoides aristata*, *Pteris comans*, *Schizaea dichotoma*, and *Christella parasitica*. *Asplenium australasicum* and *Robiquetia bertholdii* are common epiphytes. Lianas are extremely abundant,

especially *Faradaya amicorum*, *Smilax vitiensis*, *Alyxia bracteolosa*, *Jasminum simplicifolium*, *Freycinetia urvilleana*, *Alyxia stellata*, *Hoya australis*, and *Embelia vaupelii*.

In places (plots 2, 18, 35) where this forest type appears to be in a state of recovery from some past disturbance, the leading dominants are *Alphitonia zizyphoides* (33%, 76 cm) and *Elattostachys falcata* (11%, 48 cm). These are absent from the smaller size classes, which are instead dominated by the other tree species common to *Calophyllum-Garcinia* forest. *Alphitonia zizyphoides* is less common outside disturbed upland forest, but *E. falcata* is often present in low numbers throughout the upland rain forest.

Other types of vegetation, sampled semi-quantitatively, include:

VII. Strand vegetation: The species composition of the strand vegetation, like that of the adjacent coastal forest, is determined largely by the substrate. Seaward of the *Excoecaria-Tournefortia* coastal forest, and elsewhere on other bare, raised limestone benches, the vegetation consists of a shrubby layer dominated by *Bikkia tetrandra*, *Scaevola sericea*, *Clerodendrum inerme*, and *Wollastonia biflora*, with a ground layer of succulent species such as *Pemphis acidula*, *Sesuvium portulacastrum*, and the parasitic vine *Cassytha filiformis*. Seaward of the *Hernandia-Terminalia* coastal forest, on sand, trees include scattered individuals of *Cocos nucifera*, *Tournefortia argentea*, *Acacia simplex*, and *Sophora tomentosa*. The most common shrubs are *Scaevola sericea* and *Wollastonia biflora*, and the ground layer contains *Ipomoea pes-caprae*. On some sandy shores, the tree *Schleinitzia insularum* forms small, monospecific stands.

VIII. Cliff vegetation: The upper cliffs of the eastern ridge are covered in many places by a smooth canopy of wind-swept vegetation, 3–5 m high. Common species include *Diospyros elliptica*, *Citronella samoensis*, *Maesa tongensis*, *Badusa corymbifera*, *Maytenus vitiensis*, and many others. At lower elevations, where the eastern cliffs are very steep and relatively exposed to salt spray, the vegetation is open-canopied and dominated by *Pandanus tectorius*, and, in the south-east, by *Pritchardia pacifica*. Where the cliffs are less steep, though still exposed to spray, there is a low forest of *Hibiscus tiliaceus*, *Myristica hypargyraea*, *Neisosperma oppositifolium*, *Pandanus tectorius*, *Terminalia catappa*, *Schleinitzia insularum*, and *Cycas rumphii*.

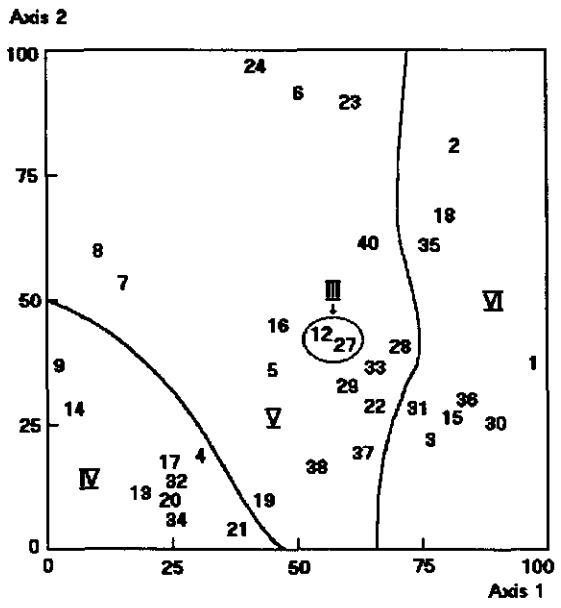

Fig. 3 Bray-Curtis polar ordination of 35 inland forest plots of 'Eua, using relative basal area of tree species. Roman numerals represent the following vegetation types: III. *Maniltoa-Pleiogynium* lowland rain forest, IV. *Myristica* lowland rain forest, V. *Calophyllum* mixed upland rain forest, VI. *Calophyllum-Garcinia* upland rain forest.

