A FIELD GUIDE TO YOUNG RAINFOREST

Much of the plant identification and ecological story about young rainforest in the Park will be told in the following field guide to the rainforest east of Kīlauea Iki Crater and north of Nāhuku (Thurston) Lava Tube. Throughout this field guide, I take the liberty of calling this young rainforest, readily accessible to cross-country travel, “Kīlauea Iki Forest.” Following the story about “Kīlauea Iki Forest” I also point out additional plant species and ecological features of other stands of young rainforest in the Park, including rainforest stands in other locations of Kīlauea summit, the Escape Road makai of Nāhuku Lava Tube, and the East Rift of Kīlauea.

“KILAUEA IKI FOREST”

My favorite young rainforest in the Park, and the focus area in the field guide for this plant community, is located east of Kīlauea Iki Crater and north of Nāhuku Lava Tube. I had not paid much attention to this forest since working in the field with Resource Management crews in the mid-1980s, when we first started controlling Himalayan ginger (*Hedychium gardnerianum*) in the rainforest of Thurston Special Ecological Area, a high priority weed-control area. This is before we had an effective herbicide, tested to demonstrate that it did not harm adjacent native plants when applied to ginger; so we were slaving away, digging ginger rhizomes from the ground with pick and shovel. Twenty-five years later, in 2010, I was asked to lead a field seminar on Park rainforest ecology for Park interpreters and commercial tour guides, and resigned myself to the Park Interpreter’s request to use the rainforest stand along Crater Rim Trail between Kīluaea Iki

Young rainforest near Kīlauea Iki Crater rim with abundant seedlings and saplings of the native trees, \`ōlapa and kāwa\`u, growing through a small light gap in the tree fern canopy. The similarity of the diameter of the \`ōhi\`a lehua trees suggests that this is an even-aged stand, probably becoming established after a catastrophic explosive eruption from Kilauea.

overlook and Nāhuku Lava Tube as the field classroom. I wanted to take them to a nearby rainforest just outside the Park with vivid examples of large epiphytic trees with masses of aerial roots dramatically descending to the ground. Leaving Crater Rim Trail and heading cross-country into the forest off Crater Rim Trail with interpreters and tours guides in-tow, my resignation turned to delight as I witnessed signs of the inspiring recovery of native trees now taking place: the abundance of seedlings, saplings, and small trees of `ōlapa (*Cheirodendron trigynum*), kōlea lau nui (*Myrsine lessertiana),* kāwa`u (*Ilex anomala*), and pilo (*Coprosma ochracea*).

The recovery of native trees in in the rainforest east of Kīlauea Iki and north of Nāhuku is the work of Park Natural Resource Management's careful fence builders, skillful hunters, and persistent weed killers. Recovery began here with the first Park pig control fences, built in 1980. This was quickly followed by eradication of feral pigs inside the fenced unit, as well as removal of a small number of feral cattle. Native forest recovery accelerated in the next two decades with the control of dense patches of Himalayan (kahili) ginger. Recently, Park resource managers began reintroducing plant species extirpated by ungulates and weeds.

NAVIGATING

Probably the best starting point to explore "Kīlauea Iki Forest" is the parking lot at Kīlauea Iki Crater overlook, located on Crater Rim Drive about one-half mile north (closer to the visitor center) of Nāhuku Lava Tube. A small patch of the forest lies between Crater Rim Trail and Crater Rim Drive and between Kīlauea Iki overlook and Nāhuku Lava Tube. You can access it by starting along Crater Rim Trail toward the lava tube. You will quickly pass a few short social trails to your left leading to views of deep earth cracks, reminding you to be wary of cracks and holes.

Large earth crack in forest near rim of Kīlauea Iki Crater. Sometimes you also find cracks well away from the rim of the crater.

(*right*) **Foot-size hole (center of image) along earth crack**. Most of this crack is hidden by an accumulation of organic matter. Best to tread well away from these small lua because it is hard to predict where the rest of the crack is located.

Continuing on Crater Rim Trail toward the lava tube, you will notice a couple of subtle and quickly fading social trails leading not to cracks but deeper into the forest; take one of these. Once inside you can wander and explore cross-country with little concern about navigation; this forest patch is bounded on the east by Crater Rim Drive and on the west by Crater Rim Trail.

A larger patch of recovering young rainforest lies adjacent to and east of Crater Rim Drive. Cross over Crater Rim Drive from the overlook parking area, looking for faint trails through the uluhe on the eastern road margin. Those informal trails also quickly disappear but you can confidently explore cross-country between Crater Rim Drive to the west, the gravel Escape Road to the east and north, and the Nāhuku Lava Tube development to the south. If you are low-tech, take a compass bearing when you enter, then wander at will, and take the back bearing to the catchlines, Escape Road or Crater Rim Drive to get out. If you use GPS, you know what to do.

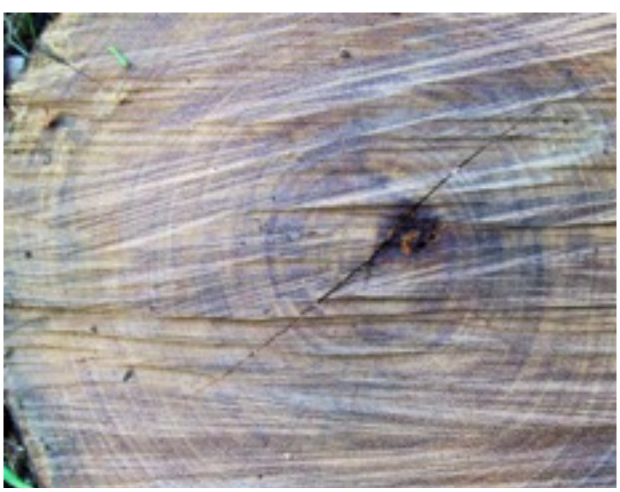
Crater Rim Trail along the edge of Kīlauea Iki Crater between the parking area at the crater and Nāhuku Lava Tube. Admittedly, there are tantalizing views of the bottom of Kīlauea Iki Crater and the Pu`u Pua`i cone from portions of the trail. However, this route does not reveal the diversity of vegetation found in the interior of young summit rainforest. The canopy gap created by the trail and its location next to the rim of the crater encourages light-loving uluhe fern (*Dicranopteris linearis*), a native fern but a little too well represented along the trail to see the complexity of the forest interior. Another reason is largely aesthetic; the margin

Common Plantain is "common" along edge of Crater Rim Trail. Common plantain is probably one of the first weed species in North America, introduced by English settlers on the East coast. The story, perhaps apocryphal, is that it was called "Englishman's Foot" by the local Native Americans because of the shape of the leaf and from the fact that it spread into areas the settlers walked and disturbed. In Hawai`i it is a fairly innocuous invasive species since it does not leave disturbed soil or trailsides and march into native forest. Hope you catch the irony of starting this field guide with a non-native plant.

HISTORY OF THE FOREST: GEOLOGICAL ORIGINS

The history of the forest east of Kīlauea Iki Crater must be inferred in a context of the recent eruptive events at the summit of Kīlauea. We know that lava flows and deposits of ash and lithics (rocks) at the summit of a highly active volcano like Kīlauea would have a profound effect on forest development. Specifically, we know that the flows beneath most of "Kīlauea Forest" were emplaced nearly 400 years ago. We also know that there were explosive eruptions depositing ash and lithic (small rocks) on the 400 and 500 year old lava flows between 1490 and 1790; some of these eruptions could have been highly destructive to established vegetation. Undoubtedly `ōhi`a lehua (also called `ōhi`a) (*Metrosideros polymorpha)* pioneered onto the pāhoehoe flows or on ash and lithic deposits, initiating the establishment of rainforest vegetation. In addition, `ōhi`a is a very long-lived tree species. Using carbon-dating techniques, some very large, recently dead individuals on other parts of Hawai`i Island were found to have lived as long as 650 years. However, there were one or more highly destructive explosive eruptions of Kīlauea since the lava flows covered this area. These could have severely impacted the forest developing in the area, resetting the successional clock.

The history of the forest east of Kīlauea Iki Crater could be precisely elucidated if we could determine the age of the trees by counting annual rings. However, remember that Hawai`i, even though blessed by cooling trade winds most of the time, is tropical. The trees in tropical environments, including Hawai`i, do not have annual rings; they have growth rings, but their growth periods may not be predictably associated with the calendar cycle. However, we can make educated inferences about forest history from the dates of lava flows and what the soil profile tells us about the sequence and types of explosive eruptions. Some layers can be roughly dated using if carbon is present. We can also make inferences about relative age of trees in a forest setting by examining forest structure, specifically the particularly the distribution, size, and growth form of `ōhi`a trees.



Growth rings of `ōhi`a lehua. These rings are not annual rings; one ring does not equal one year. In temperate environments, the cells laid down in the colder months are smaller and have relatively thicker cell walls, creating a dark ring each year. However, trees growing in tropical environments, without a marked cold season, have slower growth and darker rings because of other factors not correlated with predictable annual changes in the weather, e.g. reduced moisture. As a result there may be more than one growth period during a year or maybe even a growth period lasting longer than one year? Research is being considered to see if trees growing at very high altitudes in Hawai`i, where the climate is more temperate, may have annual rings, one ring per year.

Some of the explosive eruptions and deposits of ash and lithics between 1490 and 1790 would have been very destructive to existing vegetation; the current forest could have developed on one of these layers. So, I asked Dr. Don Swanson about the history of explosive eruptions with their deposits of ash and lithics in the area east of Kīlauea Iki Crater. Don, a senior geologist at the Hawaiian Volcano Observatory, focuses his current research on Kīlauea's explosive eruptions. My question stimulated his curiosity about the history of deposits in the forest east of Kīlauea Iki because he wanted to help explain the ecological patterns present and provide an idea what future explosive eruptions might do. So, Don dug a small soil pit in the rainforest patch near the Nāhuku end of the parking lot at the overlook. He found distinct layers of ash, sand, and small rocks, all from explosive eruptions of Kīlauea, forming about 75 cm (30 inches) of deposits above the 500 year old `Aila`au lava flows at the bottom of the pit. His carbon date from Niaulani Forest for this layer was fairly broad, 200-300 years old; he thought it was closer to 300 years. The top or youngest "several" centimeter thick layer was 1790 ash. Don said that even though the 1790 flow was highly destructive north and west of the Caldera, the thin, vertical rain of ash east of the summit was probably not forest-leveling. Below that, probably deposited between 1750 and 1790, was a layer of sandy material. Even though these fell vertically, rather than in an incandescent, horizontal volcanic hurricane or surge, Don surmised that they could have done a lot of damage. Below the ash and sand, he found a 13-17 cm (5-7 inch) thick layer of sand and gravel similar to the example on the previous page. He thought that this layer could have been resulted from a surge event; it would have been catastrophic to existing vegetation. Below this layer and above the pumice or reticulate immediately on top of `Aila`au pāhoehoe flows, were layers mostly of fine-grained ash.

Pit dug at Niaulani Forest, just outside the Park, reveals layers of deposits from eruptive explosions of nearby Kīlauea Caldera. This pit was dug down to underlying pāhoehoe to install a wooden post supporting a pig control fence. I am illustrating this as a surrogate but representative profile of the layers deposition in "Kīlauea Iki Forest**."** It would be bad manners to dig holes in the Park to satisfy my intellectual curiosity or provide an image for this story. The profile is similar to that described by Don Swanson for the research pit he read near the parking lot at Kīlauea Iki overlook. The uppermost layer just below the leaf litter on the forest floor is relatively smooth, consisting of fine particles. Below this, about 10 cm from the top, is a rough-textured layer about 10 cm thick consisting of small rocks and ash with embedded carbon indicating the occurrence of a wildfire dated 200-300 years ago. Deeper layers tend to be dominated by sand, silt, and ash particles, as suggested by their finer texture. Not visible in in this image is the reticulate overlying the pahoehoe at the bottom of the pit.

Excavated and sorted ash and lithics from the layer near the top the profile at Niaulani Forest. This sample was sorted by size using a fine mesh strainer. The fine particles of ash (< 2 mm or 1/16 inch in diameter) and slightly larger sand particles on the right made up about one-third of the sample by volume. The lithics on the left average 7 mm (1/4 inch) in diameter. The ash and rocks were stripped off the walls of the crater at the summit of Kīlauea and were deposited by a highly destructive, horizontal hurricane-velocity surge. The sand and gravel would have stripped the leaves off the forest trees. I found a few much larger rocks embedded in the sand and gravel layer at Niaulani. Don Swanson says that the bigger rocks would have retained heat and set fires, apparent from the charcoal associated with this pyroclastic layer.

So, what does forest structure imply about forest history? The relatively modest diameter of the `ōhi`a suggest that "Kīlauea Forest" is a relatively young forest. `Ōhi`a are much larger in the probably older rainforest at Niaulani, just outside the Park on the same aged lava flow and similar deep ash soil. The narrow range of tree diameters also implies that "Kīlauea Forest" is a mostly even-aged stand. The forest-form growth form of the trees implies that the trees grew up together as a cohort of closely spaced trees forming a closed forest. Forest-form trees, as opposed to open-form trees (see below) grow up in a forest environment with competing trees all around them. They do not branch laterally except in the tops of the canopy. The even-aged stands of relatively small diameter forest-form trees suggest forest development on recent ash and lithic deposits. Plant establishment and development of closed rain forest takes place more rapidly on eruption-deposited ash soil than on bare lava. More rapid succession occurs because the fine soil particles retain inorganic nutrients and water.

Young, mostly even-aged stand of forest-form `ōhi`a lehua trees just east of Kīlauea Iki Crater. Granted, there are some much smaller trees which were either suppressed by the faster growing neighbors or became established somewhat later in succession, undoubtedly in canopy gaps in the emerging vegetation.

Another feature of forest structure may shed light on the history and origin of the present forest east of Kīlauea Iki. If you look closely at the size and growth form of `ōhi`a at the summit of Kīlauea, you will find a few very large, usually open-form `ōhi`a trees, like the two depicted below, scattered in a forest matrix of far more numerous, much smaller diameter, forest-form `ōhi`a. *The larger diameter, open-form trees may be relicts of a previous forest. Their greater diameter suggests relatively greater age; the putative relicts have a diameter two to four times greater than the average diameter of the far more numerous smaller, forest-form individuals surrounding them.* The diameter of the putative relicts is similar to `ōhi`a lehua growing in known old growth forest in Volcano Village close to the HVNP, Niaulani Forest. *The open-form growth pattern suggests that the larger, older trees at one time grew in an environment without closely adjacent trees. For example, they could have survived a period in which the forest became more open, with light available horizontally, following an explosive eruption that killed most trees.* Following that, pioneer trees became established on the new deposits and formed the current even-aged stand of smaller, younger `ōhi`a lehua trees. The younger trees, growing up in dense stands of the similar aged trees, have a forest-form growth pattern. The crowns are relatively narrow because of light competition from surrounding trees.

Two large diameter, open-form `ōhi`a lehua trees in the forest just east of the rim of Kīlauea Iki Crater. The trunks of the open-form trees tend to have two major forks at 10-20 feet above the forest floor. Maybe this was close to the height of the forest which was largely leveled by a powerful explosive eruption. With adjacent trees no longer competing for light the survivors were able to spread laterally into the extensive canopy gaps created. Their open growth form has created an ideal environment for the epiphytic `ōlapa trees, typically becoming established in the forks of the major branches.

Here is my hypothesis about the history of the forest east of Kīlauea Crater, based on an possibly imaginative interpretation of eruption history and forest structure. \`Ōhi\`a lehua and other native plants undoubtedly colonized the pāhoehoe flows emanating from vents at the base of the former \`Aila\`au shield and the shelf at Kīlauea summit, 400-500 years ago or the very early ash deposits on the surface of these flows. *Early in the 1700s there was a devastating pyroclastic hurricane, a horizontal surge that deposited a substantial layer of sand and gravel layer and devastated the existing vegetation that had become established on the pāhoehoe or very early ash deposits. The \`ōhi\`a trees that became established on this layer of sand and gravel are now represented by the scattered large diameter, open-growth form \`ōhi\`a, my putative relictual trees. There were subsequent destructive explosive eruptions in the later part of the 1700s, but probably before 1790, which killed most of the trees, and leaving the putative relicts. The current even-aged stands of forest-form trees became established around the few relictual trees.*

An alternative hypothesis is that the large, open form trees became established on the pāhoehoe flows 400-500 years ago and survived the devastating surge of sand and gravel. The current even-aged forest originated on this layer of sand and gravel from the early 1700s. What bothers me about this alternative is that the forest structure is very similar on the 400 year old \`Aila\`au flows as the adjacent 500 year flows from Kīlauea summit. This suggests that the explosive eruptions following the emplacement of the pāhoehoe determined the age of the forest.

pic of forest east of Thurston (Nahuku) and if pattern the same or more like Niaulani or like near the rim of Kilauea Iki (Kilauea Iki Forest) and make a conclusion how far the blast went, with the niaulani forest structure reflecting no 1790 blast. Lots of italics. comparison with niaulan

THE FOREST PROFILE

Examining the vertical layers of the forest is one of the more informative ways to identify species and describe observable features of their natural history and ecology. The forest profile is also a revealing context for forest composition, ecological relationships among plants, and successional trends. Keep in mind that discreet layers are largely a human construct; actual forest layers tend to overlap with the layers above and below.

Emergent Canopy

The emergent (tallest) canopy of "Kīlauea Iki Forest," characteristic of almost all Hawaiian rainforest, is very simple: It is made up of monodominant \`ōhi\`a lehua. This is a very different pattern from that found in continental tropical rainforest in which there are multitudinous tree species in the emergent canopy as well as lower forest layers. Remember that Hawai\`i is the most isolated island archipelago on the planet so very few species arrived and became established here.

A common view of the emergent canopy. All of the \`ōhi\`a in this image of young rainforest along Crater Rim Drive have densely hairy (pubescent) leaves which makes the canopy foliage appear dark grey-green. The pubescent varieties of \`ōhi\`a lehua are better adapted than the hairless varieties to young volcanic surfaces. These substrates are relatively drier than older environments which are kept more moist by the shading of a forest canopy and the accumulation of organic matter on the forest floor. The scattering of light in the emergent canopy in this image results from mist blowing through the forest, a fairly common event in Hawaiian rainforest.

A uncommon view of the emergent canopy. The tree on the left with brighter, more yellow-green foliage, is an individual of a hairless (glabrous) variety of \`ōhi\`a lehua that also pioneered on the ash, sand, and gravel deposits. Tall, pioneer trees with glabrous leaves are very uncommon in the emergent canopy at Kīlauea Iki. The trees on the right side of the image have the grayish-green color foliage of the typical pioneer variety. The view is also uncommon in that the photo was taken on a dry, cloudless day. "Kīlauea Iki Forest" is located toward the dry edge of the Hawaiian rainforest environment in the Park.

The "green tunnel" formed by `ōhi`a lehua trees arching over Crater Rim Drive from both sides. Note the dense understory of hāpu`u. along the edge of the road.

`Ōhi`a lehua not arching over Crater Rim Drive. Note the thick uluhe understory.

As you travel through young rainforest along Crater Rim Drive, you will notice in a some stretches of this scenic road that the branches or trunks of `ōhi`a trees arch over the road and form a continuous canopy or "green tunnel." Ecologically speaking, the road is a gap created in the forest canopy, so it make sense that trees will grow into this gap, seeking the light available there. Notice that trees arching over the road more emphatically typically have an understory of hāpu`u tree ferns. In contrast, the `ōhi`a crowns along the road margin with an uluhe understory tend to be upright. When there is a hāpu`u understory on both sides of the road the arching `ōhi`a canopies form a "green tunnel." Time for some pleasurable eco-speculation to try to explain green tunnels. *One possible explanation for the uluhe and tree fern pattern is that overarching canopy shades out the light-requiring uluhe fern which is then replaced by shade-tolerant hāpu`u. Where the trees grow straight up, there is available light from above the road-created canopy gap so that light-requiring uluhe can persist beneath the trees next to the road. Alternatively, the presence of hāpu`u versus uluhe may have been a cause, not just an effect of formation of the green tunnel? Maybe the lateral branching of `ōhi`a is more suppressed by thick mats of uluhe which often climb high in the canopies. In contrast, the `ōhi`a lehua are capable of branching over the roadway between or through the smaller tree ferns, particularly since light is available on the edge of the forest from the roadway canopy. Why, in the first place, did `ōhi`a lehua trees arch over the road in some areas and not in others? I think this might have something to do with a pattern I see in some areas of young summit rainforest. I see same-aged, side-by-side stands of `ōhi`a lehua trees with hāpu`u understory and stands of `ōhi`a lehua trees with uluhe understory. The trees in the hāpu`u stands are larger than those in the uluhe stands. These stands also differ in micro-topography. The tree fern stands are in the swales, concave micro topography, between small ridges which support the uluhe stands. The swales probably have deeper soil and thus support faster growing, larger trees. I think I see these patterns along Crater Rim Drive associated with the green tunnels. Trees markedly arching over the road with tree fern understory tend to be in flatter or lower areas and have larger diameter trunks and branches. Trees not arching over the road tend to be on higher ground, convex micro topography,, and have smaller diameters. This pattern of tree diameter, microsite, understory type, and arching pattern is apparent in the image below.* I know that the "green tunnel" phenomenon is not a critical ecological issue for young rainforest, but this question begged to be explained. I commuted under these green tunnels on my bike for 23 years to my job at Resource Management, wondering about them.

