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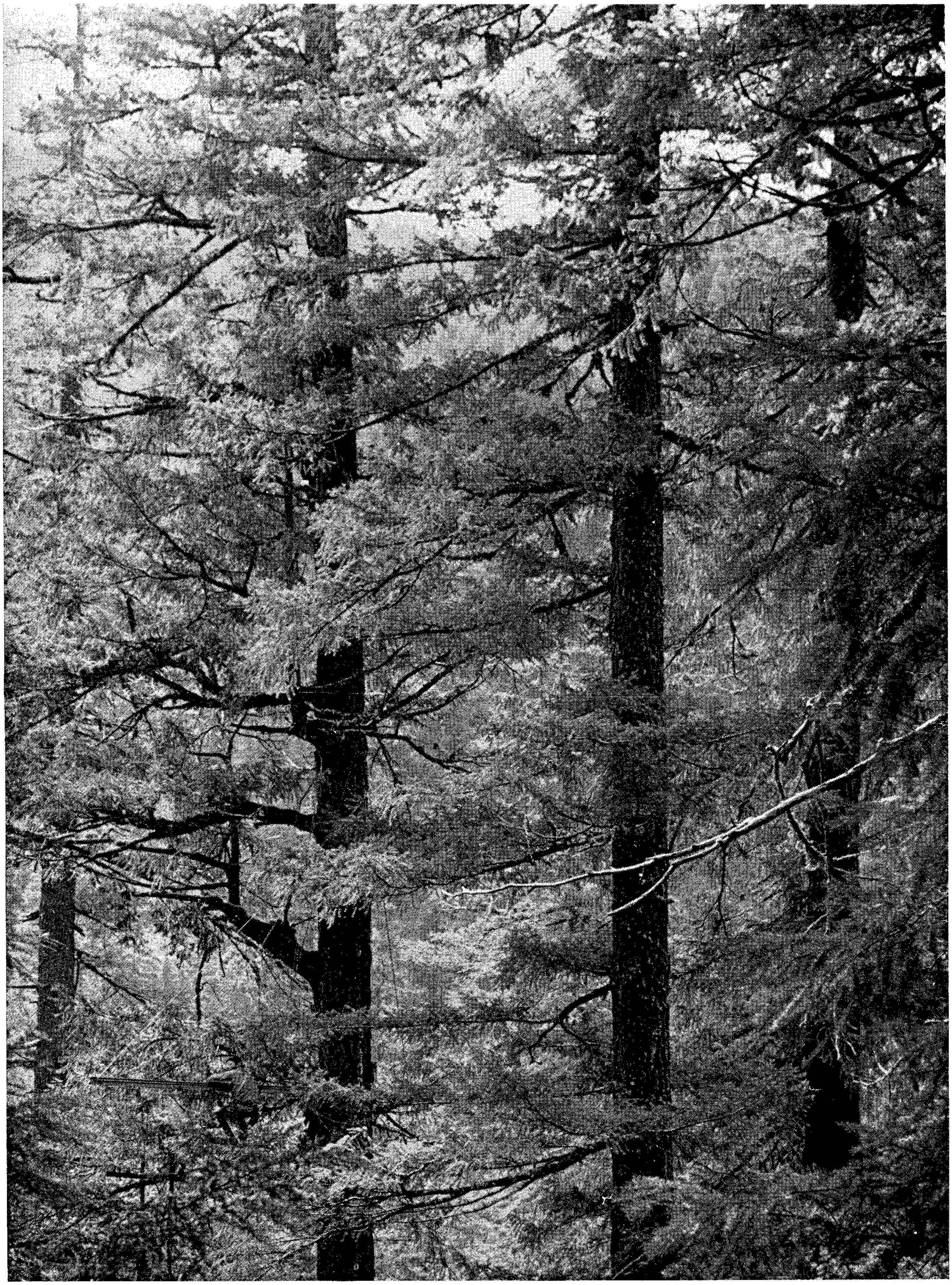


FOREST OF DOUGLAS FIRS in western Oregon dwarfs a field investigator suspended from a spar 100 feet above the ground ***(at lower left of photograph, between first and second tree trunk).*** **Use of modified rock-climbing techniques allows such closeup studies.**

LIFE IN TALL TREES

The high forest canopy consists of more than branches and leaves. Entire communities of other plants and animals dwell within this unique ecosystem, helping to provide the trees with nitrogen

by William C. Denison

A treetop in a forest, like a mountain peak or a deep canyon, is a remote world that is plainly visible but not easy to explore at first hand. Yet there is a strong urge to visit such private domains. They challenge both our curiosity and our skill. With respect to tall trees there might even be an echo of a past when our ancestors were at home in treetops.

It is perhaps a little surprising, therefore, that although investigators have been drawn to the direct exploration of mountain heights and sea floors, relatively little study has been given to the treetop world. It offers intriguing questions to a biologist. The forest canopy is a distinctive habitat, providing its own special conditions of moisture, light, temperature and other qualities. What kinds of plant and animal life does it support? Does it harbor an integrated community? What roles does it play in maintaining the forest ecosystem as a whole?