IX. Monospecific clonal stands: At lower and middle elevations, *Hibiscus tiliaceus* often forms extensive (> 1000 m^2), nearly monospecific stands that appear to have arisen through clonal growth. The stands are characterised by numerous stems growing in many planes and creating dense thickets. At middle and high elevations, multi-stemmed, clonal individuals of the banyan *Ficus obliqua* occasionally cover areas in excess of 1000 m^2, to the exclusion of most other woody species. The upper branches of the banyans support large numbers of the fern *Asplenium australasicum*.

X. Toafa (treeless) vegetation: Toafa vegetation occurs on deeply weathered soils on exposed, volcanic ridges. Although the exact composition of the toafa patches varies from place to place, the physiognomy is very consistent. A mixture of grasses, pteridophytes, and scattered woody species forms an upper stratum 0.5–1.5 m tall, beneath which numerous herbaceous and semi-woody species are found. Common species include the grasses *Miscanthus floridulus* and *Paspalum conjugatum*, the pteridophytes *Dicranopteris linearis*, *Sphaerostephanos unitus*, and *Lycopodium cernuum*, and the woody

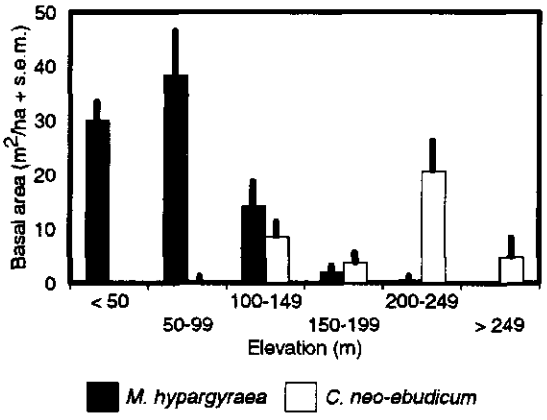

Fig. 4 Basal area of two dominant species of trees (*Myristica hypargyraea* and *Calophyllum neo-ebudicum*) at various elevations. (Community types IV, V, and VI, only; number of plots = 3, 3, 6, 10, 7, and 3, from left to right).

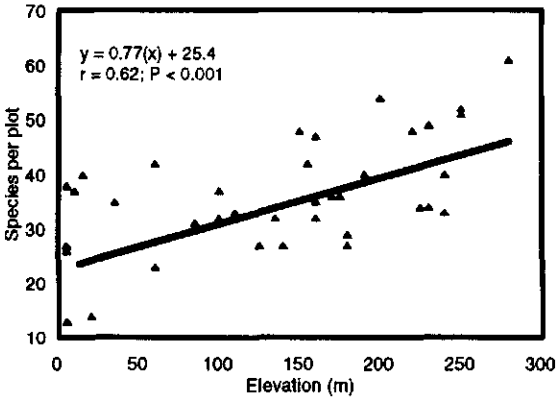

Fig. 5 Regression of species richness (number of vascular plant species per 600 m^2 plot) vs. plot elevation for the 40 forest plots on 'Eua.

species *Wikstroemia foetida*, *Alphitonia zizyphoides*, *Psidium guajava*, and *Melastoma denticulatum*. The mean number of species in five 600 m^2 plots was 26.4.

Trends

Results of the ordination corresponded well with the TWINSPAN analysis. Three of the major inland communities were spread, with little overlap, along the first axis (Fig. 3). An exception was one inland community (*Maniltoa-Pleiogynium* lowland forest), which appeared at the center of the ordination, because it lacked the dominant species of the plots that formed the end points.