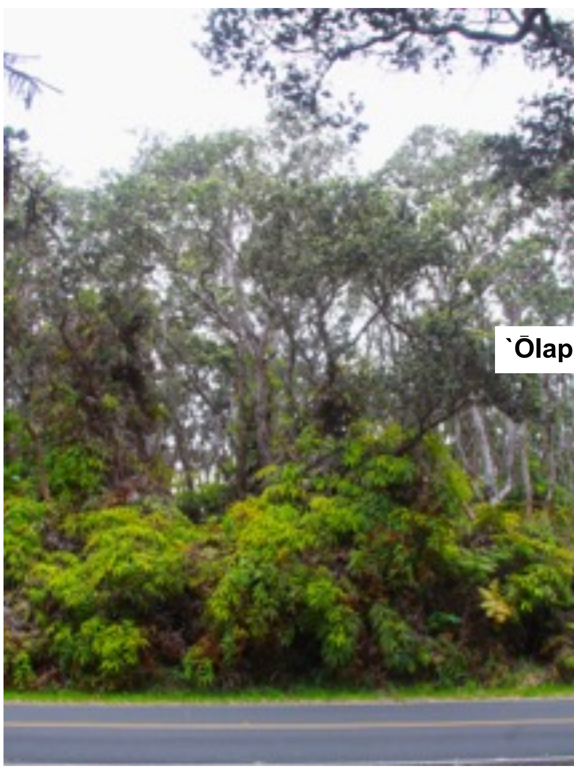
**Hāpu`u understory on left and uluhe understory on right.** The `ōhi`a above the tree ferns on the left are branching over the road more noticeably than the trees above the uluhe on the right. These trees are subtly larger in diameter than those on the right and grow in a depressed area lower than the road. The trees above the uluhe occurs on a steep ridge, probably with shallower soil. Possible reasons for the arching trees on the left are greater soil depth, faster growth, and an easier understory for lateral branches to penetrate. Of course, there are exceptions to this neat pattern. In a few short stretches of Crater Rim Drive, a few scattered `ōhi`a in uluhe patches are tall, with some trees noticeably arching over the road, as in the above image on the right side of the road. A another location, level terrain supporting tree ferns, there is a narrow fringe of uluhe along the edge of the road. DO TREES ARCH OVR HERE

Planted koa (*Acacia koa*) (center-rear, bright-green) along Escape Road, just off Crater Rim Drive. Koa naturally occurs at low density in nearby rainforest at Niaulani but not in the Park's summit or East Rift rainforest. They were planted along the edge of Crater Rim Drive and the Escape Road by overzealous Park Rangers or partners, where adequate light was available. There is a several hundred acre stand of mixed `ōhia and koa in the older `Ōla`a Forest in the Park.

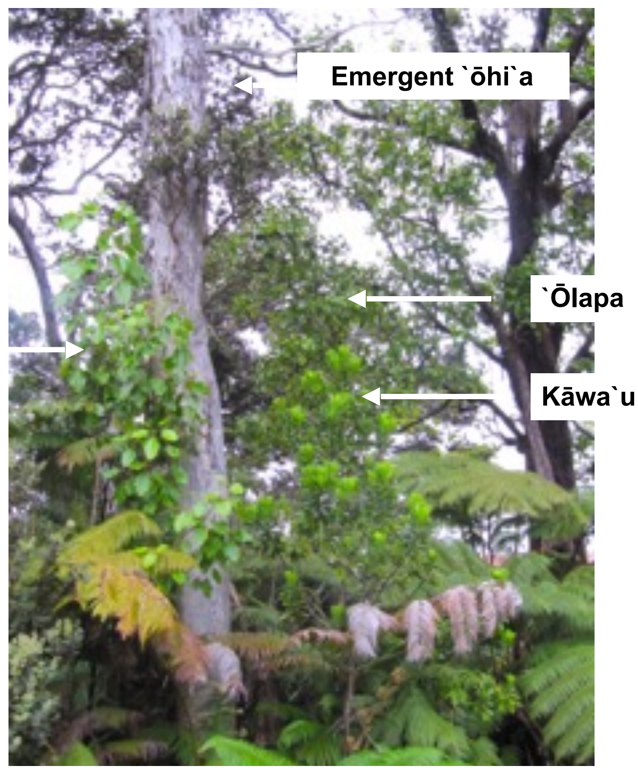
Planted māmane (*Sophora chrysophylla)* near the Kīlauea Iki overlook parking lot. The several māmane trees near here were undoubtedly planted by HVNP staff. Growing on the edge of the forest, the planted māmane here receives sufficient light to survive. Good luck finding māmane growing naturally in the rest of Park rainforest.

The Depauperate But Recovering Secondary Tree Canopy

Intriguingly, the secondary tree canopy, just below the emergent `ōhi`a lehua canopy, is poorly represented in the forest in "Kīlauea Iki Forest." Typically, in Hawaiian rainforest of this age and older, the secondary canopy consists of a scattered trees of `ōlapa, kāwa`u, and kōlea lau nui. However, in the rainforest near Kīlauea Iki, only kāwa`u is present in noticeable numbers in the secondary tree canopy. The reason for the near absence of `ōlapa and kōlea lau nui in the secondary tree layer at Kīlauea Iki is open to speculation. However, I think you can largely rule out natural succession. The premise of this argument is that the forest stands east of Kīlauea Iki are too young for the establishment of `ōlapa and kōlea lau nui, that these species get established later in succession. It is understandable that `ōlapa, kāwa`u, and kōlea lau nui are sparse in uluhe stands, an earlier stage of succession when suppressed by dense mats of uluhe fern. However, they should be present in later successional forest with little uluhe, like much of the forest east of Kīlauea Iki. These species are common in the secondary canopy of slightly older Niaulani Forest just outside the Park.



A common view of the tree canopy in the forest at Kīlauea Iki along Crater Rim Drive. Notice that there is no secondary canopy of ōlapa, kāwa`u, and kōlea lau nui below the emergent `ōhi`a lehua trees canopy and above the uluhe and tree fern layer.



A more intact secondary forest canopy layer. This is an image from the young rainforest behind the Volcano Art Center, Niaulani Forest. Protected from grazing for many decades, there is a healthy secondary canopy of ōlapa, kāwa`u, and kōlea lau nui.

There is compelling evidence from the control of ungulates and dense stands of invasive plant species in Hawaiian rainforest of various ages to indicate that these disruptive invasive species are at least partly responsible for the suppression of `ōlapa and kōlea lau "Kīlauea Iki Forest." I would first lay the blame for the near absence of `ōlapa and kōlea lau nui on the abundant feral pigs and occasional feral cattle which roamed this area until 1980. An example of the impact of stompers and chompers on native tree regeneration is demonstrated by a recently constructed exclosure in the Kahuku unit of the National Park, just above the Ka`ū Forest Reserve. The acre-sized exclosure, with almost no non-native plants present, was fenced to protect rare plants from feral pigs and cattle, as well as mouflon sheep, all present in the surrounding areas. was there assisting in planting of seedlings of some of these rare plants. Following the removal of invasive ungulates a few years ago, there are now abundant seedlings and saplings of `ōlapa, kāwa`u, and kōlea lau nui, destined to grow into the secondary tree canopy.

A more subtle demonstration is provided by the composition of the secondary canopy in pit craters at Kīlauea summit near Nāhuku Lava Tube. Ungulate-free because of their steep walls, these pit craters are about the only sites at Kīlauea summit all three secondary canopy tree species are represented in their rightful place below the emergent `ōhi`a canopy; also, without pig and cattle disturbance, all three grow from the soil.

A view of the secondary tree canopy from the rim of pit craters near Nāhuku Lava Tube. Kāwa`u and `ōlapa are illustrated here. Kōlea lau nui occurs in other areas of the pit craters. Large kōlea lau nui trees are extremely scarce in the secondary canopy "topside" (the forest outside and above the pit craters) in "Kīlauea Forest."

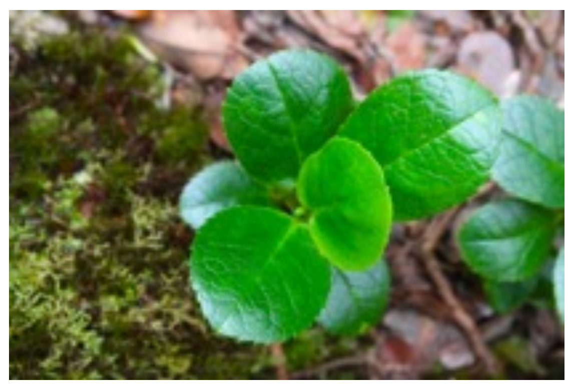
In addition to the damage done by stompers and chompers, I would also blame Himalayan ginger, which dominated the understory in many parts of "Kīlauea Iki Forest," probably since the 1960s. A good example of recovery after ginger removal is found along the east side of the administrative road down to the Research/Resource Management center of the Park. Himalayan ginger invaded patches of shaded out uluhe, the ideal site for secondary tree establishment. The wall-to-wall ginger understory here was controlled temporarily in 1980, immediately after the removal of ungulates from the area and then definitively in 2000 as the first full scale test of Escort herbicide use in the Park. Now `ōlapa, kāwa`u, and kōlea lau nui seedlings, saplings, and young trees are flourishing, with the tallest individuals growing into the secondary canopy.

One of the few `ōlapa in the forest at Kīlauea Iki which figured out a way to grow into the secondary tree canopy. This tree got established as an epiphyte, above the zone of feral pigs, cattle, and Himalayan ginger.

**`Ōlapa, the "dancer."** The leaves of this secondary canopy tree are palmately compound, that is, formed of similar leaflets, joined to the main leaf stem at the same location. The number of leaflets in `ōlapa vary from three to five per leaf. `Ōlapa means dancer in Hawaiian and this name aptly describes their movement; in even the most gentle breezes they dance in the wind. Movement in the wind is facilitated by the flattened stems of the leaflets; the leaflets move up and down perpendicular to the flattened side of the stem. The relatively large size of the thin, light-weight `ōlapa leaflets also facilitate "dancing." Flattened leaf stems also account for the "dancing" of quaking or trembling aspen (*Populus tremuloides*) on the Mainland. I especially enjoy watching `ōlapa leaflets "bounce" when hit by large drops of moisture falling from the upper canopy.

**A kāwa`u tree (right) adjacent to an a larger `ōhi`a lehua tree.** The kāwa`u trunks, with non-flaking bark and a paucity of epiphytic ferns, mosses, and liverworts, help distinguish kāwa`u from the much more abundant `ōhi`a lehua. Often in the forest near Kīlauea Iki, individuals of kāwa`u grow adjacent to an `ōhi`a lehua, probably getting started on the mosses and liverworts covering the spreading, slightly fluted trunk bases of `ōhi`a where seedlings of kāwa`u are now commonly seen. *Maybe establishment in this slightly elevated microsite, protected in some areas of the forest from pig rooting and trampling, accounts for the presence of scattered, large kāwa`u trees in "Kīlauea Forest"?* The large, scattered kāwa`u , growing at the base of `ōhi`a trees probably got established decades ago, before Himalayan ginger became a wall-to-wall understory in for rainforest at Kīlauea summit. Some of the kāwa`u in "Kīlauea Iki Forest" are as tall as the `ōhi`a lehua. *Maybe this can be explained by its relatively faster growth rate of kāwa`u?*

Kāwa`u treelet rapidly growing in a forest gap. Seedlings and saplings of this native tree species are often distinguished by a very straight, unbranched growth form, called treelets. The treelet growth form is common in continental tropical rainforest, possibly as an adaptation to reach greater light on the dark forest floor beneath several layers of overstory trees.



**Leaves of kāwa`u seedlings reveal its evolutionary origin.** Kāwa`u, also called Hawaiian holly, is a true holly (genus *Ilex*). *Ilex* species in continental ecosystems with large herbivorous mammals typically have leaf margins with spiny teeth. The leaves of saplings and mature trees of kāwa`u have smooth rather than spiny edges, presumably losing this defense against herbivory because of the evolution of this species in remote islands without herbivorous mammals. Note the intricate, anastomosing pattern of small veins between the lateral veins, depressed on the upper side and raised on the lower site. This pattern is helpful in recognizing

Kōlea lau nui. This important member of the secondary tree canopy can be recognized by its simple, alternate leaves, pronounced mid-vein and inconspicuous lateral veins. With its slightly folded leaves, it is the only tree species in the Hawaiian rainforest with the classical "drip tip" characteristic of many continental tropical rainforest trees. In addition, like many continental rainforest trees, it produces flowers and fruits close along its stems, a pattern you can see in this image, called cauliflory. These features makes sense for *Myrsine,* which is *a* pantropical genus. The ancestral species of *Myrsine* reaching Hawai`i probably came from the South

As you can see in the images below, without the "stompers and chompers" and without the dense, in many places wall-to-wall mats of Himalayan ginger, the normal resident species of the secondary canopy, `ōlapa, kāwa`u, and kōlea lay nui, are now thriving, regenerating with seedlings, saplings, and small trees, poised to find their place in the forest canopy below the emergent `ōhi`a lehua.

The impacts of feral animals and Himalayan ginger on establishment of the secondary tree canopy can be explained as a disruption of the natural successional process in wet forest The forest east of Kīlauea Iki, with a tree and tree fern canopy closing in, is transitioning from an early successional stage in which the understory is dominated by uluhe fern. At this stage of succession kōlea lau nui, `ōlapa, and kāwa`u, poking their way through gaps in the uluhe mat, should have been becoming more abundant, poised to grow above the tree fern subcanopy into the secondary tree canopy. However, this stage of natural rainforest succession was delayed for many decades by the impacts of feral animals and Himalayan ginger.

Another possible factor in the suppression of secondary canopy trees may have been the ability of hāpu`u tree ferns to survive and even spread in some areas, in spite of presence of feral ungulates and ginger; and to expand rapidly once control of these invasive species occurred. Mature tree ferns grew above the ginger and these long-lived plants persisted in spite of the wall-to-wall understory of ginger beneath them. Even when hāpu`u tree ferns fell, as they typically do, the resprouting fronds of fallen trunks of this shade-tolerant species resprouted up through the ginger canopy. The scattered patches of tightly packed, tall tree ferns in the Kīlauea Iki area clearly inhibit the establishment of secondary canopy trees. Once feral animals, and particularly ginger, were removed, it appears that hāpu`u tree ferns, already abundant, quickly recruited to expand and fill in the patches of tree fern subcanopy. Feral ungulates and ginger had suppressed and displaced other native understory plants, especially shrubs and herbaceous ferns,* *normally native species that might compete with hāpu`u tree ferns. In short, from a successional perspective, feral ungulates and Himalayan ginger, followed by the control of these species, may have increased the density of trees ferns and accelerated succession from the uluhe stage to the tree fern stage. DIETER REFERENCE FOR OLAA, PHILIP BURTON

The good news is that, all three of the secondary tree canopy species, `ōlapa, kōlea lau nui, and kāwa`u, are now regenerating prolifically in gaps in the tree fern canopy or where uluhe has been shaded out. Some of these young trees will make their way in the upper canopy below the emergent `ōhi`a. A few trees, fast growing `ōlapa and kāwa`u, have already poked through open tree fern subcanopy. Good work, Natural Resource Management!

Recovering `ōlapa and kāwa`u. These tree seedlings and saplings are recruiting through native `ohe grass in a well-lit gap in the tree fern subcanopy.

Here is a challenging question to answer about the composition of the secondary tree canopy in "Kīlauea Forest." Why did some kāwa`u, but not `ōlapa, and kōlea lau nui, manage to germinate, grow, and reach into the upper tree canopy, decades ago, while feral ungulates roamed the forest and Himalayan ginger was abundant, if not wall-to-wall? *Here is my ecospeculation. Maybe the close physical association of kāwa`u and `ōhi`a lehua can explain why kāwa`u are noticeably present in the secondary tree canopy in the forest near Kīlauea Iki. Kãwa`u seedlings and saplings, elevated on the raised, sloping trunk bases of `ōhi`a were protected to a degree from feral ungulates and exposed to greater light? It would be more complicated than that because `ōlapa and kōlea lau nui seedlings are also found in that microsite, although they rarely grow into trees starting from this site. Maybe `ōlapa and kōlea lau nui are preferentially grazed more or are vulnerable to trampling than kāwa`u? `Ōlapa does have that reputation with cattle.*

Secondary canopy tree species recovering in a gap in the tree fern subcanopy. Recruitment in this gap is dominated by seedlings and saplings of kōlea lau nui, with one noticeable individual of `ōlapa (left, rear).

`Ōlapa sapling recruiting inspiringly in a gap in the uluhe canopy. I acknowledge that this image may be redundant to illustrate this point, but please indulge my celebrating. With an opening in the tree fern subcanopy, there is greater amounts of available light penetrating to the forest floor and reduced amounts of leaf litter. Also, Don Drake, a Botany professor at UH Manoa and Linda Pratt, a Botanist with U.S.G.S. Biological Resources Division, now retired, found that falling tree ferns fronds significantly damaged and killed many tree seedlings. Greater light, less litter, and fewer injuries by falling fronds are conditions all found in gaps in the tree fern subcanopy. These conditions foster the germination and growth of native trees. Tree regeneration is sparse to absent under closed tree fern subcanopy.

**`Ōlapa growing through the tree fern canopy.** `Ōlapa is a relatively fast-growing tree species and ginger was removed from this area along the edge of the Escape Road near the Nāhuku Lava Tube, early on, around 1985. In addition, there is ample light available at this open site on the edge of the canopy gap over the road.

Kāwa`u topping the tree fern subcanopy. This image is from the forest on the east side of the road descending to the Park Research/Resource Management Center. This was the first ginger control area in the park, in 1980, just after fencing and pig removal. Wall-to-wall ginger plants were removed manually and mechanically, prior to development of an herbicidal technique. The other secondary canopy tree species, `Ōlapa and kōlea lau nui, are also growing through and above the tree fern subcanopy. Seedlings and saplings of all three species are abundant in well-light gaps in the tree ferns. *It will be interesting to see if the secondary canopy will eventually become closed, more typical of older rainforest.*

The Tree Fern Layer

Hāpu`u tree ferns in the genus *Cibotium* are signature life forms and ecological keystone species of Hawaiian rainforest. They can form a layer of the forest, beneath the `ōhi`a canopy and also below the secondary tree canopy of kāwa`u, `ōlapa and kōlea lau nui. The tree fern layer in young Park rainforest at Kīlauea summit is very strongly dominated by a single species of hāpu`u or hāpu`u pulu, *Cibotium glaucum,* the typically dominant species of tree fern in Hawaiian rainforest. In some areas of “Kīlauea Iki Forest” tree ferns have formed closed canopy patches; in other areas they grow open to very scattered. Closed tree ferns patches will persist and the areas of open or scattered tree fern canopy will eventually become closed in the forest at Kīlauea summit. This is suggested by the abundance of younger tree ferns in both closed and open areas, and by the fact that hāpu`u trees ferns are long-lived and shade-tolerant species. Don Drake and Dieter Mueller-Dombois, studying the succession of native trees and tree ferns in rainforest on Mauna Loa, found that the tree fern canopy became closed after about 400 years of succession on bare lava flows. Closing of the tree fern canopy will mostly likely happen more quickly in “Kīlauea Iki Forest” because of the relatively deep soil dominated by fine ash and sand particles. Hāpu`u tree ferns get a lot of attention in the following pages because of their interesting natural history and ecologically profound influence on Hawaiian rainforest.

Looking down on the hāpu`u tree fern subcanopy from the edge of a pit crater.

Underside of frond of hāpu`u pulu (*Cibotium glaucum).* This tree fern species can be distinguished from other species of of *Cibotium* by the whitish-green color of the underside of the frond blade. The underside of the blade is dull-green in other species of *Cibotium* in the Park.

