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Plant Succession on Pago and Witori Volcanoes, New Britain[1]

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PAGO AND WITORI VOLCANOES are situated on the north coast of central New Britain near Cape Hoskins (Blake and Bleeker 1970). Pago is an active volcano that last erupted in 1914–1917, and is mostly covered by vegetation ranging from sparse ferns and club moss to dense forest, although parts remain bare. It is situated in the caldera of an older, extinct volcano, Witori, the flanks of which are covered by rain forest. The caldera was formed about 1,500 years ago. Fig. 1, and Figs. 2 and 3 taken in 1947 and 1965, respectively, show the position and the main features of the two volcanoes and their vegetation.

On air photos the terrain appeared very suitable for a study of the development of vegetation on young volcanic deposits, and field work confirmed that the vegetation on Pago is not disturbed by fire or grazing, as the volcano has been avoided by man and beast alike.

The area has a wet tropical climate with an annual rainfall of about 4,000 mm on the coast. A dry season from May to October has monthly falls of just over 100 mm during the driest months, and a wet season during the remainder of the year has falls of over 750 mm during the wettest months. The rainfall farther inland on the volcanoes is probably higher than on the coast.

THE FORMS OF THE VOLCANOES

Pago consists of a central steep cinder cone (1 on Fig. 2), below which are a number of lava flows of different ages (2, 3[3]). The cone, 250 m high and rising to 724 m above sea level, was formed during the 1914–1917 eruption. Closely spaced erosion gullies radiate outward from the rim of the crater that forms the central part of the cinder cone. Solfataras and fumaroles occur on the flanks of the cone and inside the crater. They are most common on the upper part where the surface has hardened to a crust. The lava flows below the cone are glacierlike in form. Their surfaces range from blocky to smoothly undulating, and rocky ridges abound. Lava blocks range up to several meters across. During the last eruption the largest lava flow on the volcano was formed (2) and volcanic ash and pumice are reported to have fallen over a wide area. This flow descended the northeastern side of the volcano and was diverted eastward and southward by the caldera wall of Witori. Solfataras and steam vents are still active on the surface of the flow, and a number of hot springs issue from underneath its southern end, despite a cooling period of more than 50 years.

The floor of the Witori caldera (4), where not covered by lava from Pago, consists of pumice and debris mainly from the caldera wall (5). South of Pago most of the caldera wall is missing, and the lava flows descend to a partly swampy plain (7) formed of volcanic and alluvial deposits.

The flanks of Witori to the west, north, and east of Pago are built up of pumiceous deposits. The upper flanks are steeply dissected into a ridge-and-ravine landscape with very narrow ridge crests and deep V-shaped valleys (6). Boulders of lava occur in the narrow valley bottoms. The lower flanks, on the other hand, are gently undulating to almost flat and grade into the plains to the east and northwest. Widely spaced drainage courses have flat floors of very porous pumiceous sand and gravel and are dry except immediately after heavy rain. On these lower flanks the pumiceous deposits have weathered to form a generally highly permeable soil rich in pumice fragments. The color of the soil changes from dark brown in the top 20 cm through yellow to pale gray at a depth of 40–50 cm. Down to this depth the soil is loose and very porous, but below, on the east flank, com-

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[3] Arabic numbers refer to numbered features on Fig. 2.

