



Proceedings of the

LOCKWOOD CONFERENCE

on the

SUBURBAN FOREST

and

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March 26, 27, 28, 1962

New Haven, Connecticut

**Edited by
PAUL E. WAGGONER
and
J. D. OVINGTON**

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Foreword

This Station has pioneered in research on trees. The first Experiment Station forester in the nation began work here in 1900, and in that same year land was purchased for experiments in forestry.

Trees are plants, and it was to be expected that Station botanists, pathologists, geneticists, and entomologists would put science to work in the woodland. This they have done, and this they continue to do.

After World War II it became apparent that trees and woodlands in Connecticut had values quite different from those conventionally ascribed to the forest. The suburbanization of many areas in Connecticut proceeded rapidly. Thousands of people moved into the woodlands or near to them. They became acutely aware of trees—trees to be bulldozed, trees to be trimmed and sprayed, trees to be transplanted, trees on the ridges to serve as living backdrops for the pageant of Connecticut life.

New times called for new research on the entire plant communities called forests or woodlands. In 1957 this Station proposed the term Suburban Forest to identify the natural environment in which Connecticut citizens are building a new way of life in an old land. We devoted a whole issue of *FRONTIERS OF PLANT SCIENCE* to the subject. Our scientists critically examined our research in the sciences contributory to the scientific discipline called ecology. They found that much had been accomplished, but they sensed the need for better orientation, for a clearer statement of questions that may be answered by research.

To explore further the possibility of fruitful ecological studies in the suburban forest, we invited 10 visitors to meet at this Station for the Lockwood Conference on the Suburban Forest and Ecology on March 26, 27, and 28, 1962. They came and they considered how ecology, both experimental and observational, can improve our understanding and lead to rational improvement of suburban forests. There were seven formal lectures and three half-day discussions.

The visitors were: Marston Bates, Pierre Dansereau, F. F. Darling, Peter Farb, H. J. Lutz, H. T. Odum, J. D. Ovington, M. B. Russell, S. H. Spurr, and F. W. Went.

In addition to these visitors, H. A. McKusick of the Connecticut Park and Forest Commission and 16 members of the Station staff joined in the discussion.

The conference was divided into eight major sections concerned with the description of Connecticut forests, the definition of the suburban forest, the problem of the suburban forest, the purpose of the suburban

forest, planning of suburban forests, ecological tools and their use, local types of suburban forest from the ecological viewpoint, and uses of the suburban forest to ecology.

The papers and discussions brought together in this volume suggest that there are no pat answers, no panaceas, applicable to the suburban forest, that there is a vast diversity of interests among those who live within the suburban forest.

There seems to be, however, a preponderant opinion that experiments must be laid down to try a great variety of things and to obtain results in terms of circulation of energy and nutrients and exotic chemicals in a system of plants and their soils.

Such work was in progress at this Station. The Lockwood Conference, however, has already caused our scientists to begin even more studies of the ecology of the suburban forest. We expect it will open further vistas of research both here and elsewhere.

The Lockwood Conference was made possible by income from the Lockwood Fund, an endowment of the Station.

James G. Horsfall
Director

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The Problem of the Suburban Forest

Paul E. Waggoner

Considerable courage was required to invite 10 distinguished biologists to New Haven and assign the suburban forest as a topic for investigation. We were emboldened, however, by knowing that all, whether from England (Old or New), Texas, St. Louis, Urbana, Ann Arbor, or the Metropolitan East, were well aware of or deeply involved in some aspect of a surprising phenomenon of our times.

I refer to the miraculous increase in productivity that feeds more and more people from each acre and to the technology that taps ancient reserves of carbon for fuel and fabric.

We are, I believe, both the eyewitnesses and the heirs of the most dramatic release of resources the world has thus far known. We meet here to consider *particularly* the release of land no longer needed for tillage. The landed estate we survey, the wealth we inherit, is indeed vast. Both as eyewitnesses and as heirs, we have our limitations. We shall not be able to agree exactly in our descriptions of what we see. Eyewitnesses seldom do. We shall, I trust, disagree in some measure as to how our inheritance should be used. Heirs commonly disagree. But we can at least walk the bounds together. That is why we meet here on this beautiful spring day in historic New Haven.

Six centuries ago a less beneficent releaser of land, indeed a satanic liberator, cut a swath across Europe. Men called it the Black Death and it swept away perhaps a third of the people in its path. "The scourge passed, and a Europe [awoke] too small for its clothes." (Churchill, W. S. 1956. *History of the English-Speaking Peoples* 1:353. Dodd, Mead and Co., N. Y.)

The release of land, and of people from the land, in our time has not come with the terror of pestilence. But it has left fields untilled and farmsteads unwanted. Our clothes of productivity, so generously fashioned, hang loose upon us despite our growing numbers. We are too small for our breeches.

We are uneasy, like a farm boy newly transplanted in the city, as we seek to adjust our old and familiar ways to new realities. At the same time we know that millions of people elsewhere in the world would like nothing better than to match our opulent attire.

In this time of tumult, in this era of miraculous productivity, lies the opportunity to attain a long-sought goal. This goal of conservationists, inherited through Thoreau, Muir, Pinchot, and Roosevelt, is

the freeing of land from tillage and its restoration to perennial plants. Now it is a national purpose, stated in Presidential messages and implemented by Congressional appropriations, to accomplish this renewal of forests.

Let us make no mistake. If men are cold, they will cut trees for firewood. And if they are hungry, they will plant hillsides for corn. The petitions of the conservationists will not prevail.

Given affluence, however, the pleas can be heard. Thus with oil to warm us and power our mechanical muscles, with bins bulging with plenty to feed us, with electricity to light our way, we can and will restore trees to the land.

In a grand tradition we create new National Parks and Monuments. We envision vast wildernesses: land that will retain its primeval magnificence, a piece of earth and its community of life untrammelled by man. We set aside vacation and weekend forests, visited for the most part on long holidays by those who live in the metropolis, much trammelled by man and his works.

Within these metropolitan complexes are most of the people. They consume most of the goods and services our economy affords. Most of us find living space within the web of these metropolitan complexes, all interconnected by rapid and repeated communication. Caught within the net or web of the metropolis is the suburban forest, the greenery we see day in and day out, a medium far different from the background of the great forest we visit once a year, or never.

Like the modern public domain, the suburban forest is being enlarged. Both hard economic facts and Federal agricultural policy continue to encourage the conversion of farm lands that once nursed the city. The need for open space near cities, farms forsaken by farmers, abandoned acres, was recognized in the Housing Act of 1961, and more funds are now requested by the President. Even in the city itself, little "greenbelts" appear as old slums are leveled by redevelopment.

Farmers are abandoning land faster than it is demanded by cities. Coons and skunks multiply, having discovered their affluence in the garbage pails of the anxious exurbanite now living on forsaken farm land in the suburb.

It is these haunts of the coon and the skunk, these lands of the carpool and the PTA, that with their greenery comprise the suburban forest that concerns us here.

Suburban homes replace the apartment and summer cottage combination, suburban forests erase the clear line that once separated streets from wilderness.

"Open space" is the 1-acre that busies the suburbanite's weekends, the matrix of the turnpike exchange, the handsome grounds of the new

power plant. It is the abandoned pasture invaded by red cedars or the second-growth oak invaded by gypsy moths.

This is the suburban forest we want to understand, perhaps improve. We needn't spend our time here speculating whether it will be, whether it should be, or whether it need be promoted. It already is, it is increasing, and it will last for many years.

We need spend our time learning how to live comfortably with it. This remark introduces ecology, because ecology is the study of how plants and animals live together, how they are ruled by their environment, and how they modify the environment.

In all manner of husbandry, ecology is interesting. But in suburban forestry we hope to grow perennial plants with ease and live among them comfortably. Hence, ecology becomes critical as well as interesting.

Scouts of widely differing calibre have marched beneath the banner of ecology. There is a temptation to review this parade, to rank them from saints to knaves, to agree that some should be discharged and others recruited. If, however, we are to find those clear new paths we hope for, we'll ask not who the aids are but what they can do.

As we proceed we shall have many another opportunity for distraction. We may be aided by this advice:

The fine art of . . . decision consists in not deciding questions that are now not pertinent, in not deciding prematurely, in not making decisions that cannot be made effective, and in not making decisions that others should make. (Barnard, C. I. 1938. *The Function of the Executive*. Harvard Univ. Press, Cambridge.)

If we accept this advice we need not decide that a suburban forest should be created, for that is not pertinent; that some of the forest will again be diverted into farming, for that is premature; that more resources should be devoted to ecology, for that cannot be made effective; nor that all men should want stately trees, for that is for them to decide.

We may then ask, "What are we to talk of?" We might seem to have little left after discarding the mission for conservation, the concern for future food, the recruiting of men and money for basic research. We might seem to be displaying an unnatural disinterest in our neighbors' business and taste.

This is illusory, of course. There remains our natural business of natural science. Our hearts are not disengaged from our neighbors' business, only our minds. We are following the fruitful methods of natural science: circumscribe a system, forgetting all else; propose laws that predict the behavior of the system; test them; and use those that work. We use these methods for the same reason that the laws are used: because they work.

Because they work, an unending and ever accelerating cycle is begun. The responsibility of scientists grows with their success. The neighbor's wife feels no responsibility to be prepared or to be right when asked, "What can I do for my child's fever?" The doctor, however, wears the magical mantle of medicine and must be prepared and be right when the distraught mother turns to him.

The practitioner of science generally assumes:

. . . that the maximum benefits cannot be had from science without the continual application of foresight and forethought. But the permissive conception of science that I encounter among many educated people is entirely different: they appear to think we need not take any long-range thought for the future, because science will always stage an eleventh-hour rescue from any corner we may have boxed ourselves into. New supplies of food will be magically conjured up on demand, and new earths for habitation. It would not be exaggerating greatly to say that the triumphs of science, in this sense, have induced a general attitude of recklessness about the future of mankind. Men's age-old sense of the impossible, or at any rate of the dimension in time of the possible, has experienced a profound decay. (Fleming, D. H. 1961. *Daedalus* 90: 474.)

And want this responsibility or not, we have it. When man can do nothing, he need know nothing. When he has means to work changes, however, his knowledge of consequences must be better. A scientist is not wiser in his choices, and his vote counts no more than any other in setting a course, but as technology enables a course to be followed, scientists increasingly need to know consequences of courses—with certainty proportional to the power of the technology that makes the change effective. Unfortunately, coming to know is slower than deciding upon a course, and we must anticipate the many natural problems that will arise from a great variety of courses, state them as questions, and seek answers.

Now we could make a mistake: while we debate grand strategy, the war could be lost. Fortunately, that cannot happen here, for we have only 3 days. Also, we can stick to specific skirmishes, leaving grand strategy for another time.

I suggest these specifics may be:

What plant stand creates a microclimate that is airy in the summer and snug in the winter? Since the suburban forest is our own habitat, why should not our comfort be the first objective of this ecology? If we are wise biologists, why should we not easily achieve a comfortable medium for man, minimizing the roar of the oil burner and the whirr of the air-conditioners?

How can the forest composition be promptly bent to our will? Clearly, if the knowledge of a desirable forest is to be of more than idle interest, we must erect the forest while we are still here to enjoy it. As foresters

we can view with patience how things will be a century from now. As owners of new homes in raw clearings or bulldozed meadows, however, we see a 5-year wait as intolerable.

What are the consequences of the changes we can shape? Will the soil be lost beyond retrieve? Will songbirds fall? Will spring flowers fail? Will a panorama be closed? As scientists we cannot do with pontifical opinions or bureaucratic advice for inaction. We must buttress logic with old observations and new experiments.

How do we create variety, an insurance against oversight? Variety may be aesthetically desirable, but certainly it is a necessary safeguard both against our imperfection and against the vicissitudes that are inherent in weather.

How is a self-sustaining system established? Our enthusiasm or money may soon be exhausted, for a pleasant environment is a luxury. If the system ticks along nicely with little winding, however, it will please through all our years.

If we unchain ourselves from restrictions of the past, what startlingly different forests can we create? For without wide-ranging variety of choice and a spirit of hopeful intervention, we can no more hope for improvement in forests than can the geneticist presented with a homogeneous population.

What surprising things will arise in a startlingly different forest? The probability of unpleasant things is high, we must admit. The possibility of pleasant things exists, nevertheless, and we would be cowardly not to gamble the small stakes of acre plots.

Finally, what stands of plants yield the most water? The suburban forest is the cup in which we catch our water as well as the medium in which we live.

Description of the Connecticut Forest

Henry W. Hicock

The area of Connecticut is 3 million acres of which 2 million are forest covered. Since 1860 approximately 1 million acres have been forsaken by agriculture and are now in some kind of forest. Another million acres have never been entirely cleared. All have been very heavily burned—both before and after Europeans arrived on the scene. These settlers encountered a mixed conifer-hardwood forest on the better uplands and pine-hemlock on the stratified soils.

Unlike the shrink and spread of the forest area, population has grown consistently to the present 2½ million.

Plants will live at just a bare existence level on roughly 20 per cent of Connecticut land and 20 per cent has agricultural potential under present conditions. The remaining 60 per cent or thereabouts is unsuited to present-day agriculture but will produce fair to good forests. I do not call this forest derelict. It is in bad condition, yes, but I am convinced that most of it will respond to management. I think it has good potential for timber growing and will play an increasingly important role in the conservation of human and other natural resources.

Ninety-two per cent of the forest land is privately owned and 8 per cent is public or quasi-public. I say quasi because some of our large watersheds are privately operated but serve exactly the same purpose as the municipally owned watersheds.

Definition of the Suburban Forest

Discussion

In Connecticut this 2 million acres of woodland is not the forest primeval that we visit on rare holidays. Rather it is the suburban forest caught within the metropolis and its web of communication. Most of us live in the metropolitan complex, and the suburban forest is the greenery we see day in and day out.

McKusick. I think it would be helpful if we could identify the suburban forest. Does forest become suburban when the cost of land and the carrying charges of land exceed its productivity in timber, in wheat, or corn, or whatever? Is this what we are talking about? To me most of the acres in this State have already reached a point where people are competing in the open market for the right to own them at a price that exceeds their value for wood production.

Spurr. By this definition, most of Southern New England would be suburban forest.

McKusick. This is a spreading thing. Even the forests of Northern New England are not entirely immune as people escape from this area. If we can't own land here, we will go further north and own that half-mile lakefront further up. We have to identify the suburban forest, and then there may be individual problems of management. I like the idea that this is going to be by and large a managed and planned forest, and I think this is what foresters have been talking about for a long time.

Bates. To me, the suburban forest is an area which has a considerable tree growth and is primarily residential in purpose, e.g., New Haven, Greenwich, and Middletown. A reservoir, a park, a reservation, or a wildlife refuge are presumably something else. If this is the definition, a park within New Haven, Stamford, or Greenwich would be suburban forest as long as it was part of the urban situation or of the suburb. The main point is that the primary element of the suburban forest is human residence.

Russell. By your definition the tracts of woods far from the cities of the Midwest and managed by schools and municipalities would not be relevant to our discussion.

Spurr. It seems to me that the main criterion is that of orientation to man. Subdivide this and you've got golf courses, the Merritt Parkway, the completely urban environment which is ecologically and climatologically so distinctive, the museum pieces, areas reserved for study, and the recreational forest where you go fishing. There is a whole system and the parts have different purposes, different functions.

Darling. I think Bates is rather trying to limit the suburban forest and to define it rather heavily, more than we should. The suburban forest, wouldn't you say, is that forest which is used by a certain number of people. I know that it will vary in the amount of treading it gets, but at the same time the degree of treading is probably a very good criterion of forest use, of suburban forest use.

We have to realize that with the suburban forest, what we want more than anything else is amenity. Or, to go back to a sixteenth century English word, a "pleasance." I am sure you have used it yourself in the 18th century and you will probably use it more now than we would in England, this word, "pleasance," because you have more relict words than we have. I think "pleasance" is a very good word, and I think that is what we are after, isn't it, "pleasance"?

Bates. The reason that I restricted the definition of suburban forests was because of my interest in the animal problem of getting along with man. From the points of view of squirrels, robins, or racoons, the residential forest is different from the reservoir or the nature reserve.

Spurr. Darling has brought out a British word which we don't use. "Amenity" is a very nice summing up in one word of what some of our desires are. Another word we don't use in this country, that has always impressed me as being useful, is "derelict woodland." We have so much of this derelict woodland that we would like to convert it to amenity or usefulness.

Bates. I'll abandon my concept of the suburban forest and call it the residential forest.

Spurr. I think that this is still too limited because the suburban forest is really the whole matrix of the state.

Bates. Yes, but it is divisible into a number of distinct things.

Spurr. I can see an ownership pattern and a pattern in how it is going to be managed. A watershed forest has got to be managed differently from a woodlot that is in private ownership. A woodlot that is owned by a lawyer in New York will be managed differently from a woodlot that is attached to a farm. To me, however, all this is part and parcel of the same biological community. The suburban forest is all of Connecticut

except the strip along Long Island Sound and up the Connecticut Valley and little bits of farm land and salt flats. It is really one great ecosystem.

Bates. Yes, but if you look at it from the point of view of a red squirrel, the difference between a residential forest, a derelict forest, and a primeval forest is enormous. The squirrel's point of view leads to the interesting questions of natural history in the city. What animals have been able to adapt to New York apartments? I think John Kiernan wrote an unfortunate book with the title "The Natural History of New York." He deplored the things that had been displaced and said hardly a word about pigeons. Pigeons are greatly neglected: we have had a problem trying to find interesting colored photographs of pigeons. We can get them of ivory-billed woodpeckers more easily. I feel strongly about the need for study of the animal problems of getting along with man from the point of view of animal behavior. This should interest The Connecticut Agricultural Experiment Station because it involves basic biological research. Let us keep the residential area within the agenda somehow.

Dansereau. Couldn't you say the suburban forest is the forest that is not being used for producing either crops or timber? That would be suburban since the people who live there essentially use it as home, as recreation, for pleasure, for essentially non-economic purposes.

Collins. Our concern at this particular conference is not with azaleas and forsythias except when some insect migrating from the suburban forest threatens them. Whereas an individual may be quite concerned over plants growing in his yard, he is not going to say much about the trees growing naturally between his lot and his neighbor's, where he tends no lawn and seldom ventures. The forest we are concerned with here is sometimes found between yards, but most often between towns. I think we should distinguish it rather carefully from the horticultural aggregation in people's yards.

Dansereau. There are two extremes we have to keep in mind and the object of this conference lies exactly between the two. One extreme is the garden, no matter how much expanded, where essentially every individual plant is accounted for by the owner. The other extreme is forest, and I am sure there must be some in Connecticut, which is in a state of recovered virginity. This forest is seldom referred to and behaves essentially as a wild forest. In between is our subject, a semi-domesticated area, that we can call the suburban forest.

Russell. We are in the usual semantic difficulties. We are dealing with a highly interdependent system that is a continuum of biology, economics, and politics. If we are really going to get out of the area

of philosophy and semantics and come to grips with some of the more specific problems we must ask the Station staff to define this forest.

Stephens. The suburban forest in Connecticut is that part of our forest land which is man-oriented. It is the land surrounding and permeating the clearings for cities, farms, homes, and highways. This land contains sufficient trees to give a wooded appearance and is generally excluded from horticulture and agriculture. A suburban forest provides privacy, varied scenery, recreation, and a backdrop against which man carries out his daily activities.

Purpose of the Suburban Forest

The Forest: What It Does and How It Is Established

Frits W. Went

Before discussing some problems about the ecology of the forest I would like to suggest specific functions of a forest. What does a forest do? How do trees influence the environment? There are, of course, a number of things which were already mentioned – water conservation, soil conservation, retention of minerals, and those all will be discussed in detail later. In addition, there is wind and dust control. What I would like to stress especially is the climate control which a forest gives. Actually forests, street trees, and parks act more or less as air conditioners for a city.

Normally the total radiation which reaches the surface of the earth is largely absorbed by all objects it strikes. If this radiation strikes asphalt, cement, or stone, only a small percentage will be reflected but over 90 per cent is absorbed and is transformed into sensible heat which registers on a thermometer and which causes an increase in temperature in the adjoining air. This is exactly the same thing which happens in a desert where also 90 per cent of the incoming radiation is transformed into sensible heat.

In the case of the forest the same total amount of energy is received. Again a small percentage of the radiation is reflected, about as much as in a city, but the rest of the radiation instead of being all transformed into sensible heat is partially used for heat of evaporation. This is something which we don't measure as a temperature increase but as an increase in relative humidity. Depending on the amount of available moisture, 60 to 70 per cent of the incoming radiation is used for heat of evaporation so that a very much smaller amount of energy is transformed into heat, which means that there is also a very much smaller increase in air temperature. In addition there is a certain amount of radiation energy which is used in photosynthesis. When we add this all up, only a very small fraction of the incoming radiation is transformed into sensible heat in the forest.

At night the temperature relations in a forest are also quite different from those outside. Through radiation into space there is considerable cooling of all exposed objects. In the case of the forest the cooling caused by this night radiation at tree-top level is transferred to air which will

descend toward the forest floor keeping the inside of the forest at the same minimal temperature as outside the forest. During the following day most of the air heated by radiation absorption in the forest canopy rises so that the forest floor temperature does not rise very much during the day. This is also indicated by the fact that the average soil temperature in the forest is lower than the average yearly temperature of a particular location when measured outside the forest.

Taking all this together, a forest acts as an air conditioner, keeping temperatures much more even and preventing excessive heating during the day. This is in sharp contrast with what is measured in the desert where there are big extremes in temperature from day to night.

In an ordinary city without much planting the climate is very much like that of the desert with considerable extremes in temperature which can be prevented by having street trees, parks, or surrounding forests. For this reason alone I think that parks and suburban forests are essential for pleasant living conditions, and, therefore, cities which have lots of parks have a better climate and are more pleasant to live in than concrete deserts of the centers of cities.

Forests and vegetation in general influence the climate also in another way. This is by the production of the heat or summer haze which is due to volatile organic materials produced by vegetation in general. This haze layer has been insufficiently considered by meteorologists. This haze is important since it absorbs almost 20 per cent of the total radiation. This absorbed radiation cannot increase the surface temperature any more.

There are many areas of the world where the importance of suburban forests is recognized. For instance in Holland in the newly reclaimed land, every city (which is a completely synthetic city because it was built where the sea was previously) is laid out surrounded by forests, and this is done not just for recreation but also I think for the specific function of improvement of the environment. There, of course, in those completely flat lands, forests are also important to reduce the very strong winds.

In most of the areas we are discussing today the forest is a climax vegetation. Yet often abandoned land does not give rise to a new forest. The reasons for this are quite complex. Especially in areas with very high rainfall the soil may become sufficiently leached, so that the nutrients which were in constant rotation may be leached out of the soil. In other cases, frost hollows may appear after the disappearance of the original forest where reestablishment of the original forest vegetation is practically impossible.

Now, what are the factors in the establishment of a forest? There is in the first place seed arrival and seed storage. We find that in new forests

very often a single live tree causes the new establishment of the forest. A secondary forest usually consists of plants which have very light seeds; this is true in the tropics and I think it is true also here in these areas. Heavy seeds are disseminated mainly by animals, so that oaks or horsechestnuts do not become established unless animals are bringing the seeds in from neighboring areas, and if there are no horsechestnuts or no oaks in the neighborhood then they cannot become re-established. There is the possibility that oaks from an abandoned oak forest remain alive for a long time in areas which are regularly grazed, for instance in Australia and Israel. Here it was shown that originally the oak population was very high in the Judean hills. But 10 years ago there were no oaks growing anywhere at all anymore. When the goats disappeared with the Arabs, then suddenly oaks came up everywhere and there were definitely no acorns about. When they dug up these oaks, it turned out that each low oak tree was attached to a very heavy root which had been there for centuries probably, so that the oaks remained alive because each year a few more shoots came up which were, of course, regularly grazed off, but there was enough photosynthesis each year to keep them alive. In general of course that doesn't happen.

The second problem is one of seed survival. There must be proper sources of seed, and that is again exceedingly interesting in the case of oaks or horsechestnuts. Those seeds have to go through winter, but you cannot store the seed. If you collect horsechestnuts or acorns and keep them over winter and put them out next year, you have lost all of them. They just don't germinate. What happens in nature? In the first place, the optimum water content of those seeds can be maintained by storing them at a humidity of about 80 per cent, where they maintain their viability. When they are kept at 100 per cent they rot, and when you keep them at 60 per cent they lose their viability completely, so you must store them at a rather high humidity, which, of course, is done if they are stored in soil. This of course happens when they have been buried by squirrels or birds. These seeds usually also need stratification, such as the horsechestnut. This does not germinate in spring if it has been stored in the laboratory because it needs a cold period. Again, if we had these buried in the soil then they get that also, and that is the reason why you find horsechestnuts germinating in many places if there are areas where squirrels can bury them. So for this we need also an animal population.