The first axis score was positively correlated with elevation (first axis ordination score = 0.24 × plot elevation (m) + 15.3, $n = 35$, $r^2 = 0.52$, $P < 0.001$). This trend is further illustrated by the shift in dominance from *Myristica hypargyraea* to *Calophyllum neo-ebudicum* with increasing elevation in communities IV, V, and VI (Fig. 4). Species richness in the forest plots increased with increasing elevation ($n = 40$, $r^2 = 0.38$, $P < 0.001$; Fig. 5), with plots near the summit of the eastern ridge having approximately twice as many species as occurred in plots near sea level. The second ordination axis appeared to correspond to degree of disturbance, with vegetation subtypes judged to be recovering from some past disturbance occurring high on the second axis, and older stands occurring lower (Fig. 3).

DISCUSSION

'Eua supports a variety of plant communities; some are relatively widespread throughout Western Polynesia, while others may be found nowhere else in the Pacific.

In general, 'Eua's coastal vegetation is similar to that found in strand habitats throughout the tropical South Pacific. Species such as *Hernandia nymphaeifolia*, *Terminalia* spp., *Tournefortia argentea*, and *Scaevola sericea* are common coastal dominants elsewhere in Tonga (Stoddart 1975; Woodroffe 1983; Ellison 1990), as well as in Nauru and Kiribati (Thaman 1992), Tuvalu (Woodroffe 1986, 1991), Wallis, Futuna, and Alofi (Morat & Veillon 1985), Fiji (Garnock-Jones 1978; Kirkpatrick & Hassall 1981; Ash 1992), Samoa (Whistler 1980, 1983), Tokelau (Parham 1971), and the Cook Islands (Merlin 1991; Franklin & Merlin 1992). In contrast, *Excoecaria agallocha* appears to be of limited importance outside Tonga.

Similarly, the treeless, toafa vegetation dominated by ferns (e.g., *Dicranopteris linearis*) and grasses (e.g., *Miscanthus floridulus*) frequently noted on 'Eua (Straatmans 1964; Sykes 1978; Whistler 1992) is also common on poor, volcanic soils elsewhere in the South Pacific. It occurs in Vanuatu (Schmid 1975), Wallis, Futuna, and Alofi (Morat & Veillon 1985), Fiji (Garnock-Jones 1978; Ash 1992), Samoa (Whistler 1980), the Cook Islands (Sykes 1978; Merlin 1985, 1991), and the Society Islands (Fosberg 1992).

'Eua's secondary forests share many pioneer species with disturbed forests of other islands. For ex-

ample, *Alphitonia zizyphoides*, *Rhus taitensis*, and *Elattostachys falcata* are among the dominants on the relatively young volcanic island of Late, and the latter two are dominant in the last relictual stand of inland forest on the limestone island of Tongatapu (Palmer 1988). Straatmanns (1964) first described the dynamic relationship among 'Eua's canopy trees. He noted that seedlings of *A. zizyphoides*, *R. taitensis*, and *E. falcata* did not grow in dense forest, whereas seedlings of *Calophyllum neo-ebudicum* and *Myristica hypargyraea* did. In addition, *A. zizyphoides*, *R. taitensis*, and *E. falcata*, together with *Dendrocnide harveyi* and *Bischofia javanica*, are important components of secondary forests in Vanuatu (Schmid 1975), Wallis, Futuna, and Alofi (Morat & Veillon 1985), and Samoa (Whistler 1980).

In contrast to the secondary forests, 'Eua's old-growth inland rain forests bear little similarity to those of other regional islands. Several factors may account for the uniqueness of 'Eua's rain forests. Because the number of plant taxa in the Pacific generally decreases with increasing distance from Malesian source areas (van Balgooy 1971; Fosberg 1984; Stoddart 1992), nearly every island or small archipelago has a somewhat unique flora and, therefore, vegetation. Large islands north and west of Tonga contain many of the dominant species of 'Eua's mature rain forest, however, these species are not dominant in these richer forests. For example, Samoa's *Syzygium* lowland forest is dominated by *Syzygium inophylloides* (uncommon on 'Eua), but also contains substantial amounts of two Tongan dominants, *Myristica hypargyraea* and *Calophyllum neo-ebudicum* (Whistler 1992). In upland forests on Mt. Korobaba, Fiji, *Calophyllum neo-ebudicum* and *Garcinia myrtifolia* are common, but not dominant (Kirkpatrick & Hassall 1985). Islands east of Tonga, such as the Cook Islands, simply lack many of the Tongan dominants (Merlin 1985, 1991; Franklin & Merlin 1992). Stoddart (1992) states that "there is no more dramatic biogeographic boundary in the Pacific than that between the southern Cooks and the southern Tongan islands." This discontinuity is at least partly a reflection of 'Eua's position on the eastern margin of the continental Indian-Australian Plate.