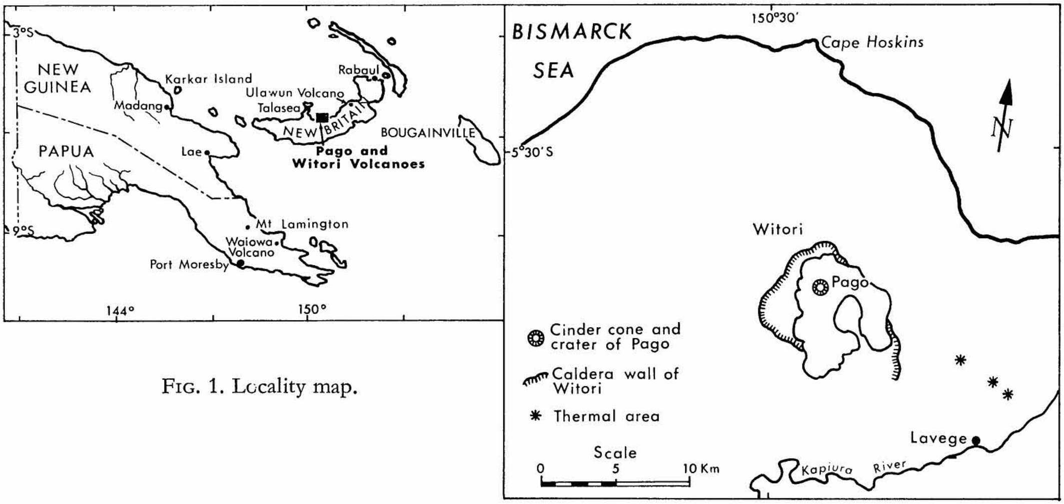

FIG. 1. Locality map.

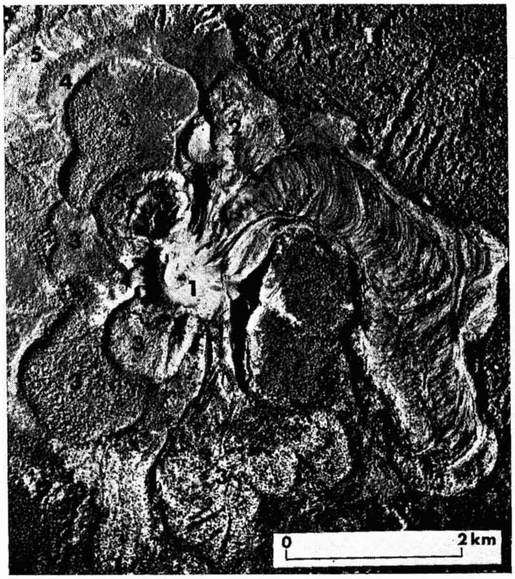

FIG. 2. Vertical air photo taken in October 1947 showing cinder cone and crater of Pago (1); youngest lava flow (2) and older flows (3) of Pago; caldera floor (4), caldera wall (5), and steeply dissected upper flanks (6) of Witori; and plain consisting of pumiceous deposits (7).

FIG. 3. Vertical air photo taken in August 1965 showing fern thicket on youngest lava flow (a) and on older flow (b); *Casuarina papuana* forest on youngest flow (c) and on plain (d); zoned vegetation pattern on older flow made up of *Eucalyptus deglupta* forest (e), mixed forest and woodland (f), and *Timonius timon* forest (g); mixed forest on older flow with emergent *Albizia falcataria* (h), partly destroyed during the 1914–1917 eruption and replaced by *Timonius* forest (i); and mixed forest with emergent *Octomeles sumatrana* and *Albizia falcataria* on upper flanks of Witori (j).

pacted ash layers occur which locally form a hardpan. On the southeast side near Lavege village are three thermal areas containing geysers, solfataras, and pools of boiling water and mud.

FIELD INVESTIGATIONS

I visited Pago during 3 weeks in July and August 1970. An ascent of the cinder cone was made from the north via the caldera floor and a valley between two lava flows. The vegetation on the southern part of three lava flows, including the youngest, was studied, the flows being reached from the south via Lavege. The area around two of the three thermal areas near Lavege was also examined. The flows are difficult to cross because they have very steep bouldery sides and there are no tracks. Progress on the flows is slow because most of the surface consists of large blocks, and the crevices between the blocks are hidden by vegetation.

The forest on the lower flanks of Witori was studied in 1966, during a timber survey, and again in 1970, en route to the cinder cone and lava flows of Pago. It is relatively easy of access.

FIG. 4. Upper surface of youngest lava flow on Pago. Saplings of *Eucalyptus deglupta* (next to indigenous tree namer), *Neonauclea* sp. (right of center), and *Casuarina papuana* (background) emerge above a dense ground cover of *Dicranopteris linearis*.