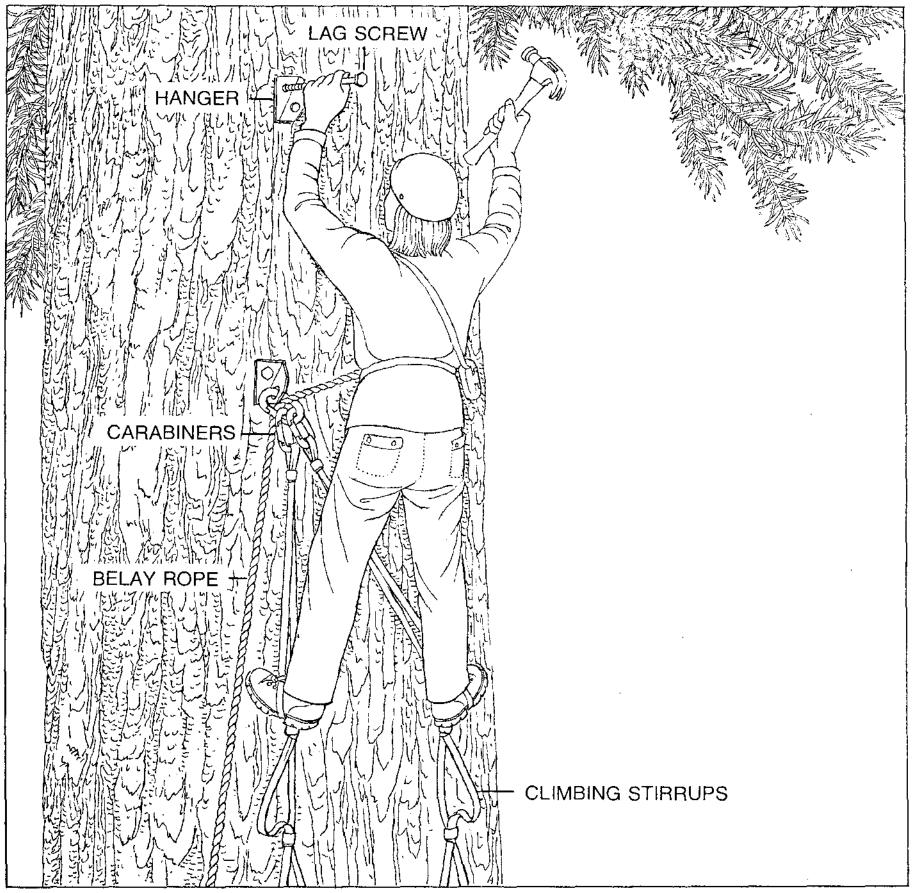
My colleague Lawrence H. Pike and I at Oregon State University undertook an exploration of treetop life as part of a U.S. study of ecosystems in western coniferous forests under the aegis of the International Biological Program. We enlisted a group of physically fit university and high school students in our climbing party and set out for the top of a 450-year-old stand of Douglas fir in the H. J. Andrews Experimental Forest in western Oregon, where the trees soar to a height of 200 feet or more and the lowest branch is usually at least 60 feet above the ground. Since the project presented a problem roughly corresponding to scaling the rock face of a mountainside, we borrowed ideas from rock-climbing to develop techniques for climbing the tall trees.

As in mountaineering, our climbers work in teams, with a teammate on the ground belaying the climber on the tree with a safety rope. The team members use small radio transceivers for communication between those on the ground and climbers far above in the canopy. In the first ascent of a tree the climber carries a hammer and lag screws (which hold better in the bark and trunk of a tree than the pitons, or spikes, used in rock-climbing) to assist the climb. The climber drives a lag screw into the tree trunk, fastening a hanger as far above his head as he can reach, attaches a pair of stirrup-loop ladders to the hanger, climbs the ladder stirrups to install the next hanger and proceeds in this way to the top of the tree *[see top illustration on next page]*. The initial climb takes several hours and is hard work, even for a person in excellent physical condition.