We have just discussed one aspect of natural stratification of seeds. This is a very important factor as I found out in my desert studies. One of the commonest desert grasses is *Bouteloua*. When seeds of this grass are picked from the plants when ripe they will not germinate at all.

On the other hand, seeds which have been lying for a year or more in soil under the natural conditions of the desert germinate right away under proper rain and temperature conditions.

We have now discussed seed dispersal, seed storage, and seed treatment as factors in the development of a new vegetation. The next step, the actual germination process, is I believe the most important single factor in the actual establishment of a vegetation.

A considerable amount of information on the desert vegetation I have been able to collect by studying its germination. Desert ecology is largely the ecology of germination, and I have become convinced that this is also to a large extent true for tropical rain forests. I know practically nothing about the temperate forest. After a good seed year in maple forests, you will find seedlings by the millions, but in the tropical forest, germination is a rare phenomenon. One of the most remarkable things about that is that you never find a seedling of the old tree, under this tree. You find them only away from the tree. So apparently there is a specific inhibition as it is shown in so many desert plants, an inhibition of germination by the mother plant. This is one of the major factors why you do not get pure stands in the tropical rain forest but why there are several hundred different species forming the mature forest. When you have pure stands, let's say the *Eucalyptus regnans* forest in Australia, one of the most magnificent forests that exists, where every single tree is 295 feet, the uniformity of that forest is due to the fact that new trees never germinate after the original establishment. I have talked with some of the men who have been studying them, who found seedlings only rarely. After a fire you get a new forest in which every tree has the same age because they all germinate at the same time.

Once established, the old trees prevent the germination of new ones. In recent years I have visited several rain forests and found relatively few seedlings. This was true also in Java where I worked more than 30 years ago. Of the few seedlings which do develop most will continue to grow and develop into small trees. There is no preferential dying of the rain forest trees at any particular age and one finds that the attrition rate is the same for seedlings and young trees as it is for older ones. This was approximately 2 per cent per year in a forest near Belem in Brazil and somewhat higher in the darkest areas. This fits fairly well with some other observations which I made in Java. There a considerable number of trees had been measured by Koorders in 1890. When I re-measured these same trees, which fortunately were numbered and could be located, it turned out that the large trees had either grown considerably in diameter or they had died. The small trees, on the other hand, which were growing in the shade of the old jungle giants, had not grown at all in most cases and had just marked time to be able

to start growing the moment the shading tree had disappeared. This is a normal pattern of rain forest growth, which we are reproducing at present in the Climatron, the new greenhouse at the Missouri Botanical Garden. We hope to establish there an actual Amazonian rain forest, but this has to be done by first planting a number of fast-growing secondary forest trees, such as *Cecropia*, *Ochroma*, *Triplaris*, etc., and underplanting them with young slow-growing trees of the primary forest. These *Ochroma* trees have grown as much as 25 feet in a 12-month period.

Another quite interesting thing in the tropical forest is that you find so very few trees fallen down, which have crashed. It is something which every collector in the tropics knows; if you want to cut a tree so that you can collect flowers and branches, you may have to cut five trees before the first one will fall down because it is so completely tied in with lianas to other trees. So in a tropical forest, very few trees actually crash. The trees just die and break down in pieces. This is a natural phenomenon, a physiological death. This is due to a gradual increase in water resistance from roots to branches, until the water resistance has become so great that no new growth can develop. Then that branch dies, then some larger branches, and ultimately the whole tree dies. Thus it falls down in pieces. The same thing occurs in the temperate forests such as on the Olympic Peninsula in Washington State, where you also do not see many trees lying down. I actually saw a piece of a tree fall down from the top; we almost got under it. Here in New England the situation apparently is very different. Here the hurricanes have an evolutionary effect in that a remarkably large number of trees can be destroyed and can be felled by such a hurricane.

Thus the first ecological interest I see in the forest of the suburb is its effect on the suburban microclimate, ameliorating the concrete deserts of the cities. The second is the establishment of a new forest on forsaken farms. My experience tells me this may be a problem of seed germination.

Purpose of the Suburban Forest

Silvicultural Objectives in Suburban Forest Management

Stephen H. Spurr

My remarks deal with the use of the scientific method in approaching the problems of the suburban forest. They are based on a very simple thesis, one which is neither unique nor original. It is the question of how we, as forest ecologists or silviculturalists, can, out of the wealth of ecological concepts and principles that are presented in the other lectures, focus our attention upon particular studies that we can make in an Experiment Station working with public funds on public problems in this deciduous suburban forest.

This forest is an ecosystem, which is defined in a broad sense as the complex of the forest as it exists together with its plants, animals, climate, and soils. This complex, as we all know, is enormously elaborate and interacting with no beginning and no end. It is not self-contained, being affected constantly by external forces and in turn affecting the external environment. Somehow we have to use our human capacity for simplification to pick from this complex some practical research projects.

In order to come up with valid research projects dealing with the suburban forest, we must identify what we have to work with and what we wish to accomplish. Our task can be expressed as a regression equation in which the aspects of the forest which we can manipulate become the independent or X variables, and our objectives become the dependent or Y variables. By altering certain factors of the environment, we can achieve certain ends. With such a simple conceptual framework expressed in the form of a regression equation, we can, perhaps, make some headway in understanding or at least working with the forest ecosystem.

By defining what we can do with the forest ecosystem and what we want from it, we can solve our philosophical regression equation and thus determine how we can get the maximum return from a given input. We can learn what we can do to the forest that will create the greatest measure of desired changes. Our interest is in the suburban forest and in its ecosystem as the medium in which suburban life exists. We are not interested in it as an ecological system independent of man.

USES OF THE FOREST

Since we want our answer in terms of dependent variables expressing human use, I will review briefly some uses for which the forest exists, concentrate our attention on the conventional uses to which the forest is put, and evaluate their importance to the suburban forest.

Starting with timber production, I think we can say categorically that we have little interest in devoting the suburban forest primarily to sawlog or pulpwood production, although these may well be welcome by-products of forest management. In the northeastern United States, timber growth rates are only moderate. Furthermore, high timber values are of secondary interest to most owners of suburban forest. The minute we try to organize a large commercial forest in the milieu of the high taxes of suburbia, we are committing ourselves to an alternate use of land that competes poorly. Devoting land to growing timber purely and simply for sale is seldom feasible in the suburban forest. I speak as one who makes his living by teaching silvicultural techniques designed primarily to grow trees for forest products. Certainly, anyone who has worked in the high-producing pine forests of our own South or in the Douglas Fir region will realize how poorly the deciduous hardwood forest competes in the world timber trade, except for the fact that, by definition, it is close to the markets.

Second, water production is another use of the forest. Dr. Waggoner has spoken of this. Certainly the water-holding capacity of the forest resulting from the creation of soil-surface structures that permit infiltration and absorption of water are important. From the standpoint of total water production, however, we all realize the truth that Dr. Went has pointed out: the forest is a tremendous consumer of water. If we wish to maximize water production without regard for flood control, then the best thing would be to reduce the amount of forest. But the forest is a water regulator as well as a water user. There is a wide range of forest vegetation that will give a watershed with sufficient capacity. Watershed management, in other words, tends not to be a limiting use. It is a use that is secondary to other purposes, and we may pass over its consideration.

Grazing and range management are in much the same situation. These uses are relatively unimportant in the suburban forest.

Of the multiple uses of the forest, therefore, we have more or less eliminated grazing and range management, and we have minimized the importance of timber production and watershed management. What is left? Perhaps there are three: (1) the use of the suburban forest in moderating the environment in which man lives; (2) the value of the suburban forest as a filter, protecting the senses of man from the sights,

sounds, and smells of civilization; and (3) the aesthetic pleasure provided by the forest.

The first of these three uses has already been emphasized: the forest moderates the environment. The suburban forest is the environment in which suburban man lives. We are 6 feet tall; the forest averages perhaps 60 in height. With a ten to one height advantage over us, the forest creates a more equable climate for man in the midst of a more variable and rigorous regional climate. The forest reduces the variation in temperature. In it, the nights are warmer and the days are cooler; the winters are warmer and the summers are cooler. Indeed, the forest reduces the variation in almost all the factors of environment — not only heat but also humidity, wind, light, and even precipitation.

Second, not only does the forest buffer us from the elements, but it also buffers us from all mankind.

I might preface this point by drawing from my own experience. For a number of years, I collaborated in studies on the gypsy moth, and these studies included one sample plot which represented for that locality the worst of all possible gypsy moth hazard conditions. When I myself came to buy a farm in New England, it just so happened that I bought the farm that contained this particular sample plot. In other words, the fact of poor forest site quality did not influence my judgment in buying the land. I wanted the land because I wanted 90 acres of space around me. This was the value that I purchased.

The value of the forest in buffering us from mankind is well stated in the definition of a primitive area given in the recent report of the Outdoor Recreation Resources Commission. There, the primitive area is defined as an area that gives man a sense of privacy and of being alone. It is, indeed, this need which the suburban forest supplies to the urbanite. Living in close contact with our compatriots, we have the urge to get apart from them, at least sometimes. When we are in the middle of the forest, we are protected because the forest is a great insulating blanket — a layer of balsam wool as it were — that not only protects us from the elements, but also protects us from the sounds, the smells, and the sights of the urban civilization which surrounds us. It is a protective cover which filters sound, filters smell, blocks our vision, and perhaps helps to filter radioactive fallout. I submit that the suburban forest is of prime importance to us in providing a feeling of space and a feeling of privacy.

Third, we come to the aesthetic or amenity use of the suburban forest. Just as it is important to us that we be buffered from civilization, it is equally important that the filtering structure which buffers us is also attractive. Here we must come to human values and judgments; for what is attractive to one of us is not necessarily attractive to another,

and what is attractive in one age may not remain so in another. Without being an expert on aesthetics, I may, nevertheless, list attributes that are generally desired in the suburban forest. One is greenness. There is a restfulness in greenness, particularly in the muted light within a vigorous forest. For another, we wish our forest to be as varied as possible. There is a monotony in numbers. We don't like too many goats on the mountainside, too many gypsy moth larvae in the trees, or even too many trees all of one kind and of one size. There must not be too much disease, or too many of any insect or other animal predators. We desire a healthy balance of plants and animals, varied in kind, size, and locality.

In this connection, we should note that many plants and animals may be attractive in small numbers but monotonous in large. One of the most monotonous landscapes in the world is in those parts of Australia where the many species of eucalyptus all provide the same grey-olive drabness for the whole landscape. The same applies to flowers and birds; the more varied they are, the better we like them. If a wildflower, however, becomes too common, it becomes a weed; and if a bird becomes too common, it becomes a pest.

In this connection, I suggest that society cares little whether a given animal or plant is native to the area or an exotic. Actually, the distinction is one made strictly from an anthropocentric viewpoint. It doesn't make any difference to a tree whether his parents arrived by free flight or in an airmail envelope. Each plant and animal is a part of the present ecosystem at the present moment of time and at a given point in space. The ancestors of each arrived at different times in the past just as did those of our human inhabitants. In the glaciated Northeast of the United States there is no such thing as a native animal or plant. All are introduced.

When we speak of preserving the native fauna and flora, perhaps we really wish to preserve our own childhood picture of the locality. If a plant or animal is part of our preconceived notion of how the forest should look, we approve of its being there. If not, its presence adds a note of incongruity. Consider the pheasant. I am sure that many people in my part of Michigan think of the pheasant as a native bird, and that there are few who, knowing that it is introduced, would like to eradicate it. There is too much pleasure in watching them cross your lawn early in the morning. Similarly, so pleasant to see are the blooms on the Japanese cherries in Washington that there are few who, knowing that they are introduced, would like to cut them down. My point is that we don't really care whether a plant or animal is introduced or native. What we do care about is whether it seems to us to be a normal part of the environment and whether it is an attractive and aesthetic part in

accordance with our own preconceived notion of how the environment should look.

In summary, the suburban forest is of limited importance in timber production or watershed protection. It is, however, of major importance in moderating the climate in which suburban man lives, in protecting him from the sights, sounds, and smells of civilization, and in providing him with an environment that is pleasing to his senses. In our research equation, our objective is to produce a protective insulating blanket which is as aesthetic as possible. We may not be able to define the nature of this blanket precisely, for the aesthetic values in particular will change and evolve as our civilization and culture change and evolve. The dependent variable in our research equation is such a forest.

TOOLS OF SILVICULTURE

So much for the objectives of suburban silviculture. How can we attain them? What are the tools of silviculture by which the forest can be modified to achieve these objectives? Although we can actually do a great many things to the forest, there are only relatively few tools at our disposal within the limits of the little money usually spent on forest management. These include cutting, fire, and mechanical and chemical treatment. With these, the forest can readily be modified at a relatively low cost so as to approximate as closely as possible the conditions that we desire.

Cutting is a basic tool of the ecological silviculturist. Trees can be cut down inexpensively and quickly; so can shrubs. Second, mechanical treatment is readily possible in our mechanistic age. With bulldozers, earth rakes, and many other implements, the trees can be torn down, brush can be cleared away, and the soil may be re-formed. Third, fire is an important tool in the hands of the forester, although it is, of course, a serious hazard when uncontrolled. Possibly, though, the very nature of the suburban forest effectively eliminates the silvicultural use of fire to any large extent. Fourth, chemical treatment offers many opportunities for improving or damaging the suburban forest. Chemicals may be applied by air or from the ground. They may be anything from growth-promoting chemicals such as fertilizers to plant and animal killers of many types. Intermediate between the extremes are growth regulators which affect the growth of different organisms differentially.

In the suburban forest, chemical treatment probably will continue to be the most important. In this environment, we are probably not going to cut much; we are certainly not going to burn much, and if we intend to keep the forest as a forest, we are not going to do much mechanical treatment. Of the various tools of silviculture, then, the

most important in the management of the suburban forest is chemical treatment. We have an enormous range of chemicals at our disposal, at different concentrations and seasons, and these affect different organisms in the forest differently. There is great room for investigation of the effect of these chemicals on the forest ecosystem. There is a great danger inherent in chemical treatment; yet there is a great potential gain in using chemicals to achieve the objectives of man.

SUMMARY

Combining the tools at our disposal with the objectives of forest management in suburbia, we may begin to define the types of ecological research that should be pursued. Essentially these fall into the category of the effects of chemical and other treatments on the value of a forest as an insulating blanket and as an aesthetic backdrop to our lives.

Specific problems are many. One that has intrigued and plagued us at the same time is the effect of DDT upon the fauna of the forest. Another is the effect of 2, 4, 5-T upon the over-all vegetation and upon plant succession. Still another is the effect of gypsy moth control upon the forest ecosystem. All are complex problems because we are dealing with a complex ecosystem in which we are consciously affecting only certain elements with the objectives of attaining only certain ends. Our independent and dependent variables are few. They have been chosen because of their practicality and because of their importance to man. Their study, however, will reveal much about the complex forest in which we live.

Purpose of the Suburban Forest

Man and Nature

Marston Bates

We have been tending, in our discussion, to a sort of ecological determinism. This morning someone referred to the ideas of Ellsworth Huntington, which I suppose could be labelled as climatic determinism. The Huntington thesis, it seems to me, can be reduced to simple terms. New Haven, obviously, represents the apex of contemporary civilization. The climate of New Haven therefore must be particularly favorable for civilized developments. Athens in the fifth century B.C. was also somewhat civilized. Therefore the climate of Athens in the fifth century must have resembled that of New Haven today.

It is easy to ridicule deterministic explanations — they represent one class of the general fallacy of single causes. Yet there is often some truth in them, even in ecological determinism. You don't expect a maritime culture to develop in Kansas, for instance.

As we talked about productivity ratios in relation to man's use, I couldn't help but think of the Mayan cities of Guatemala, or Angkor Wat in Cambodia. You can say, "All right, they disappeared." But at least they lasted longer than Connecticut has so far. I think it is very difficult to look at human action or behavior in terms of a particular kind of biological community — man, through history, has tended to become divorced from particular communities. I am saying much the same thing that Darling did, perhaps in different terms. Let's glance at this question of the relations between the human animal and the biological community.

We might try to go back to the beginnings of man and reconstruct the possible ecology of the protohominids — to use the title of an elegant article published by Bartholomew and Birdsell in *The American Anthropologist* about ten years ago. I suspect these protohominids were social carnivores, behaving in relation to the biological community much as wolves do — they are also social carnivores. We must have been social for a long time because solitary man is a pretty puny and helpless creature. We have also been carnivorous for a long time. Our physiology is adapted to the digestion of raw meat, from oysters to beefsteak — and I at least prefer my meat that way. Our ability to handle vegetables without fire for cooking is much more limited; our physiology is not adapted to the digestion of raw potatoes.

The protohominids were thus predators — high order consumers — behaving like wolf packs, or like the bands of baboons in Africa today. These higher-order consumers are curiously unimportant in the biological community. As a zoologist, I am all in favor of animals, and I like to think they are important. But you can also look at them as a sort of frosting on the cake of the biological community. Odum has been talking about El Yunque in Puerto Rico — a forest that I like, though I won't agree to call it a rain forest. But he pointed out how unimportant animals were in the biomass of the forest, and I think this would be true of any forest.

I don't know whether anyone has done it, or how it could be done: but I bet that if you could get a measure of the animal protoplasm per hectare of forest and compare it with the animal protoplasm per hectare of grassland, that the two would be similar. In some cases, the savanna or grassland would probably win — despite the much greater bulk of plant material in the forest. You can hardly find a leaf in the forest that hasn't been nibbled by something; yet most of this prolific vegetable material never goes through the animal system at all.

Man as a higher-order consumer would thus be a trivial part of the ecosystem in which he existed. Of course this changed greatly when man learned to control and use fire. But the biggest change came, I think, with what the anthropologists call the Neolithic Revolution — the discovery of agriculture and animal domestication. Man then started to destroy landscapes or vegetation he didn't want, replacing it with vegetation he could use. He was still limited by the community in which he lived — that is, the kind of thing he could grow would be determined by the characteristics of the region. Man was changing the community, altering it, dominating it if you will, but he was still directly related to a particular kind of ecosystem.

Man's independence of particular ecosystems started with what Gordon Childe has called the Urban Revolution. This turned on learning to store and transport food, which permitted the transition from village to city. Through trade and tribute many different biological communities — ecosystems — could be drawn on to support the city. Classes of men could develop who were freed from the necessity of producing their own food — soldiers, priests, philosophers and kings.

With the Industrial Revolution man started developing non-biological mechanisms of energy production and the process of separation from particular biological communities was accelerated. There is much talk now about our moving into a Nuclear Age — but I personally have little faith in the future of nuclear energy, at least for constructive purposes. The British experience with the use of nuclear fuels for generating electricity has not been reassuring, and I understand that the German

government is retreating from its plans for the development of nuclear power. Uranium is fine for making big bombs; but I suspect that if we manage to survive, the great power source of the future will be some direct method of converting solar energy. Perhaps then the Sahara will be the industrial center of the future, or maybe Arizona. But this is anyone's guess.

The series of changes since the Neolithic can thus be looked at as a retreat from dependence on particular ecosystems. When we go out to lunch in New Haven, the things we are likely to eat — and food relations are basic in the community idea — come from a wide variety of ecosystems. This always surprises me when I stop to think about it. We still can't develop a maritime culture in Kansas, but we can get lobsters there as easily as in New Haven.

The characteristics of our cities have nothing to do with the type of ecosystem that originally covered the site. The nature of Ann Arbor is not determined by the fact that the location was once covered with deciduous forest. One town may be an academic community, another a farming center, a third industrial, and so forth. The nature of the human activity is much more important than whether the original ecosystem was prairie, pine woods, or deciduous forest.

Vernadsky long ago recognized this by saying that the biosphere was gradually being replaced by the noösphere. I don't particularly like the word, but the idea is that man-altered landscapes are gradually coming to dominate the planet. Man's alteration of the ecosystem, as Darling has pointed out, is essentially a process of simplification. We have reduced the complexity of the ordinary food web with its network of interrelations of animals eating each other. With the use of fire for cooking, man has been able to move into the position of a first-order consumer, living directly on vegetation — the most efficient animal position from the point of view of maintaining large numbers of individuals — and I presume we have to maintain our numbers. Or as meat eaters, we have moved into the position of second-order consumers. We grow corn and eat it, or feed it to hogs and eat them. Only in relation to the marine environment, in eating larger fish that have eaten smaller ones and so forth, are we in the position of a higher order consumer.

Furthermore we do not tolerate competition. We don't want to share our sheep with wolves, our chickens with hawks — we won't even share our apples with worms, even though the worms might add to the nutritional value. This man-altered, simplified system, of course, is more efficient than the natural complexity. Quantitative-minded ecologists, particularly Evelyn Hutchinson and his students here in New Haven, have shown that there is a tremendous energy loss with each

shift in consumer level, the maximum transfer from one level to the next being something like 6 per cent of the energy potential.

Charles Elton, in his lovely little book on "The Ecology of Invasions," has shown that the danger of this simplification is the liability of catastrophe. It seems to me that this is fairly well documented. Attempts to set up simple predator-prey relations in the laboratory end rapidly in extinction — you have to set up a quite complex system for it to run at all. In nature, catastrophes like epidemics and locust outbreaks are apt to characterize the man-altered situation. And in relatively simple natural ecosystems, like those of the Arctic, populations are liable to violent fluctuations, as in the notorious case of the lemmings. The simplified system has less play in it, less room for adjustments, so that anything happening to one part affects the whole system. This could well apply to the management of the suburban forest. The problem is to compromise: to maintain a relatively efficient position without simplifying to the danger point.

Our whole attitude toward the ecosystem is surprising. We not only don't want to share our apples with worms, we even try to defeat the decomposing system by putting our dead in lead-lined caskets. This human tendency to try to be apart from the natural system has been going on since before the Neolithic and results in the curious paradox of man as a part of Nature, and yet apart from Nature.

We get awfully pleased with ourselves because of the clever things we do, but we haven't really repealed any natural laws. If you jump off the top of the Empire State Building without a parachute, you go splash when you hit the bottom. We haven't withdrawn the law of gravity, and I don't think we have withdrawn any ecological laws. I am reminded again of the aphorism of Francis Bacon, that you cannot command nature without obeying her. Our problem, then, is to find out how we can work with the natural system, and at the same time maintain the relatively efficient position demanded by our numbers.

I would like to shift to another point of view and look at the nature of the human environment. The problem of organisms and environment is one that has been bothering me increasingly over the years. I feel sometimes as though it would be better if we had no such words because they are constantly misleading us. When I try to define environment, I get rapidly into the state where I no longer have any idea what I am talking about — which is always distressing.

In dealing with organisms and their environments, we are dealing not with discrete and different things, but with interacting and inter-related systems. The psychologist, Hadley Cantril, has said that we should think in terms of transactions between organisms and environments. Of course the psychologists are particularly impressed with the

extent to which our environment is our own creation, the product of our sense organs and the result of our learning or conditioning. What this room means to us, how we define the colors and shapes, how we perceive the proportions of the table, depends on what we have learned.

The perception psychologists can fool us easily enough, and in the process learn about the way we order our environment. The experiments I like best involve spectacles built so that the vertical axis, for instance, is rotated at an angle of a few degrees. If you put a pair of such spectacles on a well-trained sailor and he looks at an admiral, the admiral still seems to stand straight, even though he shouldn't be perceived that way. If the sailor looks at another gob, though, he sees him slanting all right. The husband of a newlywed pair will see his wife standing straight when he has the glasses on — but after 20 years of marriage, reality comes through more clearly, and the wife will be seen slanting, as she should.

Such perception experiments demonstrate clearly that what we see is in part a consequence of what is really out there, but in large part also a consequence of our interpretation — an interaction system. This applies to many other aspects of the environment. Biologists now believe that the nature of the composition of the atmosphere, especially oxygen and carbon dioxide, is a consequence of living activity as well as a determining factor in such activity. It goes back in a way to the problem explored by L. J. Henderson in his book on "The Fitness of the Environment." You can be just as surprised at how fit the environment is for organisms as at how the organisms fit with the environment. To a group of foresters, it is obvious enough that the kind of forest growing in a region is in part determined by the nature of the soil — but that the nature of the soil is also a consequence of the kind of forest. We are dealing with interaction systems and not with discrete and different things.

There is a trivial problem of definition also. At what point does an apple (with or without worms) cease to be part of the environment and become part of you? Is it after you have swallowed it, or not until the digestive process has been completed? I suspect that if we got a stomachache from eating a green apple, we would consider this to be an environmental effect.

There are many different ways in which we can analyze the environment. We can talk about the biological environment, the physical or climatic environment, and so forth. As a scientist, I believe in the existence of external reality and in the possibility of reaching some sort of an understanding of it. This external world, I suppose, makes up the total environment, the setting for any and all organisms. But only parts of this setting have direct effects on organisms — and the parts that affect any particular organism might well be called the operational

environment of that organism. With animals, part of this operational environment is intercepted and interpreted through the sense organ systems—making up the perceptual environment of any particular animal.