**Closed subcanopy of Hāpu`u.** In places in "Kīlauea Forest," hāpu`u has formed a closed subcanopy beneath the `ōhi`a lehua, creating deep shade and a thick litter layer on the forest floor that inhibits the establishment of light-requiring rainforest plants. These properties make hāpu`u an ecological keystone species of the rainforest at Kīlauea summit.

(*left*) **Pulu-covered fiddleheads of hāpu`u pulu.** Hāpu`u pulu can be distinguished from the other large rainforest tree ferns by the copious soft reddish-brown hairs, pulu, on the fiddleheads, lower stipes, and buds along the sides of the tree fern trunks. All ferns have fiddleheads, the young frond tips resembling a violin scroll, which unfurl into new leafy fronds. This image was taken in "spring," when most fiddleheads emerge from the top of the hāpu`u trunk and then unfold in a synchronous fashion. After the new fronds emerge, some of the older fronds will turn brown and die. As they die that undoubtedly re-translocate nutrients from the dying frond back to the rest of the plant. Some neighbors in Volcano hack off hāpu`u pulu fronds after they start turning brown, while they are still re-translocating nutrients back to the rest of the plant. They wonder why the fronds get small over the years.

(*right)* **A trickle of summer fiddleheads.** This image was taken in August, a few months after the spring flush of expanding fiddleheads. This one caught my eye because there were two fiddleheads, rather than the usual solo fiddlehead, unfolding. Don Drake, tagging and following the unfolding and demise of individuals fronds, found that hāpu`u pulu fronds lived an average of 18 months; that implies that about one-half the fronds are replaced by new fronds each year.

(*left*) **Pulu-covered bud on the trunk of hāpu`u.** You can visualize and feel the outline of a fiddlehead under the dense coating of soft hairs on this small trunk bud. Pulu-covered trunk buds occur far more commonly on *Cibotium glaucum* which some naturalists call the "walking tree fern" because of its propensity to grow in a leaning fashion, fall over, and resprout from the apex of the trunk, and from trunk buds. The pulu covering of fiddleheads of hāpu`u and its close relatives was a mystery to me for many years; plants in dry environments are often cloaked with hairs to help maintain moisture. However, the trunk buds of hāpu`u are exposed for many years; a protective covering makes sense in this case. Most trunk buds you will see in the forest have not sprouted. MORE COMMON ON LEANING TREES, (PIC AT VHOUSE WALKWAY. NOT FOUND IN CIBOTUM CHAMIISSOI OR MENZIESII WHICH TEND TO STAMD STRAIGHT AND NOT FALL OVER. PIC OF

A trunk bud with some history. This is probably more typical of trunk buds which have copious amounts of pulu obscuring the outline of a cluster of several fiddleheads. However, this trunk bud cluster is also unusual in that the upper two fiddleheads in the cluster have apparently stopped growing or died, lost their pulu, and became a more stable susbstrate to allow moss to colonize

A sprouting trunk bud. Ignore the two large, dead stipe bases handing directly down and the upright one, all left of the sprouting trunk bud. This includes one small live upright frond and two dead, down-hanging dead stipes to the left and right. MIGHT HAVE GOOD SUBSTITUTES

Two, vigorously sprouting trunk buds. These are located on the left side of the trunk. Larger fronds are growing from the larger trunk bud above, beginning to form a separate trunk. These fronds are still smaller than those emerging from the top of the main trunk. Much smaller fronds have arisen from the smaller trunk bud lower and to the right of the trunk bud with the larger fronds.

Two-trunked hāpu`u pulu. Tree ferns with two or more major trunks are uncommon. Sprouting of trunk buds to create large secondary trunks seems to occur more in areas in which the crown is disturbed. This image was taken at Kīlauea Lodge in Volcano Village where the fronds are frequently removed. *Maybe disturbance such as the mass loss of fronds (and falling) stimulate the expansion of trunk buds.*

Cross section of a hāpu`u pulu trunk. The exterior is a mass of aerial roots, capable of absorbing moisture from the air. I have successfully transplanted tree ferns in even the driest weather but cutting through the trunk as above, placing it vertically in the ground, watering the exterior of the trunk. The interior pith is comprised of starch filled cells. The vascular tissue, conducting water ad nutrients, is the park edge of pith, where it meetings the roots mass on the periphery if the trynk. Introduced rats have started foraging the lower portion of the pith, used by Native Hawaiians as a starvation food.

Fallen hāpu`u pulu with sprouting trunk buds. This individual of the "walking tree fern" fell in the last two years. Two small fronds subsequently sprouted from existing trunk buds. The fiddleheads at the terminus of the trunk also sprouted.

Location of first upright tree fern

An, approximately 200 year old “walking tree fern” forming a horseshoe-shaped nurse log. My interpretation of the history of this tree fern individual is that it has fallen three time and grew back vertically from the former top of the upright tree fern and the end of the nurse logs that formed after falling. The first upright tree fern grew in the middle of the image, at the far end of the current nurse log. It then fell from left to right, and resprouted from the top of the fallen trunk. After about five decades of vertical growth it fell again to the forest floor, this time from right to left in the image. A now good-sized kāwa`u tree became established as a seedling on the nurse that was formed. After another four or five decades of upright growth at the center, front of the image, the tree fern fell yet again, this time from right to left. The upright trunk of the hāpu`u, growing from the is still standing. It would be cool if it fell to the right and closed the cumulative nurse log being created by this walking tree fern. Over several years Don Drake patiently measured the vertical growth of hāpu`u trunks in the Kīlauea summit area. Tree fern only grow at the apical ends, at the tip of the trunk where the fiddleheads emerge. Don inserted a nail at this point and established a fixed point on the ground. He regularly measured the distance between the two (sometimes science can be pretty non-esoteric). Don found that tree ferns grow slowly, about one and one-quarter inch per year or one foot per decade. Of course, if you are determining the age of this “walking tree fern” you need to include the length of the tree fern trunks lying on the forest floor.

Here is what happens to “walking tree ferns” in pig inhabited forests. This hāpu`u tree fern fell in a rainforest stand in Volcano Village not protected from feral pigs. The upper portion of the trunk has been plundered by these stompers and chompers for the starchy material in the core. What the pigs did not eat the rats consumed. The cortex or outer layer of the trunk is made up fibrous roots. Two live fronds are growing from a trunk bud near the base of the plant, probably protected by their height above the ground. Pigs tend to leave very large diameter tree ferns that fall to the forest floor.

**Hāpu`u `I`i (*Cibotium menziesii*).** Individuals of this species of *Cibotium* grow highly scattered among its first cousin or congener, hāpu`u, *Cibotium glaucum,* in the tree fern layer at Kīlauea Iki. Hāpu`u `i`i probably comprises less than one percent of the tall tree ferns in the rainforest there. Hāpu`u `i`i tends to be more abundant in older Park rainforest deep in Large Tract `Ōla`a. Here it is located at lower elevations, in areas with higher temperatures and more abundant rainfall. *Also, it may be more affected than hāpu`u by feral ungulates or invasive Himalayan ginger. Finally, it may be less abundant in younger rain and eventually become more abundant as the forest matures. For example, hāpu`u `i`i is relatively more common in the slightly older, probably 300 year old, and historically more protected forest at Niaulani, just outside the Park.*

**Hāpu`u (*Cibotium chamissoi*). (**I prefer a common name formerly used and no longer an official common name, Meu to distinguish it from *Cibotium glaucum*). I am still looking for this tree fern species in "Kīlauea Iki Forest." Like hāpu`u `i`i, it is also relatively abundant at wetter, warmer lower elevations in older Park rainforest within `Ōla`a Forest. *However, I speculate that disturbance by feral pigs and cattle may account for its apparent total absence at Kīlauea Iki, at the upper edge of its range.* Meu grows scattered in the forest at Niaulani behind the Volcano Art Center, near Kīlauea Iki. This forest was fenced and protected from feral ungulates for many decades. If you are hiking in the forest at Kīlauea Iki, keep your eye's out for a tree fern with these features: undersurface of blade light green (not white-green); stipes with golden hairs just at the base; and often a "skirt" of dead fronds dead fronds.

**Fiddlehead of hāpu`u `i`i.** One meaning of "`i`i" is reddish-brown. The reddish-brown scales or pulu at the base of the stipes are relatively soft to the touch. However, the shorter hairs higher on the stipe (center back) are rough to the touch, hence the alternate common name no longer in favor by the botanical powers-that-be, hāpu`u kāne, an, meaning male or man hāpu`u, maybe a reference to the bristly scales or pulu.

Four short tree species at Kīlauea Iki potentially grow within or often just above the tree fern layer: pilo (*Coprosma ochracea*), manono (*Kadua affinis*), alani (*Melicope clusiifolia*), and olomea (*Perrottetia sandwicensis*). Like the secondary tree canopy species, these tree species were disturbed by feral pigs and cattle and suppressed by Himalayan ginger. Now, with removal of feral ungulates and invasive ginger, seedlings, saplings, and even some small trees of the depleted tree fern layer species are now found in well-lit canopy gaps, often intermingled with young individuals of recruiting secondary canopy trees, \`ōlapa, kōlea lau nui, and kāwa\`u. Very scattered, mature individuals of pilo and manono can be found in the tree fern layer; these provide the seed source for the current cohort of recruiting seedlings, saplings, and young trees recruiting in gaps in the tree fern subcanopy. You would have to search more diligently to find the very uncommon occurring alani; you should celebrate your good fortune if you find the very rare olomea. In contrast, pilo is noticeably recruiting, with noticeable numbers of seedlings and saplings.

Alani (*Melicope clusiifolia*) (left) and pilo C*oprosma ochracea*) (right). Alani is scarce in the young forest at Kīlauea Iki. You can recognize it by the whorls of three to four leaves, attached at the same level on the stem, near the tips of the branches. The central vein on the underside of the leaf is dark red.

Pilo seedlings, saplings, and young trees are abundant, nearly as common as the secondary canopy tree species. You can recognize pilo by it opposite, flexible leaves. The leaf pairs are not aligned at 90^0 to the pair above and below. There is a tiny, triangular bract upwardly clasping the stems opposite each leaf pair.

(*below*) **Olomea (*Perrottetia sandwicensis*).** Only one small individual, about two feet tall, was found in the forest at Kīlauea Iki. This is a fairly common tree of the tree fern layer in older rain forest and historically protected young rainforest near the summit of Kīlauea. For example, olomea is fairly common in the forest at Niaulani. Olomea can be recognized by its simple, alternate leaves with red veins underneath. Māmaki often has red veins but dense, short hairs on the leaves make it feel "sandpapery."

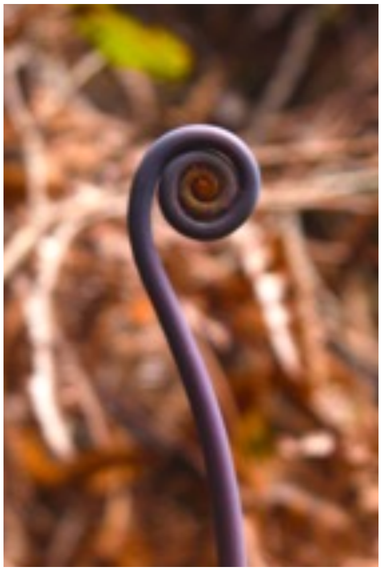
(*above*) **Manono (*Kadua affinis*).** Manono can be recognized by its leathery, simple opposite leaves, with each leaf pair attached at approximately 90^0 to the pair below and above. Manono is currently uncommon at Kīlauea Iki, However, this species is recovering well in other young rainforest at the Kīlauea summit after ginger removal. This response is anticipated at Kīlauea Iki and is suggested by the scattered seedlings there.

The Uluhe Layer

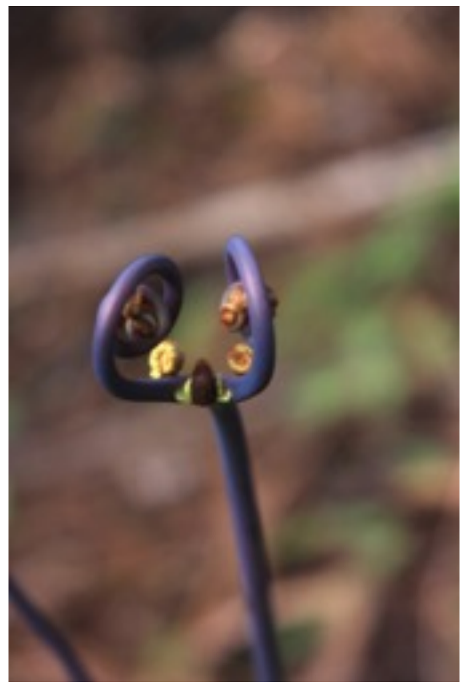
Uluhe fern is a thicket-forming, climbing fern, primarily of young rainforest in the Park; it is also a colonizer of canopy gaps left by \`ōhi\`a lehua dieback patches in older rainforest or disturbed or burned areas in young rainforest. Sometimes the tangles of uluhe, hanging on to the branches and trunks of \`ōhi\`a trees, can be more than 20 feet thick or form continuous blankets over hundreds of acres of rainforest. The thickets of uluhe must certainly compete with native plants, suppressing them or at least slowing down their establishment and growth. For these reasons, understandably, many people think uluhe is an invasive plant species. After all, this is what highly invasive plants do: they form dense patches that displace native vegetation and prevent their establishment. However, uluhe is native to Hawai\`i, and it has coevolved over the millennia with other native plant species in this environment. Its native character is confirmed by the fact that it was found and described by early European explorers and botanists, prior to the onslaught of invasive plants arriving in Hawai\`i. Also, this species is native to many other areas of the pantropical Pacific Basin, so it makes sense that it would be native to Hawai\`i. Another line of evidence is that, Native Hawaiians, utilizing native species for medicine, drank an infusion brewed from the fronds as a laxative. Finally, thickets of uluhe may be the bane of cross-country hikers in the rainforest, but this fern behaves in a perfectly understandable way, ecologically-speaking, for a native species. In young rainforest in the Park uluhe is an early successional colonizer, getting established shortly after `ōhi`a lehua, in open areas of lava flows or ash deposits. In older rainforest in the park it may fill in gaps left by naturally dying `ōhi`a. It also rapidly colonizes rainforest burned by wildfires. On older islands in the Hawaiian archipelago chain, it colonizes landslides and disturbed areas. Uluhe is eventually shaded out as the native tree and tree fern canopy closes in. It is replaced by other, later successional native species; not the other way around. Learn to love your uluhe, an

Mat of uluhe fern, climbing part way up `ōhi`a lehua trunks. Continuous thickets of uluhe like this are found where the tree and tree fern canopy is open, particularly on the edge of the Crater Rim Drive or the Escape Road where light is available from the large canopy gap created by the road. Uluhe is a light-demanding species, intolerant of shade. Uluhe mats are clones, spreading by shallowly buried, dichotomously branching rhizomes on the forest floor and above ground by dichotomously branching stems.

Relictual patch of dead uluhe. Small, decomposing patches are fairly common sights in the forest at Kīlauea Iki as the tree and tree fern canopy closes in and shades out the light-requiring, shade-intolerant uluhe.



(left) **Purple rachis and fiddlehead of uluhe arising from the shallowly rooted rhizomes on the forest floor.** This fiddlehead will very soon (below) expand into two lateral fiddleheads and a very small l fiddlehead in the center of the forking rachis.



(right) **Fiddlehead separating into three fiddleheads.** The two lateral fiddleheads of the dichotomously branching frond are expanding separately from each other. There is a very small fiddlehead at the base of the forking rachis, between the two expanding, lateral rachises. This central one will "rest" while the lateral ones expand and grow (below).

(*left*) **An expanding fiddlehead at the top of the main rachis and at the base of newly formed dichotomously branching rachises.** The smaller, "resting" fiddlehead described above is now expanding after the lateral branches expand to form leafy fronds. This central fiddlehead will also branch dichotomously, as will the lateral rachises. This dichotomous branching pattern is responsible for the English common name, "staghorn" fern. The growth of uluhe is characterized as "indeterminate." It keeps expanding dichotomously, with no predetermined fixed end point to growth. This is how uluhe can form such extensive mats. *ADD: DETERMINISTIC FOR SOME LATERAL SHOOTS SEE ANN RUSSELL PAPERS*

Uluhe starting to climb up a new host tree. Uluhe climbs differently from many climbing vines. It does not have tendrils that attach to the host, it does not twine or wrap around its host plant, and it does not root into its host. Instead, a new upward-growing or laterally-spreading shoots “reclines” on its host, in the fork of a tree or across lateral branches of the host plant. From there it can grow upward from its center rachis and laterally from the two spreading rachises. The uluhe in this image first grew vertically from the forest floor on the right side of this multi-trunked `ōhi`a lehua. A lateral rachis extended through the fork of the tree and reclined on its host. From there it can then grow upward and outward.

Uluhe climbing trees with forked trunks or low lateral branches. *I see uluhe frequently climbing trees which are forked and trees with lateral branches along the lower trunk. The second and third tree in the foreground, from left to right, are forked and support climbing uluhe. It tends not to climb trees with single trunks such as the first, fourth, and fifth trees.*

Uluhe climbing part way up a hāpu`u tree fern. Uluhe readily climbs up the trunk of tree ferns, if the tree fern canopy is open and there is available light. Uluhe can climb by reclining on adjacent vegetation and the downward angled and slowly decomposing frond stipes attached to the top of the trunk. Uluhe rarely climbs higher in tree ferns because its fronds cannot recline on the high-angled and short-lived frond stipes or main stems. Very occasionally you find uluhe tangles in the lower parts of hāpu`u fronds; in these cases, uluhe is climbing in adjacent `ōhi`a lehua trees and moving laterally into the tree fern blades.

Thin veneer of green blades over a thick mat of dead uluhe. There are typically up to three or four live uluhe fronds overtopping thick mats of dead but still attached dead fronds. These mats of dead fronds can be up to 10 (3 m) feet deep. Sometimes, climbing upon trees and tree ferns, uluhe thickets can ascend to 20-30 (6-9 m) feet or more. Dead uluhe decomposes very slowly, in spite of the rainy environment it inhabits. After two years, researchers found that more than 50% of the dead leaf mass and 77% of the dead stem mass was still present. One intuitive reason for slow compostability is that its tangles of dead fronds are elevated above the moist forest floor. Also, these slowly decomposing tangles of rachises and leaf blades also catch uluhe falling litter and hold it above the ground. The slow fern decomposition of uluhe and other ferns is under active investigation, looking mostly at plant compounds like lignin and tannins that would slow down microbial decomposition and levels of nutrients that would foster faster microbial decomposition. One researcher concluded that uluhe decomposes slowly because it has a high ratio of lignin to nitrogen. Another researcher found that uluhe is very efficient at translocating phosphorus from dying tissues back to living tissues. As a result, they concluded that litter tends to be nutrient poor with reduced phosphorus to encourage microbial decomposition. Slow decomposition in ferns is a complicated story.

Kōlea lau nui seedlings emerging through a uluhe mat. Native trees tend to emerge through the mats of uluhe, most noticeably in patches of decomposing uluhe litter without a covering of green uluhe fronds. Patches of uluhe without a veneer of live fronds are common in uluhe mats and can be rather large. *This results from the indeterminate, ever expanding and interconnected growth pattern of uluhe. Large dead patches, without a green veneer, may result from the death of a rachis near the ground level or the loss of a rhizome.*

Kōlea lau nui sapling penetrating a mat of decomposing uluhe litter on an uluhe mat climbing an `ōhi`a lehua tree.

`Ōlapa and kōlea lau nui saplings recruiting through small gaps and thin patches in uluhe on edge of uluhe mat. This is a transitional site, with an understory intermediate or transitional between closed tree fern subcanopy and continuous uluhe mats. The opening in the tree fern subcanopy provide enough light for the uluhe to persist *but the shade inhibits it from developing, thick continuous mats.*

You may wonder why uluhe has received so much attention in the field guide. The reason is that I have a newfound appreciation for uluhe, after observing this fern more closely in the forests at the summit of Kīlauea and reviewing research papers about its ecology: how it is able to colonize young, harsh volcanic environments, form thick, sprawling mats and climb trees, and why it is such an effective competitor with both native and invasive plants. Now, when I encounter tall, tangled mats of this fern, I am no longer just a frustrated cross-country hiker, wishing uluhe replaced instantly by a more diverse and navigable suite of later successional native plant species; I have become the respectful naturalist impressed by an ecologically powerful species.