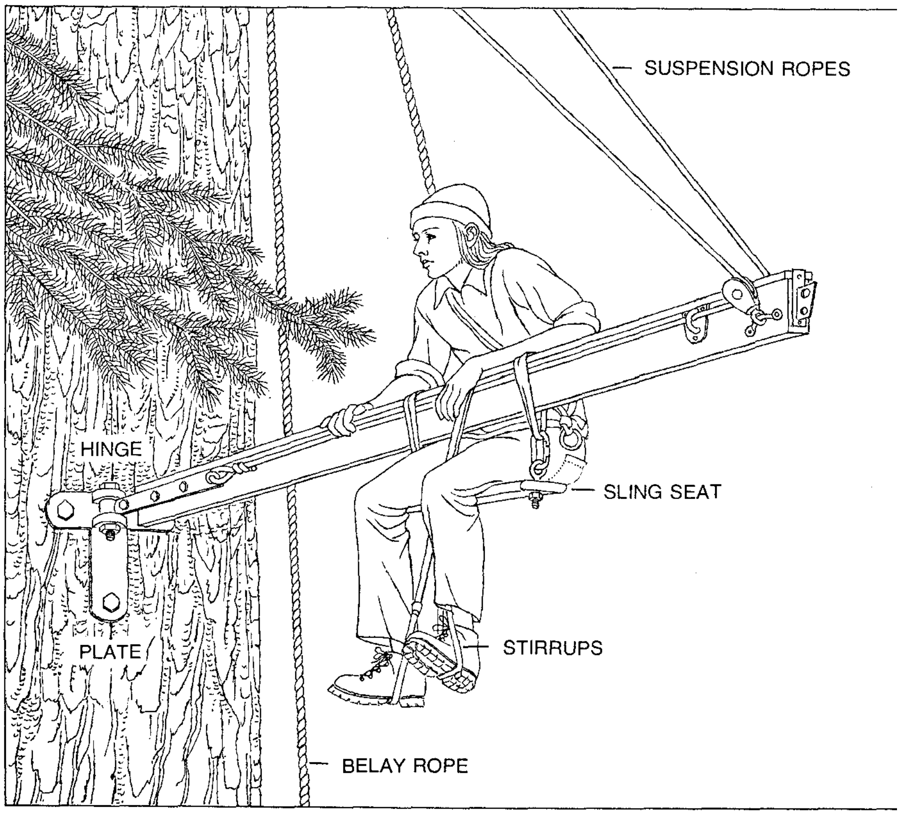
At the top of the ascent the climber attaches to the trunk a rope that will be used for subsequent ascents and a large pulley for the belaying rope that the climbers use for additional support. To ascend the climbing rope the climber holds in each hand a Swiss-made Jumar Ascender, which is a form of clamp that grips the rope tightly when weight is put on it and loosens when weight is removed. Slings of nylon webbing that serve as stirrups for the climber's feet are suspended from the jumars and the climber goes up the rope by taking the weight off one foot and stirrup, sliding the jumar up the rope with one hand, restoring the weight on the stirrup to tighten the jumar and then repeating the process with the other hand and foot. With practice one can climb the rope in this way with little more effort than it takes to climb an ordinary ladder. One can also rest one's feet from standing in the stirrups or free both hands for work at any point by sitting back on a seatlike sling that is attached to one jumar.

In addition to these devices for climbing and descending along the tree trunk, we have developed a 12-foot boom, which we call the "spar," for working in areas away from the trunk (including the ends of branches). The spar is attached to the trunk with a special hinge and is suspended at its outboard end by a pair of ropes [*see bottom illustration on next page*]. The occupant sits on a sling seat suspended from the spar and can move along the spar by alternately standing in stirrups while sliding the seat along and then moving the stirrups while sitting in the seat. By pulling one or the other of the two ropes supporting the outboard end of the spar the occupant can move horizontally around through an arc of 180 degrees. Thus we can work effectively anywhere in the canopy within 12 feet of the trunk.

After establishing access to the treetop, we carried out a systematic survey not only of the wood and foliage of the tree but also of the population of epiphytes: the many plants that grow on other plants but are not parasitic. We recorded the results of the survey on punch cards, a procedure that enabled us to store the data in a computer and to undertake computer analyses. The data were first used in preparing a "map" of the tree, showing the location and amount of living and dead matter on the tree trunk and on each branch system. The survey enabled us to estimate the biomass, or weight of living matter, of each branch system and of the tree as a whole. These estimates were compiled by considering separately the amount of foliage (obtained by observing what percent of the horizontal area within a branch system was covered by foliage), the amount of wood (in the branch and twigs) and the amount of epiphytic plant



ASCENT OF TREE is accomplished by means of the mountaineering methods designed for vertical rock faces, except that lag screws are used instead of pitons to secure hangers. The first climber up the tree rigs the climbing and belay ropes used by subsequent climbers.



HORIZONTAL SPAR provides a movable base among the tree branches. The investigator is supported by a sling seat hung from the spar and can study a 12-foot length of branch.

life inhabiting each branch. We checked our estimates of the biomass by making detailed measurements of typical systems. We found, for example, that in a Douglas fir 185 feet tall the foliage had an estimated total weight of 187 pounds and the epiphytic lichens and mosses growing on the tree weighed 38 pounds.

It was already well known, of course, that trees are inhabited by a great variety of plant and animal life. The plants that grow on tree trunks, branches and foliage include bacteria, algae, fungi, mosses, lichens and ferns. (In warm climates even advanced species of plants such as orchids are epiphytes.) The animals that live out their lives in trees show a similar range in size and diversity: protozoans, nematodes, higher invertebrates such as arthropods and mollusks, and various vertebrates (including primates in warm climates). As botanists, we focused our attention on the plant life in our exploration of treetops.

The forest canopy proved to be a subsystem of considerable complexity. The variety of its plant life reflects a variety in the habitats within the canopy. These habitats differ widely in the amount of available moisture and light, in temperature and in the age and surface texture of the supporting structure (twig or branch). As a twig grows and ages into a branch, its surface harbors *a* succession of different organisms, beginning with pioneering lichens and progressing through a series of complex communities. Diane Nielsen and Diane *hl.* Tracy, two students who started with us as undergraduates and, pioneering our climbing techniques, were the first to ascend to the canopy, found that the diversity of habitats and the number of species of epiphytic plants increased the higher they went up the tree. Each habitat has a characteristic flora, with certain species predominating. For example, most of the large fir trees in the forest where we have been working are not strictly vertical but lean *a* little to one side. As a result their trunks have an upper side and a lower side, and the upper side is moister than the lower because rainwater streams down that side. The upper and lower sides therefore differ in the prevailing lichen species growing on them. On the branches aloft in the canopy certain large foliose (flat and leaflike) lichens predominate on the upper side of the branch, and the lower side tends to favor the lower plants known as liverworts.