Other, non-biogeographic factors also contribute to 'Eua's uniqueness. Due to their combination of limestone substrate, elevation, and relief, raised limestone islands such as 'Eua, Makatea, and Mangaia tend to have distinctive floras (Stoddart 1992). As a result, their vegetation bears little similarity to that of nearby volcanic or low coral islands. Thus, 'Eua's forests differ from those of the volcanic islands in Tonga, such as Late. Sykes (1981) noted *Casuarina equisetifolia*, *Alphitonia zizyphoides*, *Elattostachys falcata*, and *Rhus taitensis* as dominant and *Calophyllum neo-ebudicum* as common on Late; in contrast, *Myristica hypargyraea*, *Maniltoa grandiflora*, *Dysoxylum* spp., and *Garcinia myrtifolia* were absent.

Even among raised limestone islands, 'Eua is relatively unique in its combination of great elevation (312 m a.s.l.), large surface area (81 km^2), age (Eocene), sharp relief, deep andesitic soils, and volcanic core. Only 'Uta Vava'u in northern Tonga has the proper combination of biogeographic position, size (95 km^2), elevation (210 m), and andesitic soils over limestone (Orbell et al. 1985) to potentially support rain forest vegetation similar to 'Eua's. However, 'Uta Vava'u's vegetation is quite distinct because many of the dominant species of 'Eua's forests are rare or absent there (J. Franklin & D. Drake unpubl. data). Given the uniqueness of 'Eua's rain forest vegetation, the Tongan Government deserves praise for the foresight they have demonstrated through their ongoing efforts to protect a large tract of it in a national park.

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APPENDIX I

List of vascular plants recorded in the vegetation samples

Since there is no recent treatment of the spermatophyte flora of Tonga, nomenclature follows several sources. Smith (1979, 1981, 1985, 1988, 1991) treats nearly all of the spermatophyte species. For species not treated by Smith, the most recent treatment from among Yuncker (1959), Wagner et al. (1990), or Whistler (1991) is followed. Nomenclature for pteridophytes follows Sykes (1978). Tongan names are from Yuncker (1959), Sykes (1978), Whistler (1991), and the present study. Voucher specimens are deposited in the personal collection of A. Whistler at the University of Hawai'i (UHAW).
Key: E = endemic, I = indigenous, P = Polynesian introduction, A = post-European introduction.

PTERIDOPHYTES
Adiantaceae
Pteris comans, I
Pteris ensiformis, I
Pteris tripartita, I
Aspidiaceae
Arachnoides aristata, hulufe leisi, I
Tectaria dissecta, I
Tectaria latifolia, I
Aspleniaceae
Asplenium australasicum, hakato, I
Asplenium marattioides, I
Asplenium polyodon, I
Loxoscaphe gibberosum, hulufe leisi, I
Athyriaceae
Diplazium harpeodes, I
Blechnaceae
Blechnum orientale, I
Cyatheaceae
Sphaeropteris lunulata, ponga, I
Davalliaceae
Davallia solida, kulutuma, I
Nephrolepis hirsutula, hulufe, I
Dennstaedtiaceae
Microlepia speluncae, I
Gleicheniaceae
Dicranopteris linearis, kahiva'e, I
Hymenophyllaceae
Trichomanes humile, I
Trichomanes saxifragoides, I
Lindsaeaceae
Sphenomeris chinensis, I
Lycopodiaceae
Lycopodium cernuum, hiku 'i pusi, I
Marattiaceae
Angiopteris evecta, hulufe vai, I
Polypodiaceae
Drynaria rigidula, I
Phymatosorus grossus, I
Pyrrosia adnascens, I
Psilotaceae
Psilotum nudum, I
Schizaeaceae
Schizaea dichotoma, masalu ngaue, I
Thelypteridaceae
Christella parasitica, I
Sphaerostephanos decadens, I
Sphaerostephanos invisus, I
Sphaerostephanos unitus, I
Vittariaceae
Antrophyum plantagineum, I