Ann Russell, then a graduate student of Peter Vitousek and now an ecology professor at Iowa State University, investigated the ecology of uluhe in the early 1990s on young lava flows on Mauna Loa. Her research focused on traits of uluhe that made it such a successful species in these harsh volcanic landscapes. In most young rainforest environments, after initial establishment of an open canopy of small \`ōhi\`a lehua, uluhe is able to form a continuous mat over open, nearly barren lava after 100-150 years. These environments are challenging, with full exposure to the sun, extreme temperature differences from day to night, frequent drying of the thin, organic soils, and low nutrient content. She found that uluhe successfully competes with other native species for the more favorable microsites on recent lava flows, e.g., cracks in pāhoehoe, microsites on \`ā\`ā with smaller clinkers or inputs of organic matter from nearby forests. It then spreads vegetatively, on to the more harsh volcanic microsites, where other native species struggle to become established. Uluhe's branching, indeterminate, branching growth pattern allows it to spread in all directions indefinitely and cover volcanic surfaces well away from the favorable starting point microsites. These spreading mats of uluhe are highly efficient. On young lava flows on Mauna Loa they carried out 74% of the photosynthesis occurring there, even though they made up only 14% of the live biomass. Of course, at the Kīlauea summit area, uluhe became established in a much less harsh environment, in ash soil more effectively retaining moisture and nutrients.

Uluhe is such an effective competitor with other early successional species not only because of the spreading mats of live fronds but also because its litter decomposes very slowly. The combination of one to several layers of green fronds and the thick, mat of mostly attached, dead frond blades and rachises, severely blocks light from reaching the lava flow surface. Also, the mat of of slowly decomposing litter acts as a nutrient sink, depriving competing plant of inorganic nutrients.

Recent lava flows, with minimal organic matter, are nitrogen-poor and phosphorus-poor environments. Uluhe is highly efficient at taking up and/or utilizing small amount of nitrogen from the environment as well as storing nitrogen. Nitrogen use efficiency is measured by the amount of organic matter produced by the of nitrogen taken up. However, Ann Russell found that other native species on the recent lava flows were just as efficient in the nitrogen use. Phosphorus is also limiting in early successional sites. They found that uluhe has high phosphorus use efficiency, much higher than competing plant species on recent flows. With greater nutrient and moisture retention, uluhe probably colonized the Kīlauea summit area faster than young pāhoehoe.

Uluhe makes slow-going for a forest killer. Often at Kīlauea summit, small patches of Himalayan ginger can been seen surrounded by the lush growth of uluhe fern. I have not observed the full dynamic over time between these two ecologically powerful species. However, I suspect the ginger invaded a small dieback patch of uluhe but its vegetative

Uluhe indeed competes with native plants. In exclusion experiments, in which uluhe was hand-removed from sites, native `ōhi`a grew faster without it overburden of uluhe. In the Hawaiian environment, where invasive plants can be overwhelming threats to native plant communities, uluhe mats act as weed mat, keeping out invasive aliens. In the same exclusion experiments, non-natives tended to invade the cleared sites. The exclusion experiments were conducted on Mauna Loa, away from Himalayan ginger. Weed invasions at the summit of Kīlauea could be more consequential. Fortunately, the thick mat of live uluhe fronds and the underlying decomposing litter not only blocks light and hogs nutrients away from competing native plants, it also suppresses the invasion of non-native plants. For example, Himalayan ginger spread widely in the summit area of Kīlauea in tree fern dominated areas, forming wall-to-wall stands in some areas. Dense patches of uluhe probably helps control Himalayan ginger in other rainforest stands at the Kīlauea summit.

Young `ōhi`a trees growing within a matrix of dense uluhe at Sulphur Banks. I have never seen uluhe overtopping and shading out stands of native trees or shrubs. This makes sense from an evolutionary perspective for uluhe and `ōhi`a. These two species have worked out their obviously competitive relationship out over evolutionary time; they are both extant, competing but adapted to each other and coexisting. I suspect that this may have something to do with how uluhe climbs, that it is largely dependent on lateral branch to "lean" on, rather than forming roots or tendrils. This may allow narrow vertical shoots to grow up above the uluhe mat. The trees are up to six feet tall in this stand and the uluhe mat is slightly shorter. In the late 18th century forest in the background, the uluhe mat is much taller because the `ōhi`a is much taller. Steam vents are apparent in the upper left hand corner of the image. *However, I would speculate that the presence of `ōhi`a in this area, and other sites of the Sulphur Banks area reflects a cooling of the substrate in portions of the area.*

Earth crack mostly hidden by uluhe. I could not help myself in ending this section on uluhe fern by repeating I story I heard when I first arrived in Hawai`i in 1982. This involved a second hand experience with uluhe and earth cracks. One of the first people I met was a bird researcher, Peter Paton, who, over mai tai's, related a deep experience he had while conducting a bird census field study in uluhe dominated rainforest near the park while working for the U.S. Fish and Wildlife. He was by himself and following a flagged and minimally cleared transect. He did not see the crack because of the mat of uluhe hiding it, and plunged down at least 75 feet. This story had a happy ending. When he did not show up at that night, fellow workers and Park rangers, knowing which transect he was following, hiked this minimally cleared trail and found his raincoat fortuitously snagged at the top of the crack, even though they could not communicate with him. They went back to Park Headquarters, brought back a climbing rope, repelled deep into the crack, found Peter with just minor injuries, and retrieved him to the surface. This experience was career changing. Peter went to the Mainland and I like to think he became a life insurance agent.

The Shrub Layer

The recovery of native trees is heartening in the forest at Kīlauea Iki, the prolific seedlings, saplings, and small trees of `ōlapa, kāwa`u, kōlea lau nui, and pilo, as well as scattered hints of the recovery of manono and even alani. However, the recovery of native woody shrubs is just beginning and much more subtle to perceive. Only one species, `Ōhelo kau lā`au (*Vaccinium calycinum*), is relatively common. Most native shrub species that you find in less disturbed rainforest are uncommon, rare, or even absent at Kīlauea Iki. Delicate native woody shrubs suffered disproportionately at the hands (metaphorically, that is; actually from the mouths and feet) of the invasive chompers and stompers that roamed the early successional forest at Kīlauea Iki, abundant feral pigs and the small number of feral cattle. In addition to feral pigs and cattle, native woody shrubs were forced into competition for over four decades with a plant life form not present in the environment in which these native species evolved. That`s right: Himalayan ginger, a tall, dense, rhizome-forming invasive herb.

`Ilihia (*Cyrtandra platyphylla*). This is the most common of the uncommon native shrubs in the forest Kīlauea Iki. You can easily recognize it by its simple, opposite, heart-shaped leaves, cloaked with dense, long hairs. For these reasons, it is sometimes affectionately called "Hawaiian petting plant." It is also call ha`iwale, which means fragile, a good descriptor of this delicate shrub. The stems of `ilihia are brittle and readily broken by browsing pigs or cattle or simply by ungulates moving through the forest, falling tree fern fronds, or even by well-intended forest hikers.

**`Ilihia regenerating by under-ground roots.** Notice shorter shoots in the center of the image and a taller shoot to the left of the `ōhi`a lehua tree. The shorter shoots probably arose as sprouts from the shallow roots of the taller, shoots. Native shrubs evolved without mammalian browsers. Imagine a pig burrowing in the soil for earthworms and arthropods, easily damaging the spreading roots and precluding the most common methods of regeneration of this species. `Ilihia can now spread in the forest near Kīlauea Iki since the stompers and chompers and light-robbing, as well as the smothering ginger were removed from the forest.

Spreading colony of kanawao *(Broussiasia arguta*). Connected by roots just under the surface of the soil, the tall shoots in the center of the image are undoubtedly the parents of the younger, short, root sprouts in the foreground. Often these older individuals are 6-10 feet tall, absorbing light above the Himalayan ginger canopy; this may account for the persistence of kanawao during the ginger era. Kanawao is one of the most common and widespread native shrub in Hawaiian rainforests. However, it is uncommon in the disturbed rainforest at Kīlauea Iki. The root sprouting colonies of kanawao, genetically identical clones, can now expand because the forest has been liberated of pigs, cattle, and Himalayan ginger.

(*left*) **Terminal leaf whorl of kanawao.** Kanawao is also called Hawaiian hydrangea; it is in the Hydrangea family and its leaves, particularly the whorled arrangement near the stem tips, resemble those of the ornamental hydrangea. Fortunately, the flowers of Hawaiian hydrangea, not manipulated by plant breeders, do not have garrishly elaborate, brightly colored petals.

(right and above) **\`Ōhelo kau lā\`au (*Vaccinium calycinum*).** This is the rainforest species of \`ōhelo, in the same genus as \`ōhelo ai (*Vaccinium reticulatum)* found on recent lava flows and open scrublands or woodlands. \`Ōhelo kau lā\`au is currently the most common shrub in the young rainforest at Kīlauea Iki. It grows equally well as an epiphyte on \`ōhi\`a lehua or hāpu\`u, on nurse logs, or terrestrially from the soil. Its ability to grow on "platforms" may account for its persistence during the ungulate and ginger decades.

The short, ama`u (ama`uma`u) tree ferns (genus *Sadleria*) are important and expanding elements of the shrub layer in the rainforest at Kīlauea Iki. As short tree ferns with narrow trunks, particularly young ama`u tree ferns are readily killed by feral pigs who push them down and eat the starch-filled interiors of the trunk. Also, they compete for available light with Himalayan ginger because of their short stature. For these reasons, the ama`u tree fern populations were depleted and now are noticeably expanding after the Kīlauea Iki forest area was fenced and ungulates were removed and Himalayan was controlled.

**Ama`u (ama`uma`u) fern (*Sadleria pallida*), intermixed with the native shrub, iliahi.** This ama`u fern is much more abundant than its congener, *Sadleria cyatheoides*, in the rainforest understory. *Sadleria pallida r*eaches its highest densities in the partial shade of the forest understory with open hāpu`u tree fern canopy.

An individual of ama`u (*Sadleria cyatheoides*) under a large opening in the hāpu`u tree fern canopy. The very scattered individuals of this species of ama`u fern occur in more open sites with greater available light.

Translucent veins of ama`u fern, S*adleria pallida.*** These are revealed by backlighting the blades and viewing the bottom surface. This is the field diagnostic feature distinguishing this species of ama`u fern from ***Sadleria cyatheoides.*

Backlit, whitish, opaque bottom surface of the blade segments of a young S*adleria cyatheoides,* without translucent veins.

`Ōhā wai (*Clermontia parviflora*). This shrub species is often one of the most common in local rainforests. It is currently highly uncommon in the forest at Kīlauea Iki. It has potential to spread, especially since the most disruptive invasive animals and plants have been removed. Expect to find it growing epiphytically, especially on the trunks of tree ferns, on nurse logs, and terrestrially, from the soil. Unfortunately, for some reason, its ability to grow in protected microsites above the ungulates and ginger apparently did not protect it in the forest at Kīlauea Iki.

`Ie`ie (*Freycinetia arborea)* (left, image from Niaulani Forest) and ha`iwale (*Cyrtandra lysiosepala*) (right). I have been searching closely (and hopefully) for these two native woody species in the forest at Kīlauea Iki. I have not found a single individual of either species. They are found nearby in less disturbed rainforest in the summit area of Kīlauea. For example, are common in the forest at Niaulani. `Ie`ie can grow as a sprawling shrub on the forest floor or nurse logs. It can also climb by tendrils up the trunks of trees as in the image above. `Ie`ie has a reputation for being sensitive to cattle trampling and browsing. Feral cattle were reported to occur in the forest at Kīlauea Iki prior to fencing and ungulate control in 1980. Ha`iwale is well-named; it means fragile. Its brittle stems and roots are readily damaged by trampling or rooting ungulates.

VINES

Hawaiian rainforest lacks lianas that characterize many tropical rainforests. Lianas are climbing vines that grow up into and expand in the canopy. Common in continental tropical rainforest, lianas are rooted in the soil, climb tree trunks, and then spread in the tree canopy, sometimes from tree to tree. \`Ie\`ie, illustrated above, is the only native vine that sometimes climbs high on tree trunks. There are a few other vines in rainforest, spreading on the forest floor and climbing on the lower trunks of trees close. There are also a few species that cannot decide if they are vines or shrubs. In some cases they are upright shrubs and in other cases that spread horizontally. However, if you expand your concept of vines beyond plants with woody tissues, then you realize that Hawaiian rainforest has a very abundant and ecologically important vine, namely uluhe. This is a sprawling and climbing vine, in some ecological settings, of high biomass. It makes sense biogeographically that a fern is the most abundant vine in Hawaiian rainforest; dispersing by light spores to Hawai\`i, fern species are disproportionately represented in the Hawaiian flora, especially diverse in rainforest.

A Hawaiian "mintless mint" (*Stenogyne calaminthoides*) climbing up a tree trunk and sprawling on the forest floor. This native vine is more of an herbaceous plant than a woody plant. Like other Hawaiian mints, *Stenognyne calaminthoides,* has little minty taste or odor. Evolving without mammalian herbivores, many Hawaiian plants have lost their chemical defenses against herbivory. The chemicals responsible the minty odor and taste are thought to serve the function of minimizing herbivory. This species of "mintless mint" is locally common in some areas of "Kīlauea Iki Forest," particularly in pit craters and large cracks, where they were protected from feral pigs and cattle, and somewhat from Himalayan ginger.

Hoi kuahiwi (*Smilax melastomifolia*), a Hawaiian briar, climbing by means of tendrils and sprawling on the forest floor. Hoi kuahiwi is a "briarless" briar, without curved prickles to ward off mammalian herbivores. The prickles on briars in the genus *Smilax* in the southern USA are responsible for the theme in the Brer Rabbit stories about the horrors of being thrown in the briar patch.

An indecisive shrub/vine, manono (*Kadua centranthoides*). This woody plant is upright in the upper image and horizontal in the lower image. NEW PIC IN CAMERA

The Herb Layer

***Asplenium* sp.** This was the only individual of the only herbaceous fern species I found growing terrestrially (from the soil) on the open forest floor, formerly subject to disturbance by pigs, cattle, and deeply shaded by Himalayan ginger. This fern and other native herbaceous fern species were found in the Kīllauea summit area in protected habitats such as some pit craters, cracks, or lava tube openings. I do not offer a species name to this fern because I did not check out the pattern of sori on the on the underside of the blade. It is undoubtedly *Aplenium contiguum* or *Asplenium polyodon*.

The native herb layer in the young rainforest at Kīlauea Iki is nearly as disturbed and disappointing as the shrub layer. This makes sense in light of its history of disturbance by pigs and cattle and displacement by ginger. The herb layer in Hawaiian rainforest, made up of rather delicate herbaceous ferns and flowering herbaceous plants, grows on the forest floor, directly under the feet of browsing ungulates and below the canopy of Himalayan ginger. Native Hawaiian plants did not evolve in the presence of life form such as mammalian ungulates and tall herbaceous plants with dense clusters of rhizomes below. The impact of ungulates and invasive plants is suggested by a natural ungulate exclosure nearby, a large skylight for Kazamura Lava Tube, located in young rainforest of the 400 year old `Aila`au flows about two miles from Nāhuku Lava Tube. The bottom of the skylight is approximately 600 square feet and is protected from pigs and human disturbance by 30 foot vertical wall. It is largely free of Himalayan ginger which has decidedly colonized surrounding forest. In spite of its small size, this protected site supports over a dozen herbaceous fern species, two species of the native herb Peperomia, and pai`niu. The skylight provides a glimpse into the natural vegetation on the forest floor at Kīlauea summit before humans and their introductions arrived on the scene. Herbaceous ferns and ala ala wainui are now strikingly absent from the forest floor of the rainforest at Kīlauea summit.

`Ala`ala wainui *(Peperomia hypoleuca*). This is one of the most abundant broadleaf herbs in less disturbed rainforest in the Park. So far, at the Kīlauea summit I have seen just one tiny patch on a nurse log (right), small patches along the trail to the lava tube, and one extensive patch, six feet across, on the forest floor. Below, I show you photos of extensive patches of *Peperomia* found in a forested pit crater historically protected from ungulates. The six foot patch was found in “Kīlauea Iki Forest” very close to the margin of that pit crater. The proximity of the six foot patch to a seed source inside the adjacent forested pit crater, along with the fact that its habitat is now protected from ungulates and weeds, explain its presence in this site. Its presence is a good sign for the future recovery of this species throughout “Kīlauea Iki Forest.”

**Pa`iniu (*Astelia menziesiana*).** One of the four native lily species in the native Hawaiian flora, this tall herb is spreading slowly spreading mostly from underground rhizomes. It is rather shade-tolerant and was able to persist as very scattered plants under the ginger canopy. However, Pa`iniu seems to be most abundant in sites with an open tree fern canopy.

`Uki (*Machaerina angustifolia*). Very scattered individuals of this large, light-loving native sedge are found in areas with well-lit gaps in the canopy.

Wāwae`iole (*Lycopodiella cernua*). You occasionally find this clubmoss growing in well-lit gaps, often with uluhe fern (dead uluhe in background.)

**A single shoot of `ohe, with leaves nearly at 90$^0$ to the stem.** `Ohe is the only native grass found in the Park rainforests. This light-requiring species is probably becoming less abundant in the forest at Kīlauea Iki as the tree fern canopy closes in.

roadside gaps with Dubautia and mix.

THE “UPSIDE DOWN” RAINFOREST

Undisturbed Hawaiian rainforest has been characterized by some naturalists in Hawai`i as the “upside down rainforest.” It deserves this catchy descriptor because its greatest biological diversity resides in the understory, near or on the forest floor, rather than in the tree canopy. In contrast, mature rainforests in the tropics, for example in South America, Southeast Asia, Australia, and Africa, typically have high biodiversity in the several layers of the tree canopy, with many tree species, each represented by widely scattered individuals. The high diversity of trees in the canopy in turn supports a great diversity of epiphytic plants, vines, birds, invertebrates, and even mammals. Probably because of the deep shade created by multiple layers of trees, there is lower diversity in the understory in continental tropical rain forests.

In contrast, greater biodiversity in undisturbed Hawaiian rainforests naturally resides on the forest floor. Hawaiian rainforests have a very simple tree canopy. The tallest forest canopy is typically made up of emergent, typically mondominant `ōhi`a lehua trees. In a few locations in Hawaiian rainforest, although not the rainforest at Kīlauea summit, there are also koa trees in the upper tree canopy. In all but the youngest rainforest dominated by uluhe fern in the understory, the secondary canopy of trees is a little more complex but still simple, characterized by `ōlapa, kōlea lau, and kāwa`u. We discussed above how the secondary canopy in “Kīlauea Iki Forest” is recovering, with abundant seedlings, saplings, and small trees, now that feral pigs and cattle, and Himalayan ginger have been controlled. The tree fern layer is simple with just a handful of tree fern and tree species. The shrub layer is dominated by just a few species although these are relatively abundant in undisturbed rainforest. The greatest plant diversity in undisturbed Hawaiian rainforest resides in native herbs and particularly ferns on or near the forest floor, in its lowest understory layers, in particularly if native ferns, and herbs, and epiphytic ferns, mosses, and liverworts on the lower trunks of trees or on nurse logs.

PICS FROM NIAULANI AND PIT CRATER SHOWING LAYERS,ESP SHRUB and fern AND HERB

Notice that I qualified my reference to Hawaiian rainforest above by referring to "undisturbed Hawaiian rainforest." The vegetation of the forest floor is potentially the most impacted by feral ungulates and invasive plants. Rainforest at the summit of Kīlauea was highly disturbed, by feral pigs and a few feral cattle, digging up soil and trampling and foraging on native vegetation. Highly invasive Himalayan ginger formed wall-to-wall stands in much of the forest at the summit of Kīlauea, displacing native understory plants. As a result, the understory of the disturbed young rainforest at Kilauea summit is highly impoverished, as illustrated by the images below. Native shrubs occur in very widely scattered small colonies. Native herbs are represented by just small patches of pa`iniu, `uki, and `ohe and one known six foot diameter patch of native `ala`ala wainui. Forest floor herbaceous ferns are virtually absent. Now that ungulates have been removed and Himalayan ginger is controlled in many areas, Park Resource Managers have started inoculating "Kīlauea Iki Forest" with species that have become rare or lost. These plantings are typically introduced in cluster and will serve as a seed source for the spread of these species.