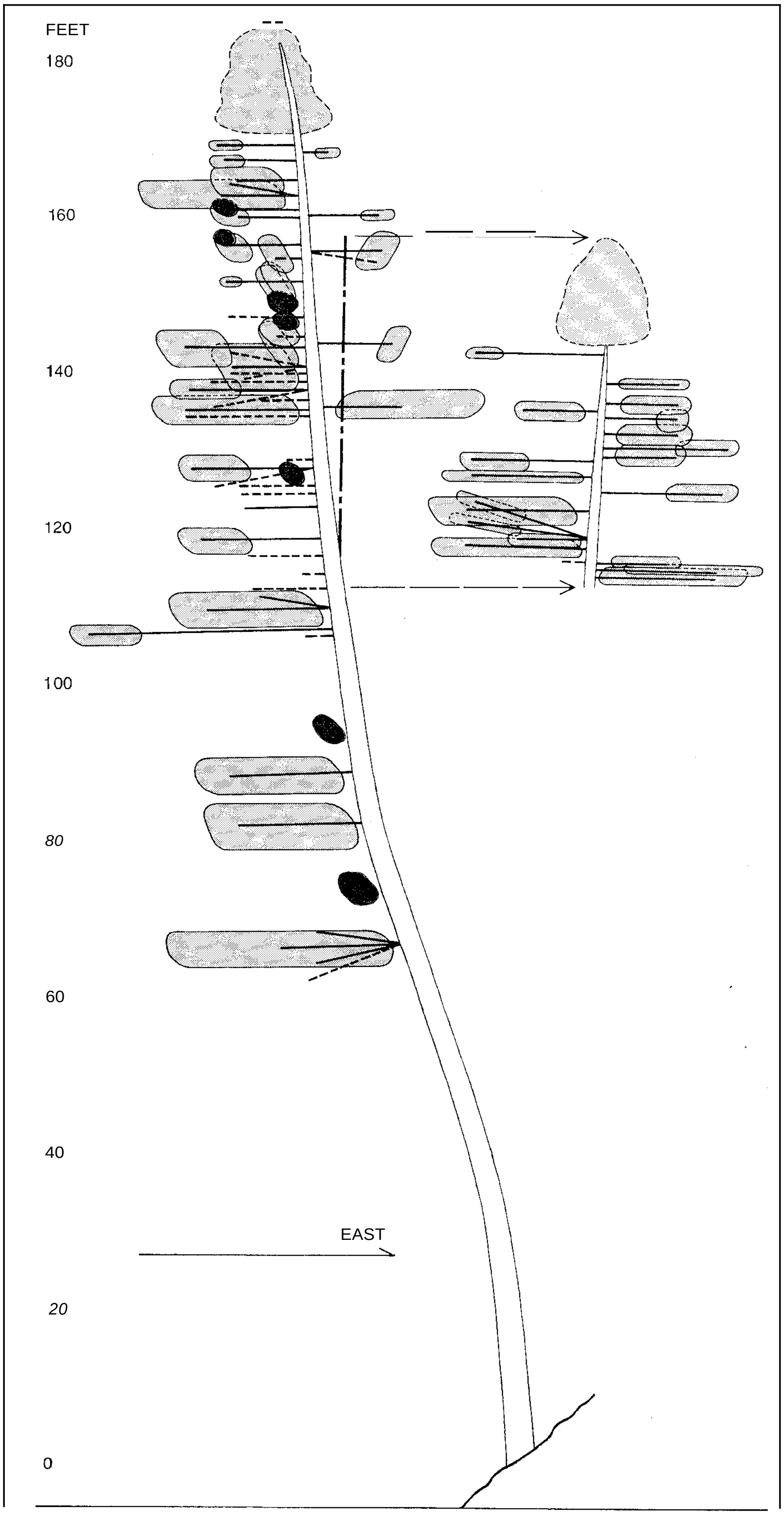
Habitat by habitat, we are cataloguing the characteristic epiphytic communities and obtaining a census of the many plant varieties. Pike has already noted 121 different species of lichens. The number will undoubtedly increase as we explore more trees.

We find, then, that the forest canopy is an active, well-populated system (comparable in many respects to the forest floor), and we must suppose that the epiphytes living in the canopy contribute substantially to the nourishment and viability of the forest as a whole. They undoubtedly take up water, minerals and other substances from the atmosphere. Through photosynthesis and other processes they produce nutrients that are released to the forest's animal dwellers and the trees. We have been particularly interested in investigating the epiphytic plants' role in capturing nitrogen for the forest's needs.