GYMNOSPERMS
Cycadaceae
Cycas rumphii, longolongo, I
Podocarpaceae
Podocarpus pallidus, uhiuhi, E

DICOTYLEDONS
Acanthaceae
Graptophyllum insularum, I
Aizoaceae
Sesuvium portulacastrum, I
Amaranthaceae
Achyranthes aspera, tamatama, I or P
Deeringia amaranthoides, I
Anacardiaceae
Pleiogynium timoriense, tangato, I
Rhus taitensis, tavahi, I
Semecarpus vitiensis, ōlahi, I
Apiaceae
Centella asiatica, tono, A

Apocynaceae
Alyxia bracteolosa, kulu, I
Alyxia stellata, maile, I
Cerbera odollam, toto, I
Ervatamia obtusiuscula, te'ete'emanu, I
Melodinus vitiensis, tuamea, I
Neisosperma oppositifolium, fao, I
Araliaceae
Meryta macrophylla, kulukulu, I
Polyscias multijuga, tanetane vao, I
Asclepiadaceae
Hoya australis, laumatolu, I
Hoya pottsii, I
Tylophora samoensis, I
Asteraceae
Ageratum conyzoides, A
Bidens pilosa, fisi 'uli, A
Conyza bonariensis, A
Elephantopus mollis, A
Emilia sonchifolia, A
Sonchus oleraceus, A
Synedrella nodiflora, pakaka, A
Vernonia cinerea, fisi puna, A
Wollastonia biflora, ate, I
Barringtoniaceae
Barringtonia asiatica, futu, I
Boraginaceae
Tournefortia argentea, touhuni, I
Cordia aspera, tou, I
Cordia subcordata, pua taukanave, I
Burseraceae
Canarium harveyi, 'ai, I
Caesalpiniaceae
Maniltoa grandiflora, tautau 'a manu, pekepeka, I
Campanulaceae
Wahlenbergia marginata, I
Caricaceae
Carica papaya, lesi, A
Cassythaceae
Cassytha filiformis, fatai, I
Casuarinaceae
Casuarina equisetifolia, toa, I
Celastraceae
Maytenus vitiensis, I
Clusiaceae
Calophyllum inophyllum, feta'u, I
Calophyllum neo-ebudicum, tamanu, I
Garcinia myrtifolia, feto'umaka, I
Combretaceae
Lumnitzera littorea, I
Terminalia catappa, telie, I
Terminalia litoralis, telie 'a manu, I
Connaraceae
Connarus sp. nov., vavatu, E
Rourea minor, va'a 'uli, I
Convolvulaceae
Ipomoea indica, fue 'ae puaka, I
Ipomoea macrantha, fue hina, I
Ipomoea pes-caprae, fue kula, I
Merremia peltata, fue mea, I
Operculina ventricosa, fue hina, A
Stictocardia tiliifolia, A
Dichapetalaceae
Dichapetalum vitiense, kili, I
Ebenaceae
Diospyros elliptica, kānume, I
Diospyros major, mapa, I
Diospyros samoensis, tutuna, kokau 'uli, I
Elaeocarpaceae
Elaeocarpus graeffei, ma'ama'alava, I
Elaeocarpus sp. nov., E
Elaeocarpus tonganus, ma'ama'alava, I
Euphorbiaceae
Aleurites moluccana, tuitui, P
Bischofia javanica, koka, I
Chamaesyce atoto, I
Chamaesyce hirta, A
Croton microtiglium, I
Drypetes vitiensis, I
Excoecaria agallocha, feta'anu, I
Glochidion ramiflorum, malolo, I
Macaranga harveyana, loupata, I
Omalanthus nutans, fonua mamala, I
Phyllanthus amicorum, E
Flacourtiaceae
Homalium whitmeeanum, I
Xylosma simulans, filimoto, I
Gesneriaceae
Cyrtandra samoensis, I
Goodeniaceae
Scaevola sericea, ngahu, I
Hernandiaceae
Hernandia moerenhoutiana, pipi tui, I
Hernandia nymphaeifolia, fotulona, I
Hippocrataceae
Salacia pachycarpa, I
Icacinaceae
Citronella samoensis, olavai, I
Lauraceae
Cryptocarya hornei, motou, I
Cryptocarya turbinata, kakala 'uli, motou, I
Litsea mellifera, mamea, I
Loganiaceae
Fagraea berteroana, pua, I
Geniostoma rupestre, te'epilo 'a maui, I
Loranthaceae
Decaisnina forsteriana, topu'uno, kainikavea, I
Lythraceae
Pemphis acidula, ngingie, I
Malvaceae
Abelmoschus moschatus, P
Hibiscus tiliaceus, fau, I
Sida rhombifolia, te'ehoosi, P
Thespesia populnea, milo, I
Meliaceae
Aglaia heterotricha, langakali vao, E
Dysoxylum forsteri, mo'ota hina, I
Dysoxylum tongense, mo'ota mea, mo'ota kula, E
Vavaea amicorum, ahi vao, I
Melastomataceae
Melastoma denticulatum, I
Memecylon vitiense, malamala 'a toa, I