THE VEGETATION ON THE CINDER CONE OF PAGO

The cinder cone of Pago was only sparsely covered by vegetation in 1970, 52 years after its formation. The fern *Dicranopteris linearis* and the club moss *Lycopodium cernuum*, growing up to 20 cm high, cover about 30 percent of the lower slopes but become lower and sparser upslope. Scattered low trees of *Casuarina papuana* are present throughout, but rare individuals of the grasses *Imperata cylindrica* and *Eulalia leptostachys* grow only on the lower slope. Ferns and club mosses are highest and densest under casuarinas. The vegetation on the upper part of the cone is very sparse but *Dicranopteris* and *Lycopodium* are less sparse locally where the surface crust has collapsed. There is little or no vegetation near the crater rim where the ground is very hot.

THE VEGETATION ON THE LAVA FLOWS OF PAGO

The Youngest Lava Flow

The main vegetation types on the youngest lava flow are fern thicket (a[4] on Fig. 3, Fig. 4) largely consisting of *Dicranopteris linearis* but including many other ferns, and *Casuarina papuana* forest (c). *Lycopodium cernuum* and grasses such as *Thysanolaena maxima*, *Eulalia leptostachys*, and *Imperata cylindrica* are present, and locally, where the fern cover is less dense, codominate with *Dicranopteris*. Trees, growing singly or in small groups, are sparse but a great variety of species are present. Areas bare of vegetation occur near groups of solfataras and hot air vents where the surface rock has been cemented by sulphurous and siliceous material, and locally on the very steep sides of the flow.

In the *Casuarina* stands the trees are mostly between 12 and 20 m high and have girths of up to 60 cm. *Timonius timon* is the most common tree below the canopy, but many other trees, and also tree ferns, are present. An occasional emergent *Eucalyptus deglupta* reaches a girth of 1.2 m. Tall ferns and gingers form the ground layer. Litter and humus accumulate in crevices and form a thick cover on flat surfaces. The blocks of lava have not yet developed weathered crusts, and appear as fresh as when the lava flow was formed. Most of the steam vents are concealed by vegetation and their

[4] Lowercase letters refer to lettered features on Fig. 3.

presence is given away only by the heat they emit.

The Older Flows

A tall thicket of *Dicranopteris linearis*, *Eulalia leptostachys*, and a thorny climber *Rubus moluccanus* covers most of the southern part of the flow on the west side of the youngest flow (b). Together these plants form an almost impenetrable tangle. Scattered groups of mixed broad-leaved trees occur, but *Casuarina* is uncommon. The southern part of the next flow to the west has a zoned vegetation pattern that shows up clearly on air photos. A forest dominated by *Eucalyptus deglupta* (e) covers the steep bouldery southern rim of this flow. Girths range from 40 cm to 1.5 m, and the maximum tree height is about 30 m, indicating that the forest is still young. To the north the eucalypt forest grades into mixed, rather open forest and woodland interspersed with patches of fern thicket (f). In contrast to the rim the terrain here is gently sloping, undulating, and not markedly blocky. Soil and humus fill the crevices between lava boulders and cover the smaller blocks. Northward the mixed forest changes abruptly to a dense forest of pure *Timonius timon* (g). Here the trees are uniformly 18–20 m high and have a small range in girths from 50–70 cm. The terrain is similar to that under the mixed forest, and the reason for the abrupt change in vegetation is not known. On the air photo taken in 1947 (Fig. 2), this flow shows less woody growth and more fern land than its eastern neighbor, yet appears densely forested in 1965 (Fig. 3), whereas the vegetation pattern on the eastern flow has not changed.

The eastern part of the flow on the northwest side of Pago in 1947 shows a vegetation of dense, very small-crowned forest (i), whereas the western part is covered by much larger crowned forest (h). This vegetation difference has, however, largely disappeared by the time the 1965 photo was taken. The vegetation on the eastern part was probably destroyed during the last eruption and by 1947 was replaced by a pioneer forest. In 1965 this forest was approaching the status of the forest to the west.