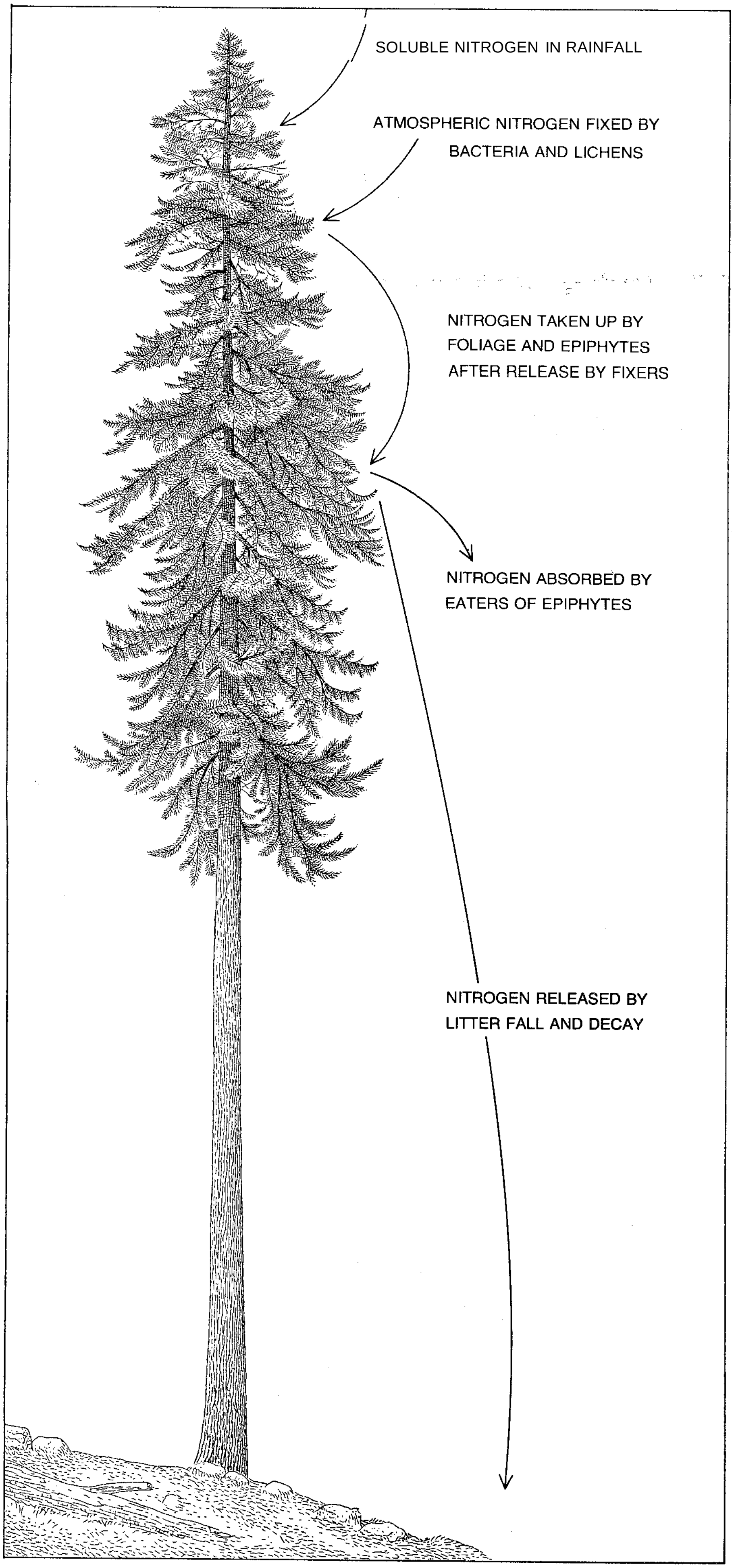
In an old-growth Douglas-fir forest the supply of available nitrogen is not abundant. Relatively little of this essential element is brought in directly from the atmosphere by rainfall, and the forest floor is largely barren of nitrogen-fixing plant life. It seemed likely, therefore, that lichens growing in the canopy, some of which wcre known to fix nitrogen, might be important contributors to the forest's nitrogen economy.

Our notice was attracted particularly to one lichen, *Lobaria oregana,* that is by far the most abundant species in the treetops. The forest floor is littered with fallen pieces of its green, lettucelike thallus (plant body). It has been established that *Lobaria* fixes nitrogen from the atmosphere, presumably through the agency of a blue-green alga that is embodied in granular packets within the thallus. In order to evaluate the importance of this lichen in the forest's overall economy, we worked out estimates of its probable annual contribution to the nitrogen supply.

Sterling A. Russell of Oregon State University, who has investigated *Lobaria's* nitrogen-fixing productivity, estimated that the lichen fixes nitrogen at a maximum rate of about 50 nanomoles (billionths of a unit of molecular weight) per hour per gram of the lichen's fresh weight, which is equivalent to 200 nanomoles per gram (dry weight). We estimate that in our Douglas-fir forest the amount of *Lobaria* growing on the trees is between 350 and 450 pounds per acre. If we took the 450-pound figure and assumed that *Loharia* fixes nitrogen at the maximum rate throughout the year, we would arrive at a figure of slightly more than 10 pounds per acre as this lichen's



SCHEMATIC MAP of a Douglas fir more than 180 feet high is based on climbers' studies. The fir had a forked top; the shorter fork, on the east side of the tree, is offset for clarity. The map shows only branches that project east or west and that are more than 1.6 inches in diameter. Solid lines indicate living branches, broken lines dead ones. The enclosed area accompanying a branch is proportional to the weight of its foliage. Where branch is less than minimum diameter only the foliage area is shown *(color)*. Treetops were not mapped.



annual production of fixed nitrogen. It is unreasonable to suppose, however, that the lichen sustains the maximum rate the year round.