Many things affect animals that are not perceived. Cosmic radiation, for instance, could be considered part of the operational environment insofar as it affects mutation rates; but without a Geiger counter it cannot be perceived. The subvisible world of viruses and bacteria likewise are clearly parts of the operational environment. I like to think that if we had evolved in a universe full of naked wires carrying high voltage electricity we could have survived either by developing immunity to high voltage electricity (as we have to viruses) or by developing a sensory system capable of perceiving this kind of danger and thus avoiding it.

There is a human tendency, I think, to confuse our particular perceptual world with the "real" world, the total environment. We perhaps almost necessarily have to describe a forest in terms of our perception—in terms of colors and shapes and a rather limited range of odors. We can, with instruments, get measures of temperature, humidity, evaporation, radiation and such like factors that are relatively "objective" and dependent on our sensory system only for interpretation. But it is very hard for us to reconstruct the perceptual world of some other animal. What is the forest like as interpreted by the sense organs of a cat, a snake, a robin? I have spent many hours of my life trying to understand the perceptual world of mosquitoes, and getting quite desperate about it. How did they find their mates, their hosts, their places to lay eggs? Their perception of radiation, of sound, of odors was so different from mine as to be unimaginable.

If we go back to man and try to analyze the human environment, we rapidly find ourselves involved with a curious collection of factors that I have come to call the conceptual environment—the world of ideas. I first thought of this as the supernatural environment—the world of spirits. I lived for a while on an atoll in Micronesia, where the spirits that governed typhoons were just as real, just as important to cope with, as the sharks in the lagoon. The suffering from the violation of a taboo can be as painful as the wound inflicted by an animal; in both cases, sometimes fatal.

From my exalted position as a scientist in the tradition of Western civilization, I could see that this fuss about spirits was a lot of nonsense. The people had made the spirits themselves, and then were reacting to them. But on thinking further, we have little reason to be holier than thou toward the Micronesians or any other culture about their ideas. We Westerners, too, live in a world of ideas, a world that we (or

our ancestors) have created and that yet influences our every action. We are back in a special case of organism-environment interaction, a case that I presume is limited to the human species, but that also involves all living men. Our value system is one part of this environment.

Our attitude toward the suburban forest is an example. Yesterday Spurr started out by talking about our need for space, how the residential forest served as a buffer between man and man, family and family; a buffer also, as has been pointed out, against noise, dirt, perhaps even fallout, and a moderating influence on climate. I think probably everyone here feels the same way that Spurr does — wants trees in his yard because we share a value system. But I remember one summer in Sardinia being struck by the way the towns abruptly gave way to open fields, with no trailing out into suburbs and isolated houses. The same thing is true of Rome, Florence, and many other Mediterranean cities and towns. There will be big apartment houses right up to the beginning of the agricultural land.

This puzzled me, and I remember asking why people should live all crowded together with all of this space about. But I was told they liked it that way — they didn't want separate, independent lives; on a holiday, even, they all crowd together again on some beach. Perhaps it has something to do with the feeling of belongingness, of reassurance from close interpersonal association.

This poses the problem of who is right — we, who want some measure of protection from each other, or they who want to crowd together. Should other people be educated to appreciate the values of the residential forest, or should we only try to give people what they want, or think they want. We can move rapidly from the specific case of the suburban forest to the general problem of the meaning of resources. Resources for what? For what purpose, what end? How is my need or convenience to be reconciled with yours?

I rapidly get lost when I try to think about this, and everyone I know seems to be about equally lost. We are caught in the problems of cultural relativism — that what may be good in one context may be bad in another. We are left without any absolute criteria for judgement. Taking off from the suburban forest and resources, we find ourselves involved with questions of ethics and aesthetics. I have been trying to talk about this lately every time I manage to catch a philosopher, but, I must say, without much satisfaction. The philosophers don't seem to be much better off than anyone else — and sometimes I get the impression that they are more concerned with Plato and Spinoza than with the problems of the contemporary world.

But how can you determine policy, say, in relation to the suburban forest without some fairly explicit statement of your value system, your

goals, your purposes, the ends of your society? Maybe The Connecticut Agricultural Experiment Station should have a department of philosophy where these questions can be pondered.

One of the few positive things I have got out of worrying about these problems is an increasing feeling that diversity in itself is a "good." Several different approaches have brought me to this conviction. One was an attempt to find positive values in our contemporary civilization — which is extremely difficult. Often when I start talking about our civilization I sound as though I wish I were living back in the Neolithic. But this isn't true. Some aspects of the Neolithic may have been fun, but I would want to have my dentist with me, and modern equipment for coping with lions and diseases. Our civilization does have values, and among the greatest of these is diversity.

In a Neolithic culture, a village culture — Micronesian society is a good example — there is no possibility of being different. The common conceptual environment of the culture is accepted wholeheartedly — what we might call deviant behavior, strikingly different ideas, become unthinkable. There is no model, no knowledge of a different style of life from that of the tribe. But as civilization has developed and become complex, it has developed a wide diversity of styles of life, and increasingly a freedom to choose among them. The freedom is limited; we weep about the organization man and the pressures for conformity, and rightly. But we still, I think, have less pressures, and conversely more freedom, in the 20th century West than in any past human cultural development. We can be professors or researchers in experiment stations or bank clerks or thieves — there are all sorts of possibilities.

In an analogous way, I think diversity has a positive value in the ecosystem, or in the biosphere. It is "good" to have a variety of ecosystems; and it is "good" to have diversity and complexity within any particular ecosystem. Diversity tends to promote equilibrium within the system, and thus has utilitarian value. I think it also has value from the point of view of aesthetics and from that of ethics. It is left, in short, as one of the few things I can cling to in this relativistic world.

In talking about values, we are clearly involved with problems of the conceptual environment. In using this phrase I have not labelled any new sort of an idea. It is the same thing, I suspect, as the culture of the anthropologists and perhaps as the superego of the psychologists. I have simply made a shift in vocabulary. But I find this useful. When I look at the world of ideas in terms of conceptual environment, I recognize more clearly that I am dealing with a man-made aspect of the world. And if man made this aspect of the environment, surely he can alter it, modify it. Not easily, to be sure — there are probably all sorts of cultural and psychological laws operating and determining the

course of development. But if the human experiment has any meaning at all, we shall surely somehow be able to devise a conceptual environment in which we no longer need to do silly things like testing atomic bombs, and in which people and groups of people learn somehow to be less mean to each other.

I have wandered away from the suburban forest. But not really. How we deal with this, what we make of it, depends on our ideas — and I suspect we shall have to study the ideas as well as the trees. So maybe Dr. Waggoner should add a philosopher to his staff for the field work. Certainly, at least, there is a great deal to learn.

Purpose of the Suburban Forest

Discussion

Waggoner. We don't need to educate the taxpayers and the lawmakers to the need for the suburban forest. They have an interest, and it is growing. For my part, I think I am the one who needs educating. I would like to know why these people want a suburban forest. What do they want from this land that they are setting aside? If I knew what they wanted, then perhaps I could suggest the sorts of biology that we should be pursuing.

Went. I would like to speak of the dimensions of the air-conditioning by the forest. It depends on whether or not the wind blows. The calm condition is most important because then local heating occurs, creating rising and descending air columns. This causes the "bumpiness" of flight on clear days. The distance between two rising air columns may be about a thousand feet. Fair weather cumulus indicates where the columns rise. This thousand feet gives an estimate of the lateral spread of the forest influence.

Waggoner. In other words, you must live in or very near this forest for it to cool you. The city park on the other side of New Haven won't do us any good.

Went. That is why one big park is of little value compared to many small parks. When the hot air rises from the city blocks of stone, cool air from nearby parks can rush in.

Dansereau. We have two different phenomena here. First, a forest is a buffer, creating a microclimate that is relatively equable in comparison with the surrounding area. It is warmer in winter, cooler in summer, cooler at midday, warmer at midnight, than the surrounding area. The most highly developed type of vegetation in an area represents the maximum possible buffering and equalization of the microclimate.

The other phenomenon is the possible change in general climate caused by differences in plant cover. Is the deforestation of an area responsible for a decrease in precipitation in that same area, or an increase?

Lutz. This is a subject that has attracted foresters' interest for many years. One of the early champions of the regional effect upon precipitation by forests was Raphael Zon. He obtained his lore mostly from Russian experience. But in 1945 Zon remarked in a symposium of the

American Philosophical Society in Philadelphia, that whether the forest actually increases the amount of precipitation is, after 80 years of observation, still a moot question. To sense these effects we must be in the forests or very, very close to them. It would be wrong to infer that we could change the regional climate by manipulating the tree vegetation.

Waggoner. Thus the only way that we can benefit from a forest, so far as our environment is concerned, is to mix the trees with ourselves, as in the suburbs.

Russell. If it comes down to it, we can adjust the physical environment more efficiently and predictably by means other than manipulating plants. To me the more important role is to provide the human need for space in aesthetically pleasing surroundings. If we are going to use the scientific approach and think of the aesthetic and human values as dependent variables, these must be reduced to quantitative terms.

Odum. How much would the suburban dweller be willing to pay to the budget of his forest system along with the budget it gets from the sun? He would pay this contribution in exchange for aesthetic demands. If we knew how far the suburbanite would go, how many dollars per acre he would put into cutting, trimming, weeding and spraying, we might then compare that with the other budgets, saying, "This is how much we have got to work with."

Spurr. A man earning \$20,000 a year and owning an acre of land is willing to pay a great deal for lawnmowers, tree surgeons, DDT sprays, barbecue pits, and other "forest" activities around his place. The suburbanite will spend a great deal to create a pleasant environment around his house. We are talking in terms of hundreds of dollars per acre that might be spent if improvement in aesthetics, space, and insulation could be safely predicted in the suburban forests. This is a very high land use.

Odum. Do you suppose we could figure out whether the sun or man has the most energy?

Russell. Is the process energy controlled? Other things go into this equation besides energy in the physical sense.

Darling. You have an immense labor potential available in the suburban forest. In addition to the effort the owner will give to his acres for pleasure, giving up his productive money-making time just to keep himself happy, that labor bill might be supplemented. Only the other day a friend of mine, who had bought up part of the suburban forest to maintain more of it, not to have it let into quarter-acre lots, found that the tax load was heavy. He talked to his tax authorities about it, and they

said "Yes, it is heavy." But they kept on insisting, "What is it you like about this place?"

He said, "Well, I like it just as it is."

The authorities said, "That's right, and that's what you're paying for. We as tax people would rather see it all cut up into lots with house-holders: we could be taking money from them. You want it like this; therefore, you can pay for it."

I think you ought to be able to say to the municipal authorities, "You are taking money in tax for the maintenance of this land as forest rather than as asphalt, and, therefore, you should put it back, too." There is, therefore, the possibility of more money to be expended on the forests than appears.

Farb. We have many outstanding examples that conservation of the suburban forests pays in dollars and cents. Westchester County, N. Y., officials have studied what has happened to taxable land bordering the park systems. They concluded that the County has been reimbursed many times by the increased property evaluations following putting this land aside. We have the example of Milwaukee, which bought flood-plain and watershed land. They estimate they they have received a financial benefit between fifty and one hundred times the cost of the land. Dover, Massachusetts, is buying scenic easements to do exactly what Darling's tax man said should be done, keep the land as it is. The community is willing to spend the money because planners have proven that greenbelts benefit the town many times the cost of paying a landowner not to put up a factory. The landowner continues to enjoy his land, but does nothing to it except provide fire protection. Of course, there have been squabbles about insect and disease control. The state of Tennessee has purchased hunting and fishing rights to private land which cover the landowner's taxes and upkeep on this land. The land is well managed, the landowner receives an income, and people can use it. This is really a perfect arrangement.

There are approximately 4,000 community parks in this country. These are suburban forests maintained by a school, church, or town. In almost every case this is land now worthless for agriculture, or building, worthless for anything except growing trees as a crop and serving as an outdoor classroom for nature study and conservation. Dr. Spurr has said that this is not financially important, but in certain communities in Ohio and Wisconsin school activities have been financed by the harvest that comes from these forest lands. In addition they are training grounds providing potential conservation allies, youth leaders, people willing to assist in managing local forests. These people can mark trees, clear plots, blaze trails. There is an army of people capable of the same sort of contribution living around and in the suburban forests.

Spurr. A few years back at the Harvard Forest in central Massachusetts, we made a survey of why people bought and owned these lands. The results were surprising: many offered their land to the University so that the land would be taken off the tax list if a guarantee was given that it would be left as it was. In other words, almost everybody was owning it to maintain the status quo. Instead of getting back the questionnaire, we were offered thousands of acres of land.

I am in precisely the same situation as these landowners. My family owns a mile of lakefront on a New Hampshire lake. Trying to pay the taxes on it is tough, but we don't want to sub-divide it into 50-foot lots. We would be delighted to give it to the state, to the Federal government, or to anybody who will keep it as it is.

One problem is managing the privately owned forest, and the other is guaranteeing orderly urbanization with greenbelts.

Bates. What are the aesthetic questions? Are we victims of 18th Century French landscape gardening? Is the present practice preferable to Versailles landscaping? Are there objective measurements of aesthetic preference as well as economics?

Dansereau. I can illustrate this by the history of landscaping and painting in Australia and New Zealand. During the Colonial period, imitation of the Old Country was the thing. Eucalyptus were painted to look like elms and they planted elms in the gardens. With the rise of nationalist feeling, the popular taste has changed to planting "our big, beautiful native trees."

Possibly the mystique of conservation has operated much in excess of its legitimate objectives, so that conservation to an American is linked with everything in its place as God made it, with letting natural areas return as nearly as possible to their primeval state. The Europeans have reached far beyond this for a long time. Their parks and even their "natural" forests are designed, are planned.

There are two applications of planning in suburban forests. One is preserving reasonably large blocks of each of the major forest types, for at present some forest types are not preserved. The blocks should be big enough to study new concepts such as energy relations which are currently coming to the fore. To test them we need a variety of areas. The rest should be planned artificially. Introduce conifers where no conifers grow if it is right for picnicking, recreation, or aesthetic purposes. These two things should be thoroughly separated: the museum and laboratory on one hand and the recreational values on the other.

Spurr. Longfellow first used the term "forest primeval." He had no concept of an uninhabited forest; his conception was of an inhabited Acadia, not a virgin forest where the hand of man has never set foot.

Planning Suburban Forests

Discussion

The discussion of planning was provoked by an account of the New Forest, which is an old wood in England.

Darling. In England, there is an ancient forest called the New Forest where, believe it or not, Mesolithic man continues. He is a forest edge exploiter, bodging about, keeping a pig and an odd cow or two. These people are there yet. They don't farm well, and they have no intention of farming well. In this New Forest you have the Forestry Commission which manages the forest in the same way that you are speaking about forest management in this State. Then you have got a lot of stuff you can't reckon up, and you have got open spaces called commons.

Now the aim of this story is to show you a piece of absolutely nonsensical planning or else the complete lack of planning in relation to resources. First of all the Forestry Commission came. The Forestry Commission was to manage areas and the commoners said, "These people are going to take our common lands from us. We have got cattle and we have got sheep around, and they are going to take common land for trees." So the Forestry Commission was so anxious to show it wasn't going to do that, it even undertook to keep their commons clear of trees. They would keep the Commission forests to the forest areas.

Now war came along, and immediately in war you must have food production whatever happens. No matter what the fantastic cost, you must have food production in England in wartime. They set to at quite ridiculous cost to bash some of this land into agricultural production. You can grow bananas at the North Pole, everybody knows that, and that is exactly what they did in the commons within the New Forest. They bashed them about until they got magnificent crops of sugar beet and everything else, at what cost is simply never known.

At the end of the war, the commoners insisted that, as agreed, this land be put down to grass. The agricultural people put it down to grass. They had to soak that land with phosphates to get it to grass. Once they had it done, by jove, here was a beautiful billiard table sward. Every blessed thing in that New Forest — every pony, every cattle beast and sheep, fed on the new leys. In fact, people were carting cattle around to put on this new grass; it was so punished by the stock of all these little Mesolithic folk that the ground packed up with helminths of all kinds. The parasitosis was epidemic throughout the whole Forest.

Then, on these poor commons that were not being grazed, there shot up a magnificent, self-regenerated crop of Scotch pine. From the forester's point of view, this was excellent, because you can't get better Scotch pine than by regeneration. But, because of the legal situation, the Forestry Commission had to go in and knock down these beautiful crops of self-regenerated Scotch pine in order to keep the commons open. The agricultural people by this time were out. They were lucky.

You can see the money that is being spent, the turmoil, the complete lack of planning due to no coordinated land-use planning notion within the New Forest. Yet, for growing trees that country is wonderful. On this poor ground they will grow faster than anywhere in Britain.

The moral of this digression is that Connecticut has a chunk of country which is undergoing change. When New Englanders first dropped in here, they had to farm it. It wasn't until the Middle West opened up that the pressure was off, and it came back to what it belonged to, which was forests. When you have acid rock, fairly high rainfall and fairly steep slopes, the chemical answer is really cellulose, it is not protein. Nature and economics have gradually pushed this eastern seaboard back to cellulose production, and here is a most wonderful opportunity for overall planning. To an outsider it always appears as if here is a mental block. The North American objects to the notion of planning from the word go.

Here in Connecticut is a most wonderful opportunity for planned use of forests. Connecticut is heavily populated with fairly small communities permeating it. I do not see much difference between the remote parts of your forests and those nearer in. Lumber is not the primary crop, it is the secondary crop now. The primary crop is amenity. This is what the people in Connecticut are going to enjoy more than anything else in these forests. You have a secondary crop of lumber and a tertiary crop of game. Managing this floral and faunal complex comes down to just sheer planning. That is what I wanted to say with all this New Forest stuff. Here is an example of no planning and the idiotic situations you get yourself into.

Waggoner. Planning is upon us. But, you see, in the New Forest they did have planning. They planned to grow food crops there, and because they had a plan rather than a lot of individual decisions, the catastrophe was a huge one.

Let's say that it is given to me today to plan the whole landscape of Connecticut. I am afraid I might be making "groundnut" type mistakes.

Darling. I am sure you wouldn't. You need to be a little sillier than we were to do that, and I don't believe it.

Lutz. Planning in itself is no guarantee of success. The planning has to

be prudent, and we need to know what the objectives are. Then we have to assure ourselves we have the necessary knowledge to put the plan into effect. We have planted red pine in the southern counties of Connecticut and, although it was carefully planned, much of that red pine forest is in poor condition today.

Darling. If you had planning, as we understand it, at least you hold up utter misuse. Stop valley bottoms from being built over and so on. Obviously we in this room couldn't imagine going ahead without research and experimentation. Always the best thing is, if you don't know, leave it alone. That's a very great lesson to learn.

An agricultural experiment station, in a state like Connecticut, which is now much more concerned with the management of human environment rather than farming, is justified in going into research on what has been up to now considered trifles of some long-haired professor in the laboratory.

Russell. We are not against planning. We do fear centralization of decision-making in the absence of knowledge. By the diffuse nature of decision-making, you tend toward inertia and pay a price for it. The question is whether decisions should be centralized to make greater use of technical information. I would be much more content to have a scientist make this grand scheme for land use in Connecticut than I would the Governor of Connecticut. Similarly, I would feel more comfortable if somebody in addition to the scientist was involved, because although I respect his judgment, he is not all-seeing.

The extent to which these decisions are reversible is important. The location of an airport or subdivision is essentially irreversible.

Farb. In New England in 1955 we had the disastrous hurricane-flood. As a result of that, people in New England now favor planning. The town of Granby, Connecticut, for example, lost a neighborhood of cottages along a river, swept away in the flood. What did people do? The people in Granby set this land aside as a suburban forest in which no building was permitted. But, what do they do next? By instinct they know that this land belongs in forest. What do they do beyond that? What kind of forest? How should this forest be managed, or should it be managed at all? This is where the problem begins, and I think this is where the session could aid. I think the people are perfectly willing and ready to undertake planning for this land, but they need guidance in ecology.

Waggoner. Our planning is racing ahead of our ability to make sensible plans. Now we must delineate those parts of the suburban forests we are going to manage for specific purposes. Most important is the

part to be managed for pleasure, amenity. We have to say what amenity is, in clear enough terms to undertake research to prevent foolhardy decisions. Clearly research in this field is fraught with many more difficulties in definition and in accomplishment than ever was forestry or agriculture.

Corn yields have gone up because the agronomist knew he was to get more bushels per acre, and he did not worry about growing some rabbits and pheasants, too. This might be the clue to the success of their method. We must go on to consider the ecological methods to apply to this difficult problem.

Ecological Tools and Their Use

Simplicity and Complexity

F. F. Darling

As we get older some of us get out of this position of really doing research, and we are looking at other folks' stuff.

Ecology, I know, must become more and more in biological terms what economics is in monetary terms. I feel these two disciplines, both named from the same root of *ecos*, are completely at odds with each other and must get nearer. The economist is dealing with money, he simply cannot count values which don't take on dollars and cents as a symbol, while the ecologist has too often in the past been brushed off by his brother biologists as being superficial and inexact. I don't think he need be afraid of being called jack-of-all-trades and master of none. He can wear that one. The time is now coming, however, when the ecologist, if he is going to justify himself, must come down to the quantitative kind of thing Odum and Ovington will give us. This is the moment and time for that. They are getting it. This is the sort of stuff which we can hand to the politicians. The politicians will have to decide on action, but when we hand those chaps these good figures, these quantitative figures which Odum and Ovington provide, then we put a much greater responsibility on the politician to say what he is going to do. He can't brush off biology anymore when these workers can give him ecology in quantitative terms which he can apply just as he can the dollars-and-cents symbol in the economic world.

I, however, remain a naturalist and thought I might talk on the subject of simplicity and complexity which constantly impresses upon me the difference between sound and unsound ecological economics.

Agriculture sets out to simplify immediately. If you are going to grow crops you simplify an ecosystem in order to grow a mono-crop. If you are going to domesticate animals, you get rid of a large number of species and grow one or two. We know that in many parts of the world agriculture and stock raising have degraded the habitat. Let us assume that this is primarily due to lack of knowledge in management; an Agricultural Experiment Station is naturally having to correct that lack of knowledge so that one could maintain the habitat in agriculture. Nevertheless, there are areas where successful agriculture and stock raising have completely altered the existing ecosystem into a vastly in-

creased output. If as a philosopher or naturalist one says that agriculture makes a primary and big mistake of simplifying the habitat to such an extent that you arrive ultimately at degradation of the habitat, what are we to do? Are we to go back to the savages or not?

I think an ecologist is entitled to ask, "Where have new practices been applied, where have they succeeded, and where have they failed?" In New England you have a most beautiful example of ground which does not lend itself primarily to sustained agriculture. There are pockets, but when people first came here from England they were faced with getting a living somehow, not necessarily only from the few pockets of good soil. But as soon as the Middle West opened up a bit, the pressure was off here, these acid rocks and steep slopes were left, and they have gone back to this suburban forest with which we are concerned today.

Now, so-called good land, which you might see in the Middle West of this country or in Southeastern Britain, is all too scarce. (When I say Southeastern Britain I mean from the Firth of Forth down to Dorset — the good lands that comprise only half of England but which she tends to be generalized by.) This land which is so good and has sustained this very, very high farming of today, will keep on. We haven't reached the top yields. I am sure that agricultural techniques are going to improve and that yields from good lands will improve by 25 per cent or even more.

But the marginal lands, of which we have many in Britain, are constantly showing their inability to uphold agriculture through the years. What is worse, the higher agriculture becomes, the less able are these marginal lands to carry it in our day. They can carry a subsistence agriculture which removes man very little from the state of being part of the indigenous fauna. As long as he stays at subsistence level and farms in subsistence fashion, he gets by; but as soon as high farming is attempted on poor land, deterioration of habitat ensues.

Here you have accepted this fact much better than we have in Britain, I feel. You are ready to look at Connecticut in terms of the suburban forest. That to me, coming to this Conference, is quite a point. If we had been in Britain now, I am quite sure there would be a tremendous effort to let us give 50 per cent grants for scrub clearance. "We must keep the land in production, don't you know," say the tub-thumpers. Of course we have a great population to feed, so you can understand our ecological wrongheadedness; you haven't got the extreme of that trouble here as yet. I hope you never will, but the poor land must, I think, go out of agriculture, leaving high farming on good lands.

Now this simplification of habitat in agriculture, what does it really mean? We are pushing succession back from possibly climax to the initial

stages. Agricultural crops are annuals for the most part. Some are biennials, but even then we often crop them in their annual stage. Seeing the amount of bare ground we lay open, we know very well that oxidation and erosion go on. Now, we ourselves are hostages to fortune. By the accumulation of skill and hard work, we get by. Good land will take this capital, skill and hard work, while the poor land will take only the hard work and leave you little at the end. High farming is simplification carried to an extreme, dependent upon advantageous soil and climate.

