In: BOUCHET P., LE GUYADER H. & PASCAL O. (Eds), *The Natural History of Santo*. MNHN, Paris; IRD, Marseille; PNI, Paris: 372 p. (Patrimoines naturels; 70).

Principal

Types of Vegetation Occurring on Santo

Jérôme Munzinger, Porter P. Lowry II & Jean-Noël Labat

The Santo 2006 expedition was designed to carry out detailed exploration of the botanical diversity present on the island. A wide diversity of vegetation types were therefore studied, covering the full range extending from what can be regarded as "extremes" on a scale from natural, nearly undisturbed areas to those that have been profoundly modified by man. Large areas have been transformed by humans —partially or completely— through clearing, fire, and other means, in an effort to meet basic needs for food, shelter, fiber, grazing land for livestock, etc., although such habitats exist only because they are created and maintained by man or by domesticated animals. At the other extreme, Santo's vegetation includes nearly pristine formations that result from the natural processes of evolution and succession and are self-maintaining, provided they are not subject to excessive human disturbance. These natural vegetation types include humid forests, which

Table 5: Vegetation types in Vanuatu proposed by Mueller-Dombois and Fosberg.

1. Lowland rain forest
a. High-stature forests on old volcanic ash
b. Medium-stature forest heavily covered with lianas
c. Complex forest scrub densely covered with lianas
d. Alluvial and floodplain forests
e. *Agathis-Calophyllum* forest
f. Mixed-species forests without gymnosperms and *Calophyllum*
2. Montane cloud forest and related vegetation
3. Seasonal forest, scrub and grassland
a. Semi-deciduous transitions forests
b. *Acacia spirorbis* forest
c. *Leucaena* thicket, savanna and grassland
4. Vegetation on new volcanic surfaces
5. Coastal vegetation (including mangroves)
6. Secondary and cultivated woody vegetation

Figure 62: View up the Penaoru Valley toward the center of the Cumberland Peninsula, with rainforest in the foreground and montane cloud forest at the highest elevations.

were the main focus of the research carried out during Santo 2006. Some areas of humid forest were only visited briefly by botanists passing through various parts of the island, but a large area on the west coast of the Cumberland Peninsula, especially in the Penaoru Valley (Figs 62 & 63), was the subject of detailed study and will be the main focus of the present chapter. Additional field work was conducted by a team on the western slope of Mt Tabwemasana (1879 m), the highest point on Santo and indeed in the entire Vanuatu archipelago.

The vegetation of Vanuatu can be divided into six main categories (Table 5):

- Lowland rain forest;
- Montane cloud forest and related vegetation;
- Seasonal forest, scrub and grassland;
- Vegetation on new volcanic surfaces;
- Coastal vegetation, including mangroves;
- Secondary and cultivated woody vegetation.

We will limit our discussion to the vegetation types that were examined during the Santo 2006 expedition (indicated in bold in Table 5).

Phytogeographic Relationships

Gordon McPherson

A visitor to the forests of Santo familiar with New Caledonia finds himself surrounded by a strange mixture of plant species, many of them completely unfamiliar but others that are only slightly different from their close relatives found to the south. The abundance of species and individuals in such Asian genera as *Myristica* (Myristicaceae), *Pterocarpus* (Fabaceae), *Dracontomelon* (Anacardiaceae), *Dendrocnide* (Urticaceae), *Pangium* (Acariaceae), *Medinilla* (Melastomataceae), *Hydnophytum* and *Timonius* (both Rubiaceae), *Vavaea* (Meliaceae) and *Cyrtandra* (Gesneriaceae) will convince the visitor that the influence of the Southeast Asian flora is much stronger on Santo than it is on the geographically more isolated and geologically much older New Caledonia. At the same time, he or she might be surprised to discover that some groups regarded as characteristic of New Caledonia are represented in Santo by distinct species. These include such genera as *Agathis*, *Ascarina*, *Hedycarya* (Monimiaceae), *Trimenia* (Trimeniaceae), *Balanops* (Balanopaceae), *Geissois* (see "Focus on *Geissois* (Cunoniaceae)") and *Spiraeanthemum* (both Cunoniaceae), *Meryta* and *Schefflera* (both Araliaceae – see "Focus on Araliaceae").