THE VEGETATION ON THE CALDERA FLOOR AND ON THE PLAIN SOUTH OF PAGO

Open irregular forest covers the northern part of the caldera floor. The main tree species *Anthocephalus chinensis*, *Eucalyptus deglupta*, *Octomeles sumatrana*, and *Rhus taitensis* each form small, almost pure stands. *Octomeles* and *Eucalyptus* have reached girths of 2 m and heights of more than 30 m. They probably were the first to start growing after the last eruption and are also the quickest growers. Both trees can reach a girth of 2.5 m in 40 years (Heather 1955).

E. deglupta dominates the forests on the caldera floor west of Pago and on the plain to the southwest, and also forms pure stands near Lavege. Forest of this tree occurs on pumiceous as well as alluvial deposits but is best developed on well-drained alluvium where the tree grows to a girth of 6 m above buttresses and to a height of about 60 m. Where the terrain becomes swampy *E. deglupta* is replaced by other trees, such as *Campnosperma brevipetiolatum*.

Casuarina papuana is the main tree in the forest just south of the lava flows (d). Here it occurs together with sago palm (*Metroxylon sagu*), *Campnosperma*, and pandans on poorly drained to permanently swampy sites. Girths are mainly between 80 cm and 1.2 m, and heights range from 20 to 30 m.

THE VEGETATION NEAR HOT STREAMS AND HOT SPRINGS

Some of the streams that issue from underneath the youngest lava flow are very hot, others are of about body temperature. In one of the hottest streams only green algae were seen on the bottom but a lush vegetation, consisting of pandans, ferns, sedges, and grasses, grew on the banks. This hot stream flows into a swamp where the water is still warm; yet normal swamp plants are present.

The centers of the two thermal areas examined near Lavege have patches of fern thicket similar to that on the youngest lava flow, and patches devoid of vegetation. *Dicranopteris linearis* and *Lycopodium cernuum* locally grow so close to boiling mud holes and solfataras that

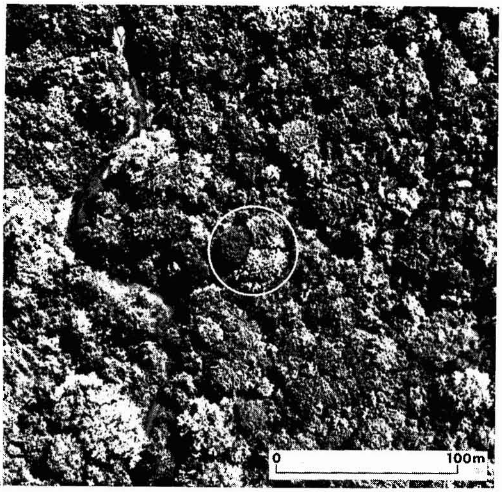

FIG. 5. Part of vertical air photo taken in 1965, enlarged, showing mixed rain forest on plain of Kapiura River southeast of Pago. Group of three tree crowns in center show crown shyness. The tree on the left is *Pterocymbium beccarii*, and the other two trees are *Celtis* sp. The three trees are of equal height which is about 40 m.

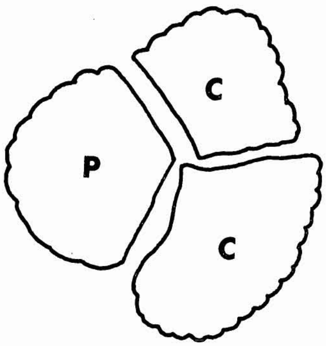

FIG. 6. Diagram for Fig. 5. P, *Pterocymbium beccarii*; C, *Celtis* sp.

their leaves are encrusted with sulphur. Various shrubs, grasses, and ferns form a narrow transition zone between fern thicket and surrounding low forest. The forest around the hot springs is growing on warm ground and here hundreds of bush hens (*Megapodius freycinet*) lay their eggs in tunnels in the loose ground where the eggs will hatch by the natural warmth of the ground. The women of Lavege and other villages have come and dug for the eggs for many years. The warm ground and disturbance of the vegetation by the egg collectors are the most likely reasons for the poor growth of the forest here.