In wild lands, on the other hand, we have become gatherers of wealth. We use the sheep because one man can manage a thousand mouths over the Sierra and the Limestone plateaus of the West. We can gather wealth very easily in that way. But we put nothing back; we only take away, not only the wool and the meat, but species of plants are grazed out, many of them the legumes essential to the maintenance of that particular habitat. Philosophically, I can't get away from the feeling that we started out with as children: We were taught that everything has its use, every animal has its use. We shed that very soon as we grow older and take an arrogant view the other way. But by "use" in biological terms, what I really mean is that each species is doing something in the habitat, that it has found itself a niche in the conversion cycle. You find that the conversion cycle in climax states is more complex as compared with earlier stages of succession, the efficiency of conversion is higher and losses from the system are less. In fact, organic matter is accumulated.

Mankind emerging from his prehistoric past has, with emergence from paleolithic conditions, begun to exploit these immense reserves built by the ecosystems of the past. He has not only learned to use the present biological resources, but has gone back to the fossil coal and oil. In the early stages where he was merely tackling the existing biological reserves, he was able to civilize because of the leisure granted by the easier existence gained. Now as time goes on, civilizations and religions grow, man has taken on the sense of *right* to do this, and now I think we are beginning to question. We are coming to a stage of questioning rights to use these things unless we manage them well for the maintenance of habitat and sustenance of yield from natural resources. That I suppose is what conservation is, if it isn't an obsolete word in these days.

Complexity means fullness of use. Let me go from this part of the world to Africa for an example. In Africa you have starkness of climatic impact, although great complexity within the environment. The actual biological activity in a miombo woodland, for example, is terrific. If you alter that biological community to try to produce a crop, you may canalize more of the energy through the guts of some human, but the

total energy turnover and conversion rate of matter is reduced. The number of ungulate species in Africa is very high. Each one of these 20 to 30 species in a habitat is making its own demands on the environment, and the carrying capacity of ungulates in an African habitat is much higher than under agriculture. I read a very important report in this country 3 years ago which said one had only to look at the number of ungulates in Africa to realize how well adapted the continent was to livestock production. That is dead wrong ecologically! He wanted to simplify, to reduce the spectrum of 20 to 30 species to 2 or 3, and expected to get as big as carrying capacity, as big an ungulate biomass, as with the 20 or 30 species that were there in Nature. This doesn't work.

The soil of much of that part of Africa where you get 6 months dry, 6 months wet, is very old; it has never been glaciated. They are senile, you might say; the base exchange and crumb structure are poor; these are not soils you can disturb without thought of consequence. You must let this existing and very beautifully integrated leguminous forest play its part in ameliorating the soils and yielding a seed crop of high protein content which is eaten by the wild fauna. With perhaps 6 months wet and 6 months dry at a fairly high temperature the whole time, the biological turnover is terrific. To change from complexity to agricultural simplicity in this rather extreme situation is to invite degradation within 10 years. In a temperate forest it takes much longer, but nevertheless the lesson is there: complexity and stability go very much together. Simplification and instability also go together; unless the simplification is backed up by knowledge, hard work, and capital, it cannot be carried through to lasting success.

The Highlands of Scotland, once well-wooded with oak, birch, pine and now cleared, have been well worked over by grazing animals. Further, the country has steep slopes, massive rocks, and high rainfall. In such country you see where the trees come in as calcium pumps. Deep-rooted trees go down towards rock faces, their root tips dissolve that rock, and the calcium comes up into the tree tops, making the young leaves rich in calcium. We then get some defoliation, which we tend to dislike. But what does 15 to 20 per cent defoliation in an oak forest in May really matter? Not much from the tree's point of view. In a recent paper Stephen Collins shows how the understory benefits from defoliation by the gypsy moth.

If you go into an English oak woodland in May when the *Tortrix* larvae are at work, you can hear as well as feel the caterpillars; the small droppings fall continually. The sound is part of the undertone of the forest, this fall of droppings onto the soil, which is well covered with species like dog's mercury. Here is material, rich in calcium and full of cellulose-splitting organisms, and the earthworms gather this

harvest in a very real fashion. This calcium-rich material is being mixed into the surface layers of this soil, and although this is in a country where calcium is scarce in the soil, calcicolous flowers grow almost as plentifully as in a soil originally much more basic. The community of the forest makes calcium available. Outside that forest you come upon an acid, peaty moorland, it is indurated as hard as rubber, and it is leached. Here are plants that simply cannot get down to the basic layer and renew the calcium in the surface.

Compared to the managed field, the forest biome is rich and stratified. Of course it has suffered immensely by the tree felling that we hear about in Connecticut. We don't know what species of animals and plants were knocked out in those fellings, but I would imagine the number would be considerable. We still don't know the full invertebrate fauna of the forest, and yet in the conversion cycle I imagine they are probably the principal agents in the conversion of organic matter. We don't even know the community structures, never mind individual species. There are still lots of them to be found. When species are lost in traumatic land use, such as clear felling, what are the means and speeds of recolonization? These are all problems which remain for us to solve, thank goodness.

Now bird life is much better known than the invertebrate fauna. This bird life is a portion of the fauna which gives great pleasure in the suburban forest.

I feel that our management of the suburban forest should be designed to keep the complexity of the ecosystem, of the biome, as full as possible, to keep it to its original complexities and not to simplify it as managers are apt to do. Having an agricultural and pastoral background, I know it is very easy to fall into management on a simplifying basis. As agriculturalists, you of the Agricultural Experiment Station likely will also need a slight change in attitude, remembering that you are going to work for a complexity rather than a simplification as in traditional agriculture.

In complexity, the tropical rain forest excels. In his big book on the tropical forest, Paul Richards said there were about 3,600 species with trunks 20 centimeters or more in diameter in that forest. This is an immense complexity. One school of silviculture looks on this complexity, wants timber of a few species, and says, "Obviously, we must get more of the desirable species and less of what we call weeds." I doubt if they are going to succeed because I would take the view, which is more generally observed now, that these other species make their own demands on the environment and make their own contributions to it. Evolution consists of differentiation. All differentiation means different demands on the environment and different species not making the same demands in the same environment.

This differential demand on the environment is not, I think, a thing that we can forget or do without. Ecology must find what demands each of these species are making on the environment. Where is their niche in the whole? We are doing this all the time, of course, but perhaps not with the definite end of determining energy cycles. Much that Ovington tells us is to the end of getting conversion of matter into quantitative terms, although he was not telling us *how* the several species did these things. He was merely giving us the final sum. There remains this plain natural history to be done: find what animals and plants are doing within the environment.

If amenity is now the primary resource in the suburban forest, isn't natural history, which is communicable to people, also one of the major resources of this suburban forest? Slightly over an acre of it for every inhabitant of Connecticut, and none of the population so remote from it that natural history is not a potential resource of the forest for the people. This comes down to education and communication. There are great fields for improvement in communication between the Agricultural Experiment Station and the people of Connecticut. I feel that in a state like Connecticut, which has been going out of agriculture, natural history is a worthy and proper end for this Station in the management of this human environment which is the suburban forest.

Ecological Tools and Their Use

An Application of Ecological Laws to Woodlots

Pierre Dansereau

A fitting preliminary to a land-use plan may well consist in an examination of ecological theory. The science that deals with environment lags so far behind those of heredity, physiology, geology, and many others that it has often been denied autonomy. It is at once paradoxically considered to be too specialized (because we have built a protective coating of vocabulary around some of our activities?) or to have remained too general, to have no area of its own and to live entirely upon borrowings.

This, of course, I hardly agree with. It seems to me that the holocenotic view, as it has been variously developed by ecologists (some of whom did not call themselves so), has provided a central focus. This will stand just as sharply whether or not one is willing to accept the community as an organism (or super-organism) not behaving merely as the sum of its parts but having proper functions of its own, or whether this is merely a commodious analogy which is useful methodologically. We are at least bound to recognize some processes and trends as properly ecological and not reducible to their components. Admittedly, ecology has borrowed from other disciplines and will continue to do so for its analytic and synthetic purposes without losing its ground. In fact, general ecological theory has contributed much to the advancement of anthropology, geography, sociology, physiology, genetics, etc.

Appendix A is entitled "A tentative formulation of ecological laws." I will not paraphrase each proposition or justify the four levels of generalization, and then apply each to the Northeast, and particularly to woodlots. I am hoping that much of this will come up in the discussion.

I will stress, however, that the problems at hand can be properly focused only if the study of environmental relations considers not only the features which are apparently or demonstrably responsible for the role played by individual species in plant communities, but also the historical factors which are as limiting as the immediate physiological requirements of the plants. Such is the case where a low timberline is not clearly due to the physiological inaptitude of woody plants to grow there but to some past circumstance which has deprived the regional flora of suitable species for this function. Many such places are known,

notably in Australia. Australian ecologists have done much to restrict some of the classic concepts such as that of climax vegetation and zonal soil, and the rest of us have paid attention to what they have said. Australia holds the key to some of the most crucial problems.

I have tried to formulate the ecological laws as precisely as I could, although I recognize that they are only remotely comparable to the laws of physics and chemistry which the molecular biologists hope will eventually encompass all of our thinking. Until such an event does occur, these approximations may serve as guideposts, as beacons along the way or at least as mutually limiting hypotheses. These laws as I have expressed them myself or reformulated them from the work of others, are therefore primarily intended for discussion. There might even be some contest as to the credits I have assigned, and I shall be happy to make amends.

In the study of vegetation we are ruled by two things: we should try to maintain our sights on the community and also to grasp the interacting physiology of the component species. Maybe the ecosystem is more of a real object of study than the community in a narrower sense. We should try to focus upon the community, but anything that we say about the community is very largely governed by what we know about the physiological aptitudes, conflicting or cooperating, of the component species. Therefore, it seems to me that our initial attention is levelled at the physiological *laws of ecotopic fitness*.

These physiological laws are empirically derived from observation: they do not necessarily consider the innate aptitudes of individual species so much as actual performance in the field.

What led me to formulate the first, the *law of the inoptimum*, was experiments that show that almost all transplanted wild plants can be made to flower sooner or longer, grow more rapidly, withstand drier or wetter habitats. In other words: to exceed, and sometimes by far, the conditions to which it is seemingly confined in nature.

One of the best examples in this region is silver maple (*Acer saccharinum*). It is planted as a shade tree all over North America, often in rather dry areas, on very poor soils. In nature, however, the silver maple does not escape the floodplain; it is found in riverside habitats where the soil is flooded in the spring and well aerated during the summer. Germination seems the weak link in this case, since the germinating power of the silver maple is rapidly lost. This would not seem to preclude its being carried by wind, which is very likely because of its winged diaspore, to temporarily wet areas where, once rooted, it would seem to be able to persist, which it does not. So there are possibly several factors, historical, ecological, climatic, and no doubt a combination of these, which do in fact confine the silver maple to the floodplain

habitat, maybe in a narrower sense, to a certain type of floodplain community, a certain type of muck and a rather closed forest.

The frequent observation of such phenomena has led me to formulate the *law of the inoptimum*.

Plants that grow together certainly illustrate the paradox that they grow together: a) because *they have*, and b) because *they do not have* the same requirements. Both of these statements are true, because of the particular tapping mechanism of the plant. Competition is no explanation: competition is not a thing-in-itself. There is a differential exploitation of the resources of the environment which allows certain species to use up a greater share of what they are able to use. Rarely do they use up the full amount of what they are equipped to use, because some other species takes up a smaller or greater share. Sharing is, I think, an extremely important act, since it balances the conflicts of competition and cooperation. Recently Herbert Baker, who has contributed so much to our understanding of pollinating mechanisms, has developed the idea that it was necessary for insects to share the same plant and necessary for plants of different species or genera to share the same pollinators. In both cases the persistence, survival, and maintenance of an ecological position is dependent upon cooperation or sharing. (Maybe sharing is a more objective, less anthropomorphic term and should be preferred to cooperation.)

The *law of tolerance* and the *law of valence*, as I have put them down here following Good's earlier formulations, and Mason's and Cain's, are reducible to a seemingly simple proposition that "plants grow where they can." (This led someone to say that ecology was an elaboration of the obvious.)

Are some other laws, 5 and 6 for instance, in contradiction? The late John Curtis (whose early death is such a great loss to us) had developed a theory of the continuum: in any area that one studies carefully, with an eye upon the holocenotic nature of the community, there is a gamut of niches. Precisely because the plants that habitually grow together do so upon this contradiction of their having similar and dissimilar requirements, the coinciding spectrum of their valences shows a staggered optimum (or a maximum?). Therefore, a slight shift in the environment — a little more wetness, a little more sandiness, a little more shade — will move the sub-dominant to dominant and so on. Curtis and his students were able to present a considerable number of data which substantiate the view that there are indeed many apparently slight differences in site quality and in microclimate which favor these replacements. Are they minor or major shifts, and what do we witness from the beginning to the end of the spectrum? Is it possible to cut anywhere? Are there any discontinuities, or is all vegetation a continuum?

I think this calls for serious doubt, and I have been led to formulate a law seemingly but not really in opposition with the preceding one: the *law of cornering* (No. 6). Whereas the continuum will unquestionably express itself to the full if it is ordained upon a gradient whose segments are roughly even, it will have step-wise hiatuses in all steepenings of the gradient. In the first instance the segments of the gradient are at least broad enough to allow the development of the various niches in which species of equivalent total spectrum can develop to dominance. On the other hand, hiatuses or unconformities are common both on the ecological and on the geographical scale. On a river bank, for instance, the zonation reflects slope and duration of flood in well-developed vegetation belts. But all river banks are far from having a gradual slope. More often they are variously contracted and designed. And this is so too of climatic gradients. A rainfall map of eastern North America gives us a good idea why instead of having a prairie, a savanna, and a forest zone, in that order, with decreasing rainfall, the gradient is so tight in the potential savanna area that the latter (presumably "oak opening") does not develop to any geographical magnitude. This is *cornering*. There is no place for the plant association that reaches its optimum here in this segment; it is completely eliminated, and the adjacent, the heretofore noncontiguous members have come into contact. I believe this phenomenon to be very common, to occur under a great variety of conditions.

One of the applications which I have proposed concerns the pines, the white pine in particular. This tree does not seem able to dominate, at least in pure stands, for an indefinite period of time in the eastern North American forests. It is replaced by broadleaf species, or at least it falls down the ecological scale to a relic or at best a sub-dominant. However, pollen analysts show a consistent trend whereby, in post-glacial times, there are long periods during which some kind of pine dominates. How could this happen? Some palynologists are convinced that the pedogenesis was so slow as to allow this species to persist very long as a sub-climax dominant. This is not unlikely. An alternative is the restoration in post-glacial times of a segment now missing in the climatic zonation which would then have allowed white pine (or red pine?) to dominate a woodland. This would have been a much more open type of forest than either the broadleaved forest which followed it or the spruce forest which preceded it. But maybe there was never any spruce forest either in the early post-glacial time, but also a spruce savanna, something like the Hudsonian lichen woodland of today, and then a jack pine and finally a red or white pine, open woodland. In fact, on the western side of the continent, ponderosa pine does indeed behave in this way and forms extensive open woodland or savanna stands.

The process of cornering may have been very important, and we

should not, in my opinion, reconstruct the post-glacial sequence, or any former vegetation, by guiding ourselves exclusively on contemporary vegetation. Obviously some other combinations have been possible in the past.

If you will permit me, I will go even further and ask: What is the origin of *Thuja occidentalis* and *Tsuga canadensis*? How can we explain what they are doing now? There is a rain forest on the Pacific coast dominated by *Thuja plicata* and *Tsuga heterophylla*, which thrives upon high, constant rainfall under an equable climate. Such equable climates have been superseded in eastern America for a long time, ever since the deciduous forest arose. When this came about, what was to remain of the coniferous rain forest? Conceivably its two dominants went in different directions: one was absorbed as a climaxial dominant in the emerging northern segment of the deciduous forest, the beech-maple-hemlock phase; and the other pushed, as it were, down the ecological scale to a sub-climaxial stage. However, in the Maritime Provinces one encounters an extreme northern phase of the mixed mesophytic forest, with red spruce (not black and white), hemlock, fir (with maybe a few genes persisting from *Abies fraseri*, the so-called var. *phanerolepis*), and the tallest and most forest-like specimens of *Thuja occidentalis*. These are a hundred feet high and grow in closed stands, not on open hillsides or the edges of marshes. These speculations illustrate cornering on a very broad time scale.

We can hardly consider one by one all of the laws. But let me quickly run the gamut, starting on a physiological plane and thinking of the adjustment of the individual species. Let us call it a taxon because very often we shall be dealing with a local sub-species or a variety. The ultimate reality is, of course, the regional race, and it is its performance that we should try to evaluate.

A few years ago, in quest of the *varieties of evolutionary opportunity*, I tried to bring all this together and to compound, as it were, the geographical and ecological position, as a frame for the behavior of a number of species that I had seen in the field, some through their entire range. I tried to put one inside the other, the geographical characteristics (not only in historical terms, but primarily in terms of extent and continuity), the valences of the species, and the structure of the population. Above all, it seemed pertinent to ask: to what ecosystem, to what dynamic group did it seem to be related?

Some plants, like the bracken fern, show a tremendous aptitude in all dimensions: geographical, ecological, and physiological. Others like the sugar maple have a smaller area. As members of the climax community, and almost exclusively so, they are stenotopic, very narrow, but always present (constant) and very abundant as individuals. Such species

are also successful, but in a restricted sense. (It will be noted that sugar maple, in fact, does well under a measure of disturbance although it is relatively wasteful, for it has to produce a great number of seedlings that die in order to keep up its effectives. Beech does not do that to obtain the same result, and seems more "economic." These are physiological incidences which are potentially important.)

And so it goes for a number of other species. An orchid, like *Listera borealis* which has a tremendous circumboreal range, is linked with certain ecosystems in that it does not readily venture outside of fairly mature and not badly disturbed spruce, fir, or pine forest. Nevertheless, its constancy is not high. One can walk through miles of good timber of the kind which is hospitable to *Listera borealis* and not find it, and when one does, it is seen to build up a very small population. The sugar maple, this orchid and the bracken fern all show a great measure of ecological success. Their chances of survival would seem to be high, but for completely different reasons.

If we are to understand the *strategic laws of community adjustment*, what really needs the most careful identification are the regimes: the climatic regime, the pedogenic regime. These are fairly well defined, but the corresponding *vegetation regime* is not. This is for us to do now if we are to correlate climate, soil, and vegetation. This basic triangle can be understood only on one condition: that we not define vegetation by climate or soil by vegetation, and that we stop this circular reasoning to which we have all fallen victim, partly because of vocabulary, tradition, and in the end, partly because of necessity. Some maps, which purport to show the soils of such and such a state, were drawn on the evidence of known vegetation, not on the grading of soil particles. Some vegetation-maps were compiled very largely on the basis of information on climate. And so it goes. What are the real determinants or the mutual inferences or influences between soil and climate and vegetation?

There are many ways of representing climate. The hythergraphs which are used by many authors are especially useful if one is concerned with regime. There can be detected various thresholds which mark the efficiency of a particular regime.

In fact, there are thresholds between each and every one of the major vegetation types. But what are the major vegetation types? Have we defined them in a completely satisfactory fashion yet? Or, indeed, is it more significant to identify the trends? For instance, to know what Northern New Zealand is exposed to should there be a modification in climate? That it is exposed to becoming a mediterranean area and may well have been so in the past? Pollen analysis shows some evidence of this and many of the plants that live in New Zealand today have the small, hard, evergreen mediterranean type of leaves!

Turning to the third point in the triangle, what is *vegetation regime*? Whereas we can speak of laterization and podzolization in soils and of monsoonization and mediterraneanization in climate, what is a parallel manifestation in plant physiology and morphology? Admitting that morphology does not *in every case* respond to physiology, that form and function do not correspond, we must not be blind to what we should be looking for. What are we looking for? Herbaceous versus woody growth: woody plants do not grow in some areas and what are those areas? What is it in a given environment, a given climatic area, or — more narrowly — in an ecosystem within that area, that allows the herbaceous way of tapping soil and air resources to prevail to the exclusion of woody plants? Is there a basic difference, as Theophrastus thought, between woody and herbaceous plants? Is this real or are some woody plants more like herbs and some herbs more like woody plants? Of course we should not stop there even if we drew such a line. We should also have to think in terms of leaf types, periodicity, and genetics.

Some communities, if analyzed, will reveal that a majority of their members depend upon the production of seed for the continuance of the spatial occupancy which they now enjoy. In the desert, annuals may not form the larger part of the biomass, but they are in the order of 60 per cent of the flora, and are dependent upon renewal or maintenance of their effectives by seed. On the contrary, in an Arctic tundra, the bypassing of sex is frequent and many species maintain their position, continue their strategy by purely vegetative means or apomixis.

Other responses of plants, deciduousness versus semi-deciduousness and evergreenness, and leaf size and type and texture, and the variety of dispersal devices, and various combinations of these features are apparent on a geographical scale and will be revealed by a functional analysis, one that is not primarily geared to taxonomy. In the mediterranean areas, whether the component species are derived from the stock of the temperate Southern Hemisphere (Chile and South Africa) or of the Northern Hemisphere (California, Spain), the emergent structure is so similar in these widely separated areas that it shows as a response to a similar climatic regime.

I think I have almost exhausted my time so I will not comment on the rest of the laws, but will hope to apply these concepts, in the course of discussion, to the forests of the Northeast.

I have provided a basic bibliography. Appendix B bears upon ecological theory, and Appendix C concerns the North American forests, more specifically the eastern American, and more intimately Connecticut. I would especially draw your attention to a very fine bibliography of Connecticut and of eastern North America by Frank Egler.

APPENDIX A

A TENTATIVE FORMULATION OF ECOLOGICAL LAWS

Some of the following are transcribed, sometimes in an altered wording, from P. Dansereau, 1956 and 1957 (see bibliography). Responsibility for the concepts which are recorded here is assigned to various ecologists and plant geographers, who are not necessarily quoted verbatim, as I have sometimes felt that a more concise or a more complete statement was more useful.

A. PHYSIOLOGICAL LAWS OF ECOTOPIC FITNESS (1-8)

1. *Law of the inoptimum.* No species encounters in any given habitat the optimum conditions for all of its functions (Dansereau).
2. *Law of aphasy.* "Organic evolution is slower than environmental change on the average, and hence migration occurs" (Cain).
3. *Law of tolerance.* A species is confined, ecologically and geographically, by the extremes of environmental adversities that it can withstand (Good).
4. *Law of valence.* In each part of its area, a given species shows a greater or lesser amplitude by its relative efficiency in various habitats (or communities); this is conditioned by its requirements and tolerances being satisfied or nearly overcome and by its capacity of utilizing the resources of the ecosystem, which are being checked by its commensals (Dansereau).
5. *Law of the continuum.* The gamut of ecological niches, in a regional unit, permits a gradual shift in the qualitative and quantitative composition and structure of communities (Curtis).
6. *Law of cornering.* The environmental gradients upon which species and communities are ordained either steepen or smoothen at various times and places, thereby reducing utterly or broadening greatly that part of the ecological spectrum which offers the best opportunity to organisms of adequate valence (Dansereau).
7. *Law of persistence.* Many plants, especially dominants of a community, are capable of surviving and maintaining their spatial position after their habitat and even the climate itself have ceased to favor full vitality (Dansereau).
8. *Law of evolutionary opportunity.* The present ecological success of a species is compounded of its geographical and ecological breadth, its population structure and the nature of its harboring communities (Dansereau).

B. STRATEGIC LAWS OF COMMUNITY ADJUSTMENT (9-13)

9. *Law of ecesis.* The resources of an unoccupied environment will first be exploited by organisms with high tolerance and generally with low requirements (Cowles).
10. *Law of succession.* The same site will not be indefinitely held by the same plant community, because the physiographic agents and the plants themselves induce changes in the whole environment, and these allow other plants heretofore unable to invade to displace the present occupants (Cowles).
11. *Law of regional climax.* The processes of succession go through a shift of controls but are not indefinite, for they tend to an equilibrium that allows no further relay; the climatic-topographic-edaphic-biological balance of forces results in an ultimate pattern which shifts from region to region (Clements).

12. *Law of factorial control.* Although living beings react holocenotically (to all factors of the environment in their peculiar conjunction), there sometimes occurs a discrepant factor which has controlling power through its excess or deficiency (del Villar).
13. *Law of association segregation.* Associations of reduced composition and simplified structure have arisen during physiographic or climatic change and migration through the elimination of some species and the loss of ecological status of others (Braun).