Travelers coming from lands to the north or west of Santo or from most of the islands of the Pacific will enjoy seeing other familiar genera. These include *Calophyllum* and *Garcinia* (both Clusiaceae), *Castanospermum* (Fabaceae), *Dacrycarpus* (Podocarpaceae), *Dysoxylum* (Meliaceae), *Elaeocarpus* (Elaeocarpaceae), *Freycinetia* (Pandanaceae), *Joinvillea* (Joinvilleaceae), *Metrosideros* and *Syzygium* (both Myrtaceae), *Morinda* (Rubiaceae), *Neuburgia* (Loganiaceae), *Pittosporum* (Pittosporaceae), *Rapanea* and *Tapeinosperma* (both Myrsinaceae) and *Semecarpus* (Anacardiaceae), although in most cases the species on Santo will be unfamiliar. Figs (members of the genus *Ficus*; Moraceae) and orchids (Orchidaceae) abound here, as in most tropical forests.

Figure 63: View down the Penaoru Valley, with rainforest in the foreground and seasonal forest at lower elevations.

MEDIUM-STATURE FOREST

Figure 64: Understorey of medium-stature forest above Penaoru base camp, showing numerous buttresses on large tree trunks.

Medium-stature forest (Fig. 64), which is characteristic of low elevation sites, is frequently degraded as a result of its proximity to inhabited areas. Many of the trees are tall (Fig. 65) and especially at lower elevations some deciduous species can be found such as *Antiaris toxicaria* (Moraceae) and *Pterocarpus indicus* (Fabaceae). The most characteristic element is *Castanospermum australe* (Fabaceae), known locally as *puilapuila*, and easily recognized by its majestic habit, straight bole and especially its beautiful flowers, which vary from orange to red depending on their maturity (Fig. 66). This is one of the largest trees in medium-stature forest, and it stands out when in flower because the ground underneath is carpeted with flowers and the emergent canopy above is multicolored. This type of forest is also distinctive in having a well developed layer of small trees 6 to 15 m tall. Charateristic species include *Dendrocnide latifolia* and *Pipterus argenteus* (Urticaceae) with their small flowers. Various species of fig also occur in this type of forest, such as *Ficus wassa* (Moraceae), a cauliflorous tree that bears numerous clusters of fruits on the trunk (Fig. 67) and produces abundant white latex, along with more discrete members of the genus such as *F. kajewskii*. *Gardenia tannaensis* (Rubiaceae), locally named "*uka*", is usually 5 to 10 m in height but can occasionally reach 20 m, has large white flowers (Fig. 68) with a strong, pleasant odor and is thus often planted around villages and in fields.

On ridges at about 500 m elevation, the lower stature forest is dominated by several species, including *Meryta neoëbudica* (Araliaceae) (Fig. 69; see "Focus on Araliaceae"), *Myristica inutilis* (Myristicaceae) and *Ficus septica* (Fig. 70), all of which are often covered with climbing plants belonging to several species of *Freycinetia* (Pandanaceae), whose large strongly scented flowers are eaten by bats (see "Focus on Pandans").

Figure 65: Jean-Noël Labat examining the canopy in medium-stature forest.

Figure 66: *Castanospermum australe*, one of the largest trees in lowland forest, is easy to spot when it flowers because the ground is carpeted with its red-orange petals.

Figure 68: Flower of *Gardenia tannaensis*, a sweet-smelling member of the coffee family.

Figure 69: A female individual of *Meryta neoëbudica* with young multiple fruits above a whorl of large leaves.

Figure 67: *Ficus wassa*, a member of the fig genus whose fruits are borne directly on the trunk.