FIG. 7. The three trees in center of Fig. 5 photographed from the ground.

THE FOREST ON THE FLANKS OF WITORI

The steeply dissected upper flanks of Witori volcano are covered by a rather open irregular forest (j), with wide-crowned *Octomeles sumatrana* and *Albizia falcataria* trees emerging above the canopy on ridge crests.

Very mixed, well-closed, and moderately tall rain forest covers the lower flanks of Witori volcano, except for the creek beds. The height of the canopy is 25–30 m, and emergents reach about 50 m. *Pometia pinnata* is by far the most common tree in the canopy. Basal areas were measured with a Bitterlich wide-angle relascope at 100-m intervals along a number of lines through the forest on the east side of the volcano. Total basal areas range between 20 and 31 m^2/ha, which is slightly below the average for tropical rain forest; they are lowest, 20 to 23 m^2/ha, where a hard pan is present in the soil.

Canopy trees in the forest on the lower flanks of Witori locally show a peculiar feature. This feature, which I have termed "crown shyness," is reported here because it was first observed on large-scale vertical air photos of the forest on Witori and was checked on the ground. Normally in mixed tropical rain forest the branches of neighbor trees intermingle to some extent after the crowns have grown so that they touch. In some cases, however, the outer branches of a crown appear to avoid those of its neighbor. Their growth is retarded and the crowns flatten against each other, leaving a narrow gap between them. This feature is illustrated in Figs. 5–7. Fig. 7 was taken after most of the undergrowth had been removed. Various tree species were involved in four cases where crown shyness visible on air photos was checked on the ground, but one species, *Pterocymbium beccarii*, was a neighbor tree in three of the four cases. Crown shyness may be fairly common throughout tropical rain forests, but is likely to escape notice from below because the undergrowth screens the canopy from view; and it is not readily visible from above on air photography of conventional scales.

DISCUSSION

The cinder cone of Pago was still sparsely vegetated in 1970, and the vegetation pattern hardly appears to have changed between 1947 and 1965. The main hazard for plant growth there is lack of moisture. Rainwater runs off the surface crust or sinks away in the loose rubble where the crust is absent. Moisture conditions near the surface are more favorable under casuarina trees, where maximum temperatures and hence evaporation are lower, and the tree litter retains some water, forming a habitat for nutrient-recycling microorganisms. As a result, the fern vegetation under these trees is more lush than elsewhere.

In contrast to the vegetation on the cone, that on the youngest lava flow has developed rapidly since 1947. Clusters of casuarinas have spread to form forests, and the pattern of rills and furrows visible on the 1947 photo is largely obscured by vegetation on the 1965 photo. On this flow the plants grow from crevices which retain some water and small-sized material that serves as anchorage for the roots. The presence of soil does not appear to be essential for pioneer plants (Eggler 1971). The distribution of fern thicket and forest appears to be more or less random, except that the north and south parts of the flow have more forest than does the center. Stands of *Casuarina* and *Timonius* are present north and south of the flow and these probably have been the main sources of seed supply.

Dicranopteris linearis and *Lycopodium cernuum* are the most common colonizers on Pago and grow nearest the summit of the cinder cone. They are also abundant in the centers of the Lavege thermal areas and are recorded near fumaroles on Java (van Steenis 1965). The same two species are also common colonizers on the volcanoes of Bougainville island (Heyligers 1967). Both are little demanding species that occur throughout Papua New Guinea on open sites which have poor topsoils or have lost their topsoils by erosion.

The most common pioneer grasses on Pago, *Thysanolaena maxima* and *Eulalia leptostachys*, are somewhat less tolerant than are *Dicranopteris* and *Lycopodium*. *Saccharum spontaneum* was not found on Pago at all, and *Imperata cylindrica* occurs only sparsely, although both play an important part in the colonization of other volcanoes on New Britain (van Royen 1963), and of Mt. Lamington on mainland New Guinea (Taylor 1957).