C. REGIONAL LAWS OF CLIMATIC RESPONSE (14-19)

14. *Law of geoecological distribution.* "The specific topographical distribution (micro-distribution) of an ecotypic plant species or of a plant community is a parallel function of its general geographical distribution (macro-distribution), since both are determined by the same ecological amplitudes and ultimately by uniform physiological requirements" (Boyko).
15. *Law of climatic stress.* It is at the level of exchange between the organism and the environment that the stress is felt which eventually cannot be overcome and which will establish a geographic boundary.
16. *Law of biological spectra.* Life-form distribution is a characteristic of regional floras which can be correlated to climatic conditions of the present as well as of the past (Raunkiaer).
17. *Law of vegetation regime.* Under a similar climate, in different parts of the world, a similar structural-physiognomic-functional response can be induced in the vegetation, irrespective of floristic affinities and/or historical connections (Schimper).
18. *Law of zonal equivalence.* Where climatic gradients are essentially similar, the latitudinal and altitudinal zonation and cliseral shifts of plant formations also tend to be; where floristic history is essentially identical, plant communities will also be similar.
19. *Law of irreversibility.* Some resources (mineral, plant, or animal) do not renew themselves, because they are the result of a process (physical or biological) which has ceased to function in a particular habitat or landscape (Crocker and Wood).

D. GEOGRAPHIC LAWS OF DISTRIBUTION (20-26)

20. *Law of specific integrity.* Since the lower taxa (species and subordinate units) cannot be polyphyletic, their presence in widely separated areas can be explained only by former continuity or by migration (Gray).
21. *Law of phylogenetic traces.* The relative geographical positions, within species (but more often genera and families), of primitive and advanced phylogenetic features are good indicators of the trends of migration (Camp).
22. *Law of migration.* Geographical migration is determined by population pressure and/or environmental change (Good).
23. *Law of differential evolution.* Geographic and ecological barriers favor independent evolution, but vicariant pairs are not necessarily proportionate in their divergence to the gravity of the barrier or the duration of isolation (Gray).
24. *Law of availability.* The geographical distribution of plants and animals is limited in the first instance by their place and time of origin (Good).

25. *Law of geological alternation.* Since the short revolutionary periods have a strong selective force upon the biota, highly differentiated life-forms are more likely to develop during those times than during equable normal periods (Russell).
26. *Law of domestication.* Plants and animals whose selection has been more or less dominated by man are rarely able to survive without his continued protection.

APPENDIX B

SUMMARY BIBLIOGRAPHY OF ECOLOGICAL THEORY

- Braun, E. L., 1935. The undifferentiated deciduous forest climax and the association-segregate. *Ecology*, 16:514-519.
- Cain, Stanley A., 1944. The foundations of plant geography. Harper and Brothers, New York, xiv + 556 pp.
- Camp, W. H., 1947. Distribution patterns in modern plants and the problems of ancient dispersals. *Ecol. Monogr.*, 17:123-126, 159-183.
- Clements, Frederic E., 1936. Nature and structure of the climax. *Journ. Ecol.*, 24(1):253-284.
- Cowles, H. C., 1901. The physiographic ecology of Chicago and vicinity; a study of the origin, development, and classification of plant societies. *Bot. Gaz.*, 31:73-108, 145-182.
- Crocker, R. L., and J. G. Wood, 1947. Some historical influences on the development of South Australian vegetation communities and their bearing on concepts and classification in ecology. *Trans. Roy. Soc. S. Austr.*, 71(1):91-136.
- Curtis, J. T., 1959. The vegetation of Wisconsin: an ordination of plant communities. Univ. Wisconsin Press, Madison, xi + 657 pp.
- Dansereau, Pierre, 1956. Le coincement, un processus écologique. *Acta Biotheoretica*, 11(3/4):157-178.
- Dansereau, Pierre, 1957. Biogeography, an ecological perspective. Ronald Press Co., New York, xiii + 394 pp.
- Dansereau, Pierre, 1961. The origin and growth of plant communities. In: "Growth in Living Systems," Proc. Symp. on Growth, Purdue Univ. (Indiana), June 16-18, 1960; ed. by M. X. Zarrow; Basic Books, New York, pp. 567-603.
- Du Rietz, G. E., 1931. Life-forms of terrestrial flowering plants. I. *Acta Phytogeogr. Suecica*, 3:1-95.
- Egler, Frank E., 1942. Vegetation as an object of study. *Philosophy of Science*, 9(3):245-260.
- Good, Ronald, 1931. A theory of plant geography. *New Phytologist*, 31:149-171.
- Good, Ronald, 1953. The geography of flowering plants. Longmans, Green and Co., London, New York, xiv + 452 pp.
- Gray, Asa, 1846. Analogy between the flora of Japan and that of the United States. *Amer. Journ. Sci. & Arts*, 52:135-136.
- Gray, Asa, 1873. Comparative study of the floras of Eastern North America and of Eastern Asia. *Proc. Amer. Assoc. Adv. Sci.*, 21:1-31.
- Holdridge, L. R., 1947. Determination of world plant formation from simple climatic data. *Science*, 105(2727):367-368.
- Mason, Herbert L., 1936. The principles of geographic distribution as applied to floral analysis. *Madroño*, 3:181-190.
- Mason, Herbert L., 1946. The edaphic factor in narrow endemism. I. The nature of environmental influences. *Madroño*, 8(7):209-226.
- Odum, Howard T., John E. Cantlon, and Louis S. Kornicker, 1960. An organizational hierarchy postulate for the interpretation of species-individual distributions, species entropy, ecosystem evolution, and the meaning of a species-variety index. *Ecology*, 41(2):395-399.

- Raunkiaer, C., 1934. The life forms of plants and statistical plant geography. Clarendon Press, Oxford, xvi + 632 pp.
- Russell, R. J., 1941. Climatic change through the ages. In: "Climate and man," U.S. Dept. Agric. Yearbook 1941, pp. 67-97.
- Schimper, A. F. W., 1903. Plant geography upon a physiological basis (transl. by William R. Fisher). Clarendon Press, Oxford, 839 pp.
- Stebbins, G. Ledyard, Jr., 1950. Variation and evolution in plants. Columbia Univ. Press, New York, xx + 643 pp.
- Tansley, A. G., 1946. Instruction to plant ecology. George Allen & Unwin, Ltd., London, 260 pp.
- Villar, E. Huguet del, 1929. Geobotánica. Editorial Labor, Barcelona-Buenos Aires, 339 pp.
- Warming, E., 1909. Oecology of plants. An introduction to the study of plant communities. Oxford Univ. Press, London, xi + 422 pp.
- Watt, Alex S., 1947. Pattern and process in the plant community. Journ. Ecol., 35(1-2):1-22.

APPENDIX C

SUMMARY BIBLIOGRAPHY ON NORTHEASTERN AMERICAN FORESTS

The ecological and the silvicultural literature on the Northeastern forests is very considerable, not to mention the geographical, pedological, and sociological items. The most comprehensive is certainly E. Lucy Braun's (1950) book. As for vegetation studies, Egler (1948 and 1959) has provided an excellent bibliography. Additional items are listed here, some of them more recent than Braun or Egler's contributions, some of them otherwise pertinent to the present discussion.

- Beetham, Nellie, and W. A. Niering, 1961. A pollen diagram from southeastern Connecticut. Amer. Journ. Sci., 259:69-75.
- Braun, E. Lucy, 1950. Deciduous forests of eastern North America. Blakiston Co., Philadelphia, xiv + 596 pp.
- Collins, Stephen, 1956. The biotic communities of Greenbrook Sanctuary. Palisades Nature Assoc., Englewood, N.J.
- Collins, Stephen, 1961. Benefits to understory from canopy defoliation by gypsy moth larvae. Ecology, 42(4):836-838.
- Egler, Frank E., 1948. Regional vegetation literature. I. Connecticut. Phytologia, 3(1):1-26.
- Egler, Frank E., 1959. A cartographic guide to selected regional vegetation literature. Part I. Northeastern United States (Connecticut, pp. 24-31). Sarracenia, 1:1-50.
- Egler, Frank E., 1961. Nature of naturalization. In: "Recent advances in Botany," Univ. Toronto Press, pp. 1340-1345.
- Gilbert, Adrian M., and Victor S. Jensen, 1958. A management guide for northern hardwoods in New England. Northeastern For. Exp. Sta., Upper Darby, Pa., Sta. Paper 112, 22 pp.
- Goodwin, Richard H. (ed.), 1956. Six points of especial botanical interest in Connecticut. Conn. Arboretum Bull. 9, 32 pp.
- Gottmann, Jean, 1961. Megalopolis, the urbanized northeastern seaboard of the United States. Twentieth Century Fund, New York, xi + 810 pp.
- Hicock, Henry W., 1956. Connecticut forests . . . asset or liability. Northeastern Logger, Nov. 1956, pp. 20-22, 30-33
- Hill, David E., and Arthur E. Shearin, 1960. Soils and urban development in Hartford County. Conn. Agric. Exp. Sta., New Haven, Circ. 209, 8 pp.
- Koroleff, A., 1946. Practical woodlot management. How to use the forest soundly and profitably. Canad. For. Assoc., Montreal, 60 pp.
- Leak, William B., and Robert W. Wilson, Jr., 1958. Regeneration after cutting of

- old-growth northern hardwoods in New Hampshire. *Northeastern For. Exp. Sta., Upper Darby, Pa., Sta. Paper 103*, 8 pp.
- Lunt, Herbert A., 1948. The forest soils of Connecticut. *Conn. Agric. Exp. Sta., New Haven, Bull. 523*, 93 pp.
- Niering, William A., and Richard H. Goodwin, 1962. Ecological studies in the Connecticut Arboretum Natural Area. I. Introduction and a survey of vegetation types. *Ecology*, 43(1):41-54.
- Olson, Jerry S., Forest W. Stearns, and Hans Nienstaedt, 1959. Eastern hemlock seeds and seedlings; response to photoperiod and temperature. *Conn. Agric. Exp. Sta., New Haven, Bull. 620*, 70 pp.
- Ritchie, Alexander, Jr., and C. L. W. Swanson, 1957. Soils and land use, Hartford County, Connecticut. *Conn. Agric. Exp. Sta., New Haven, Bull. 606*, 36 pp.
- Trimble, George R., Jr., 1959. A problem analysis and program for watershed-management research in the White Mountains of New Hampshire. *Northeastern For. Exp. Sta., Upper Darby, Pa., Sta. Paper 116*, 46 pp.
- Society of American Foresters, 1954. Forest cover types of North America (exclusive of Mexico). *Soc. Amer. Foresters, Committee on Forest Types, Washington*, 67 pp.
- Westveld, Marinus, and Committee on Silviculture (Society of American Foresters), 1956. Natural forest vegetation zones of New England. *Journ. Forestry*, 54(5):332-339.

Ecological Tools and Their Use

Man and the Ecosystem

Howard T. Odum

With vast flows of energy man now begins to possess the ecosystems that spawned him. The suburban forest of Connecticut, which once nursed Pilgrim America, and the green bays of Texas, which nourished Karankawa Indians with shellfish, are such systems suddenly under energy control and management by man.

A forest with man's energy subsidies is still an ecosystem, but the combinations of flux are new and the steady states which will prevail are little known. Conversely, the specifications of inputs and outputs necessary to produce preplanned environments are little known. A new enterprise, ecological engineering, is required to fashion synthetic systems partly under old energy budgets of nature and partly with special power take-off from civilization.

How can we provide guides and know-how for the new enterprises? What are man's tastes in ecosystems? What kinds of action can couple available energy to his tastes? Are his tastes energetic hangovers, potentially lethal? What are the formulae and the costs? Consider some general features of ecosystems, energy, matter, and man.

METHODOLOGY OF ECOSYSTEM STUDY, DEFINITIONS, AND EXAMPLES

The flows of energy and matter in the ecosystem, whether involving man or not, involve some basic definitions and principles long used for study and manipulations of small and simple ecosystems, mainly of aquatic type. The problems of the suburban forest and the Texas bays do not differ in abstraction regarding flow of matter and energy. By considering first an example from a synthetic system that somewhat simplifies the problem of a Texas bay, and then considering some preliminary efforts to make similar measurements in a forest system, the methodology of the ecosystem approach may be indicated.

The Oyster Reef System

In Figure 1 is a concrete pond ecosystem. In broad areas exposed to the sun, plankton are photosynthesizing and on a reef a concentration of consumers are respiring a considerable fraction of the system's

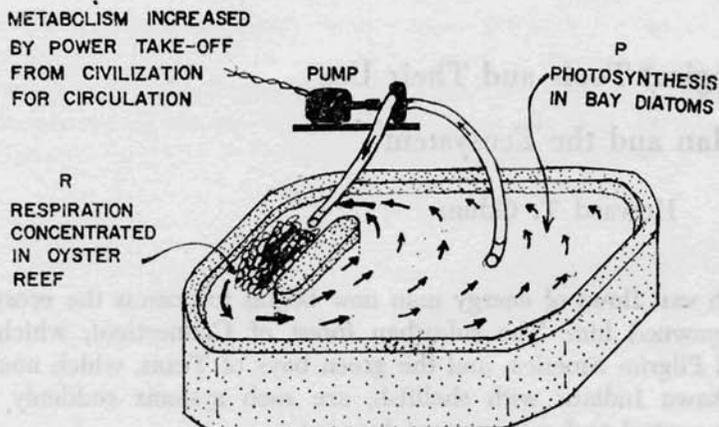


Figure 1. Synthetic system of oyster reef and bay phytoplankton, one of three units recently built of concrete.

metabolism, using the plankton for food and releasing the inorganic nutrients to the plankton. The small ratio of reef area to the larger bay area resembles the upper, low-salinity areas of the bays of the Gulf of Mexico. Whereas wind and tidal driven currents supply the necessary circulation of food to the reef and carry nutrients back to the broad bay areas, in the small, synthetic, tank system, a pump does this work with electrical energy, a power take-off from man's civilization.

By measuring changes of oxygen and carbon dioxide hourly, rates of total photosynthesis and respiration are computed; then the ratio of the processes P and R can be compared (Odum and Hoskin, 1958). Three sets of such experiments show that after initial imbalances, the metabolisms approach a steady state as long as there are no changes in regular fluxes of material. The data of Figure 2 show a flux pattern classified somewhere between the balanced case in Figure 4c and the yield system in Figure 4d where oyster growth is comparable to the timber removal.

Recently three new concrete ponds were constructed like that in Figure 1. Multiple seeding at first caused the populations in the tanks to develop differently with different species in dominant ascendancy in the plankton. Then we arranged the pumps and tanks in series so that they were intermixed for several days. As in early experiences with aquarium microcosms the mixing treatment causes the systems to develop similarly. Multiple seeding followed by mixing so as to attain replications is the microcosm method. It permits the study of basic principles in types of systems. Inferences can then be extended with suitable field studies to systems of larger size, more difficult to control. The ability to replicate ecosystems is a breakthrough for experimental ecology.

A sequence of P and R from a pond (Siler and Odum) is presented in Figure 2. That these pond systems resemble larger, natural systems is indicated by the similarity of their metabolism, the species that dominate the two, the ratio of number of species to individuals, and finally their efficiencies of photosynthesis in the two systems (one agitated by a motor and one by wind and tide).

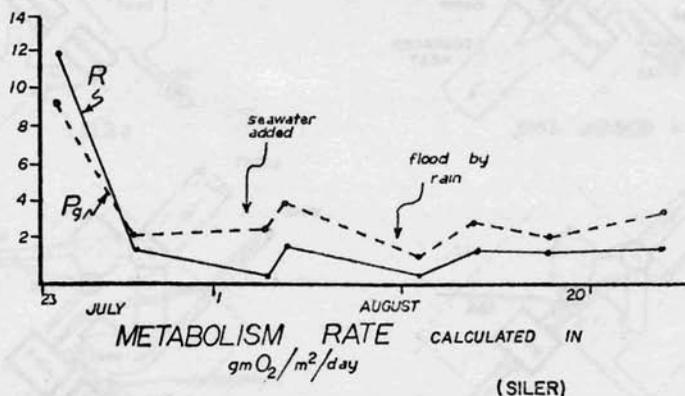


Figure 2. Photosynthesis (P) and respiration (R) in one sequence of stabilization of the oyster reef system. Data were taken by Walter Siler in 1960 in a plastic prototype of the unit in Fig. 1.

The General Case

The carbon metabolism of the oyster reef, Figure 4c, is only a special case of the general 4a, where 4c is created by the lack of flux save light and mechanical energy. In general, if one establishes the fluxes in and out, provides an evolutionary pattern by seeding and allows time to pass, a relatively rapid succession and a stable equilibrium follow. Let us use the old term climax to mean any open steady state with its stable structure and function.

Then we can classify the climax and succession in terms of P, R, and fluxes. Thus the city, 4b, is an extreme consumer with both biological and physical work accomplished by inflowing food and fuel. The oyster reef is the balanced 4c with no food or fuel being imported or exported. Finally, the Connecticut forest of the past is the productive 4d with wood as an export.

The four ecosystem types are again represented in Figure 3. Here the biochemical are separated from the heat engines. $T\Delta X$ indicates fluxes of energy content from the system that are an inherent part of the process even under the theoretical condition of thermodynamic re-

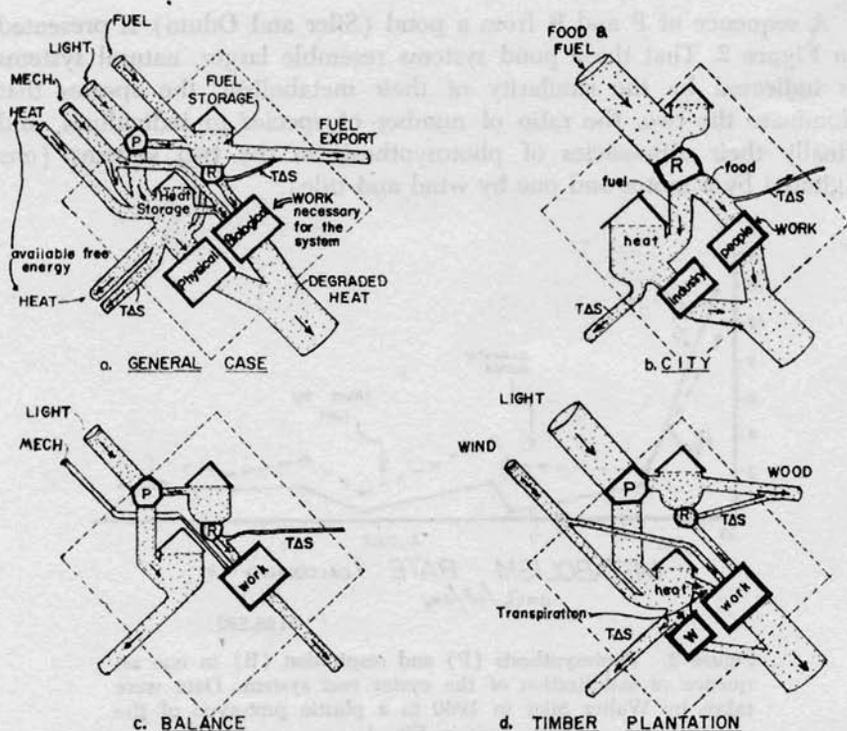


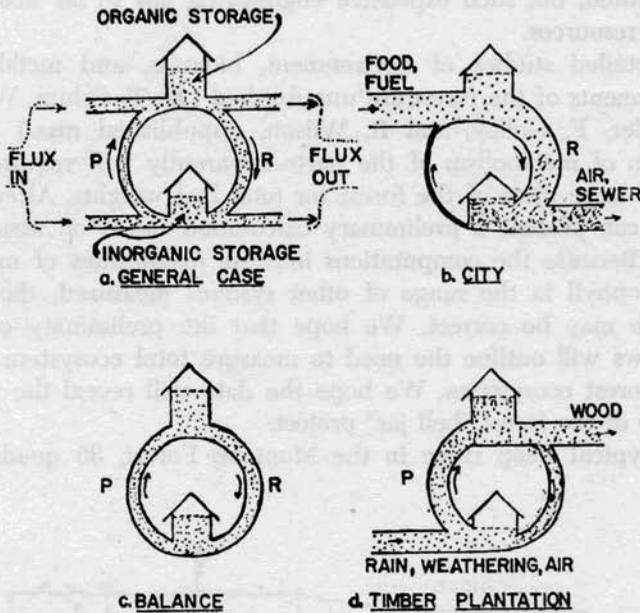
Figure 3. Generalized energy diagrams. *a.* General case with many of the major flows of energy of most ecosystems shown; *b.* a city with predominant basis of industrial fuels and human food flux; *c.* a balanced system in which photosynthesis and respiration are similar; *d.* a timber plantation representative of photosynthetic ecosystems that have net yields of stored energy in the form of exported organic matter. The W indicates physical work.

versibility when no energy is available for work. For example the heat of vaporization of transpired water leaves the system without being available for other work.

In such abstract matters, the land community differs not at all from the aquatic system. Because of the difficulties of technique our knowledge of land ecosystems with respect to P, R, and fluxes is less crystallized. Since this Conference concerns the suburban forest, perhaps it is useful to show some attempts to make the necessary P and R measurements on a forest system, even though the techniques are still imperfect.

The Montane Rain Forest of Puerto Rico

Over the past 5 years with the help of the Rockefeller Foundation and the cooperation of Dr. Frank Wadsworth of the U. S. Tropical Forest Station, we have attempted to estimate the biomass and metabolism of



**CYCLE AND FLUX OF CARBON
& ASSOCIATED ELEMENTS**

Figure 4. Generalized diagrams for the flux of matter associated with carbon metabolism. *a.* General case with four main fluxes; *b.* a city with predominant inflow of organic carbon and outflow of inorganic carbon dioxide and related inorganic wastes; *c.* balanced system with no fluxes of matter and with photosynthesis (P) equal to total respiration (R); *d.* a timber plantation, agriculture, or cultivated lawn with net yields balanced by influx of carbon dioxide and fertilizer (in rain or artificially added).

some main forest components of the lower Montane rain forest of Puerto Rico east of El Yunque. The approach is logically simple: (1) measure the gm^{-2} of leaves, animals, small roots, and other main metabolic components; (2) measure the photosynthesis and respiration per gram of the separate components with an infrared CO_2 analyzer in gas flow systems in the field; and (3) multiply the gm^{-2} times the metabolic estimates per gram to estimate total P and R of the system. Estimates for a patch of red mangroves at La Parquerra were recently published (Colley, Odum, and Wilson, 1962). Putting a large 70-foot bell jar over part of the forest and installing powerful air recirculation and refrigeration along with louvres for admission of rain may be a

better method, but such expensive engineering has so far been beyond available resources.

The detailed studies of environment, biomass, and metabolism of the components of the forest are unpublished (H. T. Odum, W. Abbott, R. Selander, F. Golley, and R. Wilson, unpublished mss.) and final summation of metabolism of the parts apparently will require massive cutting of large plots of the forest for total leaf weights. Already, however, we can present a preliminary calculation based on assumed leaf quantity. Because the computations indicate magnitudes of metabolism and chlorophyll in the range of other systems measured, the order of magnitude may be correct. We hope that the preliminary calculation that follows will outline the need to measure total ecosystem functions in large forest ecosystems. We hope the data will reveal the feasibility and value of the forest "bell jar" project.

On a typical steep ridge in the Montane Forest, 36 quadrats were

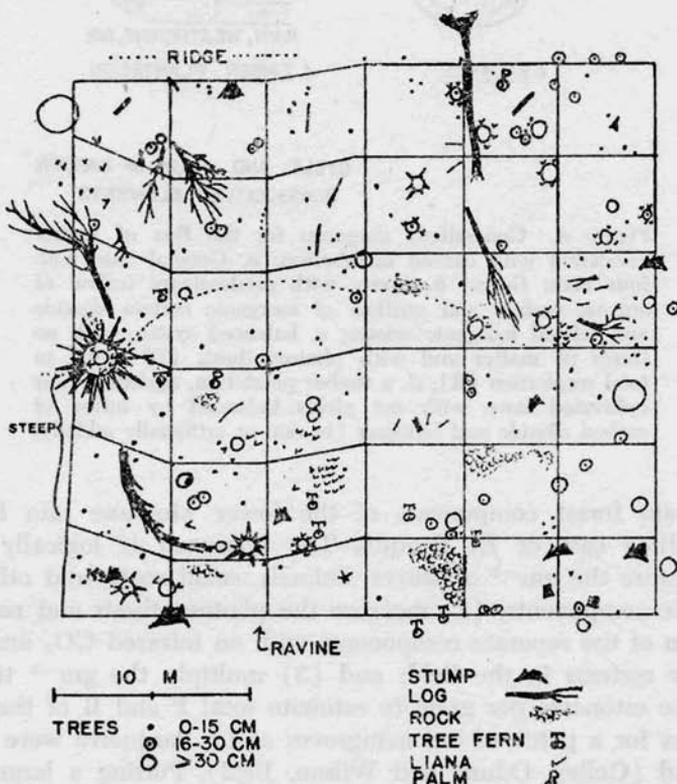


Figure 5. Quadrat with string grid used for preliminary computations on a patch of rain forest (see Tables 1 and 2).