FOREST FLOOR PLANTS IN PROTECTED HABITATS

The deleterious effects of feral pigs and cattle on the understory of the rainforest at Kīlauea summit is demonstrated dramatically by comparing the shrub and forest floor herbaceous layers in areas disturbed by stompers and chompers and areas naturally protected from grazers/browsers. Typically the protected areas will have noticeably higher diversity and dramatically higher cover of native shrubs and forest-floor broadleaf herbs and herbaceous ferns. The protected areas include forested pit craters and collapsed portions of lava tube caves—both inaccessible to ungulates because of their steep walls. Characteristically, there are also very few invasive plant species in these protected area, even Himalyan ginger, suggesting that disturbance by ungulate smay facilitate their establishment. Protected areas provide a model of a relatively intact plant community, a reference community, for resource managers in the restoration efforts; they certainly elicit hope and inspiration to resource managers. From the plethora of images below you can see that I really enjoy these areas. My apologies, but I cannot provide directions to navigating to these precious, fragile, and hazardous areas. However, you can find many of the species portrayed below on the trail to Nāhuku Lava Tube. These species persisted here because of the high density of human traffic for many decades inhibiting disturbance by feral ungulates and because of the inaccessible moist cliff faces at the cave entrance.

Ilihia (*Cyrtandra platyphylla*) with two kinds of forest floor herbs beneath them. Ilihia is the most common native shrub in the protected areas and is far more abundant here than on the forest floor "topside." In my favorite, secret protected area at the summit, ilihia typically has an understory of the mostly herbaceous native vine, *Stenogyne calaminthoides*, an herbaceous vine, or dense mats of \`ala\`alawainui, both of which are abundant in this special site. It is inspiring to see both the shrub layer and a forest floor herbaceous layer together.

Kāmakahala (*Labordia hedyomisifolia*). I found just one plant , less than a foot tall, of this subshrub (just woody at the base). This was in my favorite protected area at Kīlauea summit. The exposed underside of the leaf is appropriately overexposed; it was whitish-green.

`Oali (*Pteris cretica*). I found this species only on a moist cliff face in a protected area, and in rocky sites along trails.

Asplenium contiguum growing from soil in a pit crater.

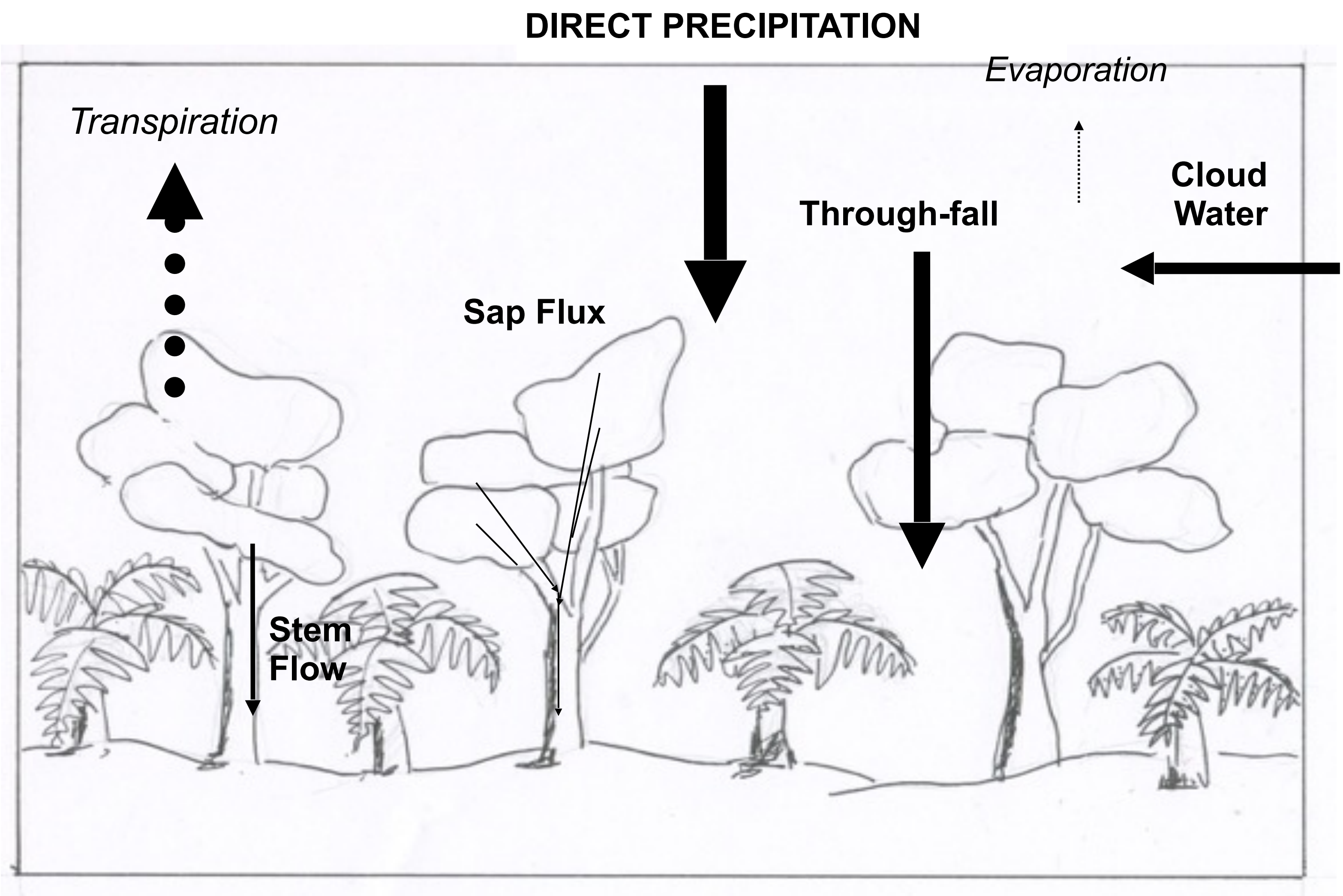
Ho`i`o Kula (*Cyclosorus sandwicensis*) is one of the five native fern species I found in protected areas that I have not seen in Kīlauea summit areas protected from ungulate disturbance starting in 1980.

Ho`i`o (*Diplazium sandwichianum*). Ho`i`o is often the most abundant fern on the forest floor of undisturbed or restored rain forest. Some of the larger individuals have a short, woody trunk.

`I`i (*Dryopteris fusco-atra*). I have never never seenw `i`i in the rest of the Kīlauea

RAIN IN THE RAINFOREST

Preliminary research by climatologists at a field site near Nāhuku Lave Tube suggests that about one-third of the moisture reaching plant tissues in young rainforest at Kīlauea summit is derived from cloud interception or fog. More refined measurements are being taken and evaluated.



Conceptual model of rain forest precipitation. Cloud water is horizontally moving clouds or fog, intercepted by the canopy, which also to some degree condenses water vapor. Cloud water is very important in the precipitation budget of the Hawaiian rainforest. Most water reaching plant tissues is from direct precipitation. The rainforest east of Kīlauea Iki Crater and north of Nāhuku average about 100-120 inches of direct precipitation per year, as measured near ground level in open areas, away from trees. Some of this rain gets hung up in the canopy and evaporates. Some rain falls to the forest floor as “through fall” or descends the surface of vegetation as “stem flow.” A very small amount is absorbed by leaves through their stomata and enters the vascular

A misty day in the rainforest at Kīlauea summit. As a resident of the adjacent community of Volcano, just east of "Kīlauea Forest," I know that foggy days at the summit are fairly frequent events. Also, as a Biologist I know that cloud water contributes a fair amount of the moisture to the summit rainforest. However, I am not sure I would call the forest at Kīlauea summit a "cloud forest." Part of the problem of deciding if "Kīlauea Forest" is a cloud forest is that there is no standardized and certainly no quantitative definition of a "cloud forest." Since I am free to make up my own definition, I will follow my mental images of cloud forest that contains a greater abundance, a luxuriance of epiphytes.

Another cloud forest day.

Forest mist in the early morning.

EPIPHYTES

In spite of living and botanizing in Hawai`i for over 30 years, I am still fascinated by the abundance and diversity of epiphytes in Hawaiian rainforest, as you will infer from the plethora of images below. This persistent intrigue might have something to do with first learning native plants in the oak woodlands of the dry, coast range of California, where about the only epiphytes I would see were lichens and occasionally small patches of mosses in moist areas on tree trunks. I will admit that I was not totally unfamiliar with rainforest and epiphytes before moving to Hawai`i in 1982. I spent 3-5 months each summer in the 1970's hiking the trails of the lowland temperate rainforest in North Cascades National Park as a Backcountry Ranger. I particularly enjoyed the abundance of mosses, covering the trees, drooping from branches, and coating the forest floor. But, I did not know what I was missing until I transferred to Hawai`i Volcanoes National Park and became acquainted with Hawaiian rainforest. Rainforests in Hawai`i not only have an abundance of mosses and leafy liverworts on the trunks of trees and tree ferns but also a rich epiphytic flora of ferns as well as shrubs and trees. The rich range of epiphytic life-forms is illustrated in the two images below. The abundance of ferns and especially woody plant epiphytes help distinguish tropical rainforest, including Hawaiian rainforest, from temperate rainforest.

Hemiepiphytes

A host hāpu`u with woody plant epiphytes, including seedlings of `ōlapa, kāwa`u, `ōhi`a, and `ōhelo kau la`au. These native trees and shrubs germinated in a matrix of mosses and leafy liverworts.

Hoe a Maui (Maui's paddle) (*Elaphoglossum crassifolium*) growing epiphytically on an `ōhi`a tree in a matrix mostly of mosses and leafy liverworts, along with a small patch of filmy ferns.

Epiphytes are plants growing on other plants; “epi" and “phyte” are the Greek roots for “upon,” and “plant.” The most common question I am asked about epiphytes is this: “Do epiphytes harm their hosts; are they parasitic”? Epiphytes are not parasites; their roots anchor them to their host plants but do not penetrate the tissues of their hosts to extract water and nutrients. They do indirectly utilize nutrients from their hosts. Nutrients are leached from the outer bark or surface of their hosts and washed down to the roots of the epiphyte by stem flow. In this way, epiphytes also take advantage of the nutrients from not only the host tree but also organic litter deposited on the host, from adjacent trees.

The host plants for epiphytes serve as light-rich platforms above the deeply shaded rainforest floor, the latter often covered with thick mats of leaf and branch litter. Very low light levels and mats of organic litter, plus the hazards of falling tree fern fronds, present a challenging environment for terrestrial (from the soil) plant establishment and growth.

The abundance of epiphytes in Hawaiian rainforest can be explained by the abundance of moisture in this environment. Epiphytes grow on a relatively poor surface for retaining moisture, the bark of a tree or the dense mass of tiny aerial roots that make up the surface of tree ferns. However, moisture in the Hawaiian windward rainforest environment, supplied by nearly daily trade wind showers, cloud interception, is not limiting. There are near daily trade wind showers, occasional heavy rains in the winter and summer tropical storms in the summer, as well as frequent episodes of cloud water.

**\`Ōlapa getting started as an epiphyte on its favorite host, \`ōhi\`a.** \`Ōlapa is a highly successful epiphyte in Hawaiian rainforest. It frequently becomes established (*left*) in the fork of \`ōhi\`a trunks on small compost piles of moisture retaining and nutrient-rich leaf litter. This microsite is also well-watered by stem flow descending from multiple trunks. The “groove” on the \`ōhi\`a host (*right*) probably receives or retains significant stem flow, as suggested by the presence of the moss. Note the single, thin aerial roots descending within the groove. Although it is out of the image, you can take my word that it reached the ground and penetrates the soil. Aerial roots reaching down to the soil and mining the nutrients and steady supply of moisture there also account for why \`ōlapa is such as successful epiphyte in Hawaiian rainforest.

(*left*) **`Ōlapa tree with aerial roots on an `ōhi`a**.” This `ōlapa became established in the fork of a host `ōhi`a. Almost all of the larger, epiphytic `ōlapa in “Kīlauea Forest” are growing on `ōhi`a, a stable and very long-lived host. Note that this `ōlapa epiphyte has several aerial roots, descending on the surface of the host to penetrate the soil and mine the richer nutrient and consistent moisture supply from this source. The aerial roots penetrating the soil account for why `ōlapa can grow into relatively large trees on their `ōhi`a hosts. Only two species in Hawaiian rainforest consistently produce aerial roots, `ōlapa and `ōhi`a, and become large trees on their hosts. Trees producing aerial roots that reach down into the soil are called “hemi-epiphytes.” I have observed hemiepiphytes only in tropical rainforest, not temperate rainforest. Yes, Hawaiian rainforest is tropical rainforest. The flagging tape on one of the aerial roots marks the corner of a permanent vegetation plant established by the Park’s Resource Managers to monitor the recovery of native vegetation after the removal of invasive species.

`Ōlapa seedlings with bent stems epiphytic on hāpu`u. `Ōlapa seedlings are common on hāpu`u hosts at Kīlauea summit. Notice how the stems of the epiphytic `olapa seedlings below are also curved at the base. This happens early in the growth of the `ōlapa seedlings, as can be seen in the seedlings in the image to the left. I will offer an explanation, based on the governing principle that seedlings grow toward the light. *The surface of hāpu`u trunks is cluttered with the bases of old fronds broken at near the base, aerial roots, and sometimes mats of pulu hairs. These block light so maybe the best strategy for the `ōlapa seed is to grow laterally away from the hāpu`u trunk to reach light; once at a distance from the trunk they grow up toward the light. SUBSTITUTE PIC FROM SANFORDS OR OLAPA FROM LEAF BASE*

Two small `ōlapa trees epiphytic on hāpu`u and with aerial roots. Ōlapa this size on hāpu`u usually send down aerial roots to the ground. The aerial root of the `ōlapa is apparent in the image on the left. There was an aerial root apparent in the individual on the right, just below the `ōlapa stem but embedded in the root fibers of the tree fern trunk. However, I did not trace the aerial root to the soil because I did not want to excavate the fibrous trunk roots of the host hāpu`u. It's a national park; you can take pictures and leave footprints but do not excavate tree fern trunks. There are some of the largest epiphytic `ōlapa I have seen on a tree fern substrate (maybe a better term than "host"?) Both occur near the edge of Crater Rim Drive near the lava tube.

Aerial Root

Host hāpu`u.

Large `ōlapa epiphyte on hāpu`u host. This is the only large `ōlapa tree I have seen in "Kīlauea Forest" with an obvious history of starting life as an epiphyte and not supported by adjacent trees or tree ferns.

Large `ōlapa epiphytic on hāpu`u but supported by adjacent `ōhi`a trees. I took this photograph in Volcano Village outside the Park. The dangling roots are from planted Monstera epiphytes.NEED PIC FROM MAILE LANE.

ohia aerial roots, on hapuu, prop roots, reason they are quite successful starting on tree fersn. stress roots. roots on surface of ground, stress roots, extra roots on itself. aerial roots of chia on chia (try Rohner Lane)

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OHIA EPIPYTICS ON OHIA, SEEDLINGS IN FORK AND TALLER TREE WITH AERIAL ROOT FROM OUTSIDE FOREST.

**Kāwa`u acting as a hemi-epiphyte.** `Ōhi`a and `ōlapa are the champion hemi-epiphytes of the Hawaiian rainforest. However, in hiking mindfully through "Kīlauea Forest" I found some aerial roots with slightly different bark from `ōlapa. Looking up into the host `ōhi`a, perched in the typical fork of the tree, was a kāwa`u, extending a narrow aerial root down to and penetrating the soil. Looking more closely from then on, I found several trees acting hemi-epiphytically. The easiest one to see at the summit of Kīlauea is about 50 feet down the trail from the lava tube to the bottom of Kīlauea Iki, on backside of an `ōhi`a host, rooted right next to the right (north) side of the trail. I have never heard of or read about kāwa`u acting act a hemi-epiphyte. Making a new discovery is a satisfying reward for carefully walking and observing in the forest.

Facultative Epiphytes

One of the most unusual features of Hawaiian rainforest epiphytes is that many of the larger species of epiphytes—trees, shrubs, and herbs—are not specialists in the epiphytic way of life, dependent on a tree or tree fern host substrate; they also readily grow "terrestrially," that is, from the soil on the forest floor. Epiphytes in continental tropical rainforest tend to be specialists, growing just as epiphytes. You could call them obligate epiphytes. The three tree species above, kāwa`u, and especially `ōhi`a and `ōlapa, grow from the soil and as epiphytes. Pictured below, the shrub, `ōhelo kau lā`au (*Vaccinium calycinum*), and herb, pa`iniu (*Astelia menziesiana*) usually grow terrestrially but also as epiphytes. You could label them as facultative epiphytes. *I can think of a couple of reasons for the versatility of many Hawaiian epiphytes. Very few plant species were dispersed to the Hawaiian Islands, the most isolated archipelago on Planet Earth. These numbers did not include the epiphytic specialists found in continental tropical rainforest. Also, the paucity of species established in Hawai`i provided ecological opportunities for the few Hawaiian plants that did successfully arrive and evolve in the Islands. Opportunities were available to thrive as plants growing from the soil or as epiphytes. Ferns, mosses, and leafy liverworts tend of be substrate specialists, either growing terrestrially or on tree and tree fern*

The shrub `ōhelo kau lā`au, established on an `ōhi`a host. This is the Hawaiian rainforest "huckleberry" (same genus as Mainland huckleberries).

`Ōhelo kau lā`au growing terrestrially. Soil is a more common substrate for `Ōhelo kau lã`au.

Pa`iniu, growing as an epiphyte among filmy ferns on a hāpu`u "host," that is, platform.

Pa`iniu in its more typical habitat on the forest floor.

`Ōhā wai (`Ōhā) (*Clermontia parviflora*) growing as an epiphyte. Almost all individuals of this species grow terrestrially.

Ilihia (*Cyrtandra platyphylla*) growing epiphytical on hāpu`u. This is the only individual of this species I have seen not growing from the soil.

retake photo to show soil

Ferns

Filmy ferns are among the most abundant epiphytes in Hawaiian rainforest, including "Kīlauea Forest." This is in terms of biomass, not species diversity. So far, I have found only two species of filmy ferns in the summit rainforest at Kīlauea, Palai hinahina (*Hymenophyllum lanceolatum)* and ōhi`a kū (*Hymenophyllum recurvum*). The fronds of ferns in this family are just one cell layer thick. As a result, their shiny fronds are somewhat translucent, hence the term "filmy." Physiologically, filmy ferns are similar physiologically to mosses and leafy liverworts in their response to moisture changes and ability to tolerate dessication. When dry conditions prevail, their fronds lose moisture and filmy ferns become physiologically inactive. When wet conditions return, they readily absorb moist and within minutes become physiologically active again. It is not surprising that filmy ferns are very similar in size and morphology to mosses and leafy liverworts.

Palai hinahina *(above and right)* is by far the most abundant filmy fern in Park rainforest. In the "Kīlauea Forest" it typically grows in the most moist sites for epiphytes, such as the bottom of `ōhi`a tree trunks (*right*) or in major major forks. It can be distinguished by its smaller size and sparse hairs

Ōhi`a kū *(above and left)* is less common than palai hinahina. It is larger and hairless.

A common scene at "Kīlauea Forest" in 2014, when this photo was taken: large patches of dead filmy fern fronds, especially palai hinahina, following extended periods of dry weather in the previous years. The dead fronds should be distinguished from dry, dormant, but alive and green filmy ferns fronds. The rainforest at the summit of Kīlauea is located on the drier margin of rainfall so may be more vulnerable to the impacts of drought.

**Live `ōhi`a kū on the more moist side of a leaning hāpu`u,** receiving direct through-fall precipitation. Dormant or dead fronds of palai hinahina grow on the drier, "leeward" side of the hāpu`u trunk. Note that the lower stem of the `ōlapa seedling is characteristically curved as discussed above.

Dry, physiologically dormant filmy fern (top), moss (middle), and leafy liverwort (bottom), during a four week drought. The leaves of filmy ferns, mosses, and leafy liverworts are just one cell layer thick, and respond similarly to moisture changes. When living in rainforest environments with nearly constant moisture, they are usually moist and physiologically active. During periods of dry weather, they readily lose moisture and become physiologically dormant. You can detect dry weather induced dormancy because mosses and leafy liverworts fold their leaves together so that the branches contract. Filmy fern fronds lose their shiny, moist appearance and curl downward. All of these species readily absorb moisture over their entire leaf surfaces, as well as from roots, and become physiologically active again when the near-daily rains resume.