The genus *Casuarina* is a common pioneer on fresh volcanic deposits. The species *C. papuana* has a very wide ecologic amplitude, occurring on the dry cone and lava flows of Pago as well as on swampy sites south of the flows. Another species, *C. cunninghamiana*, is common on Waiowa volcano on mainland New Guinea. I visited the crater of this volcano in 1969, 26 years after the last eruption. The sides of the crater wall are as blocky and devoid of soil as is the youngest lava flow on Pago; yet they are covered by a forest of *C. cunninghamiana*, the trees of which are twice as large as those of the *C. papuana* forest on Pago. They have had only half the time to grow; however, high temperatures may have prevented plant invasion for much longer after eruption on the youngest lava flow of Pago than on the crater of Waiowa. Another species, *C. junghuhniana*, is a common pioneer on the volcanoes of Java (van Steenis 1965).

Eucalyptus deglupta, well known by its com-

TABLE 1

SUCCESSIONAL TRENDS ON PAGO AND WITORI VOLCANOES UNDER DIFFERENT SOIL MOISTURE CONDITIONS

SOIL MOISTURE LACKING: BLOCKY LAVA FLOWS, PUMICE CONE				
Sparse low vegetation of *Dicranopteris* and *Lycopodium* with scattered *Casuarina* trees →	Open *Casuarina* forest with undergrowth of *Dicranopteris*; abundant climbing *Stenochlaena* →	Moderately open to well-closed *Casuarina* forest; subcanopy layer of *Timonius*; sparse shrubs and a variety of saplings in lower layer; dense ground layer of ferns and gingers; mainly fleshy climbers →	Dense mixed forest with scattered *Casuarina* emerging above canopy; open layer of slender shrubs; sparse ground layer of herbs and tree seedlings →	Dense to locally open, mixed forest; shrub layer generally open; ground layer generally sparse but locally dense; fleshy and woody climbers
SOIL MOISTURE VARIABLE: CREEK BEDS, CALDERA FLOOR, RIVER FLOODPLAINS				
Open to dense stands of *Eucalyptus* with dense to open ground layer of tall gingers and ferns; climbing *Stenochlaena* in later stages →	Well-closed *Eucalyptus* forest; *Pometia* and other rain forest trees in lower stories →	Tall mixed forest; *Pometia* locally predominant; *Endospermum*, *Laportea*, *Pimelodendron* common →	Tall, very mixed forest	
SOIL MOISTURE IN EXCESS: SWAMPS, FLOOD-OUT PLAINS				
Green algae in hot streams →	Tall herbaceous vegetation of *Hanguana* and *Saccharum* in warm swamp →	Tall gingers with pandans and scattered low trees of *Casuarina*, *Rhus*, *Macaranga* →	Open forest predominantly of *Casuarina*, also *Campnosperma*, *Endospermum*, *Euodia*, *Cerbera*; tall pandans and sago palm common below canopy; ground layer of tall gingers →	Open mixed forest; *Alstonia* emerging above canopy; *Campnosperma* common in canopy

mon name, kamarere, is another pioneer that has a wide ecologic amplitude, although not as wide as that of *Casuarina papuana*. It tolerates flash floods but not permanently swampy conditions and grows poorly on ill-drained sites. Like *Octomeles sumatrana*, kamarere does not regenerate under its own shade. Species of the mixed tropical rain forest gradually invade initially pure stands, and the last stage of the succession is a mixed rain forest that has huge, overmature, widely spread kamarere trees emerging above its canopy. Kamarere regenerates profusely on abandoned logging roads and timber-hauling areas on the western lower slopes of Witori. Together with *Casuarina* it also colonizes almost unweathered pumice slopes on Ulawun volcano, New Britain (Heather 1955), but it had not been recorded on young lava flows before.

On young lava flows in Hawaii the most common pioneer vascular plants are *Metrosideros*, a tree, and *Nephrolepis*, a fern, followed by the shrubs *Styphelia* and *Dodonaea* (Eggler 1971). Species of *Metrosideros* are also early entrants of successions on rocky surfaces in New Zealand (Atkinson 1970). Of these four genera only one, *Nephrolepis*, was seen on Pago where at least four species occur. One of the others, *Dodonaea*, is recorded as a pioneer on lava flows on Karkar Island (Fig. 1), but the other two genera have not been recorded from volcanoes in New Guinea.