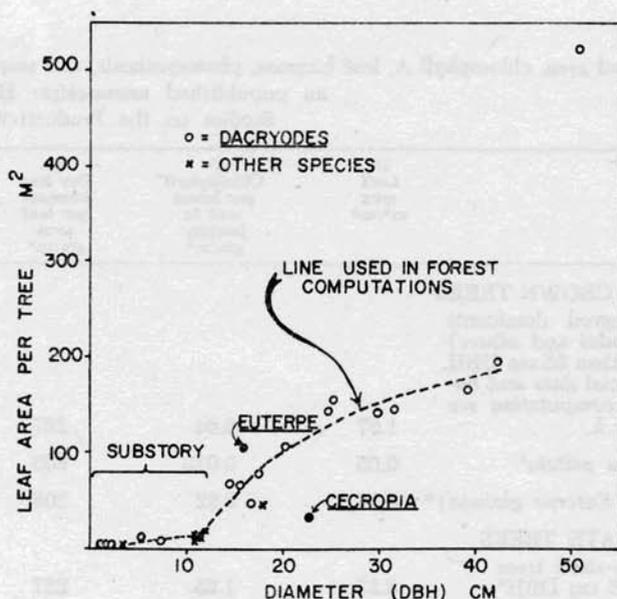


Figure 6. Leaf area as a function of trunk diameter for some trees in the lower Montane forest.

laid out with string (Figure 5). The principal trees were drawn in by size class: lianas, palms, tree ferns, and bromeliads were also counted. Chlorophyll A per area of representative leaves was measured (Odum, McConnell, and Abbott, 1958). Photosynthesis and respiration per area of leaf was measured in the field (Golley, Odum, and Abbott, 1962). Leaf area was related to tree diameter for one of the common dominant tree species *Dacryodes excelsa* (Figure 6). From Figure 6 we estimated the leaf area of 10 of the broad-leaved dominants, 29 medium-sized trees, and 132 small trees (Table 1). In other words, for this preliminary computation it was assumed that *Dacryodes* had a reasonably representative ratio of leaf area to trunk diameter. Then amounts of leaves were determined from the size classes. From leaf areas thus estimated, chlorophyll A and metabolisms were computed (Table 1). Details of the calculation are in the footnotes.

Estimates of soil respiration, respiration of animals, and leaf metabolism, Table 2, were taken from the manuscript cited above. The role of animals in metabolism was small.

If the preliminary calculations for the patch of Montane rain forest were correct, the following comparisons would be made with other ecosystems. The resulting area index (Table 1) of 7 m² leaf per m² ground would be two or three times that of the usual agricultural system. On the other hand, Varischi (1951) found 2.0 in a Montane tropical

TABLE 1. Leaf area, chlorophyll A, leaf biomass, photosynthesis, and respiration computed
an unpublished manuscript: H. T. Odum, W.
Studies on the Productivity of the Lower

	1 ^a Leaf area m ² /m ²	2 ^b Chlorophyll per forest area in January gm/m ²	3 ^c Dry leaf biomass per leaf area gm/m ²	4 ^d Dry leaf biomass per area of forest gm/m ²
DOMINANT CROWN TREES				
10 Broad-leaved dominants (<i>Dacryodes</i> and others) greater than 25 cm DBH. For special data and bases for computation see footnote k.	1.67	0.64	227	380
3 <i>Cecropia peltata</i> ¹	0.05	0.019	203	10
3 Palms (<i>Euterpe globosa</i>) ^m	0.34	0.22	208	70
INTERMEDIATE TREES				
29 Medium-sized trees 15 to 25 cm DBH ⁿ	3.23	1.25	227	734
8 Tree ferns (<i>Cyathea</i>) ^o	0.06	0.016	117	7
132 Small trees 2 to 15 cm DBH ^p	0.95	0.22	155	147
27 BROMELIADS ^q	0.01	0.0009	38	0.5
GROUND HERBS AND SEEDLINGS^r				
	1.03	0.30	41	41
TOTALS FOR LEAVES	7.34	2.67	1390

^aLeaf area was obtained for trees from Fig. 6. The ratio of area of leaves to area of forest is sometimes called the leaf area index.

^bChlorophyll A values per leaf area were multiplied by values in preceding column 1. Values of gm/m² chlorophyll found were: broad-leaved crown trees, 0.42; *Cecropia*, 0.37; palm, 0.61; medium trees based on shade *Dacryodes*, 0.38; small trees based on mean of 14, 0.23; *Cyathea*, 0.27; bromeliads, 0.09; ground herbs and seedlings, 0.29.

^cData from the manuscript cited in the Table caption.

^dProduct of values in columns 1 and 3.

^eProduct of values of area in column 1 and data on respiration per leaf from the manuscript cited.

^fProduct of values of net photosynthesis and leaf area in column 1.

^gSum of columns 5 and 6.

^hProduct of values of net photosynthesis and leaf area in column 1.

ⁱSum of columns 5 and 8.

^jValues in column 5 multiplied by 2.

^k150 m² leaf area per tree computed from Fig. 6 for 30 cm DBH Crown (10-15m). Light regime on sunny day included: 2 hr, 2000 fc; 2 hr, 4000 fc; 2 hr, 6500 fc; 2 hr, 8500 fc; 4 hr, 10,000 fc. Photosynthesis was taken as 0.15 gm C/m² of leaf area/hr in 85 per cent of crown tree leaves within crown above 10 m, and 15 per cent in shade also as 0.15. Respiration was taken as 0.027 gm/m²/hr. Light regime on rainy days was: 2 hr, 200 fc; 2 hr, 500 fc; 2 hr, 1500 fc; 2 hr, 2200 fc; 4 hr, 2700 fc.

for principal components of a 900 m² quadrat of the lower Montane rain forest. Data from Abbott, R. Selander, F. Colley, and R. Wilson.
Montane Rain Forest of Puerto Rico, Part 1.

5 ^a Night respira- tion gm/m ² /12 hr	6 ^c Net daytime photosynthesis on a sunny day gm/m ² /12 hr	7 ^e Gross photosynthesis on a sunny day gm/m ² /12 hr	8 ^b Net daytime photosynthesis on a rainy day gm/m ² /12 hr	9 ^f Gross photosynthesis on a rainy day gm/m ² /12 hr	10 ^l Total respiration per day gm/m ² /24 hr
0.54	3.02	3.56	2.50	3.04	1.08
0.024	0.23	0.25	0.076	0.10	0.05
0.08	0.46	0.54	0.20	0.28	0.16
1.83	5.68	7.51	3.58	5.41	3.66
0.011	0.07	0.08	0.007	0.018	0.02
0.74	1.61	2.35	0.76	1.50	1.48
0.0067	0.0036	0.0103	0.002	0.009	0.0134
1.27	1.07	2.34	0.62	1.89	2.54
4.50	12.14	16.64	7.745	12.25	9.00

¹0.13 m² per leaf; 314 leaves per quadrat; light regime as in footnote k; photosynthesis rate as in the manuscript, respiration 0.040 gm/m²/hr (mean of 4 determinations).

^m101 m² leaf/tree (Fig. 6). Light regime as in footnote k. Photosynthesis at 8500 fc, 0.12 gm/m²/hr; respiration, 0.01 gm/m²/hr.

ⁿ100 m² leaf per tree for 20 cm DBH. Half was computed as crown leaves above 10 m as in footnote k; half was computed as in shade leaves in footnote p. Light regime: 10 hrs above 560 fc, 2 hr at 300 fc, and photosynthesis, 0.10 gm/m²/hr. Respiration of shade leaves 0.065 gm/m²/hr; respiration of crown leaves, 0.027 gm/m²/hr.

^o0.1 gm/m²/hr; respiration, 0.015 gm/m²/hr; net photosynthesis on rainy day, 0.010 gm/m²/hr at 200 fc.

^p6.5 m² leaf area per small shade tree (mean of 10 trees: 3.4, 10.5, 17.5, 10.1, 9.0, 9.8, 2.1, 0.7, 0.94, 0.70). All leaves of small trees were computed as shaded; light in the shade on a sunny day: 14 hr, above 500 fc, with photosynthesis 0.15 gm/m²/hr; 2 hr at 400 fc and 0.10 gm/m²/hr. Respiration of shade leaves, 0.065 gm/m²/hr; respiration of crown leaves, 0.037 gm/m²/hr.

^q0.40 m² leaf per bromeliad; photosynthesis 0.010 gm/bromeliad/hr; respiration, 0.0093 gm/individual/hr.

^rLeaves were picked from quadrats and dried. 82 gm/m² leaf biomass on open canopied ridge; 0 in ravine; mean 41 gm/m² of forest; 40 gm/m² of leaf area. Photosynthesis in shade, mean of 13 herbs and seedlings, 0.087 gm/m²/hr; respiration, mean of 7 determinations, 0.103 gm/m²/hr.

TABLE 2. Some overall metabolic estimates for a plot of lower Montane rain forest^a

P, TOTAL GROSS PHOTOSYNTHESIS (Table 1)	12-16 gm/m ² /day
R, TOTAL RESPIRATION	
Total leaf respiration (Table 1)	9.0
Soil, litter, and root respiration ^b	5.8
Animal respiration by 3.7 gm/m ² animals (dry)	0.18
Total ^c	15 → 15 ←

^aThese include some unsubstantiated assumptions about leaf quantities as indicated in the text and in Table 1, column 1.

^bEmploying an infrared CO₂ analyzer in an open system beneath a shelter of foil, the metabolism of the natural forest floor surface was found to be a function of the rate of air flow across the litter. From ammonium chloride smoke measurements in April, 1962, air velocities averaging 14 cm/sec. were found 2 cm above the litter. Under the disc or shelter of aluminum foil supported about 0.5 cm above the irregular litter surface, a velocity of 14 cm/sec occurred when air was drawn at about 30 liters/min. The respiration rate of the forest floor surface that was equivalent to this flow was about 0.24 gm/m²/hr. This estimate is probably high since the natural air flow at 0.5 cm is likely less than that measured with smoke at 2 cm.

^cRespiration of stems and trunks was not measured.

forest at Rancho Grande, Venezuela. The large difference between two estimates for Montane forest emphasizes the need for total leaf counts. The chlorophyll A of about 3 gm m⁻² is somewhat larger than the usual 0.5 to 2.0 gm m⁻² in land and water communities. The total gross photosynthesis of 14 to 20 gm m⁻² day⁻¹ corresponds to an efficiency of about 10 per cent of the usable light reaching the forest and is in the range of the most productive systems so far measured: algal cultures, sewage ponds, the best agriculture, coral reefs, and underwater grass flats.

The preliminary calculations provide a possible solution to one question troubling Dr. Frank Wadsworth and associates, tropical foresters managing this forest. The growth rate of the trees measured over 20 years has been small, 0.05 to 0.12 inches per year. The dominant trees are several hundred years old. Is this slow growth due to lack of light, lack of nutrients, or inadequate photosynthesis for other reasons? The calculation of respiration as 9.0 gm² day⁻¹ due to leaves and 5.8 due to the soil, root, and litter indicates very little production is left for any net growth with most of it being used to sustain leaf and soil activity. The apparent reason for slow growth is thus not any inhibition of gross photosynthesis, but the full development of the ecosystem structure requiring most of the production for respiratory maintenance. Such metabolic arrangements are not unexpected in a climax system where nutrients must be mainly recirculated. The forest could be manipulated to divert more of its production into products desirable by man whether timber or aesthetic aspects, but it is very unlikely that total output could be increased without adding auxiliary energy since the efficiency may

already be as high as has ever been measured in other systems (if the leaf assumption is of the correct order). In other words, the Montane forest is more like Figure 4c than 4d.

The behavior of the Montane forest seems similar to the microcosms of balanced aquaria in the constant temperature rooms at the Institute of Marine Science where Beyers (1962) has done exhaustive studies on the intricate coupling of P and R, one complementing the other in the supply of nutrients. The coupling is so close that the ecosystem has a total metabolism independent of temperature even though the separate organisms have the usual responses to temperature. For 4 years, close coupling of P and R also was seen in the Texas Laguna Madre, an example of the general case (Figure 4a) (Odum and Wilson, 1962). The unity of aquatic and terrestrial systems provides a powerful, single ecological theory for predictions about unstudied systems like the Connecticut suburban forest. To maintain diversity both the climax Montane forest and the aesthetic forest channel energies similarly.

PRINCIPLES OF ECOLOGICAL ENGINEERING

Power Take-off From Civilization

There is a spectrum of energy budgets from systems in which power supplements by man are small to those in which the power subsidies are large. At one extreme are the completely natural forest or pond whose many processes run on such natural energy sources as the sun or inflowing organic matter. At the other extreme, where power subsidies from man dominate, are the environmental industries: agriculture, traditional forestry practices, and waste disposal engineering. Characteristic of technological progress in man's use of the natural environment has been the ever increasing ratio of subsidized power to the natural power supply. In the mechanized production of food, the power from gasoline may exceed that from sunlight. Knowledge of the natural ecological systems and the environmental industries has been growing, but relatively little is known of the potentialities in the zone where the power subsidies by man are small, but sufficient to keep the system within bounds. The suburban forest and the Texas Bays are of this type. Recognizing the shared energy sources from nature and from power take-off from civilization, we suggest the term ecological engineering for those cases in which the energy supplied by man is small relative to the natural sources, but sufficient to produce large effects in the resulting patterns and processes. Because man's aesthetic desires may be often related to properties of complex and climax systems and because these systems are more nearly self-maintaining and require relatively small power subsidy, the suburban forest will involve ecological engineering.

Power take-off from civilization into a forest may take many forms such as: regular fertilizing, spraying, pruning of particular species, food subsidy for some animal, wildlife management, and seeding. Whereas we may have a good idea of the immediate result of one of these actions, we know relatively little about the long-range effect on the whole system. We know relatively little of its readjusted successional and steady states when the auxiliary energy supply is on a regular basis. Experimental plots with auxiliary power inputs on a regular basis can provide answers. Some idea of the sustained power requirements for significant changes should soon emerge.

Synthetic Systems and Domestication

Synthetic ecosystems include conditions and combinations of organisms never before in existence. Just as in the above example of an oyster reef pond where a new synthetic system was developed by combining previously existing species complexes (prototypes) with some new imposed conditions, so with man in the suburban forest a new synthetic system is being developed by combining the natural species complexes with some new imposed conditions such as interspersed houses and clearings. When multiple species seedings are done in artificial aquatic systems, a functional ecosystem soon evolves with species-number distributions like those in wholly natural systems (examples, Odum and Hoskin, 1957; Beyers, 1962). Presumably, similar processes will act in a synthetic system of multiple natural seedings plus the imposed habitations of man. In the terrestrial systems, however, dispersal and rapid introduction of multiple species may be retarded, especially the larger components. Multiple introductions from throughout the world may permit more diverse combinations to evolve, more closely integrating the habitation of man.

Domestication is a special development of synthetic systems through multiple importations and genetic adaptations. In domestication, few species have yet been fully adapted to such purely human systems as cities. However, in the semi-inhabited suburban forest, enough evolutionarily-old prototypes may remain for the existing species to develop in a reasonable time the diversity for stability. Eltonian population invasions need to be recognized as simplified preliminary phases in the early organization of new systems from preadapted components.

Past emphasis in research on physiology, horticulture, and husbandry of single species in systems involving man may not enable us to predict results where diversity, complexity, and self-sustaining complexes are needed without large energy subsidies. We need to know something about the nurture and manufacture of synthetic systems.

A fictional account of man's house as a synthetic, evolutionarily-young system was developed by Ordish (1960). In an interesting account of 500 years in the history of a house, he includes reasonable though fictional time graphs of populations of roaches, wood borers, humans, and other animals. He considers the rise and fall of the system including such sophisticated considerations as relative metabolic energies of the human and other dwellers. He considers the invasion and domestication of species new to the human system. In the crudeness of data so far available, ecosystem science may be no less fictional, and the approach is identical. In drawing together a substantial bibliography on the human house and in providing a broad-brush plan for its study, the book, however intended, is a contribution to the methodology of quantitative ecology, and perhaps a guide to the studies needed for the system of man and the suburban forest.

A different approach was used by Odum, Muehlberg, and Kemp (1959) and by Arvid Anderson (1960) in considering man as part of the Texas bay system, using dollar-per-acre equivalents to compare cultural and biological metabolism.

Arresting a Successional Stage Into a Climax

If a successional stage is developing towards a steady state by accumulation of some quantity such as organic matter or nutrients bound in soil systems, one may arrest the successional stage and hold the system in a new steady state by introducing a new flux that removes the organic matter or nutrients.

Ecosystems have been manipulated in this way in sewage algal systems by Oswald where, by control of rate of flux, the populations were maintained in various climax adjustments comparable to successional stages from 1 to 14 days old. The principle is well known in fire management. Acknowledging the abstract flux idea underlying the old practice may aid in developing new procedures for new systems. Similar influxes may essentially change the type of ecosystem. For example, by changing the fluxes of organic matter and water through the spraying of wastes into a forest, Little, Lull, and Remson (1959), produced a mesic herbaceous system instead of the normal forest system in New Jersey.

Abbreviating Succession

Where succession involves accumulation or consumption of quantities between starting and final climax, the successional stages may be abbreviated by artificial addition or removal of that quantity. If the critical quantity is an inorganic elemental substance, such manipulation

may be especially practical once the nature of the quantities controlling these transient states is known.

ECOLOGICAL DETERMINISM

Progress and the Balance of P and R

Here in New Haven where Ellsworth Huntington wrote on a geographical determinism, it may not be courteous to discuss ecological mechanisms determining early civilizations of man, since Huntington's proposed influences were physiological rather than ecological and so naive that a generation of sociologists was repelled.

Nonetheless, full activity by men obviously depends on a full flux of energy, and one may consider the patterns of energy availability in time and space as major causal agents in the cultural evolution of man. In times prior to the era of fossil fuels, man's supplies of energy were obtained immediately from photosynthetic products of the land: timber and foods. Productivities of plants and their dependent animals were highest in communities with unlimited raw materials for photosynthesis. This happened along the boundaries of land and water and especially where mechanical energy of water along rivers, reefs, and shores concentrated raw materials and foods for organic growth. The high yields of energy from such environments may have been the essential reason for human colonization in such places rather than communication, transportation, or direct use of water. High productivity of the environment was an essential but not a sufficient condition, for the energy flows of many highly organized ecosystems are large but so branched that little energy is available at any one spot or time for one large species in competition with hundreds of specialized types.

In ecosystem terminology, man could flourish to the extent that P (photosynthesis) was not only large but in excess of R (respiration). In situations where R was balanced with P, organic matter was used as fast as it was produced by the metabolism of the biotic community and little was available for man. We may speculate on the metabolic types of natural ecosystems most amenable to man as he emerged from some restricted animal niche.

Is progress and human culture possible in either primitive or oil ages only when energy beyond subsistence becomes available? In the pre-fossil fuel eras extra energy became available in nature only when photosynthesis exceeded the respirations of the ecosystem *in situ* or when P and R became separated either in time or in space and organic matter accumulated temporarily. The balance of ecosystem processes is the metabolic basis for ecological determinism based on energy budgets.

P exceeded R with temporary storage excesses in the temperate and

higher latitudes where the seasons were keeping the processes out of phase. Accumulations of animal biomass for a hunting economy were possible in such oscillating systems. Tropical areas with dry and wet seasons may similarly have had peaks in P and R separated in time and hence had temporary food accumulations. Areas with net growth also occurred in succession when fire, clearing, or flood reduced matter and a recovery scheme of P greater than R followed. Early cultural progress in semi-arid and temperate areas; along temperate water, seashores, and rivers; in areas with seasonal energy pulses; in monsoon areas; in savanna belts of Africa; and in the dry-wet seasons of middle America are not inconsistent. Wherever extra energy was available momentarily, culture and progress flamed, new know-how for getting a larger part of the energy emerged and was absorbed into the cultural memory. Thus the evolution was one of widening energy input paid for by the energy expenditure during surplus periods.

Then man's role began to increase as a larger fraction of energy was taken, but the opportunity from system failure due to actions of man also began to increase as his role became greater. Progress spread, and cultural developments of primitive man beyond status quo and subsistence were nurtured where P was already in excess of R or in other localized areas of organic matter accumulation.

Many things about this early development of man may make energetic sense when the distribution of P and R are considered. The development of primitive agriculture with power take-off from the photosynthetic system via domestic animals is in the anthropological record. Did small shifts in climactic belts transform the seasonal dry-wet forest of the Mayans into more of a steady state rain forest with vast decreases in P/R ratio and available energy for man?

Only in the 19th century did new energy sources become available beyond the immediate photosynthetic process; only recently was the P and R basis of survival superseded. With cultural survival so recently on a new basis, are man's instinctive attitudes to nature mainly inappropriate but lingering to be reckoned with in the Connecticut suburban forest and the fishing waters of Texas?

Two Extremes in Man's Ecological History

Man's cultural development is thus directly related to the energy budget available in excess of his previous level of sustenance. Where he was adapted like the pigmy to the heavy non-seasonal forest, he adjusted like the pigmy to a small percent of the total metabolism taken regularly from a system of great stability but with little excess for progress and the future. In a stable climax ecosystem such as a coral

atoll or a Darien rain forest man was maintained by the system, but with relatively little net growth; there was little opportunity for the human population once at its equilibrium to gain surplus energy for new purposes. Thus in the stable climax, man may have been stable but unable to innovate. Only a tiny percentage of the human populations could spend time in activity other than subsistence. Here man was fully at the mercy of the system of which we was a part. Perhaps fortunately for him, he controlled only a small proportion of the total energy of the system. The long evolution of the natural systems had provided some stability as his reservoir of protection.

Where man inhabited the variable ecosystems, energetics were different. There were wide variations and temporary energy excesses and with the temporary excesses invested in progress his culture blossomed and died like the desert flowers. When man converted a primitive hunting system to an agricultural system, the carrying capacity was increased. His new available energy sources were those products of forests or fields that he could divert from other consumers that would otherwise have eventually respired the organic matter. Control was easiest for him in fluctuating ecosystems where instability had prevented the tight organization of branching food chains of biotic specialists to preclude collectively his access to the energy flux.

Many aspects of the early history of man are understandable in terms of the irregular pulsing of energy for progress. The development of nomad and military mechanisms of adapting to irregular energy flows gained control of the system's energy flows. The more rapid cultural developments in the Near East and Asia are consistent with the wider variations in the pulsing of ecosystem energy availabilities. The rich but irregular cultures of the monsoon belts and subtropics are of P and R imbalance.

ECOLOGICAL ROOTS OF THE AESTHETIC

Deep within man's physical and cultural inheritances are environmental preferences that create strong desires even in modern times, as in the Connecticut suburban forest or the Texas Lagunas. One may speculate about instinctive drives and their possible significance for survival in the former eras when man's energy supplies were ecologically different.

To some extent these feelings now seem contradictory, for some seem to relate man to the stable climax and some to relate man to successional, aperiodic, and oscillating systems. It may well be that the relict instincts of man would place him on the forest edge between the successional plot and the climax, on shores for their high productivity, and in places where several kinds of productivity may be tapped.

What are some of man's preferences that seem related to climax?

Love of diversity, color in animals, multiple flowers, complex bird songs, mesic atmosphere, green softness, mossy-covered forest floors, shade?

What are some of man's preferences that seem related to successional stages? Love of a panoramic view, forest borders, and sunny spots, masses of homogenous herbs like the bluebonnets of the Texas sage. Whence come his likes? Are they completely unrelated to early survival? Are they related to survival as a part of a stable system, or are his likes tied to the momentary high pulsing of some less permanent system?

Whatever may be the functional roots of his inheritance of aesthetic preference, the excess energy of cultures rich in energy are soon diverted from survival into the satisfactions of the aesthetic preference whether they are still related to survival or not. Well-developed love of Nature, like other more formal arts, is an indicator of a high ratio of energy influx to subsistence energy demand.

If the aesthetic needs of man were formed in the past and nourished in relation to the hard realities of energy budgets, it is a reciprocal corollary that a system retaining the wrong aesthetics in diversion of its energetics may be eliminated in competition as in the ages past. Are the ecosystems like the suburban forest to be managed according to relict aesthetics related to the positions of tribal lodges or according to new aesthetics yet to be evolved according to new energy bases? Dare we manage the forest for the objective of a former aesthetic system when it may be non-essential and diverting energy needed for making gains for survival? Will competitive political and cultural systems roll over a society managing its modern ecosystems according to its tribal lores?

How sure are we of the continuance of the new energy sources? Are the precious decades of excess fossil energy now available for progress part of a receding flame? Should we manage our planning for survival in a P and R system that will prevail again? Should the forests and the bays be studied for maximum energy output for man at a later time? If man is again to be on a photosynthetic basis, the forests and bays might best be prepared for management no longer unsubsidized by present power feedbacks from the fuel-rich industrial complex.

Is it possible that non-functional aesthetic systems serve as energy buffers? Survival of a system may require the availability of great power reserves for short, violent periods of competition, disaster, and fluctuations of conditions. A system which builds its populations and reproduces its basic functional units to the maximum carrying capacity, like overcrowded grain beetles, has no power reserves. Is it possible that the persistence of the arts and the aesthetics in the human system serve to bleed off enough energy during ordinary times to prevent its preemption for maintenance so that during system stress, this power

drain can be immediately tapped into the main survival functions that may be unexpectedly critical?