A small patch of filmy fern fronds surviving the dry spells of weather, 2010-13. In this image taken August, 2014, almost all of the surface of the larger `ōhi`a trunk is covered by brown, dead palai hinahina fronds. Note the small patch of green, surviving filmy fern fronds below the `ōlapa seedlings in the center of the image. *The surviving patch is located in probably the moist microsite on the trunk of this tree. The presence of the tree seedlings suggest that there is a relatively constant supply of moisture in this microsite. This area is exerted from the trunk, nearly level, so it receives an additional soaking from water flowing down the stem and then accumulating laterally. It is not visible in this image, but in most forks with `ōlapa, leaf liter accumulates, creating a moist compost pile. Finally, this level sites most likely intercepts some direct vertical through-fall rain penetrating the canopy.*

Recovering filmy ferns

Just starting to recover palai hinahina. This image was taken in September, 2014. I did not notice the subtle handful of live fronds resprouting in the center of this image until I was searching my photo library in 2016 for an example of recovering filmy ferns. The rhizomes of palai hinahina run beneath the mat of dead and live fronds, on the surface *of the bark of the host substrate. We can infer that a portion of the rhizomes apparently survived.* I *would guess that this knob, projecting from the rest of the tree trunk is the moist microsite visible in this image for the same reasons the fork microsite in the image above is. It may not be as wet, as suggested by the fact that a patch of fronds survived the drought in the fork above but not on the knob.*

My favorite epiphytes in the young rainforest are what I will call the "regular herbaceous ferns." This distinguishes them from tree ferns and from the filmy ferns. These tend to be epiphyte specialists, rarely growing terrestrially. The filmy ferns are much more abundant. However, I am aesthetically drawn to the "regular herbaceous ferns." I suspect because they have diverse shapes and forms, because they project out from the matrix of the more abundant mosses, liverworts, and filmy ferns, and maybe because they are distinctly uncommon in the rainforest at the summit of Kīlauea.

(*above)* Wahine noho mauna (literally: "woman living on the mountain") (*Adenophorus tamariscinus*). It is a treat to occasionally find this delicate and intricate epiphytic fern. *(below)* Tiny frond emerging from blanket of leafy liverworts.

Kolokolo (=wandering) (*Adenophorus tenellus*). To the uninitiated, this fern looks like a grass. However, look carefully on the underside of the fronds and you will see roundish sori, cluster of spore producing structures called sporangia. This may be the most dense cluster of kolokolo I have ever seen.

I can only speculate about the reasons they are relatively uncommon. The diversity and abundance of epiphytic ferns minimally affected by the presence of feral pigs prior to 1980 because of their safe location on tree trunks. Dense patches of Himalayan ginger undoubtedly suppressed herbaceous fern establishment at the lower tree trunks. *This is an optimal habitat for many epiphytes because of the slow diameter growth of the lower trunks and consequent reduced sloughing off of bark, providing a more stable substrate for epiphytic plants. In addition, the lower portions of the main tree trunks often receive additional inputs of moisture. The trunk bases tend to be sloped rather than vertical. They therefore receive not only the flow of moisture down the trunk (stem flow) but through-fall from direct precipitation and cloud interception. Maybe the fact that the rainforest at the Kīlauea summit lies on the drier edge of the ecological range of Hawaiian rainforest may limit the success of regular herbaceous fern to become established.*

Pai (*Adenophorus hymenophylloides*). Although regular herbaceous, epiphytic ferns are uncommon in "Kīlauea Forest," pai is the most commonly encountered species. Maybe this is perceptual bias on my part; at least it is more common here than any other location I have explored in Hawaiian rainforest.

(*left*) **Māku`e (*Elaphoglossum paleaceum)*** growing as it typically does on the trunk of an `ōhia among a matrix of filmy ferns. (*above*) Mākue growing from soil in a site historically protected from pigs and cattle. I have seen mākue growing terrestrially more frequently than any of the other typically epiphytic ferns.

(*above)* **Hoe a Maui (= Maui's paddle) (*Elaphoglossum crassifolium*).** Species in this genus are often called tongue ferns because of their shape (*glossum* = tongue). The dark color on the backlit fern in the center of the image are remnants of the spore-producing sporangia that covered the underside of the frond base. (*below*) More typical view.

A medley of epiphytic ferns including a matrix of the filmy fern,`ōhi`a kū, along with "regular herbaceous ferns," mākue above and kolokolo below.

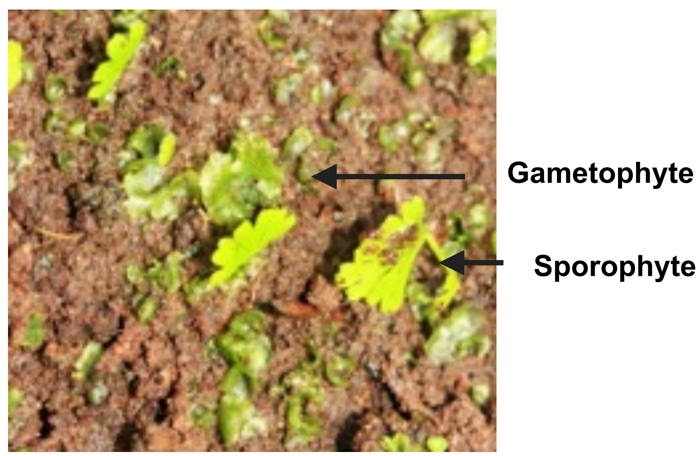
(*right*) **Moa or whisk fern (*Psilotum complanatum*).** This fern-relative is sometimes seen growing epiphytical on tree ferns or less commonly on `ōhi`a in rainforest. They are characterized by flattened, arching, downward-bending stems. The globular structures arranged in two rows along the margins of the flattened stems produce spores. Wisk ferns are distant relatives of the ferns and traditionally called fern "allies." They reproduce in the same way that ferns do, with two life stages, a spore producing sporophyte stage (pictured here) and a tiny, short-lived and rarely seen gamete producing or gametophyte stage. See the description of fern reproduction below.

Ferns are dispersed by wind-borne spores, which is one reason fern species are so well represented in the native flora of Hawai`i. Carried in the jet stream from Southeast Asia during the winter months or transported aloft in tropical storms during the summer from the southern hemisphere, lightweight fern spores ferns could arrive in a few days. Ferns spores are produced in most fern species on the lower surface of the frond blade. But, reproduction is ferns is more complicated that spore production. The spores germinate into tiny, cryptic, and flattened leaf -like structure called gametophytes that, not surprisingly, produce gametes, sperm and eggs. These unite happily and produce the spore-producing ferns, frond-bearing ferns we are familiar with, of course called sporophytes (you knew that the Greek root "phyte" means plant).

Māku`e lau li`i (*Oreogrammitis hookeri*). The sori in this species are classically rounded and located in two parallel rows on the underside of the frond.

Linear sori on the undersurface of ama`u fern.

Dispersed sporangia in mākue. Note the specialized slender upright frond in the center of the image. The dark surface of the frond results from the dense, even cover of minute spore-producing sporangia. Most ferns have sporangia organized in distinct, distinctively shaded sori, located on the underside of all the fronds. The sporangia in some ferns like mākue cover the entire lower surface of specialized fronds.



Tiny fronds of spore-producing stage (sporophytes) emerging from the gamete-producing stage (gametophyte). I first I read about gametophytes in a botany text in 1966 but I had never actually seen one in the wild until 2008 The gametophytes above, along with emerging sporophytes, were lining the moist bare soil excavated below the foundation forms for a house I was building.

Bryophytes

Mosses and liverworts are the little but mighty epiphytes of the Hawaiian rainforest. They are undoubtedly the most species-rich group of epiphytes in the young rainforest at Kīlauea summit, and cover more surface area of their hosts than any other life-form of rainforest epiphyte. Finally, they play an important ecological role in the rainforest environment as preferred sites for the germination and establishment of woody plants, both on tree host plants or on the forest floor. We often do not pay much attention to them because they are tiny so that species differences and biodiversity are hard to discern. Actually, up close, they are fascinatingly diverse, have architecturally intriguing spore reproductive structures, and grow on their hosts in patterns piquing the curiosity to explain.

Most of us hold a mental image of mosses, and some of us may call all small, simple green plants "mosses." Once you look closely on the trunks or trees and tree ferns, as we will in the following pages, mosses are just one of the life-forms of bryophytes. In fact, the most abundant bryophytes in young rainforest at the summit of Kīlauea are actually leafy liverworts, both in terms of biodiversity and cover. There are two other kinds of bryophytes in "Kīlauea Forest," thalloid liverworts and hornworts. However, they are very scarce, but I include some search images of them to challenge you to keep your eyes open and find them.

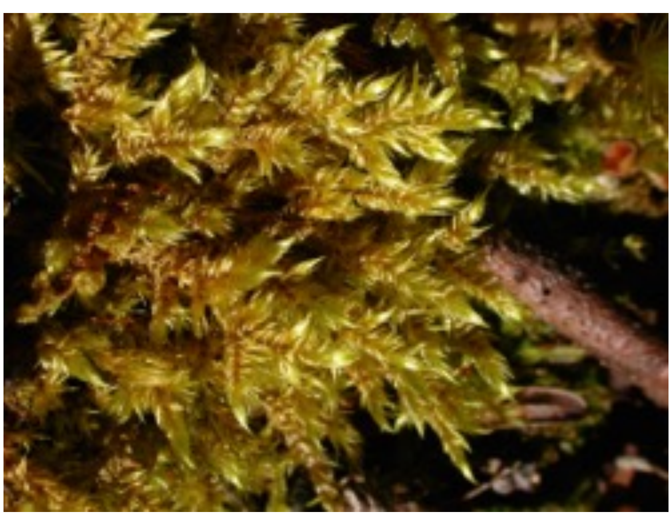
The bryophytes—mosses, leafy liverworts, thalloid liverworts, and hornworts—are small simple plants, almost all without specialized water and nutrient conducting tissue and almost all are a single layer thick. The other feature that unites them is that the spore producing stage in the life cycle is short-lived and lives on the larger, gamete producing stage. We will go into all this because it explain the bryophyte features you see in the forest, when you look closely.

Pyrrhobrum spiniforme. This species is probably the most abundant moss in "Kīlauea Forest." The stalks with capsules at the tips produce spores. *Pyrrobrum* illustrates the acrocarpous growth form, one of the two growth forms of mosses, with upright branched or unbranched shoots and sporophytes attached at the tips of the branches.

Branch of *Pyrrhobryum spiniforme*. The leaves of mosses are attached spirally around the stem. Usually they spread around radially from the stem.

(left and above) **Whitehead moss *(Leucobryum Seemanii).*** Here is a readily recognizable moss in rainforest; it even has a common name. It sometimes forms globular colonies. Whitehead moss turns a distinctive light-green color when it dries out. The white color is due to the accumulation of dead cells on the surface of the leaves.

(*right*) **Whitehead moss (*Leucobryum gracile*).** This species of whitehead moss is also a common epiphyte in young rainforest. The plants in the image are fully hydrated and bright green, in contrast to dried *Leucobryum above*. *Leucobryum gracile* can be distinguished from the larger *Leucobryum seemanii* by the small size of it leaves, 4-6 mm long in *L. gracile* and versus 7-12 mm long for *L. seemanii.*



(left) ***Acroporium fuscoflavum.*** I include this moss even though it is not an abundant epiphyte. It is distinctive and easy to recognize. Also, it is one of my favorites, aesthetically, because of its distinctive glossy green leaves. This photo is courtesy of Mashuri Waite, whom I had hired to prepare a moss inventory of HVNP. This is included in the publications listed for the young rainforest chapter.

A leafy liverwort, *Bazzania* sp. Leafy liverworts are not only the most the most common kind of liverwort in young Park rainforest but may be more abundant than mosses. At last count (2006) there are thought to be 11 species of the genus *Bazzania* and they are among the most abundant leafy liverworts in Hawaiian

***Bazzania* sp. close up** The leaves of leafy liverworts are attached in flattened fashion on both sides of the other on the stems. They never have a midrib like some moss species and the leaf tips are often lobed or toothed. Often there is a row of forward-facing leaves along the stem, on the bottom or top of the stems.

Two leafy liverworts. You will have to excuse me for not identifying the species. I did find an identification key to the genera of liverworts, written in 1960, without a single illustration. Wish someone would write a flora of the mosses and liverworts.

A moss with flattened branches. *Homaliodendron flabellatum* is an uncommon but distinctive moss, one of the largest in Hawai`i. Like other mosses its leaves are spirally attached to the leaves but project from the stem in flattened manner so that this moss resembles a small fern or leafy liverwort. Just to make things more interesting, when you think you can can distinguish leafy liverworts mosses from liverworts, you need to know that there are some mosses with flattened branches and leaves arranged in one plane. *Homaliodendron* also illustrates the pleurocarpous growth form of mosses, with creeping or ascending, extensively branched.

***Riccardia* sp.** is the most abundant thalloid liverwort in young rainforest at Kīlauea summit. However, you have to look closely to find it because *Riccardia* is often mixed in with mosses and leafy liverworts. There are many more leafy liverwort species, certainly with much greater total biomass, than that of thalloid liverworts, which are never differentiated into leaves and stems. Thalloid liverworts are much more noticeable in older rainforest in the Park.

ISOPTYGERIUM PHOTO OP AT NIAULANI

Horn-like sporophyte growing from from the thallose, lobed gametophyte of *Phaeoceros carolinianus*. *The sporophyte is green and photosynthetic*

Hornworts. Hornworts resemble thallose liverworts in that they have flattened thalli with lobes. They are distinct in that the sporophyte is a horn-like projection, hence its common name. The thallus is one cell layer thick on the edges and thickens in the middle. There are only six hornworts species in Hawai`i. They are probably most often seen on wet, disturbed soil but also on humus but also on decomposing logs in the rain forest and maybe as an epiphyte.

Mosses and liverworts reproduce in the same way. Understanding their life cycle will enable you to identify the fragile, small, and short-lived reproductive structures that are occasionally present of bryophytes. They have two alternating generations, one producing gametes and the other producing spores. The green, leafy plants, the gametophyte stage, produce sperm and eggs which unite and form the sporophyte, which produces spores. Many other plants, e.g., ferns , have alternation of generation. The big difference is that the short-lived sporophytes of mosses and liverworts lives on ("parasitizes") the perennial gametophyte (in ferns, the sporophyte is the big, independent stage and the gametophyte is tiny and short-lived). The sporophytes in mosses are fairly conspicuous. They are usually well excerpted and fairly persistent. You have to develop an eye for the short-lived, small sporophytes of the liverworts but finding the may be more rewarding.

Moss sporophytes, spore-producing capsules and capsules, growing on the out-of-focus leafy, gametophyte.

(*above*) **Sporophytes of a leafy liverwort.** I know this is an out-of-focus image, that of a very abundant liverwort in young rainforest. The sporophytes are the tiny, white round structures at the tips of branches with smaller leaves. (*below*) I have included a more dramatic cockroached image of a leafy liverwort sporophyte of a different species below to give you a search image; leafy liverwort sporophytes are quite common once you know what you are looking for.

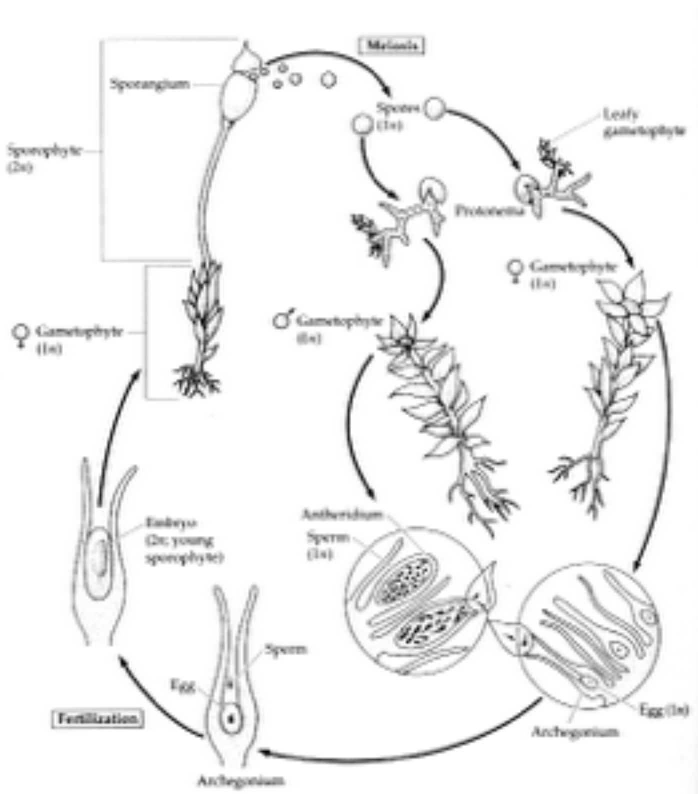
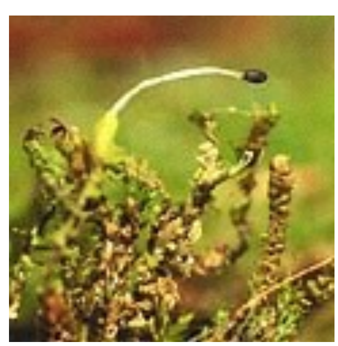


Diagram of the life-cycle of mosses.



Microphotograph of a moss leaf revealing similar sized cells arranged in a single layer, except for the multilayered midrib. Photo courtesy of Mashuri Waite.

Bryophytes are ideally suited to the reduced lighting and nearly constant moisture of the rainforest environment. The leaves of most bryophytes species are just one cell layer thick (except for midribs when present). In addition, the surface of their leaves, unlike those of ferns and flowering plants, are not masked by a waxy cuticle. They therefore absorb nutrients and water over their entire surface, not just the root-like rhizoids that attach them to their hosts. Without a waxy cuticle, they can photosynthesis at low, rainforest levels of light. This gives them a net photosynthetic gain, i.e., produce more food from photosynthesis than burning it through respiration in a very low-light environment. Only a few bryophytes have specialized tissues for conducting water and nutrients from place to place in the plant; this is one of the reasons they are so small.

Once I started looking for patterns in the distribution of bryophytes in the young rainforest, this became one of the most intriguing features of my off-trail forays. I am amazed that I did not notice these patterns before I deliberately looked; they are so obvious. One pattern is that the favorite host tree for epiphytes is by far `ōhi`a. This is also true of filmy ferns and "regular herbaceous ferns." *I can only speculate about the reasons why `ōhi`a is the favorite host for bryophytes (and other epiphytes). `Ōhi`a grows slowly, so that bark is sloughed off very gradually, allowing slow-growing epiphytes to colonize and spread and laterally recolonize surfaces with patches of bark that slough off. Even though the bark tends to be shed, it has a porous texture hat may facilitate bryophyte rhizoides to penetrate and anchore to the substrate. How convenient for epiphytes to colonize `ōhi`a since this is the monodominant tree in young rainforest.*

A second pattern that became apparent is that leafy liverworts seem to be the most abundant epiphytic bryophytes in "Kīlauea Iki Forest," covering more surface area of their host tree substrates than mosses. A distributional pattern among bryophytes that reliably repeats itself in young rainforest is that mosses will be more abundant at the base of the tree host but leafy liverworts tend to dominate the upright trunks. Some more subtle patterns apparent in some circumstances is that bryophytes tend of occupy more moist microsites on the trunk or branches.

Bryophytes coating the base of the tree but little represented in upper portions of the tree. *One of the reasons for this pattern may be that the tree may be slower growing at the base, providing a more stable substrate for epiphytic bryophytes (or "bryophytic epiphytes"). In addition, the fluted base made up of prop roots provides a more horizontal surface that receives not only water flowing down the stem but direct through fall rain. Finally, habitat near the ground in rainforest tens to be shadier and more humid.*

\`Ōhi\`a host tree with moss at base and leafy liverworts above. This image was obtained during a drought so moss at the base of the tree is dry and shriveled. Take my word for it.

(*right*) **Small patch of bryophtes in fork of \`ōhi\`a.** This is a moist microsite because it accumulate moisture flowing down the stem and also partially from vertical through-fall. It probably does not hurt that \`ōhi\`a leaf litter accumulates in the fork, providing a moisture-retaining compost pile. Notice the \`ōlapa seedling in the fork, also testifying to the extra moisture on site, plus possible nutrient benefits of the tiny compost pile there.

