If more Canadian foresters understood the concepts discussed here and in the previous issue¹ by J. P. KIMMINS (Faculty of Forestry, University of British Columbia) they would be better able to discuss environmental issues with the public and our forest land resource would be better managed.

Forest ecology: the biological basis for the management of renewable forest resources

¹The ecology of forestry: the ecological role of man, the forester, in forest ecosystems. *Forest. Chron.* 48: 301-307. These two articles are based on a series of lectures entitled *The ecology of forestry* presented through the Center for Continuing Education at UBC.

La mise en application d'un système mécanique ou électrique dépend de la connaissance et de l'application des lois de la physique qui déterminent les caractéristiques d'un tel système. Il en est de même de la forêt qui représente un ensemble de systèmes écologiques (écosystèmes) dont les facteurs sont tout autant contrôlés par les lois de la biologie, de la physique et de la chimie que l'est un poste de pouvoir électrique par les lois de la physique. Un grand nombre de forêts de par le monde sont aménagées, même de nos jours, en ignorant ce principe de base. L'auteur passe en revue quatre des principes fondamentaux de l'écologie forestière et explique la mise en application de ces connaissances en aménagement forestier. L'auteur ajoute que tout aspect touchant l'aménagement actuel de la forêt, au Canada, (et ailleurs dans le monde) devrait être orienté à la lumière d'une connaissance fortement améliorée du caractère écologique de cette richesse. C'est seulement de cette façon que le forestier canadien pourra éviter cette dégradation marquée du milieu, témoin de ses activités passées. C'est également en agissant ainsi qu'il verra sa profession atteindre un niveau plus respecté, niveau qui caractérise bien des forestiers européens secondés par le public de leur pays.

The forester of today is constantly confronted by the criticisms and demands of environmental groups. He is assailed not only for those of his activities which are clearly detrimental to the total yield of goods and services to society, but also for many activities which have long been cherished as "good forestry". Because the vocalisations and writings of the critical public are frequently both spirited and uncompromising, and because the reaction of many foresters to such public attention is defensive and even negative, the positions of both parties in many discussions of contemporary forest land management rapidly become polarised.

The level at which the public and the forestry profession interact is all too often that of polemic: the vigorous and uncompromising exercise of contrary and conflicting opinions. It often appears in such exchanges that neither party is exactly sure why it thinks it is correct, and it would seem to be highly desirable to provide both parties with a sound basic knowledge of the ecological nature of the problems they are dealing with. Such knowledge would help the forester to achieve a better understanding of the ecological nature of his management operations, reducing the risk of self-inflicted loss of future economic values and public respect. It would help some environmental groups to understand that the obverse of "all that glitters is not gold" might be "all that appears to be environmentally degrading may not be of great ecological significance". Environmental alteration which appears to understand that the obverse of "all that glitters is not gold" might ecological significance (although there may be a loss of important short-time social values), while activities which produce little visible impact may have profound and undesirable ecological consequences. The time has come to recognize clearly those aspects of forest management which produce unacceptable changes in the ecology of certain areas from those whose outcome is ecologically acceptable given today's knowledge and values. The day for blanket commendation or condemnation of ubiquitously applied forest management techniques is past.

In what follows I shall attempt to make the case that all forest management, even to the extent of economic investment in the forest endeavour, should be soundly based in forest ecology. I shall suggest that the best way to ensure maximum sustained production of goods and services from forests is by understanding the biological potential and ecological limitations of the resource being managed.

To this end I shall summarise four fundamental aspects of forest ecology and attempt to demonstrate the utility of these basic ecological concepts for the forest manager. The ecological impact of contemporary forest management practices has been presented already (Kimmings 1972).

The forest as an ecosystem

Today's forester is becoming increasingly aware of the fact that a forest is more than merely a stand of trees. Just as the farmer con-

siders his farm to be more than just the present crop of plants and animals, so the forester is being forced to realise that the public resource placed under his management is composed of several components. His perception of this fact is aided by the increasing social value and demand for other components of the forest such as wildlife and water.

A forest is much more than just its trees: it is a highly complex ecological system of interacting, interdependent living and non-living components. It includes a highly variable layer of soil underlain by parent material, a varied collection of plants of various sizes and arranged into a number of definable vertical layers, a characteristic group of animals associated with these plants, a wide variety of microbial forms of life such as bacteria and fungi, and, finally, the atmosphere (including water) which permeates through all the other components. Such a system is called an **ecosystem** (Tansley 1935).