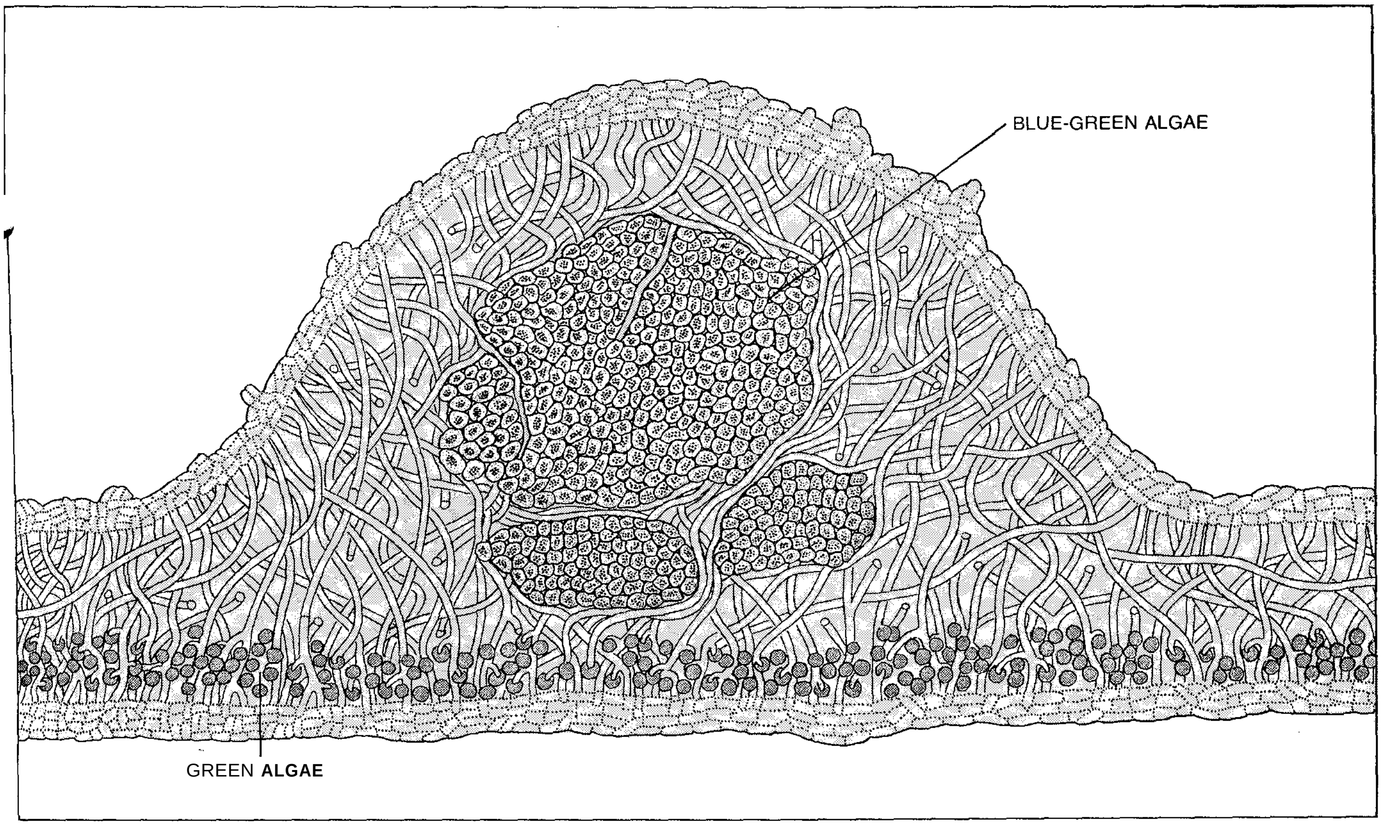
We decided to calculate a lower limit: the minimum amount of nitrogen *Lobaria* must fix to support its own growth. Its thallus, we estimate, adds about a fourth (in dry weight) in new growth each year. Taking the lower estimate of the amount of *Lobaria* in the forest (that is, 350 pounds per acre), the annual new growth would amount to 90 pounds per acre. Since the nitrogen content of the thallus is 2.1 percent of its total dry weight, the 90 pounds of yearly new growth per acre would contain roughly 1.8 pounds of nitrogen per acre.

Thus we conclude that *Lobaria oregana* contributes from 1.8 to 10 pounds of nitrogen per acre per year to the forest—certainly less than 10 pounds but probably substantially more than 1.8 pounds. The nitrogen trapped by the lichen is released in several ways for the eventual nourishment of the trees.

The chief route of the contribution is through *Lobaria's* fall and decay. The annual fall of dislodged *Lobaria* from the canopy to the forest floor amounts to roughly 80 pounds per acre; most of this fall is peeled off by rain, snow and ice during the winter. Decomposing on the ground, the fallen thalli release about 1.8 pounds of nitrogen per acre per year to the roots of the trees and other plants.

Animals feeding on the lichens in the tree provide a second means of conveyance of the nitrogen. We have observed great numbers of invertebrates, including nematodes, mites and insects, eating away at *Lobaria* thalli. Certain vertebrates, such as the rodent called the red tree vole, supplement their diet with this lichen, among other plants. The animals consuming the lichen are

NITROGEN PATHWAYS in the forest canopy are indicated schematically. First (top) some nitrogen (less than one pound per acre annually) is washed into the canopy by rain. Far more nitrogen enters the system through the action of nitrogen-fixing bacteria on the fir needles and of blue-green algae in some lichens. The nitrogen-fixers pass the vital element along three pathways. Rainwater leaches some nitrogen from the living and dead tissue of the fixers; both the tree and its epiphytes absorb the rainwater. Fixed nitrogen follows a second path when herbivorous animals feed on epiphytes and then excrete. Finally, litter from the death and decay of both the epiphytes and the herbivores adds further nitrogen to the ecosystem.