**Bryophytes only at the base of a kāwa`u tree.** Bryophytes tend to be concentrated at the base of kāwa`u, `ōlapa, and kōlea lau nui, with scarce or no cover in higher parts of the trunk. *These species tend to grow faster than `ōhi`a, presumably sloughing off bark and slow-growing bryophytes beginning to colonize this substrate. Also, they have have smooth, thin bark that lacks a soft, porous texture that would enhance penetration and anchoring.*

Bryophytes preferentially colonizing a burl on the side of the trunk. This site receives direct through fall of rain, plus stem flow that may accumulate on a horizontal surface. *The growth of this structure may be slower than the surrounding trunk area and the bark may not slough off as readily.*

The are two noticeable patterns of bryophyte distribution on hāpu`u in young rain at the summit of Kīlauea. The bryophytes understandably tend to concentrated lower on the hāpu`u trunk, below the dynamic upper trunk dominated by recent frond bases. The lower trunk is made up of a cortex of tiny, stable aerial roots. The second pattern is that bryophytes have the highest cover on the top surface of leaning tree ferns which receive more moisture from through-fall.

(*left* and *above*) **Bryophytes on upper surface of leaning individual, with low cover at top of**

One of the first patterns I noticed is that when bryophytes grow intermingled with filmy ferns, the predominant and often only obvious bryophyte is *Bazzania*.

hapuu patterns, bryophytes on older, stems,lower parts of stems, and leaning tree ferns. away from

Lichens

With low species diversity and biomass, lichens are a very minor element of the epiphytic flora of young rainforest. The most noticeable and abundant lichen in "Kīlauea Forest" is old man's beard (*Usnea hawaiiensis*), growing epiphytically on trees, especially on the edge of the forest stands where light is most available. Most lichens do best in environments, unlike rainforest, that have ample but not constant moisture. Lichens live on the knife-edge. They can only persist in environments where photosynthesis outpaces respiration; the algal component must produce more carbohydrates through photosynthesis than the fungal (and algal) partner consumes. The optimal moisture for lichen photosynthesis is 50-70% moisture saturation; the optimal moisture for respiration is fully saturated. The nearly constant moisture and the low light levels in rainforest therefore favor respiration over photosynthesis. When lichens are present in rainforest, they tend to be found in lower moisture, higher light environments such as the tree canopy. For the same reasons lichens are also scarce in non-epiphytic environments within young rainforest.

(*left*) **A fruticose (bushy) lichen, old man's beard growing on the dead branches of an `ōhi`a adjacent to Crater Rim Drive.** It is highly unlikely that the lichen killed the leafless branchlets on which it is growing. Lichens are not parasites; lichens do not penetrate the living tissues of a host to absorb nutrients and water. Instead, lichens are epiphytes, simply growing on and attached to their hosts. They undoubtedly take up nutrients leached from dead host tissues or from dust and organic matter blown on to the host plant. Old man's beard is often found on dead branches. Lichens thrive on the dead branches of their hosts, probably because there is more light available there, in the absence of the host's leaves. In addition, the growing surface of a dead branch is more stable, without new bark continually being produced and old bark being sloughed off actively growing stems.

(*right*) **Closeup of *Usnea hawaiiensis*.** Lichen associations are relatively stable so lichens function as individual organisms and resemble species in that they have a similar appearance in different areas. For this reason, they are given species names and classified in genera, families, and orders, even though they are not "true" species.

***Lepraria* sp. on the surface of a dead hāpu`u.** This is not a typical habitat for *Lepararia.* When growing on hāpu`u, *Lepararia* is typically found in small patches low on the trunk because of the dynamic nature of the upper trunk with frond development and frond base persistence. You can see some residual patches of pulu covering trunk buds near the top of the image. The `ōhi`a on the margin of the trunk are epiphytic seedlings.

Lepraria is a crustose lichen, forming a thin crust on the surface of its substrate. If you rubbed the lichen with a finger tip, a greenish powder would come off on your finger. This powder consists of tiny packets of algal and fungal cells (called soredia if you really wanted to know). They readily detach from the lichen plant and become propagules for dispersing the lichen. I use the name *Lepraria* sp. because there are apparently many "species" in this genus but lichenologists are still trying to sort them out. I take this philosophically for lichens; they really do not have true species anyway.

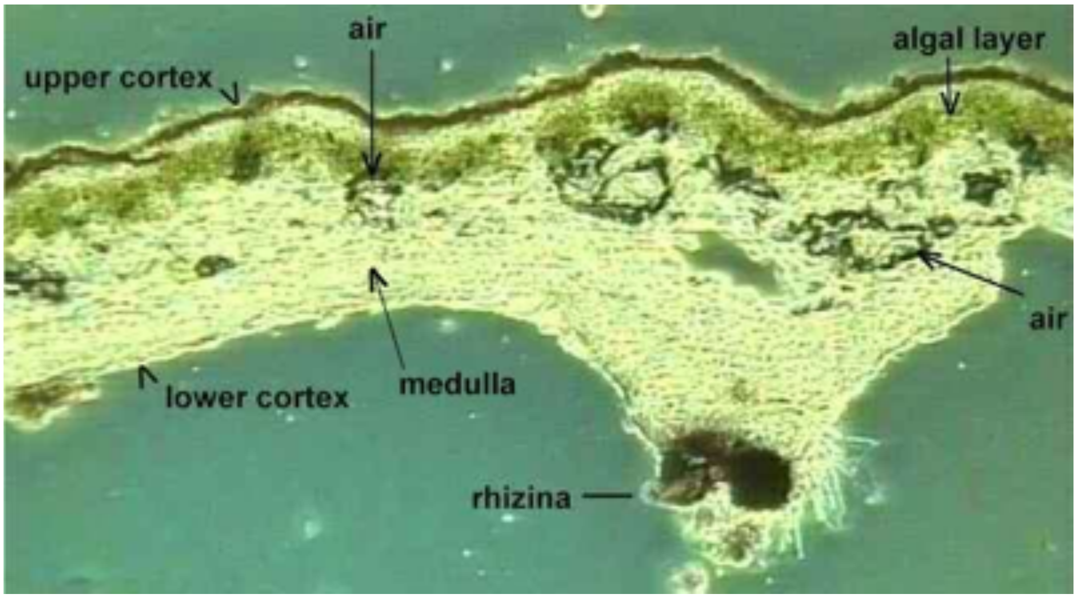
More typical habitat for *Leparia* sp. in young rainforest. This light-green crustose lichen is growing on the leeward, dry side of the trunk of an `ōhi`a tree. It absorbs sufficient moisture from the air. in this locations, it does not have to compete with the moisture-requiring bryophytes found on the exposed side of the trunk. The lichen may have the advantage in the leeward location. Lichens are generally found in "left-over" habitats where they do not have to compete with the "bully" flowering plants and ferns. Most of these left-overr Mosses and , or the abundant bryophytes in rainforest.

Two small patches of a "species" of the genus *Cladonia* growing among mosses and leafy liverworts on the bark of an `ōhi`a tree. This "species" may be more tolerant of high, constant moisture and consistently low light levels than most other lichens. Its abundance may be limited by competition from the luxuriant masses of epiphytic bryophytes which occupy the same substrates. *Cladonia* has tiny, basal leaf-like structures and upright stalks which usually produce fungal spores and soredia. Even though the same color of light green, these structure distinguish *Cladonia* from the "dusty" Lepraria.

Sticta tomentosa. This is a fairly common lichen in older rainforest in the Park. I have not noticed it yet it in young rainforest without success, but I include it here because of the story it tells. All the other lichens pictured above have green algae as their algal component or photobiont. The algal photobiont in *Sticta* is a cyanobacteria (formerly called blue-green algae). Many cyanobacteria can tolerate low levels of light so lichens so with cyanobacteria tend to be found in low light environments like rainforest. The orange structures on the margin of the lichen produce spores for the fungal component (mycobiont). Here is a mystery about lichen reproduction. The fungi spend a lot of energy producing spores. However, to successfully reproduce, the spores must land on the free-living algal species, and the phycobionts often live a different type of habitat from the lichen association.

The classical view of the lichen association is that lichens are a mutualistic partnership between the two component organisms, a fungus (mycobiont) and an alga (photobiont), with both partners benefitting more or less equally. Supporting this view is the fact that the association allows the lichens to grow in habitats where neither of its component species could live on their own. You can see the physical association of fungal and algal components in the illustration below. The photosynthetic alga resides just below the outer protective skin or cortex of the fungus and provides food for both partners. The fungus absorbs inorganic nutrients from the substrate, provides a food and moisture storage area in the center of the lichen, the medulla, and protects the alga from too much light. A more recent interpretation is that a lichen is a controlled parasitism of the alga by the fungus. The fungus makes up 90% of the biomass of a lichen association with their cells often penetrating the algal cells. Also, the lichen mycobionts, like other parasitic fungi, are not ordinarily found free-living outside the lichen association, whereas most of the algal components belong to genera or species that can live independently. Finally, the fungal partner determines the morphology of the lichen. There is just one fungal species per lichen "species"; there may be different algal species in that lichen "species" from area to area. Maybe the expression "Freddy Fungus took a 'liken' to Alice Alga" is appropriate in describing the controlled parasitism relationship.

Cross-section of a lichen. *Notice that the lichen thallus is made up of mostly fungus which surrounds and protects the photobiont. The photobiont, made up of green algae in this and most lichens is a relatively thin layer located near the upper surface to capture light. The fungi form a protective upper cortex and a lower cortex. The medulla, made up of loosely packed fungal filaments, is a food and water storage area.*



NURSE LOGS

Nurse logs are one of the defining features of Hawaiian rainforest. They are the horizontal trunks of tree ferns or trees, typically lying on the forest floor, and serving as a substrate or nursery for the establishment of plant species, especially trees and shrubs. Nurse logs are occasionally found in the more moist mesic forest environments of the Park such as Kīpuka Puaulu. Nurse logs also are found in temperate rainforest, like those in the Pacific Northwest of the Mainland. However, they are very abundant and play an important ecological role in Hawaiian rainforest. Nurse logs provide a more well-lighted platform for plant establishment, above the often deep leaf and branch litter on the forest floor. As the images below reveal, moss and leafy liverwort covered nurse play an important role in the regeneration of rainforest woody plants, compared to litter dominated adjacent sites on the forest floor. In Hawaiian rainforest less than one percent of the light striking the upper forest canopy reaches the forest floor. If you add the sometimes deep litter of tree fallen tree fern fronds, there is very little light available for the germination and growth of woody plant seedlings. There may be a more abundant supply of moisture and maybe nutrients in the forest soil than on nurse logs. However, moisture is not limiting in the rainforest environment so trees and shrubs can germinate and grow on nurse logs, even though nurse logs potentially vary more in moisture content than soil.

In the rainforest at the summit of Kīlauea, fallen hāpu`u tree ferns provide the overwhelming percentage of the nurse logs present. This species of tree fern, nicknamed by Park Interpreters the “walking tree fern,” often tends to lean and eventually fall. Trees tend to contribute minimally to the nurse log supply in“Kīlauea Forest.” This forest is relatively young, very few of the long-lived `ōhi`a, by far the most abundant tree species, have fallen.

Fallen hāpu`u tree fern, ready to serve as a nurse log. The lack of a noticeable upright trunk and the horizontal disposition of some of the fronds suggest that this tree fern fell recently. Mosses and leafy liverworts have already developed a nearly complete blanket on the surface of the fallen tree fern trunk. Bryophytes seem to readily colonize horizontal surfaces of hāpu`u, perhaps in part because of the reception of direct precipitation in this orientation. As suggested by the images below, bryophyte cover seems to facilitate the germination and growth of native woody plant species in Hawaiian rainforest. This suggests that tree and shrub seedlings will soon become established on this new nurse log. Because the host substrate is often living, maybe plants establishing on live hāpu`u tree fern nurse logs could also be considered to be epiphytes. The `ōhelo kau lā`au adjacent to the base of the hāpu`u trunk appears to be growing from the tree fern. In reality, the tree fern fell on this native shrub and it is growing around the trunk of the hāpu`u. The hāpu`u also fell on a small, recovering kōlea lau nui tree (mid-way up the trunk).

Hāpu`u nurse log with kāwa`u and `ōhelo kau lā`au, seedlings. Note the nearly complete bryophyte cover on this nurse log.

Dead tree fern nurse log with growth of `ōhelo kau lā`au. Note that `ōlapa has established at the tip of the nurse log. Note the absence of seedlings on the forest floor dominated by `ōhi`a leaf litter and adjacent to the nurse log.

Nurse log, probably a dead tree fern, with young kāwa`u, `ōlapa `ōhelo kau lā`au, and hāpu`u. Again, note absence of seedlings in leaf litter in adjoining areas.

N**urse log with `ōhi`a seedlings.** This nurse log is near the edge of the forest in a site with high light level favorable to light-requiring `ōhi`a seedlings. The surface is dominated by leafy liverworts rather than mosses.

Nurse log with kolea lau nui and kāwa`u seedlings. Note the absence of tree and shrub seedlings on the forest floor behind the nurse log. Also note that I mention only woody plants on nurse logs; in the young rainforest at the summit of Kīlauea, depauperate of herbaceous native species on the forest native, herbaceous plants are rare on nurse logs.

(*left*) **`Ōhi`a and `ōhelo kau lā`au seedlings growing just on moss pads and not from leaf litter on forest floor.** Small, elevated moss pads like these often develop over fallen branches, chunks of bark, or exposed larger roots of `ōhi`a.

(*above*) **Moss pad on top of a fallen branch.** The underlying branch substrate is visible to the left of the moss pad. (below) moss on shallow roots.

(*above, left*) **`Ōhelo kau lā`au and kāwa`u seedlings growing in leaf and branch litter on forest floor.** I will acknowledge that my observation above that rainforest woody plants become established more frequently on moss than leaf litter is a natural history-level observation, albeit one shared by several botanist friends. I will admit that no studies have been conducted in Hawai`i to determine if bryophytes are more favorable to seed germination and plant establishment germination than forest litter, or if this applies just to certain species; note the difference in species in the paired images. If bryophytes indeed favor establishment, I would like to know why; this is not obvious to me. *I suspect that there is more light available in moss mats than in piles of leaf litter. There seems to be very little woody plant establishment in areas with dense tree fern litter but more in `ōhi`a litter, which creates a thinner litter mat. Damage to seedlings from falling tree fern fronds may also be a factor inhibiting establishment in sites with relatively high densities of tree ferns. Maybe there is more consistent levels of moisture available to seedlings in the moss mats. Mosses on the forest floor are almost invariably hydrated. Maybe moss pads are like miniature nurse logs, slightly but significantly elevated above the litter on the forest floor. Like nurse logs, maybe the moss pads serve as platforms above the litter on the forest floor.*

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Type to enter textNEWLY INVASIVE AND INCREASINGLY SO. COLLECT THIS ONE AND ONE IN DRY OHIA WOODLANDS TO SHOW TO LINDA VERY FEW INVASIVE UNDISURBED HABITAT, HIGHLY SPECIALIZED.

SUCCESSION

You might expect that the rainforest vegetation at Kīlauea summit is changing, maybe even in fairly dramatic ways. After all, it is relatively young vegetation, *probably established on deposits of ash and lithic deposits following explosive eruptions 250-300 years ago.* You can see some changes taking place now, with noticeable clusters of native tree seedlings and saplings, lots of young hāpu`u tree ferns, and dead patches of uluhe fern. I believe we can describe the vegetation changes underway and predict the future composition of plant communities at Kīlauea summit, based on studies of plant succession in other areas of Hawai`i Island and an understanding of the ecology of the plant species present in the young forest at the summit. Of course, these predictions should be qualified by the inevitable future occurrence of destructive explosive eruptions, new lava flows, and the potential demise of the emergent `ōhi`a canopy from *Ceratocystis* wilt disease.

Don Drake, Dieter Mueller-Dombois, and Kanehiro Kitayama studied primary succession of Hawaiian rainforest on Mauna Loa Volcano outside the Park near Saddle Road. These researchers developed what is called a chronosequence, a description of the sequence of plants communities ("sere"" that develop over time. Hawai`i Island provides ideal opportunities for determining a chronosequence because of the location of nearby lava flows of different ages at the same elevation and rainfall. The researchers studied vegetation plots on 8, 50, and 140 year old lava flows and also on flows of approximately 300, 400, 3000, and 9,000 years. All of their closely located plots were located at 4,000 foot elevation, assuring very similar temperature and rainfall. The assumption in developing this chronosequence is that with elevation and rainfall the held constant, vegetation differences that are observed result from the age of the plant community, which is a function of the age of their lava flow substrates.

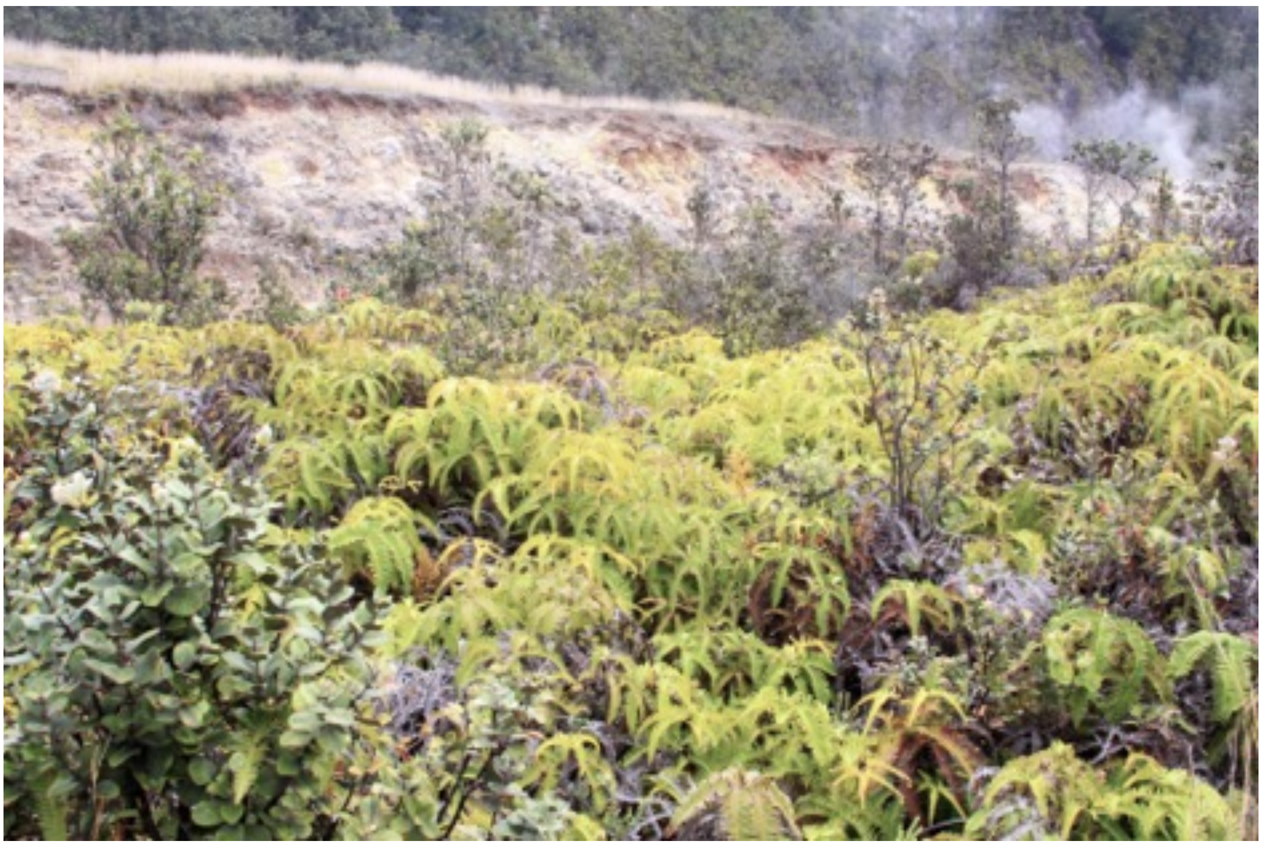
The chronosequence on Mauna Loa is relevant to succession in young rainforest at the summit of Kīlauea but differs in some respects. The Mauna Loa plots were located in a wetter environment, 140 inches versus a 100-110 inches per year at Kīlauea summit. In addition, the plots were located on `a`ā, rather than on deep ash deposits. The researchers, however, concluded that the light ash deposition in their study area accelerated the rate of succession but not the sequence of successional stages. Finally, the Mauna Loa plots were located on `a`ā which protected the forest stands they studied from pig disturbance. "Kīlauea Forest" was highly disturbed by feral ungulates until 1980, and invaded by Himalayan ginger until control efforts began in the mid-1980s.