With some humor, the artist, the Connecticut woodland pruner, and the Texas sea trout fisherman can imagine their energetic role as the vital protector of power reserves. No doubt, however, there is some proper percentage of the total budget for the artist's power flywheel.

Apparently, therefore, there are three main possibilities:

1. Management according to man's present aesthetics with the values and risks of diverting energy.
2. Management towards a time of declining subsidies of non-solar energy with study and forest system planning for timber and agricultural use once again.
3. Management according to man's present power systems with aesthetics retuned and controlled by the imagined realities of survival.

If we knew which of these or other objectives should dominate our energy planning, we could readily indicate the basic energetic boundary conditions to be used in ecological synthesis and engineering. Apparently, the momentary facts of economic life in forested Connecticut as along the Texas Gulf coast are demanding management for existing aesthetics.

SUMMARY

Using theoretical diagrams and the oyster reef pond ecosystem as an example, the methodology of studying and manipulating the gross photosynthesis and total respiration of ecosystems was outlined with techniques of ecological engineering: multiple seeding, self stabilization, replication by intermixing, energetic subsidization with power from man's civilization, and regulation by flux control.

To indicate the methodology as applied to a forest system, preliminary calculations were made of total photosynthesis and respiration of a patch of lower Montane rain forest of Puerto Rico. The slow growth of tree trunks was attributed to large respiration of leaves and forest floor rather than to any limitations of initial photosynthesis. Thus some approaches to management were indicated from metabolic considerations.

A theory of ecological determination involving the distribution of P and R in space and time was discussed in relation to man's early cultural role within ecosystems including two extremes, one with man as a minor component of complex, climax, and stable systems of long evolutionary history; the other with man the dominant consumer in erratic, successional, wildly fluctuating and unstable systems with temporary energy excesses to pay for progress. The possible ecological roots of his aesthetics in these systems were discussed and questions raised about their role in emerging new systems with shifting energy bases.

Literature Cited

- Anderson, A. 1960. Marine resources of the Corpus Christi area. Bureau of Business Research, Univ. Tex. Research Monograph 21, 49 p.
- Beyers, R. 1962. The metabolism of twelve aquatic laboratory micro-ecosystems. Ph.D. Dissertation, Univ. of Texas. 195 p.
- Golley, F., H. T. Odum, and R. Wilson. 1962. Trophic structure and metabolism of a Puerto Rican red mangrove forest in May. *Ecology* 43: 9-18.
- Little, S., H. W. Lull, and I. Remsen. 1959. Changes in woodland vegetation after spraying large amounts of waste water. *Forest Science* 5: 18-27.
- Odum, H. T. and C. M. Hoskin. 1957. Metabolism of a laboratory stream microcosm. *Publ. Inst. Mar. Sci. Univ. Tex.* 4: 115-133.
- Odum, H. T. and C. M. Hoskin. 1958. Comparative studies of the metabolism of marine waters. *Publ. Inst. Mar. Sci. Univ. Tex.* 5: 16-46.
- Odum, H. T., P. E. Muehlberg, and R. Kemp. 1959. Marine resources, p. 39-53. *In Texas Natural Resources, Report of Resource Committee, Houston Chamber of Commerce.* 104 p.
- Odum, H. T. and R. Wilson. 1962. Further studies on reaeration and metabolism of Texas Bays, 1958-1960. *Publ. Inst. Mar. Sci. Univ. Tex.* 7: in press.
- Odum, H. T., W. Abbott, R. Selander, F. Golley, and R. Wilson. Studies on the Lower Montane Rain Forest of Puerto Rico, Part I. Manuscript.
- Ordish, G. 1960. *The Living House.* J. B. Lippincott Co. 265 p.
- Siler, W. and H. T. Odum. Metabolism of a synthetic oyster reef-bay ecosystem. Manuscript.
- Vareschi, V. 1951. Zur Frage der Oberflächenentwicklung von Pflanzen-gesellschaften der Alpen und Subtropen. *Planta* 40: 1-35.

Ecological Tools and Their Use

The Application of Ecology to Multipurpose Use of Woodlands

J. D. Ovington

INTRODUCTION

The main purpose of my contribution is to show ways in which ecology can be applied to this general problem of land use in the suburban forest. There has been a great deal of research in forestry, particularly during the last 25 years. Although forest biological research has generally followed lines similar to those pioneered in agriculture and horticulture, greater importance has been attached to the multipurpose values of forest-covered land. Traditionally, forest land is expected to fulfill a number of functions, for example, to supply timber products, clean water and food, to reduce climatic extremes, soil erosion and flooding, to serve as a sanctuary for wildlife, and to be a source of recreation and aesthetic satisfaction. A rapidly multiplying world population and a higher individual standard of living invariably result in greater demands being placed on forest land and certain types of use occasionally become of overriding local importance.

The returns from timber production are considered to be of little significance in some woodlands. Epping Forest near London and Forêt de Soignes near Brussels both serve primarily as playgrounds for the urban populations nearby and in Highland Britain the returns of timber from small woodlots are negligible compared to the shelter they provide for domestic stock. Clearly, forests are no longer being regarded generally as wild crops, to be harvested periodically and left to restore themselves naturally, but to an increasing extent will be managed intensively and selectively for specific purposes.

If forest management and use are to be placed on a more rational and scientific basis, it is necessary to be able to specify the limits to which a particular use can be extended, without adversely affecting other essential forms of use and endangering the whole community. We need, for example, to understand more fully the effects on productivity and woodland biology of converting natural woodlands or deforested areas to intensively managed and harvested forests. Similarly, we must know the capacity of a woodland to withstand recreational pressure; the sheer

weight of people may so compact the soil that the vegetation is changed. Again, where the hunting interest is uppermost, we need to know the most appropriate population level of deer. Frequently when the aim is to provide as many deer as possible, the natural regeneration of the trees is completely eaten by the deer, who are literally eating themselves out of a home. The evaluation of woodland potential for different purposes under various types and intensities of management presents to woodland ecologists a complicated but challenging problem of considerable practical significance. This challenge can be met by the development of a more dynamic, quantitative and integrated approach to woodland ecology, but formidable difficulties have to be faced.

For example, few of the existing forest data can be applied readily to the problem of the suburban forest. Although numerous routine forest mensuration records are available in the form of yield tables, their ecological value is diminished because they have been prepared mainly for commercial purposes and only give volumes of marketable tree trunks with little, if any, description of site conditions and no indication of the value of other uses. Frequently the results of different types of woodland research cannot be brought together because critical background records are omitted. It is not unusual to see detailed descriptions of woodland soils or understorey flora with virtually no information of the tree cover. The results gained by the various scientific disciplines involved, e.g. zoology, pedology, botany, or climatology, are expressed in different terms and on different scales. The zoologist may be thinking in terms of a rotten log, the pedologist of a certain soil type, the botanist of a vegetation continuum and the climatologist of a regional climate.

Another difficulty is that, because of the great age the trees attain, it is impossible in forestry to set up critical experiments like those of agriculture which, within a few years, give results covering the life histories of several crops or even of the successional developmental stages of a single generation of trees. Consequently much research has to be carried out in existing woodlands and experimental plots with all their imperfections, e.g. lack of knowledge of past conditions and inadequate statistical replication of treatments. Since new long-term experiments in woodland ecology may span several generations of research workers, continuity of observation cannot be assured.

Finally, the great size and diversity of woodlands means that sampling and recording have to be planned on a relatively massive scale, despite various ingenious systems of selective sampling that have been developed. The handling and statistical interpretation of the resultant mass of data constitutes a tremendous task for which computing facilities are essential.

A useful means of synthesis, by which to bring together past research and to plan future work, is provided by the ecological concept of ecosystem, which encompasses living organisms and their remains as well as all relevant environmental factors, both biological and physical. Woodland ecosystems can be considered best in terms of four dynamic functional processes, namely (1) the organic system, (2) nutrient circulation, (3) energy flow, and (4) water circulation. It should be emphasised that no clearcut division between these processes occurs in nature since all are inter-related in numerous ways.

The ecological contribution to a better understanding of how woodlands function under different forms of use can be envisaged as being based on two distinct but complementary research operations. These should be centred around the four processes of ecosystem physiology and consist of (1) the bringing together of existing data to distinguish the relative importance of different facets of woodland dynamics so as to provide tentative answers to immediate problems, and (2) the establishment of new, long-range research programmes designed specifically to give a comprehensive answer to such questions of land use as are being posed at this symposium. These programmes should embrace several scientific disciplines and be confined to particular woodland types, or if necessary to woodland plots, so as to ensure that it is possible to link together different types of research and understand the relationships between the many different parts of woodland ecosystems. In view of the complexity of the problem these programmes must be carefully located in woodland ecosystems, which are likely to give results capable of projection to woodland areas in general. The scope of this contribution and its potential use can be demonstrated by briefly sketching the main features of the four functional ecosystem processes.

THE ORGANIC SYSTEM

Few comprehensive records are available of the production, accumulation and loss of organic matter in individual woodland ecosystems, but it is clear that, compared with most other terrestrial ecosystems, woodlands are characterised by the great mass of plant organic matter that accumulates within them. This accumulation of organic matter occurs despite periodic harvesting and a high rate of decomposition. Natural oakwoods in Minnesota, for example, contain about 25 times as much plant organic matter as neighboring prairie ecosystems (Ovington and Heitkamp, in press).

In Connecticut, the invasion of old fields by red cedar and oak is also resulting in organic matter accumulation. The amount and distribution of the plant organic matter in woodland ecosystems varies

greatly depending not only upon the type of management but also upon site conditions and the maturity of the woodland.

No reasonably complete biomass figure is available for the total fauna of a woodland but the existing evidence suggests that the fauna is considerably less in weight than the plants so that the total organic biomass probably does not greatly exceed the plant biomass in weight. There seems little doubt that the animal biomass is also greatly affected by different forms of management.

The first need of investigations into the dynamic nature of the organic system is to determine if the weights of the different types of organic matter are changing from year to year to give a long-term trend, and if so, the rates of change.

Presumably, in relatively stable natural woodlands the amount and type of organic matter present remains fairly constant but, in intensively managed woodlands they may change rapidly, e.g. successful afforestation normally results in a rapid increment of organic matter. The Breckland region in Britain, an area of sandy soils, formerly with an herbaceous plant cover, has recently been afforested mainly with pines and various alien conifers. If we take 22-year-old plantations there as examples, where *Pseudotsuga taxifolia* was planted there has been an average annual increment of organic matter into the ecosystem of $9.0 \cdot 10^3$ Kg. per Ha. and for *Alnus incana* $5.3 \cdot 10^3$. In the Douglas fir stand the increase results mainly from the annual build-up of the tree and litter layers ($+8.9$ and $+1.0 \cdot 10^3$ Kg. per Ha. respectively) with a decrease in the herbaceous layer ($-0.9 \cdot 10^3$ Kg. per Ha.) whilst the comparable figures for the alder plantations are $+5.7$, $+0.2$ and $-0.6 \cdot 10^3$ Kg. per Ha. respectively. Besides differences in weight, there are great differences in type of organic matter, the litter layer formed under the Douglas fir is unlike that under alder and the same species of plants are not present in the ground flora of the two woodlands.

Whilst information of biomass and its rate of change is valuable, it cannot provide a complete picture of the functional processes of the organic system, for more organic matter is produced by the trees and understorey plants than accumulates within woodland ecosystems (Fig. 1). Part of the primary production is used up as the green plants respire; values have been given for the use of photosynthate in this way which range from about 60 to 240 per cent of the net primary productivity. In addition some organic matter is harvested and a large proportion of the production is decomposed.

Annual net primary productivity figures for woodland ecosystems in temperate regions of over $10 \cdot 10^3$ Kg. per Ha. are not uncommon and in some tropical woodlands the net primary productivity amounts to about $40 \cdot 10^3$ Kg. per Ha. per annum (Ogawa, 1961). Dry matter production

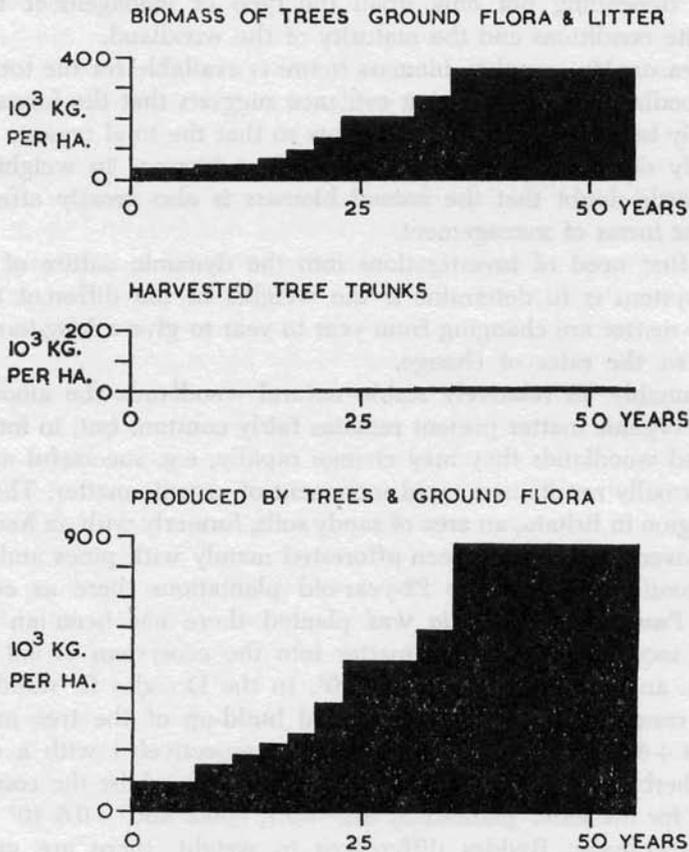


Figure 1. Organic system for Scots pine plantations, oven-dry weights.

by forests is presumably limited by various site factors, thus in Europe the maximum possible net primary production for the period April to September has been calculated by Wit (1959) from solar radiation figures, to be about 36×10^3 Kg. per Ha. but the actual annual production by actively growing woodlands in this region is only about half of this. Nevertheless, in general, woodland ecosystems appear to be relatively efficient producers of organic matter, comparing well with agricultural crops even though management is more intensive in agriculture. The relative efficiency of woodland ecosystems can be attributed to several obvious factors such as the multi-layered structure of the plant community, the great mass of tissue containing chlorophyll present for much of the year, the large leaf area and the extensive root system. Other, less obvious, attributes of woodland ecosystems may also be

important for high productivity, e.g. root grafting between forest trees occurs commonly and it may be that, when some trees are harvested or are cut down during thinning, their roots persist to serve the surviving trees so that recovery after selective cropping is more rapid than might be expected.

With greater demands being placed on forest land, the problem of increasing the biological productivity of woodlands becomes important. The complementary roles of the different plant layers must not be overlooked in this respect, for if the trees are not fully utilising the site so that the tree crowns provide only a light cover, the shrub and herbaceous layers become correspondingly more luxuriant. In deciduous woodlands the overstorey and understorey plants frequently exhibit remarkable phenological synchronisation, the peak productivity of the herbaceous layer being achieved in early spring before the tree buds are fully opened. On the whole the best means of improving the productivity of the trees are probably (a) to improve site conditions, e.g. by irrigation and applying mineral fertilisers and, (b) to breed trees capable of high rates of photosynthesis and which are resistant to disease, drought and cold. The effects of silvicultural operations, such as pruning and thinning, on the functional ecosystem processes and biological productivity, as distinct from the production of high quality tree trunks, are controversial.

The difference between net primary productivity and the amount of organic matter accumulated in woodland ecosystems results mainly from the loss of plant material by harvesting and decomposition. A variety of organic matter may be cropped from forest land; timber, foliage, Christmas trees, cones, litter and wildlife, but normally tree trunks constitute the bulk of material removed by man. The loss of organic matter from the ecosystem through harvesting accounts for only a relatively small proportion of the primary production. Taking plantations of Scots pine in Britain as an example, if all the tree boles produced were harvested at 35 years of age, their combined weight would only amount to about one third of the net primary production of the ecosystem.

The greatest loss of organic matter results from decomposition within the ecosystem. Breakdown processes begin on the living plants and are continued in numerous ways by a variety of agencies, physical, chemical and biological. In 55-year-old Scots pine plantations, the average annual turnover of above-ground organic matter is about $8 \cdot 10^3$ Kg. per Ha., i.e. three fifths of the primary production but values of up to $25 \cdot 10^3$ Kg. per Ha. have been recorded for tropical gallery forest (Ogawa et al., 1961). Undoubtedly, a large annual turnover of organic material also results from root breakdown (Orlov, 1955) but few measurements of this

are available. In view of the importance and complexity of decomposition in the organic system, there is a great need to bring together detailed studies of the inter-relationships of the soil organisms and their environment and quantitative studies of litter fall and breakdown.

Although the organic systems of woodlands vary greatly in magnitude, woodland ecosystems clearly have a potential for high rates of organic matter production, accumulation and breakdown. Because of the multi-layered woodland structure and the complementary roles of woodland organisms, there is considerable scope for modifying the organic system without destroying the woodland character. Balance sheets of organic matter show that the forester is taking off only a small part of the total produced. In addition, he harvests a greatly restricted type of material; harvesting could, however, take place at different levels, both producer and consumer, in the organic system. Because you have this massive system there is considerable scope for man to interfere, and he has a handsome opportunity for more scientific use.

NUTRIENT CIRCULATION

The organic matter in woodland ecosystems contains many different chemical elements, and associated with the production and breakdown of organic matter these chemical elements are transferred within the ecosystem. For example, since forest production is mainly carbohydrate production, large amounts of carbon dioxide are taken up from the atmosphere and immobilised in the organic mass. Much of this carbon dioxide is released later at ground level by the decomposition of the surface litter.

Some of the chemical elements contained in the organic mass are nutrients essential for plant growth. In highly productive woodlands, the build-up of organic matter results in a large annual accumulation of plant nutrients, about 23 Kg. of K per Ha., 53 of Ca, 8 of Mg, 6 of P, and 60 of N, of which approximately a quarter is in the tree trunks. Nevertheless, the average annual removal of nutrients by the harvesting of tree trunks is relatively small compared to that in agricultural crops, varying from about a half to a fiftieth, depending on the nutrient and on the woodland type.

Much greater amounts of plant nutrients are taken up by the woodland plants than are harvested or retained within the plant biomass. Smirnova and Gorodentseva (1958) found that of the 111 Kg. of N per Ha. taken up by the trees of a 30-year-old birch wood, 45 Kg. was retained within the trees and the remaining 66 Kg. was shed in the litter fall. In older birch woods the difference was even more marked, only

10 to 20 per cent of the annual nutrient uptake being held within the trees. There is, therefore, a considerable annual interchange of nutrients between the woodland plants and the soil. The understorey vegetation may also play an important part in the nutrient circulation of woodland ecosystems, particularly in poorly stocked woodlands. P'Yavchenko (1960) has shown that in old spruce and pine woods in the U.S.S.R. nutrient absorption and circulation by the understorey vegetation is over 16 times greater than that of the trees.

Fear has been expressed that intensive harvesting of forest ecosystems will decrease the nutrient capital and ultimately reduce productivity as the soil reserves are depleted. Nutrient balance sheets indicate that the greatest danger is likely to be Ca depletion because the tree boles contain a relatively high proportion of Ca compared with other nutrients. In order to counteract possible nutrient depletion through exhaustive harvesting and to improve woodland productivity, mineral fertilisers are now being added to some woodlands but different results have been obtained by this treatment, varying according to site and woodland type. If, as it seems at present, the use of mineral fertilisers is to become widespread, maximum benefits can be obtained by relating this to the individual nutrient cycles.

In considering nutrient circulation and the dangers of depleting the nutrient capital by harvesting, it is important to take into account various external factors which affect the nutrient capital within the ecosystem. Significant amounts of nutrients are added to woodland ecosystems in precipitation, in airborne dust intercepted by the vegetation mass, by rock and soil weathering and by fixation of N from the atmosphere. Nutrient loss through leaching as well as harvesting then has to be set against these credits.

The long-term effects of heavier cropping of woodlands on the nutrient capital and the need to remedy any nutrient loss must, therefore, be considered not only in terms of the internal capital of the ecosystem, but also of the credit and debit factors affecting this capital. Ecological balance sheets for the individual nutrients permit the ecologist to evaluate the components of the ecosystem and to forecast the changes that will result as succession occurs in the suburban forest vegetation and as man interferes.

ENERGY FLOW

About half of the solar radiation reaching the earth's atmosphere penetrates to the earth's surface and only part of this is available for photosynthesis. Since woodlands, compared with other terrestrial ecosystems, are capable of producing large quantities of organic matter, it

follows that energy fixation is also relatively high. In Scots pine plantations in Britain, about 2.5 per cent of the incident radiation within the wave-lengths utilised by photosynthesis or 1.3 per cent of solar radiation is fixed within the primary organic matter produced, and for tropical forests the corresponding photosynthetic efficiency is not greatly different, the available figures giving a value of about 3 per cent.

The solar energy, captured as a result of photosynthesis by green plants, supplies the needs of all the other living organisms in woodland ecosystems. As organic matter passes through the food chain and is broken down by the various agencies, the contained energy is released, so that there is a pattern of energy fixation, storage, and release broadly comparable to that of the organic system (Fig. 2). The release of energy at different consumer levels can be summarised in the form of balance sheets similar to those prepared for different chemical elements. Since virtually all other living organisms depend upon the green plants for their energy supply, the efficiency of the trees and understorey plants in capturing solar energy sets an upper limit to long-term energy flow and biological activity within woodland ecosystems.

Woods (1960) has recently outlined some of the possible applications of a knowledge of the energy relationships of forests to woodland management and suggests that silviculture can be based on energy flow. The most noteworthy application of energy dynamics is to determine site potential. Since the annual input of solar radiation to an ecosystem is relatively constant and uncontrollable by man, the energy available for photosynthesis gives the primary upper limit of site potential. Where the energy is not being fully utilised, other factors are limiting organic matter production, e.g. photosynthetic efficiency of plant stock, water supply or soil conditions.

WATER CIRCULATION

Except in arid regions, water has generally been regarded as a cheap, abundant, renewable natural resource, but with increasing use of water for domestic and industrial purposes shortages of water are being experienced in areas normally thought to be well endowed with this resource. In Britain, for example, where the amount of water used annually is only about a fiftieth of the average annual rainfall, shortages of water are occurring with increasing frequency during the summer months, even though large areas of hill land have been set aside as water collecting grounds and enormous quantities of water are stored in reservoirs. The problem is further aggravated by the fact that the centres of population are in the drier areas. Since many catchment

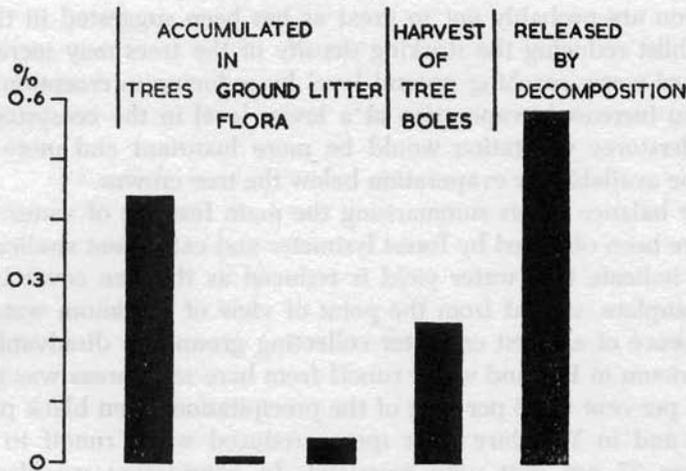


Figure 2. Fate of the 1.3 per cent of solar energy in plant production of Scots pine plantations 23 years old.

areas are forest covered or are regarded as suitable for afforestation, it is important to know the effects of woodlands and different types of woodland management on the pattern of water circulation, particularly in relation to water yield. The movement of water through woodland ecosystems differs greatly from that of organic matter, nutrients or energy, the annual increment of water into the organic matter is less than 1 per cent of the annual rainfall, there being a very rapid transfer of water into and out of woodland ecosystems.

Part of the precipitation is caught on the vegetation and some of this is evaporated back into the atmosphere without ever reaching ground level. In Britain as much as 50 per cent of the precipitation may be evaporated in this way and the remaining water that penetrates to ground level is distributed unevenly as it drips from the tree crowns or flows down the tree boles following interception. The amount of water penetrating to ground level and its distribution over the forest floor depends largely upon the type of vegetation cover and the amount of rainfall falling in individual showers. The forester is therefore able to control, to some extent, the supply of water to the soil by modifying the forest vegetation. He may also influence water storage in the soil by various management techniques, e.g. the construction of drains. The amount of water withdrawn from the soil and transpired by woodland plants also varies greatly according to the type of vegetation cover.