PRINCIPAL NITROGEN-FIXER among the epiphytic lichens in the forest-canopy community, *Lobaria oregana*, is shown in cross section. Like all lichens, *Lobaria* is a symbiotic association of a fungus *(gray areas)* and two algae *(colored areas)*. One of the Chlorophyta, or green algae, is the principal symbiont; it lives in the *Lobaria* thallus *(light color)*. Populations of a blue-green alga, *Nostoc*, are also present *(solid color)* in bulges called cephalodiums. *Nostoc*, one of the Cyanophyta, fixes atmospheric nitrogen at a significant rate. As a result *Lobaria* contributes from 1.8 to 10 pounds of nitrogen per acre to the fir-forest ecosystem annually.

fed on in turn by predators, and the nitrogen is transferred to the forest soil through the predators' excreta.

Lobaria undoubtedly provides some transportable nitrogen even from its position high in the treetops. At its maximum rate of nitrogen-fixation it probably traps more than it uses for new growth, and this soluble excess of nitrogen may he leached from the thallus by rain and washed down the tree. The rain also picks up nitrogen from dead thalli decaying in the canopy. Rainwater flowing down over the branches and leaves loses nitrogen to mosses and other epiphytes that do not fix nitrogen, and perhaps some nitrogen is fed to the tree itself through its foliage. In any event, the epiphytes that take up nitrogen from the rainwater eventually release it to the ecosystem through their decay. We estimate that in our old-growth Douglas forest the contribution of nitrogen to the soil by epiphytesthat do not fix the element amounts to roughly 5.4 pounds per acre per year.

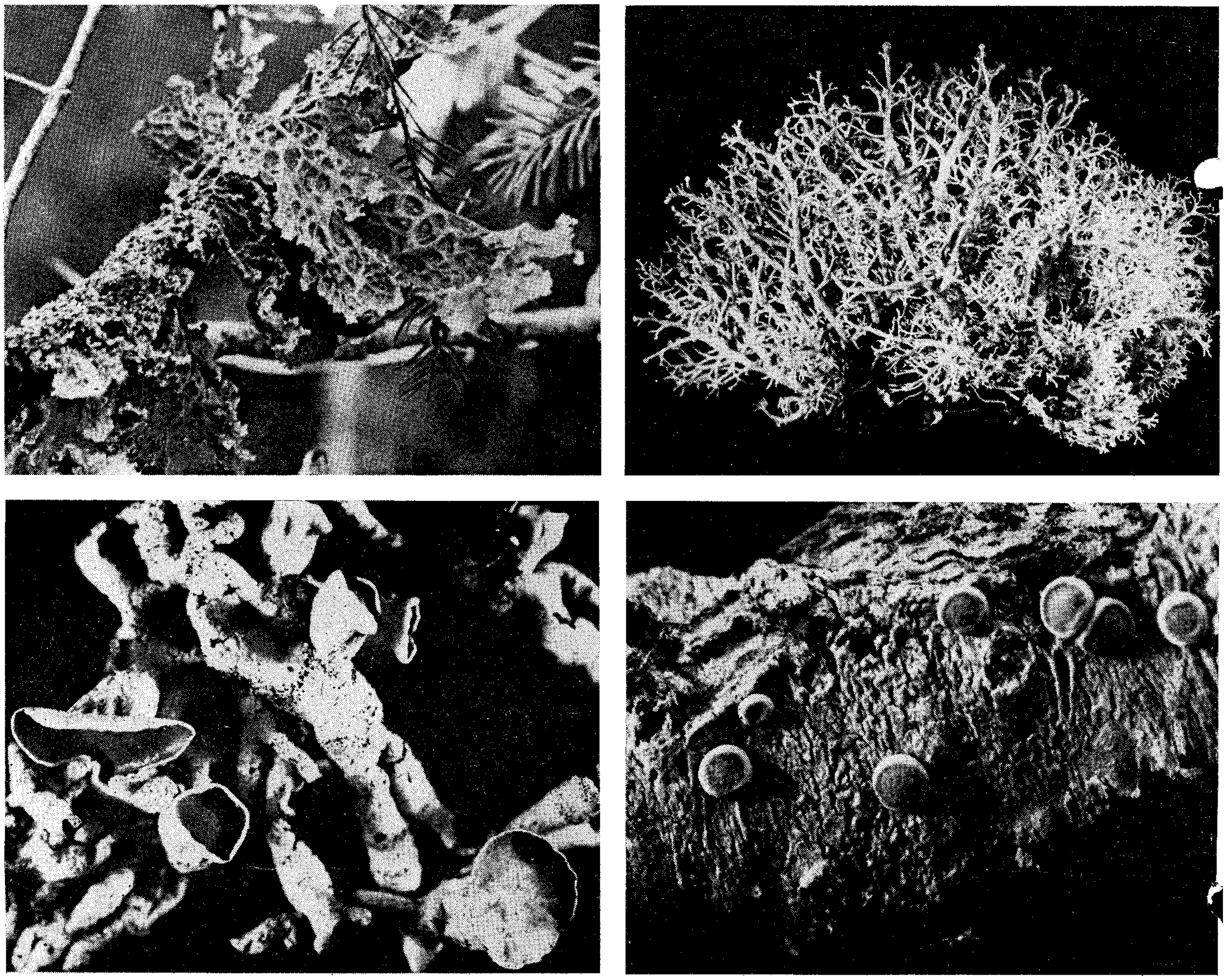
We do not yet have an estimate of the aggregate amount of nitrogen supplied to the forest by all the nitrogen-fixing epiphytes (of which *Lobaria* is certainly the most prolific). Probably the total is less than the 44 pounds per acre that is sometimes applied in the form of fertilizer to promote growth in Douglas-fir forests. Our survey indicates, however, that in an old-growth stand of Douglas fir the nitrogen-fixing plant life in the canopy can serve as the main pathway for the introduction of new nitrogen, an element required by all forest life-forms, small or large, plant or animal.