Unfortunately, it is not possible to construct a chronosequence at the summit of Kīlauea. There are large precipitation differences from east to west at the summit. The explosive eruptions and ash and lithic deposits affected broad areas, across the different aged lava flows. In addition, and the impact of the ash and lithic deposits on vegetation varied geographically in uncertain ways with distance from the source. One inherent weakness of the chronosequence approach in revealing the details of the succession process is the age gap of the different seres in the sequence. In the Mauna Loa studies, for example, the sere jumps from 400 to 3,000 years, and 3,000 to 9,000 years; a lot happened in those time intervals. I will be filling in the gaps with observations at Kīlauea and what we know about the ecology of the key plant species, particularly `ōhi`a, uluhe, and hāpu`u tree ferns.

I speculate below on early forest succession east of Kīlauea Iki Crater, based on the Mauna Loa chronosequence and what I have observed on very recent flows near Kīlauea summit. Primary succession at the summit on the pāhoehoe flows that effused from vents at the base of the `Aila`au Shield in the early 1600s undoubtedly started with colonization of `ōhi`a lehua, our keystone pioneer species in Hawai`i. *A rain of fine ash, deposited vertically and gently, may have added ash deposits to the pāhoehoe surface after the pahoehoe flows were emplaced. This undoubtedly accelerated the rate of succession,* in part because of greater amounts of nitrogen available to colonizing plants in the fine ash particles. *However, the maturation of this forest was cut short because of a hot and high speed sand and gravel horizontal surge, maybe in the early 1700s. This explosive eruption would have devastated the existing vegetation and reset the successional clock. A new `ōhi`a forest began to recover on this new ash and lithic substrate; however, this forest was mostly destroyed by sand deposits in the late 1700s. I believe a small number of `ōhi`a survived the sand deposits of the late 1700s to grow into the large open-form `ōhi`a now scattered in "Kīlauea Forest."* The succession story below is about the development of the rainforest east of Kīlauea Iki Crater after the sand-depositing explosive eruption in the late 18th century, the forest in change we see changing and recovering today.

A view of early pioneer succession on a 40 year old lava flow near the summit of Kīlauea. This image of the 1974 Keananko`i flow provides a simulation of very early succession of lava flows from the `Aila`au shield at Kīlauea summit. On pāhoehoe `ōhi`a lehua nearly always gets established in cracks. Organic matter from adjacent vegetated areas (note forest edge in background) can accumulate in cracks and provide a much richer and stable supply of water and nutrients, particularly nitrogen, than the sterile surface of the low flow. Notice the lehua flowers on the young `ōhi`a. In 1983 I saw young `ōhi`a lehua trees flowering on a 1973 Mauna Ulu flows. Pretty adaptive for a lava flow pioneer to flower early on; make seeds starting while young, adding to the local seed rain and just in case another flow is on the way nearby. Not seen here are the small native shrubs that also colonize the cracks and establish concurrently with `ōhi`a. Note the patches of grey-green lichens the have colonized the pāhoehoe to the southwest of the `ōhi`a in the center of the image. Leaf litter fall immediately down-wind from the `ōhi`a may be an important factor in lichen establishment.

Succession on new lava flows and ash deposits always starts with colonization by our champion pioneer tree species, `ōhi`a lehua. On the `pāhoehoe flows at the summit, the `ōhi`a undoubtedly became established in cracks initially. The successful establishment of stands of small, open `ōhi`a provided organic matter, nutrients, as well as a modicum of shade and cloud water interception, factors undoubtedly facilitating the subsequent establishment of uluhe fern. Uluhe fills in the openings in the `ōhi`a scrub. It competes with the `ōhi`a and slows down its growth. However, the fern does not overtop the trees and kill them; notice below how at least the tops of the `ōhi`a remain above the uluhe mat. Uluhe creates a challenging light environment for the establishment of other tree species, tree ferns, and other understory plants, suppressing them for decades. The understory of the 140 year old lava flow in the Mauna Loa chronosequence was dominated by dense mats of uluhe fern. The widespread abundance of uluhe in the rainforest at Kīlauea summit, in spite of the presence of ash soil that accelerates succession, suggests to ecologists that the rainforest here is relatively young. This interpretation is reinforced by the appearance of even-aged stands and the history of stand-replacing explosive eruptions.



Uluhe invading the understory after establishment of`ōhi`a. This image, from an early successional forest at the Sulphur Banks, simulates succession following the initial colonization by `ōhi`a lehua. In the Mauna Loa chronosequence and at Kīlauea summit, uluhe is the second invader and densely to completely fills in the gaps between the young `ōhi`a trees which establish first. Cooling of portions of the substrate at the Sulphur Banks area may have permitted fairly recent colonization by `ōhi`a and uluhe.

Tall, mostly closed canopy of \`ōhi\`a lehua with a continuous uluhe understory. This seems to be the next stage in forest development at Kīlauea summit. Researchers found in the chronosequence on Mauna Loa that \`ōhi\`a lehua trees on ash grew faster, taller, and with larger diameter than \`ōhi\`a on bare lava. Maybe this accounts for why \`ōhi\`a are fairly well developed on this site, without secondary canopy tree species starting to become established. Maybe the deep ash soil also contributes to the luxuriance of the uluhe and its ability to suppress \`ōlapa, kōlea lau nui, and kāwa\`u. I do not think animals were a factor in suppression of secondary canopy trees at this stage because of the density of the uluhe mat.

You find extensive dense mats of uluhe in relatively young rainforest but in somewhat older rainforest you find a secondary canopy of tree species, \`ōlapa, kōlea lau nui, and kāwa\`u, and a subcanopy of tree ferns. So, how does this transition take place? Looking around the forest at the summit, there seems to be two main factors: 1) the increasing size of the \`ōhi\`a trees and the greater crown closure that results and 2) the gradual establishment of hāpu\`u tree ferns trending toward a closed subcanopy. Both of these changes decrease light penetrating to the forest understory and shade out the light-requiring uluhe fern.

Example of hāpu\`u fern invading a nearly closed canopy \`ōhi\`a/uluhe forest stand at Kīlauea summit.

Small dead patch of uluhe in a stand being invaded by hāpu`u tree ferns.

Relictual patch of dead uluhe in a forest being invaded by hāpu`u and ama`u tree ferns. The ama`u tree ferns are the shorter individuals in the foreground.

Secondary canopy trees did not contribute much to shading out uluhe fern. They did not recruit prolifically through the uluhe mat where they would have been partially protected from ungulates and ginger threats. The widespread establishment of the secondary canopy tree layer at Kīlauea summit was delayed until ungulates and ginger were removed. However, at Kīlauea summit, I found very scattered kāwa`u getting started in fairly thick patches of uluhe fern in some places. I found little to no `ōlapa and kōlea lau nui penetrating the thick uluhe mat. In contrast, `ōlapa was the first secondary canopy tree to get started during the reign of uluhe in the Mauna Loa chronosequence.

**Kāwa`u growing up through uluhe.** Kāwa`u seedlings and saplings, with their single stem treelet growth form can reach fairly rapidly toward light. This uluhe patch in which the treelet is relatively thin, located between taller vines climbing up `ōhi`a hosts.

**Small kāwa`u trees to the left and right of the large `ōhi`a.** Hāpu`u is invading this site and may be partially suppressing uluhe in the site of the kāwa`u on the left.

LOOK SOME MORE IN BASICALLY PURE ULUHE MAY BE SCATTERED OLAPA AND KOLEA

Many understory patches in "Kīlauea Forest" reflect the transition from the continuous uluhe understory to the closed hāpu`u canopy. These transitional environments provide optimal light conditions for the establishment of seedlings, saplings, or small trees of `ōlapa, kōlea lau nui, kāwa`u, and pilo, and invading ama`u fern or native `ohe grass. These stands tend to be characterized by recently shaded-out uluhe patches, with vestiges of live and more extensive dead mats of uluhe and an open subcanopy of hāpu`u tree ferns.

Native tree seedlings and saplings, along with ama`u fern, growing recruiting into an area of mostly shaded-out, dead uluhe.

Small trees of kāwa`u and `ōlapa and young hāpu`u ferns invading an area of dead uluhe.

Abundant seedlings, saplings, and small trees of secondary canopy species, `ōlapa, kāwa`u, and kōlea lau nui, in an optimal sites for native tree regeneration. You can see vestiges of dead and live uluhe and background of the image. Ama`u and hāpu`u fern are also becoming established in this site.

**Ama`u fern understory.** In some areas in which uluhe is shaded out, and the hāpu`u subcanopy has not completely closed in yet, ama`u fern (*Sadleria pallida*), the rainforest species of this genus, can become abundant. This would not have been possible with pigs in the forest. They are able to knock down this small tree fern and eat the starchy core of the trunks, killing the tree ferns. Before I fenced my property in Volcano, feral pigs had killed about but one ama`u tree fern. Now that it is fenced, I am seeing numerous small ama`u. Note the `ōlapa sapling in the center of the image.

Native grass understory in small canopy gap. `Ohe forms scattered, small understory patches in some well-lit canopy gaps in the rainforest near Kīlauea Iki. Note the dying uluhe patch in the background. I wonder why `ohe patches occupy some gaps in the tree fern subcanopy and not others? You can ask the same question about the ama`u patches. Maybe there is some subtle environmental correlate associated with `ohe establishment, such as a need for higher levels of light than ama`u requires. I have noticed that the only `ohe in my home forest in Volcano Village is located on the edge of the forest facing south and west where light levels are very high. Or maybe there just happened to be a sufficient `ohe seed source present. Trying out answers to these kinds of questions makes hiking in the Park rainforest intellectually pleasurable.

In other forest patches, the closing `ōhi`a crowns form a closed canopy, and spreading hāpu`u fronds form a partially or fully closed subcanopy beneath the `ōhi`a emergent canopy. When the tree fern subcanopy is closed, there is characteristically is little or no shrub and herbaceous vegetation on the forest floor, an environment of very low light, deep litter, and hazardous falling fronds. The paucity of seed and spore sources in the area also limit the develop the establishment of the shrub and forest floor herbaceous plant layers.

A spreading tree fern subcanopy. Note the dense hāpu`u tree ferns in the background and recently shaded out uluhe fern on the right. A few kāwa`u and `ōlapa saplings, as well as Himalayan ginger, are taking advantage of the available light in the gap and minimal litter. There are ama`u ferns in the left foreground and more young hāpu`u in the center of the image, suggesting that this gap will filled in a few years with a hāpu`u subcanopy.

A young stand of hāpu`u tree ferns forming a closed subcanopy. Note the thick tree fern frond litter, fallen fronds, and absence of shrubs and forest floor herbaceous plants.

Forest patch with a completely closed tree fern. With trunk growth rate measured in a study in the Park by Lars Walker, at one foot of trunk growth per decade, most of the tree ferns here are at least 60-70 years old. Note the small hāpu`u tree fern in the front and center of the image. Although hāpu`u tree ferns create a very shady environment suppressing light-requiring species, tolerant of low levels of light themselves, they are able to continue to recruit in this environment.

The major conclusion we can draw about the direction of ecological succession in young rainforest at the summit of Kīlauea is this: the forest here is transitioning from an`ōhi`a/uluhe community to an `ōhi`a/hāpu`u community with a mostly closed tree fern subcanopy and with just a hint of a shrub and forest floor herb layer. Fortunately, in the absence of feral ungulates and widespread Himalayan ginger (thanks, Natural Resource Management), the secondary canopy tree species are recruiting prolifically in the temporary canopy opening gaps created in the uluhe mat, gaps gradually filling also with hāpu`u tree ferns.

**A hint of native shrub recovery under a closed hāpu`u tree fern subcanopy.** Note the abundance of fallen, potentially damaging dead fronds and small hāpu`u tree ferns recruiting to the left of the taller ilihia shoot.

A good question about succession from the `ōhi`a/uluhe community to the `ōhi`a/hāpu`u community is why are both communities, and intermediate stages, present across the landscape? If the successional clock were last reset about 250 years or so ago by a widespread explosive eruption, why are not all forest stands at the same successional stage, e.g., all `ōhi`a/uluhe or all `ōhi`a/hāpu`u? Typically the patches of `ōhi`a/uluhe or all `ōhi`a/hāpu`u are small and adjacent to each other. I puzzled over this until I took a hike from the leg of the Escape Road that intersects with Highway 11 near the Volcano School, walking south toward Nāhuku Lava Tube. I traversed over a small ridge, through dense uluhe, then down into a swale with dense tree fern, and then another uluhe-choked ridge and followed by a broad flat areas dominated by tree ferns in the understory. You can more easily detect the same pattern from Crater Rim Drive. You will see continuous uluhe in the understory when the terrain is higher, above the road, with cutbanks present along the road edge. created with the highway cutting through cutbanks formed in the ridge, all hidden by dense uluhe. You will see well-developed `ōhi`a/hāpu`u stands on concave or flat topography, usually below the road level, which has been built up.

pics from convex areas and concave or level

Why would minor topographic differences, ridges versus swales or lower, flat terrain, make a difference in plant community composition and stage of succession? One difference could be that the swales or flat sites have deeper ash soil than the ridges because of erosion from the convex, higher topography of the ridge, and deposition to the swales. The ridges may have greater exposure and lower soil moisture. In any case, environmental differences between the ridge and swale environments translates into a difference in the growth rate of the `ōhi`a trees and the closure of the `ōhi`a canopy. The `ōhi`a in the uluhe areas tend to grow more slowly, with small diameter and height and more forest-form, and with lateral branches spreading less in the crown, thus less shading of the understory. The `ōhi`a in the tree fern areas are growing faster, with greater diameter and height, and with lateral branches can more readily develop in the crown and form a more closed canopy. Greater canopy closure tends to contribute to the shading out of the uluhe understory and facilitating the development of the tree fern layer.

`Ohi`a Succession

SUCCESSION OF OHIA, SMALL DIAMETER TREES, FULL STORY OF PUBES AND GLABS

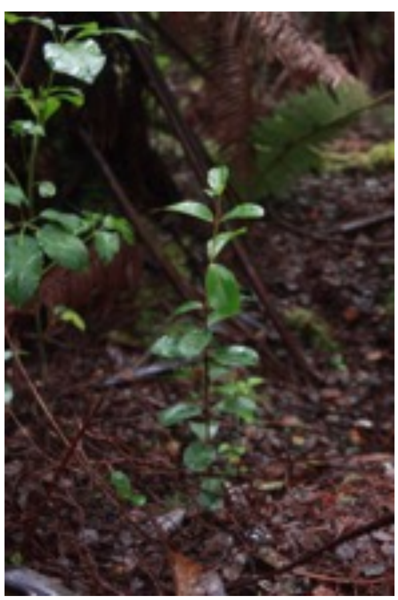
`ohia is also the climax, no classical climax, make due

here is something unusual, pubescent seedlings
and and an ohia nurse log

No classical climax in overstay.

var macrophylla found not to be genetically
distinct, lump under glabberima

(AFTER SUCCESSION, THREATS AND RESTORATION NEEDS)



EXISITING THREATS, RESTORATION OF SHRUBS, WHAT REMAINS (HERBACEOUS PLANTS—MAYBE ON THEIR OWN OVER TIME, EASILY TRANSPLANTED

qy1 ‘/7uy

NEED POLYMOPRHA TYPE HAPII AMD BDETTER ONE ON LAVA FLOW pic of ginger as an epiphyte

‘diplazium, Pneumatopertis, coniogramme at lava tube or trail down to kilauaea iki

SUCCESSION. FINISH WITH RESTORATION OF RARE SPECIES, PICS AT THE LAVA TUBE AND ESCAPE ROAD.

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pic above of tree ferns stands getting denser
another pic below of young tree ferns invading
more open areas.

East Rift
ohia phenology, flushing flowering
Ohia shallow roots and deep roots shallow because shallow soil, not so much sterile except for humus and organic. deep in cracks, soil can be shallow.
Ohia psyllids, sooty mold, Bark anatomy, shallow roots, (CHECK "WOODY PLANTS"
Uluhe, backing spreading bracts, tiny fiddleheads, spreading laterally after main lateral rachis expands.
Falling tree fern fronds crushing aloha, breaking chia (stage this in front yard).
uluhe, big dead patches from loss of just one rhizome, often lots of dead when climb trees

Aerial roots: Roots originating from above ground portions of a plant and descending, often to the ground and penetrating the soil.
Ash: Fine particles of pulverized volcanic rock blown from an explosion vent, measuring less than 1/10 inch in diameter,
Canopy: The uppermost layer of branches of trees or shrubs.
Clambering: Shrubs or vines spreading laterally, sometimes on top of other vegetation.
Climax: The culminating stage of plant succession in a given ecosystem.
Ecology: The study of species and their environment; also used to express the relationship of species to their environment.
Ecosystem: A community of organisms and their physical and biological environment.
Emergent: Growing above the rest of the vegetation, e.g. emergent trees.
Endemic: Native only to a restricted area, e.g., endemic to the Hawaiian Islands.
Epiphyte: A plant growing on another or host plant but not deriving nutrients and water from that host plant.
Establish/Establishment: A plant getting started successfully by germinating from seed or sprouting from roots.
Fiddlehead: The curled portion of the fern frond prior to unfolding.
Frond: Branch of a fern, including the stipe (stem) and blade (leafy part of frond).

HAWAIIAN/COMMON NAME	SCIENTIFIC NAME
PLANTS, LICHENS, FUNGI	
\`Ala\`ala wainui	*Peperomia cookiana, Peperomia hypoleuca*
	Peperomia membranacea
\`Akōlea	*Athyrium microphyllum*
Ama\`u (āma\`uma\`u)	*Sadleria cyatheoides*
	Sadleria pallida
English ivy*	*Hedera helix*
Gemmed puffball	*Lycoperdon perlatum*
Gold back fern*	*Pityrogramma austroamericana*
Hāhā	*Cyanea pilosa*
Ha\`iwale	*Cyrtandra lysiodsepala*
Hāpu\`u pulu	*Cibotium glaucum*
Hāpu\`u \`i\`i	*Cibotium menziesii*
Hō\`i\`o	*Diplazium sandwichianum*
Himalayan raspberry*	*Rubus ellipticus*
Hoi kuahiwi	*Smilax melastomifolia*
Hō\`i\`o kula	*Cyclosorus sandwicensis*
\`Ie\`ie	*Freycinetia arborea*
\`Ilihia	*Cyrtandra platyphylla*
Japanese honeysuckle*	*Lonicera japonica*
Kāhili ginger*	*Hedychium gardnerianum*
Kāmakahala	*Labordia hedyosmifolia*
Kanawao (Hawaiian hydrangea)	*Broussaisia arguta*
Kāwa\`u	*Ilex anomala*
Kīlau	*Dryopteris glabra var. nuda*
Koa	*Acacia koa*
Kōlea lau nui	*Myrsine lessertiana*
Koli\`i	*Trematolobelia wimmeri*
Kolokolo	*Adenophorus tenellus*
Maile	*Alyxia stellata*
Māku\`e	*Elaphoglossum paleaceum*
Māmaki	*Pipturus albidus*
Manono	*Kadua affinis*
Meu (hāpu\`u)	*Cibotium chamissoi*
Moa	*Psilotum complanatum, Psilotum nudum*
\`Ōhā kēpau	*Clermontia hawaiiensis*

HAWAIIAN/COMMON NAME	**SCIENTIFIC NAME**
***PLANTS, LICHENS, FUNGI* (continued)**	
\`Ōhā wai	*Clermontia parviflora*
\`Ōhi\`a	*Metrosideros polymorpha*
\`Ōhi\`a kū	*Hymenophyllum recurvum*
\`Ōlapa	*Cheirodendron trigynum*
Old Man's Beard	*Usnea hawaiiensis*
\`Ōhelo kau lā\`au	*Vaccinium calycinum*
Olomea	*Perrottetia sandwicensis*
Pa\`iniu	*Astelia menziesiana*
Pala	*Marattia douglasii*
Palai hihi	

STRESS ROOTS, OTHER ROOTS, THATS WHAT THEY DO
AERIAL ROOTS WHEN GROWING ON OHIA
LOOK FOR OHIA EPIPHYTIC ON OTHER OHIA.

Ohia shallow roots, grew into pots makes sense shallow soils, adapted to new lava flows. tropical trees with shallow roots but not a nutrient limitation problem. also deep roots into cracks, handing lava tubes and on lava tube floors.

PHOTOS OF SHALLOW ROOTS WITH MOSS ON THEM, LAVA TUBE ROOTS

Other summit areas
Waldron Ledge, uluhe on small ohia, why do they not overtop since lateral branched to clim on all the way to the top.

OTHER YOUNG RAINFOREST AT KĪLAUEA SUMMIT

HALEMAUMAU TRAIL
BYRONS LEDGE
ROUTE UP FROM BYRONS—ULUHE
NAHUKU
THURSTON NEAR TUBE
ESCAPE ROAD

MAYBE 10 SLIDES

EAST RIFT RAINFOREST