Figure 70: A branched infructescence of *Ficus septica*, another fig species.

KAURI-TAMANU FOREST (= *AGATHIS-CALOPHYLLUM* FOREST)

A remarkable type of forest occurs on the west coast of the Cumberland Peninsula at altitudes above about 600 m, with trees so large that a person's arms can not reach around the trunk. These majestic giants no doubt live for many years: in 1938, Guillaumin reported to have seen an individual with a circumference of 10 m (i.e. a diameter of about 3.15 m). The largest tree observed during the expedition had a diameter at breast height of 2.4 m (a circumference of about 7 m). The most impressive of these is the Kauri (*Agathis macrophylla*), easily recognized by its distinctive cones (Fig. 71) and by its bark which forms plates (Fig. 74). Also, resin can often be seen oozing out of the trunk, which hunters use to start fires. Kauris belong to the family Araucariaceae, which also includes the columnar pine (*Araucaria columnaris*), endemic to New Caledonia but sometimes found planted as an ornamental tree in Vanuatu. Kauris not only dominate the forest by the diameter of their trunk, but also by their height, emerging far above the canopy (Fig. 74). Species of *Agathis* produce a high quality wood, which has led to heavy exploitation in most places, including Vanuatu, where it is still being harvested today. The forests where members of the Santo 2006 team conducted field work, however, have thus far escaped this fate, making the Penaoru area one of the few remaining anywhere in the Pacific where true Kauri forest still exists.

The second species characteristic of the Kauri-Tamanu forest is *Calophyllum neoëbudicum* (Fig. 72), locally known as "*Tamanu*" ("of the bush"). It too can easily be recognized by its distinctive bark and also by the yellow-orange latex that exudes when the plant is cut or bruised (a characteristic of many members of the family Clusiaceae) and its small leaves with closely spaced parallel venation. Clusiaceae are abundant in the Cumberland forest, with a second genus, *Garcinia*, represented by three species, *G. vitiensis, G. pseudoguttifera*, and a third as-yet unidentified species, locally known as "*Malkevic*", which is by far the most common of the three. Unlike *Calophyllum*, the species of *Garcinia* do not have closely spaced parallel secondary veins in their leaves, and their fruit is fleshy, with several seeds, the best known being the mangosteen (*G. mangostana*).

Another species deserves to be mentioned as well, *Astronidium novaeëbudaense* (Fig. 73), a shrub or small tree belonging to the family Melastomataceae, which was the most frequently encountered of all in our studies. We recorded individuals from between 600 m and 1 200 m altitude, indicating that this plant is capable of growing in a fairly wide range of forest types, from Lowland rain forest to Montane forest. The Melastomataceae are a large family occurring throughout the tropics.

Figure 71: Cone of a giant Kauri (*Agathis macrophylla*), a dominant tree in forest above 600 m elevation.

Figure 72: A ripe fruit of *Calophyllum neoëbudicum*, common tree in mid-elevation forest.

Figure 73: *Astronidium novaeëbudaense*, bearing young green fruits and showing the characteristic venation of the family Melastomataceae.

They can almost always be recognized by the very distinctive venation in their leaves, in which the tertiary veins are parallel to one another and oriente at right angles to the secondary veins, giving them an appearance that resembles a ladder, as clearly observed on *Astronidium novaeëbudaense* (Fig. 73). Some members of the family are also epiphytes, such as *Medinilla cauliflora* and *M. heteromorphophylla* (Fig. 77). Two tree species in the olive family (Oleaceae) should also be noted,

Figure 74: The huge trunk of a giant Kauri (*Agathis macrophylla*) with its characteristic bark forming large plates.

Chionanthus brachystachys, observed at 600 m and 900 m, and *Ligustrum neoebudicum* (Fig. 78), reaching up to 1 200 m elevation. Oleaceae have opposite leaves (or sometimes sub-oppposite at the top of branches) and are easy to recognize when flowers are present as they have four sepals, four petals and only two stamens. We also encountered *Hedycarya dorstenioides*, a member of the ancient, primitive family Monimiaceae, which occurs sporadically at 600 m and more commonly at 1 200 m,

How Old are the Kauri (*Agathis microphylla*) Trees?