Menispermaceae
Pachygone vitiensis, I
Mimosaceae
Acacia simplex, tātāngia, I
Adenanthera pavonina, A
Entada phaseoloides, sipi, I
Mimosa pudica, mateloi, A
Schleinitzia insularum, feifai, I
Monimiaceae
Hedycarya dorstenioides, I
Moraceae
Ficus obliqua, 'ovava, I
Ficus prolixa, 'ovava, I
Ficus scabra, masi 'ata, I
Ficus tinctoria, masi 'ata, I
Malaisia scandens, hiehieapo, I
Streblus anthropophagorum, I
Myristicaceae
Myristica hypargyraea, kotone, I
Myrsinaceae
Discocalyx listeri, E
Embelia vaupelii, I
Maesa tongensis, I
Myrtaceae
Decaspermum fruticosum, nukonuka, I
Psidium guajava, kuava, A
Syzygium brackenridgei, fekika vao, I
Syzygium dealatum, fekika vao, I
Syzygium quadrangulatum, I
Syzygium richii, heavula, I
Nyctaginaceae
Pisonia grandis, puko, I
Pisonia umbellifera, I
Olacaceae
Anacolosa lutea, I
Oleaceae
Chionanthus vitiensis, 'afa, I
Jasminum didymum, tutu 'uli, I
Jasminum simplicifolium, tutu 'uli, I
Onagraceae
Ludwigia octovalvis, A
Oxalidaceae
Oxalis corniculata, kihikihi, P
Papilionaceae
Canavalia cathartica, I
Canavalia sericea, fue veli, I
Desmodium triflorum, A
Inocarpus fagifer, ifi, I or P
Mucuna gigantea, valai, I
Pueraria lobata, aka, A
Sophora tomentosa, lata, I
Strongylodon sp. nov., matafu'i, I
Vigna marina, lautolu tahi, I
Passifloraceae
Passiflora maliformis, vaine tonga, A
Passiflora subpeltata, A
Peperomiaceae
Peperomia tutuilana, I
Piperaceae
Macropiper puberulum, kavakava'ulie, I
Pittosporaceae
Pittosporum arborescens, masi kona, I
Pittosporum yunckeri, E
Rhamnaceae
Alphitonia zizyphoides, toi, I
Colubrina asiatica, fiho'a, I
Rhamnella vitiensis, I
Rosaceae
Osteomeles anthyllidifolia, I
Rubiaceae
Antirhea inconspicua, I
Bikkia tetrandra, siale tafa, I
Cyclophyllum barbatum, I
Geophila repens, tono, I
Guettarda speciosa, puopua, I
Gynochtodes epiphytica, I
Hedyotis foetida, I
Ixora calcicola, ola, I
Morinda citrifolia, nonu, I
Morinda myrtifolia, mamange, I
Mussaenda raiateensis, monomono 'a hina, I
Neonauclea forsteri, afa, I
Psychotria carnea, I
Psychotria leiophylla, I
Psydrax odorata, olamaka, I
Spermacoce assurgens, 'aselemo, A
Tarenna sambucina, manonu, I
Rutaceae
Melicope retusa, I
Micromelum minutum, takafalu, I
Santalaceae
Santalum yasi, ahi, I
Sapindaceae
Elattostachys falcata, ngatata, ngatata kula, I
Guioa lentiscifolia, E
Harpullia arborea, filiamaama, I
Sapindus vitiensis, ngatata hina, I
Sapotaceae
Burckella richii, kau, I
Planchonella garberi, kalaka, I
Planchonella grayana, kalaka, I
Solanaceae
Capsicum frutescens, polo, polo fifisi, A
Solanum amicorum, I
Solanum mauritianum, pula, A
Surianaceae
Suriana maritima, ngingie, I
Thymelaeaceae
Phaleria glabra, I
Wikstroemia foetida, lala vao, I
Tiliaceae
Grewia crenata, fo'ui, I
Triumfetta procumbens, I
Ulmaceae
Celtis harperi, I
Trema cannabina, mangele, I
Urticaceae
Dendrocnide harveyi, salato, I
Pipturus argenteus, 'olongā, I
Procris pedunculata, I
Verbenaceae
Clerodendrum inerme, tutu hina, tutu tahi, I