A broad correlation exists between the age of a flow and its vegetation. However, the rate of establishment of vegetation on different flows may differ greatly, and the succession on different flows may not follow the same pattern (Eggler 1971). A thicket of *Dicranopteris*, as present on Pago, probably retards the succession as it hinders the establishment of other plants. For instance, on Hawaiian lava flows the regeneration of *Metrosideros* practically ceases as *D. linearis* spreads and forms dense tangled thickets (Atkinson 1970). Once pioneer forests of such trees as *Casuarina* and *Timonius* have formed, conditions are favorable for further development toward the mixed forest climax. Many other plants then invade the forest, and the pioneer ferns and grasses gradually disappear.

The local dominance of *Eucalyptus deglupta* and *Casuarina papuana* on the caldera floor and on the plain south of Pago, and the common occurrence of other tree species characteristic of secondary growth, indicate that here the forest is seral, and that most if not all of the former forest was probably destroyed during the 1914–1917 eruptions. On the lower flanks of Witori the local abundance of *Pometia pinnata* and the above-average frequency of trees normally common in secondary forest may indicate a late seral stage. If this is so, this stage must be due either to human or volcanic activity. The history of human occupation is not known. Eggler (1959) has suggested that centuries may be required for the vegetation of volcanic deposits to approach something like the prevolcanic conditions. However, inasmuch as a period of 1,500 years is probably sufficient to restore the forest climax, the local seral stage of the forest on Witori is unlikely to be due to the caldera eruption of Witori, and may be the result of volcanic activity from Pago.

Successional trends that are thought to be typical for Pago and Witori volcanoes are presented in Table 1.

CONCLUSIONS

As on volcanoes elsewhere (Eggler 1959, van Steenis 1965) both spore and seed plants appear to invade bare areas on Pago more or less simultaneously, initial dominance being determined by the availability and chance distribution of propagules.

The vegetation of Pago is not specific to volcanoes. The same plants that pioneer on Pago and other volcanoes also colonize other sites devoid of vegetation, such as landslides, steep stream banks, roadsides, etc.

The youngest lava flow of Pago is a more favorable habitat for plant growth than is its cinder cone, although both areas are devoid of soil.

High ground temperatures have impeded or prohibited plant growth, particularly of trees, on the cinder cone and youngest lava flow of Pago and around thermal areas of Witori. High water temperatures do not appear to affect the vegetation on the banks of hot streams.

The end result of plant succession on Pago and Witori is undoubtedly a mixed rain forest, but the course of events leading to the climax varies. Succession may be retarded, locally and temporarily, by *Dicranopteris* fern thicket, or may progress relatively rapidly via stands of *Casuarina*, *Timonius*, and *Eucalyptus*.

SUMMARY

The vegetation and its correlation with edaphic conditions are described for two volcanoes on the north coast of central New Britain. The active volcano Pago consists of a central cinder cone and a number of lava flows of different ages. It is situated within the caldera of an extinct volcano named Witori. The vegetation on the two volcanoes ranges from scattered low fern and club moss on the cinder cone of Pago, through fern thicket, woodland, and low forest on the youngest lava flow and in two thermal areas, to closed rain forest on the weathered pumiceous deposits on the lower flanks of Witori. The rate and manner of plant establishment and changes in the vegetation pattern on Pago are discussed by means of air photos taken in 1947 and 1965 and of a visit to the area in 1970. The ecology of the most common pioneers, the tree *Casuarina,* the fern *Dicranopteris*, and the club moss *Lycopodium*, and of other pioneer species is discussed, and comparisons are made with plant establishment on other volcanoes of New Guinea and Hawaii. Attention is drawn to a feature termed crown shyness.

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Figures 3 and 5 are Crown Copyright and have been made available by the courtesy of the Director, Division of National Mapping, Department of National Development, Canberra.

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