Jonathan Palmer

One of the most common questions to ask when standing in a forest is how old are the trees? After climbing up past 600 m above sea-level and first encountering the large kauris at Santo, you have a feeling of awe at their majestic size and sense that they must have been standing there for a very long period of time. But exactly how long? This was the question I wanted to try to answer.

I would describe the trees as being wide but with short trunks (boles) holding up massive, open, spreading crowns. Buttressing is absent but there are large rounded roots spreading over a considerable distance from the trunk. The open architecture of their crowns is no doubt a means of withstanding passing cyclones. Typically kauris appear most abundant along ridges, where they sometimes form groves of mixed sized trees.

The main method used to obtain the age of a tree is simply to count the rings. This is fine for temperate locations but this approach can be difficult in tropical climates. The time constraints prevented us from using other options such as placing markers into the wood (pinning method) or bands around the tree and periodically returning to measure the change in circumference (dendrometer bands). Our approach was to obtain small cores from a selection of 15 trees using manual increment corers (Fig. 75). These have been widely used throughout the world and found not to cause any harm to trees. The cores extracted from the trees were stored in straws and transported back to the laboratory where they were dried, glued onto mounts and then sanded to produce a highly polished surface. They were then looked at under a binocular microscope and the number of visible rings counted. Normally the growth rings are measured and their pattern is compared to other cores from the same tree and then to other trees. If patterns match between different trees they are said to "crossdate" and in many situations this has led to the successful reconstruction of past climatic conditions.

Figure 75: The extraction of small samples of wood being taken from a kauri tree using an increment corer. The samples are used to try to count the number of rings formed so that the age of the tree might be estimated.

The Santo kauri cores were found to have ring boundaries that varied greatly from distinct to diffuse and impossible to determine. In some situations there were no "visible" rings over many centimetres of growth. Although the visible rings were counted, we knew the age estimate would not be accurate. Even so, we then checked if there was a general systematic relationship between the number of visible rings and the diameter of the trees (Fig. 76). There is no relationship. Many other studies have shown the same result: tree size ≠ age. This means for a tree found of a certain size, there is a large range of possible ages or visible rings. To check this we submitted two samples for radiocarbon dating. They were taken from inner-most ends of cores, the part closest to the centre (i.e. oldest) portion of two different trees. The results (Table 6) showed us two things. Firstly, that both samples were too young for accurate radiocarbon dating. The second thing was that although the tree Santo-15 was twice the diameter of Santo-14 (208 cm vs 102 cm respectively) there was not the same magnitude of difference in their calibrated radiocarbon ages; the trees were in fact fairly similar in probable age (note: the dates in Table 6 show the reverse trend if anything). Again, this supports the earlier result of tree size not being directly correlated to age.

Table 6: Radiocarbon dating results from two *Agathis microphylla* wood samples. (Waikato Radiocarbon Dating Laboratory, New Zealand).

Tree label	Trunk diameter (cm)	Radiocarbon date (years BP: before 1950)	Calibrated dates (95 % probability) AD (Christian calendar)
Santo 14.1	102	241 ± 30	AD 1630-1690 AD 1730-1810
Santo 15.1	208	149 ± 30	AD 1660-1890

What can we conclude? Firstly, the kauri tree-rings are not clearly defined enough to enable accurate counting and there was no consistent pattern found either within or between trees. This is despite trying to sample trees on exposed ridgelines and also towards the upper end of their elevational range (i.e. where growth might be more well defined by climatic conditions such as seasonal drought and exposure). Secondly, based on the radiocarbon dates, the trees are not immensely old. Unlike *Agathis ovata* in New Caledonia, the trees on Santo are unlikely to be much more than 350 years old. Thirdly, there seems to be a great range of possible sizes for any given age, a result that is consistent with many other studies.