Epiphytic lichens such as *Lobaria* seem to be particularly susceptible to poisoning by pollutants in the atmosphere. In western Oregon these lichens are disappearing from forests as urbanization and industrialization of the land advance toward the woodlands. Here is further evidence that the atmospheric pollution that too often accompanies increasing density of population is inimical to nearby forested lands.

Our climbing around in the treetops so far can only be considered an early stage in the exploration of the microenvironinent of trees. We hope to learn a great deal more about the communities of epiphytes living in the trees of our Douglas-fir forest and about how they are related to various tree environments.

The question of the differences in microclimates is particularly interesting. The climate at the top of the canopy is obviously very different from the climate low in the tree, so that an epiphyte high in the canopy is subjected to greater intensities of light and sharper fluctuations of temperature and humidity than one on a low branch. In the top of the tree lichens dry out within a few minutes after a rain, whereas those on the lowest branches may stay damp for months in the season of intermittent rains. As we have seen, there are marked climatic differences even between the upper and the lower sides of a branch, with resulting differences in the epiphytic communities of the two sides. Climatic differences within the tree also affect the growth of the branches themselves; for example, branches in the deep shade have a tendency to prune themselves. By installing meteorological instruments at various points in the tree we expect to obtain more specific information relating the growth of epiphytic communities and individual branches to factors in their immediate environment.

The trees to which we have given the



trunks and branches in fir forests are the nitrogen-fixing *Lobaria (top left)*, a highly ramified species, *Sphaerophorus globosus* (top *right*), *a* species with cuplike fruiting bodies, *Hypogymnia enteromorpha (bottom left)*, and a buttonlike species, *Ochrolechia oregona (bottom right)*: Lichens are easily poisoned by urban and industrial air pollutants.

most study are the Douglas fir and the western hemlock. Viewed from a distance, both have about the same general shape: a slender come consisting of relatively short branches extended laterally from a massive central trunk. Closer up, howcver, they are seen to have substantially different builds. An old-growth Douglas fir has relatively few branches and they are widely spaced, sometimes with gapsof up to 70 feet between branches on the shaded side of the trunk. Each branch is a complex system; often it is fan-shaped with a wide spread, and in many cases the system is a group of two or more young branches that have grownout from places where the original main branch broke off. In contrast, an old-growth western hemlock has more branches per length of trunk even in heavy shade; the branches are more evenly spaced up the tree, and they have most of their foliage concentrated at the end of the branch.

In his book *The Adaptive Geometry* of Trees Henry S. Horn has observed that the form of a tree can often be related to the tree's ability to take hold and thrive under specific conditions. One shape, for example, is characteristic of trees that spring up as the early settlers in place of a forest that has been felled by fire or clearing; other shapes allow the trees to invade an established forest at later successional stages. Examining our Douglas firs and hemlocks in this light, we find that the widely spaced, fan-shaped branches of the Douglas fir (formingwhat Horn describes as a "multilayer") fit his description of trees of the early successional type, and the western hemlock, with its evenly distributed foliage (forming a "monolayer"), corresponds to the late successional type. The old branches of a large tree show a pattern of developmental response to environmental factors that seems to be characteristic of its species and therefore probably is genetically influenced. The further exploration of the structure of big trees should provide useful information about the adaptive capacities of individual species.

I hope this brief description of our explorations in the treetops will encourage other investigators to extend the exploration to other forests and other types of trees. The investigation of living things in the forest canopy probably will also prove to be as attractive and rewarding to zoologists as it has been to us, botanists. The study of small arboreal animals at home in the treetops should provide information that cannot be obtained by observing them in captivity.

LICHENS AND AIR QUALITY

Portland State U.
28 February 1974

SPECIES	FREQUENCY[1]		SO_2 SENSITIVITY[2]
Parmelia sulcata	.94	.75	70-125 ug/m^3
Parmelia subaurifera	.88	.59	65
Xanthoria polycarpa	.88	.37	50+
Ramalina farinacea	.86	.43	60
Evernia prunastri	.78	.37	40-70
Usnea subfloridana	.74	.42	40
Lepraria membranacea	.70	.25	no data
Physcia adscendens	.62	.12	less than 70
Hypogymnia physodes	.35	.08	60
Physcia aipolia	.20	.000	40
Lobaria pulmonaria	.04	.006	30

1. Frequency of occurrence at 174 sites in the Willamette Valley. First collumn based on presence: second collumn based on presence above 5% cover on two or more segments or above 25% on a single segment.

2. Data from a variety of sources, but based chiefly on growth on the trunk, not the twigs of the host tree.

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