The possibilities of controlling water yield, as distinct from influencing the pattern of water circulation, by manipulation of the forest

vegetation are probably not so great as has been suggested in the past. Thus whilst reducing the stocking density of the trees may increase the amount of water reaching ground level by reducing interception, it also results in increased evaporation at a lower level in the ecosystem since the understorey vegetation would be more luxuriant and more energy would be available for evaporation below the tree crowns.

Water balance sheets summarising the main features of water circulation have been obtained by forest lysimeter and catchment studies and in general indicate that water yield is reduced as the tree cover becomes more complete, so that from the point of view of maximum water yield the presence of a forest on water collecting grounds is disadvantageous. At Castricum in Holland water runoff from bare sand areas was reduced from 77 per cent to 30 per cent of the precipitation when black pine was planted and in Yorkshire sitka spruce reduced water runoff to 28 per cent from 37 per cent with grassland. In considering woodland ecosystems in terms of water, the reduction of water yield must be set against the value of the timber crop, as well as the effects of the trees in improving water quality and the reduction of flooding, caused by delaying and reducing peak runoff of water after heavy storms.

CONCLUSIONS

The ecological ecosystem approach to woodland management and utilisation permits a better appreciation of the dynamic complexity of woodlands. Once the main patterns of the four functional ecosystem processes are characterised it is possible, using techniques such as that of analogue circuits, to forecast with some precision the effects of different management practices on each of these processes and the woodland organisms. In this way the long-term results of different combinations of use of the suburban forest can be evaluated and ecologists enabled to specify the limits to which a particular use, say, the harvest of litter, can be developed to meet man's requirements. However, woodland ecosystems should not be considered in isolation; in urban landscapes they are frequently only one of several types of ecosystem present, all of which are inter-related in various ways and whose relative proportions may give a pleasing and balanced landscape.

Whilst woodland ecologists can contribute greatly to more rational utilisation of wooded areas, woodland ecology can never be a panacea for all problems of woodland utilisation. The aesthetic values of forests are difficult to assess quantitatively and diversity of woodland type may be more important than maximum use. It seems inevitable that the final strategy of woodland use will always be a compromise between



West Rock, a Connecticut trap ridge.



Trees find living room on old fields.



ecological, social and economic factors. It is imperative, if the ecologist is to play his full part in land use, that he equips himself to be able to say what the consequences will be as man impinges increasingly on the suburban forest.

References

- Ogawa, H., Yoda, J. and Kira, T. (1961). A preliminary survey of the vegetation of Thailand. *Nature and Life in Southeast Asia* 1, 21-157.
- Orlov, A. J. (1955). The role of feeding roots of forest vegetation in enriching soils with organic matter. *Pochvovedenie* 6, 14-20.
- Ovington, J. D. and Heitkamp, D. (in press). Comparative studies of prairie, savanna, oakwood and maize field ecosystems in central Minnesota. (1) Plant biomass and productivity. *Ecology*.
- P'Yavchenko, N. I. (1960). The biological cycle of nitrogen and mineral substances in bog forests. *Pochvovedenie* 6, 21-32.
- Smirnova, K. M. and Gorodentseva, G. A. (1958). The consumption and rotation of nutritive elements in birch woods. *Bull. Soc. Nat. Moscow (biol.)* 62, 135-147.
- Wit, C. T. de (1959). Potential photosynthesis of crop surfaces. *Ned. J. Agr. Sci.* 7, 141-149.
- Woods, F. W. (1960). Energy flow silviculture — a new concept for forestry. *Proc. Soc. Amer. For.*, 25-27.

Ecological Tools and Their Use

Discussion

Ovington. Earlier we discussed problems of planning. Another problem of planning is to allow for the variable area of the suburban forest. At present we must deal with it as it is whilst recognizing its changing nature. We can, however, apply the same basic ecological tools for examining its use for different purposes. The same ecological principles apply whether you use your forest for amenity or for timber.

Dansereau. The same principles apply, but the principles and processes involved vary in widely different proportions. For instance, in the planted forest, the trees were deliberately planted, the species were chosen, the individuals were placed in certain positions, so the problems of dispersal are not involved as in the derelict forest where you wonder how the beech got there.

Ovington. If we haven't got a discipline in ecology, we might as well not be sitting here. We may compare managed woodlands with derelict woodlands. To understand how these function, however, the same basic ecological principles must be applied. All are taking up energy and this is passing through the system in various ways. All intercept rainfall and water goes through the system. The same fundamental patterns occur. Man is only manipulating the vegetation and so changing the magnitude of the various systems.

The amount of energy it costs to make sure that a plant is there can be determined by analyzing a man's efforts. If he did any less than was needed the weeds would come in, and if he did any more, it would be unnecessary.

Spurr. In an ecological study we have to realize that we frequently work mistakenly at different levels at the same time. For our trees we go to a stand in the Eli Whitney Forest, for our climatic data we take the weather records of the New Haven Weather Bureau, and for our soils data we dig a soils pit. We have got to learn to generalize our soils data and to localize our climatic data into the particular community we are working with.

Darling. We tend to think far too much of the visible flora and the visible fauna. The whole field of so-called wildlife management is crazy to neglect the invisible. They don't realize what they are dealing

Local Types of Suburban Forest

From the Ecological Viewpoint

Discussion

ABANDONED FIELDS

Waggoner. Of the 2 million acres of suburban forest in Connecticut, old fields represent an important part, 1 million acres, a third of Connecticut. These old fields have been out of cultivation for different periods of time. Let us consider a specific area of 100 acres made up of old fields last tilled 20 years ago. It grows red cedars, briars, and honeysuckle. You cannot walk across it as you will, but must follow rabbit paths. In one corner it is occasionally pastured or a farmer comes in August, mows some hay to take home. This is not a building lot. It seems impossible that there is so much of it, but there is. Someone is going to plan a use for this land. They are going to carry the plans out, or at least, they are going to start.

We are called upon to suggest some things to him and to anticipate significant research problems that are going to arise out of our suggestions. Before we can get on with this job, we have to know our goal. Because of the preceding discussions we can set goals.

Amenity was accepted as the primary purpose of the suburban forest. It can be specified by six attributes. It must be 1) green promptly, 2) stable and trouble-free, 3) provide a screen that gives privacy but remains passable to breezes and an occasional walker, 4) varied, which is both a good in itself and an insurance against oversight, 5) free of things that bite us, 6) a home to interesting animals.

By suggesting actions to the owner of this tract, we can visualize the significant scientific problems. The first action is the commonest action, "do nothing."

Now let's appraise the degree to which doing nothing accomplishes the specifications of amenity, thinking of the accompanying research. The old field is already green and will continue so. It is not stable and will appear different 30 years from now. It is a good screen but not passable to you or the breezes. It is certainly varied. It harbors pests. It is temporarily the best of all possible worlds for small animals. What things need doing either to buttress the decision to do nothing or to foresee problems that grow from it?

Ovington. In contrast to doing nothing, I am inclined to think about intervention. If I were the landowner I would decide what proportion of this hundred acres I wanted under woody, perennial vegetation and what proportion under grass. One of the most pleasing landscapes I know is the Swedish Enge which is a patchwork of pasture and clumps of shrubs and trees. Over a long period, the Swedes developed a system with the right proportion of woody areas to pasture. The open areas were no wider than the shade cast by the trees and all parts were at some time of the year shaded by a tree.

You can wander between these wooded areas, into meadows of a wonderful variety of sizes and shapes. It is extremely stable, requiring little effort to maintain. Invasion of woody plants into the pasture was prevented by cutting or grazing. This system is disappearing now in Sweden because it is uneconomic, but with affluence, you could put in the extra effort needed to create a landscape of this type in Connecticut.

This would give greenness, it lacks complete stability, there is a great variety of color and form, it provides a screen but not an impenetrable one, its diversity gives resistance to pests, and many animals find it an excellent home.

All kinds of scientific problems need to be examined: the relationships between the wooded and pasture areas, the means of maintaining pasture, the maintenance of soil fertility in the pasture areas through the blowing of tree leaves into them, the movement of animals who find shelter in woodland areas or go to the pastures to graze. In such areas you shouldn't look at the woodlands individually. You must view their role within the whole landscape.

Spurr. I question the specification "stable." We look for variability in space, why shouldn't we look for variability in time? We tire of a set landscape and of a landscaped garden for it is pleasant to watch things change. One of the missing elements is the successional hardwood forest and this could be desired, at least locally. If we were dealing with a hundred-acre lot of this old field, we could encourage dynamic activity in certain areas.

The specification of "pest free" is an example of Bates' "conception environment." A pest to one person may not be to another. You don't want stability everywhere, do you? Variety and change are necessary. Change is where things happen, whether it is in the mind or in a natural habitat. Change is part of our intellectual environment, because unconsciously we find it interesting. We don't really want stability except in the overall picture.

Russell. The Experiment Station will be asked by various people to achieve different objectives. Perhaps you should take several such tracts,

or maybe divide this one into four pieces and, by different management, achieve various objectives. This approach leads to an infinity of situations, but you should study a wide variety since you should consider the diverse tastes of people.

Another important feature is time. It takes 20 years to create a situation, but by creating diversity, you establish the wider range of ecosystems wanted 20 years hence. A responsibility of the Connecticut Station may be to set in motion the kind of management systems which, 20 years from now, will give the ecologist a diversity of systems to study and also give the public an opportunity to experience a variety of particular combinations.

Spurr. There is danger in talking of a research program based on the needs of the day. Mankind and economics change faster than experiments mature. Something happens in the local economy and none of the treatments is practicable or the local culture moves past you. It is, therefore, necessary to orient your research biologically. What are the problems of speeding or stabilizing succession, of favoring "pests" or eliminating them? Only when you have the biological alternatives can you figure what is economic in a given situation.

Waggoner. A surprising appreciation of the attractiveness of open fields has been revealed. McKusick has said that Connecticut landowners want to preserve distance, the sense of distance to the hills. The critical ecological problem is the arresting of succession to maintain their openness and to do this economically.

Farb. Frank Egler is doing this in his forest in Norfolk. He is keeping glades open, some of them quite economically, by basal spraying of trees with herbicides. I have visited there at 5-year intervals and find he has arrested succession. Carrying the knapsack sprayer around a forest, however, is not effortless, nor is it a job for the layman.

Odum. To arrest succession is, from the energy point of view, to produce a climax in which respiration and renewal equal photosynthesis. You remove what you were storing and preparing for the next step. The farmer removes the hay. Or you upset the nutrient complex by bringing in invertebrates which disturb your neatly prepared soil. Upsetting the harmony of the system to control succession by subtracting nutrients would be slow, whereas adding something that, say, upsets the calcium/phosphorus ratio might control succession in a special way as occurs in an aquatic system.

In aquatic systems photosynthesis can be reduced to equal respiration

by making the water turbid. The same result might be achieved in terrestrial systems by the use of opaque plastic spread for a few days.

Went. A great amount of the organic matter produced by forests is not harvested and it should be possible to harvest more material by developing an ecosystem clipper.

Waggoner. Mr. Hicock and Mr. Olson of this Station spent a great deal of time from 1940 to 1950 trying to find some marketable use for low-grade wood. They developed a charcoal kiln and a means of treating poles economically. If a large market for this could be found, the situation would be changed greatly. Here would be ecosystem clippers, paying their way. Fire, of course, is an economical means of "harvest," but difficult to manage in the suburb.

Spurr. We agree amenity values are important in Connecticut. But hardwood pulp also has real meaning for New England. I might illustrate this by what has happened over the last 10 years in Michigan. The regional pulp industry in Michigan, as in southern New England, had disappeared except for a few mills using imported pulp from Canada. With the development of new chemical processes and the need for insulating board, the hardwoods of Michigan are being used in new pulp facilities. The owners of the pulp mills moving into Michigan discovered immediately that they could not afford to buy any land because lawyers, doctors and auto mechanics like to own 40 acres and will pay \$40 an acre for barren sand plain. Foresters were trained to help landowners prepare management plans for the land along the lines the landowners wanted. The forester's services are contributed free and the lumber is bought at the going market price to help pay taxes. This has been highly successful and it is a booming business in what is basically amenity forest.

Hicock. Something similar could easily happen in Connecticut and perhaps in the not-too-distant future. Amenity may be uppermost now but the potential to produce 2 million tons of fiber annually, in perpetuity, and still have the amenities, should not be dismissed lightly.

Collins. The old field is the beginning of a series of successional stages that leads to forest. It is one of the least stable and, therefore, the cost of stabilizing it is high. We can maintain our old fields in one of two ways. Either pay the higher cost of arresting succession by frequent management, or pay a lower cost by rotating land so that a portion is always passing through an old field stage. On a 100-acre plot one could cut 10 acres every 10 to 20 years, allowing them to revert to old

field stages. Then, somewhere on the plot you would find old fields represented even if they weren't always at the same location. If we lack the data for arresting succession at an old field stage, we may find that the rotation system is cheapest because nature automatically takes the cleared land in that direction.

Russell. Before we design treatments to maintain old fields, we must recognize that this will be a long-time experiment. First we need the type of quantitative analyses that we have discussed here: look at the fluxes in and out of the system, at the metabolism rates, at the turnover rates, and at the nitrogen cycle. Given the greater amount of quantitative information perhaps we can identify the bottlenecks or the control mechanism in this complex system and make a rational approach to its management.

Dansereau. This conference has shown that we have new means of estimating the meaning and rate of succession. There is still a great deal we don't know about it. After 20 years I have revisited plots which I had previously studied. Some are completely different, and others surprisingly stable. Why? Does this process go on continuously or does it operate in relays? Are certain elements critical at one time and no longer so at a later stage? Some of the things we have been hearing from Ovington and Odum indicate such a possibility. It can only be tested if you work on the same site for a period of time and do nothing in the real sense of the word, just let it happen. Apply these modern concepts to parallel series of these successional phases involving the juniper savanna which is a middle stage, neither pioneer nor climax, and see what happens. That would be a very important program.

Ovington. You can go into the woods, find a range of situations and by taking things as they are reach some conclusions. Unfortunately you can never be sure that these woods are not unique. You must therefore lay down long-term experiments in which treatments are well documented. In these field experiments you should try not only the commonplace things, but also the unusual things, even the ridiculous. You might manage a woodland for butterflies!

I state emphatically that this is the role the Station should have: looking at the existing conditions and creating a new variety of conditions to evaluate.

However, while you are doing this, these old fields are becoming reforested and you really can't await the results of long-term research. This is another problem. For the present you must look at your existing woodlands and make do scientifically with the variations you have while trying to arrange a sensible long-range project.

TRAP RIDGES

Waggoner. Trap ridges are a significant portion of the 20 per cent of our acres where tree growth is poor. Although of little interest for forestry and a home to few people, they are a striking feature of the Connecticut landscape. When their oak cover is denuded by gypsy moth, the trap ridges no longer form an attractive backcloth. Then some people demand spraying with insecticides which others fear. This is a suitable problem for ecological discussion, for the trap ridges give extremes of environmental conditions, the annual organic cycle is hastened by the defoliation, and the application of insecticides introduces a largely unknown factor into the system.

Collins. The trap ridge is a resistant mass of igneous rock brought into relief by geological erosion of softer adjacent rocks. Water and nutrient drain from such a ridge, watering and fertilizing lower slopes where better tree growth is found. The basic rock weathers into a thin acid soil.

Trees are either absent or stunted on the most shallow soils. This enables some of the rare, low plants to escape tree competition and prosper. Trees developing on the less shallow soils are generally stunted by periodic drought and high transpiration of the windy summit. They are frequently broken by glaze storms. On deeper soils of lower slopes, trees may be uprooted by periodic windstorms, whereas their oak and hickory companions on the drier summit may occasionally be defoliated by gypsy moth larvae.

Hitchcock. The gypsy moth has one generation a year. It overwinters as an egg, comes out in the spring as a larva and feeds until it pupates in July. Feeding and defoliation occur during May and June. The oak then refooliates later in the summer. No fully adequate means of biological control have been found, and at the moment spraying is the only effective control. I feel that spraying is economically unsound, but it does keep woodlands green and therefore more pleasant.

Wallis. This year, for instance, 50 per cent of the leaves will be eaten from 105,000 acres, most of this on trap ridges and sandy plains scattered over much of western Connecticut. It costs about \$1 an acre to spray from the air and you have to keep on spraying year after year.

Waggoner. Returning to specifications of amenity, the cover of the trap ridge should be green, stable or trouble-free, a screen for people, varied, pest-free, and home to interesting animals. Although we were going to live in or near the old field, we are now talking about the backdrop. The greenness which was first in importance in the case of the old field, is still first in the case of the trap ridge. The stability or freedom from

trouble that was second is still second. Screen has no meaning in the case of the ridge because the whole is a rock screen. Variety in the backdrop is desirable. This freedom from pests that bite us has little meaning up there. Thus the requirements are easier for the ridge.

What action can one take and what weaknesses in our fundamental knowledge does this action expose?

The first plan is "do nothing." The plan to do nothing is forsaken when the gypsy moth arrives and doing nothing often becomes spraying, a recurring expense and irritation to people. I think we should pass from doing nothing to another plan: remove the favorite food, oak.

Farb. In addition to being a reservoir for pests, the trap ridges are sometimes sanctuaries for wild animals, such as coyotes and bobcats. People are afraid of these animals close to the suburban homes. The ridge forms a psychological screen, therefore.

Lutz. It has been suggested the oak be removed to overcome the gypsy moth problem but the public would be substantially more excited if within the next year all of the oaks were to be taken off the hillsides. You would spend as much money removing the oak as the gypsy moth. Removing the oak would take a bit of doing and the oak is going to return, unless you pull the seedlings, an annual chore.

This trouble is primarily a gypsy moth problem. What would happen if instead of removing the oak we reduce the proportion of oak? Would you get a reduction in defoliation?

Spurr. Controlling defoliation by reducing the proportion of oak to, say, 40 per cent is questionable. I never saw any evidence that the percentage of oak was a factor in gypsy moth resistance. Dr. Bess' work and the circumstantial evidence we saw in the gypsy moth region, led us to believe defoliation was largely a function of moth mortality. Mortality occurs when the insect is on the ground where it is eaten by rodents. On these dry trap ridges where the larvae spend time in the trees rather than on the ground they survive in high numbers. I suspect that defoliation would continue if you had 20 per cent reduction in oak, but it wouldn't be as much of an eyesore.

Lutz. I think it would be better to increase the proportion of hemlock at the expense of the oak, rather than obliterate the oak. You could introduce some white pine there, too.

Collins. Historically there may have been more pines. Being a fire climax species, pitch pine is slowly retreating with better fire protection, giving way to scrub oak. However, hemlock appears to be increasing in the absence of fire.

The only trouble with introducing conifers, such as hemlock, is that once defoliated they die. You must remove enough oak to prevent the increase and spread of caterpillars to the conifers.

Spurr. Certainly it is desirable to bring in conifers, laurel, and all sorts of resistant trees and shrubs. I do not think it matters whether shrubs or trees cover a traprock ridge. It is undesirable to let the ridge become a public nuisance. Spraying at the right time together with bringing in resistant plants may be the best prescription.

Dansereau. Isn't managing a low canopy simpler than managing a tree canopy? Isn't it possible to cover this trouble area at the top with some low canopy economically and wouldn't this influence the gypsy moth population under oak?

Are there any climax stages of this forest in which oak would disappear more or less automatically?

Lutz. There are some native white pines around Mt. Carmel Sleeping Giant. Some of the extreme ridge tops have a climax of red cedar. On top of Mt. Carmel are the biggest red cedar stumps I have ever seen. Red cedar is there because other vegetation does not produce a canopy to shade cedar. On the upper parts of the ridges you could maintain red cedar and increase the proportion present.

Hicock. If we searched on one of these ridges, we could find at least 60 species of woody plants. If we limit ourselves to red cedar or laurel, we are not using all we've got to work with.

Went. To let the moth remove the oak would be an ecological means of working toward a type of stand where oak does not normally occur. Our function here is to spotlight such ecological devices.

Spurr. We must realize that spraying sometimes tends to perpetuate the problem. If you just let the gypsy moth eat all it wants, it starves itself out. Then it may be 10 years before you get another outbreak. Spraying results pretty much from public excitement rather than economic justification. Oak mortality occurs only when defoliation is combined with secondary defoliation in the same year.

Ovington. I find it difficult to believe that if you leave the moth and oak together, the moth will destroy all the oak completely. By spraying you may be killing off a potential pest of the animal so you are making the situation worse. I wonder if there are some areas left where no spraying has been done and if anyone has looked to see just what happens there.

Spurr. A number of experiments can be done in the field which lie somewhere between the strict observation work and the strict laboratory experiment.

You can spray insecticide along a swath down the middle of a rock ridge, the strip being wide enough that the gypsy moth invasion doesn't come from the side. You can keep the gypsy moth off the trees by banding the trees. You can study the effects of rodent predation on gypsy moth by trenching around trees and putting in wire screens which will allow everything to move through except the rodents. A large gypsy moth population may be planted on an oak tree in the middle of a red maple forest to see if it will be defoliated.

Dansereau. If experiments are to be set up they must be done in the right place. Observation will show if the experiment is situated in a transition area which is not typical. It is dangerous to experiment too much in areas where the full complexity of the natural condition has not been explored. Large-scale mapping of the vegetation and the analysis of plant communities would give a better understanding of the vegetation in Connecticut as a whole.

Collins has indicated that in some areas the gypsy moth will accelerate succession and in others it will hold it back. Where is the hinge? At what point can the scales be tipped one way or the other?

Odum. How about looking at the ridge, the slope, and valley system? As we go further down we have net gains in the organic building up of the soils and plants toward the succession you wish to arrest. On top of the ridge there is not enough building up of the soil. Why not take the excess cuttings that are necessary to manage the succession below and carry them up to the top of the ridge? Can we do something with the water system, simply pump the water to the top?

Waggoner. Clearly, we need not only to collect and synthesize information but also to run experiments. Because of the rarity with which the gypsy moth comes back to the same spot, the challenge is here for ecologists to devise suitable experiments.

The Use of the Suburban Forest in Ecology

Discussion

Dimond. We have discussed the suburban forest from the standpoint of amenity and management. Now I would like to consider it not as a resource but as a medium for research.

Odum. What is now needed in the basic science of ecosystems just happens to coincide with the needs of the State of Connecticut. Often I have been involved in efforts to do a total budget of a system and always it has been with two or three people. Inevitably this leads to too few replications. Yet in an effort to get a synoptic picture, a simultaneous picture, we have made this sacrifice. Here at the Connecticut Station you have a magnificent facility and a staff with the techniques for doing all the things that have been mentioned: the inorganic cycles, e.g. of nitrogen and calcium, the metabolism and photosynthesis and the energy fluxes. These can all be measured by you.

In aquatic ecology we have also encountered many logistic difficulties in study of large systems. Some workers take long cruises, but I feel they often fail to focus on one area long enough to understand the system. On the other hand, we prefer to concentrate on our small marine bays, 12 feet deep. We can put dikes around representative segments and set up different management types to study. We have found you can change small aquatic systems by various techniques, and some of these can probably be adapted to terrestrial ecosystems. For example, you can seed terrestrial ecosystems continually with different plant species. If you hold your boundary conditions constant, you can see what combination comes up rather than trying to say this or that species might fit. Multiple seeding is a valuable method in water systems and may become so in terrestrial systems.

Ovington. It is unwise with a problem of such complexity to spread your efforts to too many sites. You have to concentrate on collecting basic data of the organic, nutrient, energy, and water systems in well-defined ecosystems. Once you have these data the results can be projected to other ecosystems. When you know how much solar radiation is coming in and being retained, the background is set to view certain actions. If there is surplus energy can you cash in on it further? Can the vegetation be manipulated to give a larger surplus? Is a coniferous canopy better than a hardwood canopy for energy fixation? Is a patch-

work of field and woodlots more efficient than a continuous woodland system?

Another problem is how to harvest the system. At what position of the cycle is it best to harvest, as woody material or as gypsy moth? What are the consequences of harvesting? For example, if you remove all the litter, as was done in Germany, you are removing nutrient-rich material and immediately there is a danger of lowering the site potential. Only long-term experiments will show you are slowly running down the system. The Experiment Station can contribute much by starting carefully planned long-range experiments in land use. See what opportunities are presented where someone began 20 years ago! Long-term experiments are needed to answer these questions.

In the suburban forest, where interested people live, you have the opportunity to begin and to persist in these long, difficult and important experiments.

Darling. I thought to myself, well now, this is magnificent opportunity to be a keeper for landscaping a very large area of this State for pleasure. How many more places in the world can this even be thought of at the moment?

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Participants in the Lockwood Conference. Left to right: H. T. Odum, H. J. Lutz, F. W. Went, F. F. Darling, Marston Bates, S. H. Spurr, J. D. Ovington, Peter Farb, Pierre Dansereau, and M. B. Russell.

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