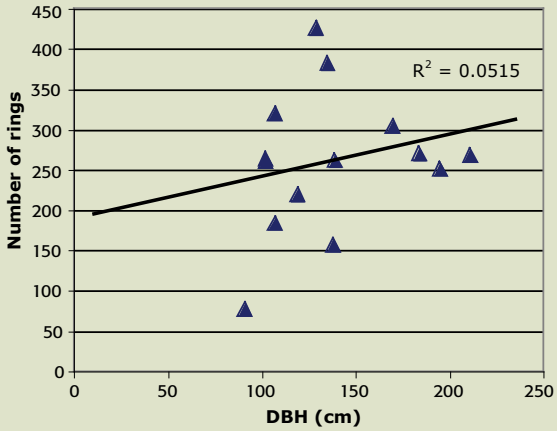

Figure 76: Plot of the number of visible rings against the diameter at breast height (DBH) of the Santo kauri trees. The regression line shows there is no significant relationship.

Figure 77: Flowers of the epiphyte *Medinilla heteromorphophylla*, which grows on trunks of large trees.

Figure 79: Fruits of *Hedycarya dorstenioides*, a member of the ancient, primitive family Monimiaceae.

Figure 81: Flowers of *Tapeinosperma netor*, a member of a complex genus.

and whose flowers have separate carpels each of which develops into a bright red drupe (Fig. 79).

Some species are very abundant in the shrubby component of this type of forest, such as *Cyrtandra efatensis*, a member of the African violet family (Gesneriaceae) (Fig. 80) and several species of *Tapeinosperma* (Myrsinaceae) (Fig. 81) that are particularly difficult to distinguish from one another. Members of the coffee family (Rubiaceae) were also frequently encountered, notably in the genus *Psychotria*, including the spectacular species *P. milnei*, which has an enlarged, showy calyx (Fig. 82). We also encountered herbaceous plants, as for example *Begonia vitiensis*, with distinctive white flowers in the understorey (Fig. 83).

Figure 78: *Ligustrum neoebudicum,* a member of the olive family whose distinctive flowers have four white petals (which are quickly shed), four persistent sepals, and only two yellow stamens.

Figure 80: Young flowers of *Cyrtandra efatensis* in humid forest.

Figure 82: *Psychotria milnei*, a member of the coffee family, is easy to recognize by it showy white calyx that persists long after the petals fall off.

Figure 83: *Begonia vitiensis*, a native relative of the commonly cultivated begonias grown throughout the world.

MONTANE CLOUD FOREST

Figure 84: Mist covered canopy (above) and understorey (below) of montane could forest at about 1 500 m above Penaoru valley.

The montane cloud forest (Fig. 84) is typically dominated by species belonging to several genera, including *Metrosideros* and *Syzygium* (both members of the family Myrtaceae), *Weinmannia* (Fig. 85) and *Geissois* (see "Focus on *Geissois* (Cunoniaceae)") (both Cunoniaceae), *Quintinia* (Quintiniaceae) and *Ascarina* (Chloranthaceae). Species of *Metrosideros* are easy to recognize by their abundant adventitious roots, which reach from the branches down to the ground: the longest seen during the expedition reached 1.9 m in length. This plant has small leaves (2.5-8.5 × 0.8-6 cm) that are opposite and a dry fruit, which distinguishes it from species in two other genera of Myrtaceae that occur in the forests

on Santo, *Syzygium* and *Eugenia*, whose fruits are fleshy. The flowers of *Metrosideros collinum* are variable in color, ranging from red or pink to yellow (Fig. 86). In humid summit areas, the trees are smaller and covered with epiphytes, mostly filmy ferns and liverworts, but also epiphytic shrubs such as *Vaccinium* (Ericaceae) (Fig. 87), which is easily recognized by its small, pink, urn-shaped flowers.