Faradaya amicorum, fufula, I
Lantana camara, talatala, A
Premna serratifolia, volovalo, I
Stachytarpheta urticifolia, hiku 'i kumā, A
Violaceae
Melicytus samoensis, I

MONOCOTYLEDONS

Agavaceae
Cordyline fruticosa, I or P
Furcraea foetida, faumalila, A
Araceae
Amorphophallus paeoniifolius, teve, P
Epipremnum pinnatum, Alu, I
Arecaceae
Cocos nucifera, niu, I
Pritchardia pacifica, piu, I
Commelinaceae
Rhoeo spathacea, fainā kula, A
Cyperaceae
Fimbristylis cymosa, I
Fimbristylis ovata, I
Mariscus sumatrensis, A
Scleria polycarpa, mahelele, I
Dioscoreaceae
Dioscorea bulbifera, hoi, I
Liliaceae
Dianella aff. *intermedia*, lave'imoa, I
Orchidaceae
Corymborkis veratrifolia, I
Goodyera rubicunda, I
Hetaeria whitmeei, I
Liparis disepala, I
Malaxis latisegmenta, I
Malaxis resupinata, I
Phaius tankarvilleae, I
Robiquetia bertholdii, I
Spathoglottis plicata, lave'i moa, I
Taeniophyllum fasciola, I
Pandanaceae
Freycinetia urvilleana, I
Pandanus tectorius, I
Poaceae
Botriochloa bladhii, A
Chrysopogon aciculatus, matapekepeka, P
Cyrtococcum oxyphyllum, P
Digitaria ciliaris, A
Imperata conferta, I
Ischaemum murinum, I
Lepturus repens, I
Miscanthus floridulus, kaho tonga, I
Oplismenus compositus, mohuku laukofe, P
Panicum decompositum, A
Paspalum conjugatum, vailima, A
Paspalum vaginatum, A
Stenotaphrum micranthum, I
Thuarea involuta, kefukefu, I
Smilacaceae
Smilax vitiensis, matafu'i, I
Taccaceae
Tacca leontopetaloides, mahoa'a, P
Zingiberaceae
Zingiber zerumbet, angoango, P