Figure 85: Flowers of *Weinmannia denhamii*, a typical dominant in montane cloud forest on Santo.

Figure 86: *Metrosideros collinum* in its yellow flowered form.

In some places the montane cloud forest can take a distinctive appearance when tree ferns and/or palms are present. In the Penaoru Valley, at about 1 200 m elevation, we visited an area of forest in which a single regionally endemic palm was frequently seen, *Cyphosperma voutmelense* (Fig. 88). The species name refers to the place where it was first collected, Voutmélé Peak. This palm alone represented fully 14 % of the trees with a DBH (diameter at breast height) of 5 cm or more, but the presence of several tree ferns, belonging to three different genera, *Cyathea, Dicksonia* and *Leptopteris*, was even more striking as they accounted for 20 % of the individuals with a DBH ≥ 5 cm. The showy white flowers of *Fagraea ceilanica* (Gentianaceae) were also very distinctive (Fig. 89), although only a few individuals were observed.

Figure 87: A flower of the epiphytic shrub *Vaccinium whiteanum*, which grows high in the trunks of the largest trees.

Figure 88: Flowers and fruits of the rare endemic palm *Cyphosperma voutmelense*.

Figure 89: Large, showy flowers of *Fagraea ceilanica*.

SEASONAL FOREST, SCRUB AND GRASSLAND

Figure 90: Gaiac (*Acacia spirorbis*) is characteristic of a "gaiac forest".

The seasonal forest, scrub and grassland can also be divided into three variants (Table 5), one of which, *Acacia spirorbis* (Fabaceae) forest (Figs 90 & 91), is locally referred to as "gaiac forest". Another characteristic species of this vegetation type is *Kleinhovia hospita* (Sterculiaceae) (Fig. 92), locally known as Matalo and recognizable by its pink flowers and light, ribbed fruits. This formation can contain sandalwood, and in drier locations it may be dominated by introduced shrubs such as *Leucaena leucocephala* and *Acacia farnesiana* (both Fabaceae) and *Psidium guajava* (Myrtaceae). Sandalwood (*Santalum austrocaledonicum*; Santalaceae) is an important element of the flora from a historical point of view, as this shrub or small tree was exploited for centuries for its prized, long-lasting essential oils that are used for perfumes, incense and in aromatherapy. Sandalwood trees can be distinguished by their opposite leaves that are slightly bluish below, their cream-colored flowers with four petals, and their angular fruit.

Figure 91: *Acacia spirorbis*. Its fruits open to reveal black seeds and their brightly colored arils that attract dispersers, primarily birds.

Figure 92: *Kleinhovia hospita* is another characteristic species in low elevation gaiac forest.

COASTAL VEGETATION

Figure 93: Coastal vegetation along the beach, Cumberland cape.

The littoral forest (Fig. 93), with characteristic species such as *Pandanus tectorius* (Pandanaceae) (Fig. 94) and *Casuarina equisetifolia* (Casuarinaceae) (Fig. 95), is common in coastal areas on Santo. These two species are quite easy to recognize; *Pandanus tectorius* has bluish leaves and a typical round, pineapple-like "fruit"[6] and *Casuarina* resembles a conifer, with long drooping branches and small, odd-looking bumpy-spiny multiple fruit that open by many small pores. *Callophyllum inophyllum* (Clusiaceae), which occurs in coastal areas (Tamanu of the sea), is also easy to distinguish as it bears the same characteristics as the Tamanu of the bush (see above), but with larger leaves and round fruits like golf balls scattered on the beach.

6 - The "fruit" of members of the Pandanaceae family is technically not really a fruit, but rather a compound fruit, developing from an inflorescence made up of many individual flowers instead of just a single flower.

Figure 94: *Pandanus tectorius*, a widespread coastal tree in the Pacific, with its typical "fruits".

Figure 95: *Casuarina equisetifolia*, a common species in littoral forest along the coast, has leaves and multiple fruits that resemble those of a conifer, but it is in fact a flowering plant.