Energy-flow in forest ecosystems

Forest ecosystems appear to be very different from other ecosystems, such as lakes, grasslands, or salt marshes. However, all ecosystems have the same basic functions: they are biological systems which are driven by the input of sunlight energy and which concentrate the nutrient chemicals necessary for organic growth and maintenance. The animals and plants in various ecosystems may look very different in terms of size, shape, and colour, but they all have the same problem in life: the need to obtain energy and nutrients with which to live, grow, and reproduce. This common need for energy has led to the formation of characteristic series of energy dependencies in ecosystems:

Sunlight → green plants → plant eaters → animal eaters
(herbivores) (carnivores)

Such a sequence is referred to as a grazing food chain. It is not the only way energy flows through the ecosystem, however. Although it very often appears (in terms of the size and visibility of the animals concerned)

to be the most significant pathway of energy-flow, in many ecosystems, and particularly in forest ecosystems, it is generally of considerably less functional significance than a second pathway, referred to as the detritus or decomposer food chain. The input to this food chain is made up of all dead plant and animal material, and all animal excreta. These materials are decomposed by a complex of microbes and small animals which are consumed by other animals which in turn fall prey to carnivores. These two major pathways of energy flow in a forest ecosystem are shown in Figure 1.

The transfer of energy from one component or level of a food chain to another is a rather inefficient affair. For example, in a grazing food chain plants only capture about 1% of the incident sunlight energy, and successive transfers to herbivores and carnivores are only 5-30% efficient with between 70% and 95% of the energy being lost at each stage or link of the food chain (Phillipson 1966, Kormondy 1969). Much of this inefficiency is the result of the loss of energy as heat (through the process of respiration) in accordance with the second law of thermodynamics. The rest represents transfers of energy to the decomposer food chain where it is also eventually lost as heat, again in accordance with the laws of thermodynamics. Because of these energy losses, there is a rapid reduction in energy flow as one moves up food chains and this controls the relative numbers or biomass of plants and animals. For example, in forests there is a far greater weight of plants (e.g., trees) than of herbivores (e.g., deer) and a far greater weight of herbivores than of carnivores (e.g., mountain lions).

Thus the forest, which at first glance might appear to be a random, unstructured collection of plants and animals, is in fact a highly structured system in which each living component is a source of food (i.e., energy) for some other component. The relative abundance of each type of organism (e.g., herbivores and carnivores) is a direct function of the basic laws of physics which dictate the

Fig. 1. Diagrammatic representation of energy flow in forest ecosystems. All energy is eventually lost through respiration, such losses being continually replaced by inputs in the form of sunlight.

overall pattern of energy movement through the ecosystem.

Ecological energetics (as the study of energy movement and distribution in ecosystems is called) is of more than mere academic interest. Energy does not simply flow through ecosystems: it is also stored in the various components. Trees are an example of storage of sunlight energy in plants, and deer are an example of storage of plant energy in herbivores. The production forest manager is vitally concerned with maximizing the rate of capture of sunlight energy and its storage in trees (i.e., maximizing current annual increment — c.a.i. — of his crop trees). The wildlife manager or recreation manager, on the other hand, may be more interested in moving the energy on up the grazing food chain and having it stored in herbivores (i.e., increasing the size and productivity of a deer or moose population).

Thus, intensive forest management in the most fundamental ecological terms is concerned with maximizing the rate of entry of sunlight energy into forest ecosystems and its storage in the components of the system which are of greatest social or economic value. To achieve the desired distribution or flow of energy, the forester must understand the factors affecting these ecological parameters.

Nutrient cycling in forest ecosystems

Many factors affect the dynamics and distribution of energy in forest ecosystems. Some factors are relatively unaffected by the activities of the forester; of those that are, the availability of nutrient chemicals is of great importance.

The significance of nutrients for tree growth lies in the fact that they act as the medium by which plants capture sunlight energy, and by which this energy is stored or passed on through food chains. Plants absorb inorganic nutrient chemicals from their environment and assemble them into complex organic molecules containing large amounts of energy

in the chemical bonds between the component atoms. This energy can be recovered for use by the plant or an animal (or is released in a forest fire) by breaking the complex organic molecules into their component parts, thus releasing the bond energy. By the time all the energy has been turned into heat and lost, the organic molecules have been broken down into their inorganic building blocks. These are then available for reabsorption by plants, and so the process repeats itself indefinitely.

This successive use and re-use of inorganic nutrients is referred to as the biological cycle of nutrients. The major pathways of nutrient movement in forest ecosystems are shown in Figure 2. For some elements or atoms the cycle can be very rapid, being completed in as little as a few days. For other elements or other atoms, a single cycle may take centuries. Whatever the details of the cycle, however, one characteristic of nutrient cycling in undisturbed forest ecosystems appears to be common: the cycle is highly efficient at retaining nutrients within the ecosystem, net losses (primarily in groundwater) being very small and apparently in approximate balance with such inputs of nutrients as dust, precipitation, and bedrock weathering (e.g., Likens *et al.* 1967, Cooper 1969). This is of great importance since forests, especially those in mountainous regions or at higher latitudes, are frequently growing on thin, nutrient-poor soils or under conditions of low nutrient availability (Gorham 1955, Prusinkiewicz and Plichá 1965, Eyre 1968). The highly efficient retention of nutrients under these conditions is vital to the continued productivity (rate of energy fixation and storage) of the forest.

Since all nutrients must pass at some stage or other through the decomposer food chain, the litter layer of the forest is a pivotal point in the nutrient cycle. If conditions are such that the decomposition of organic material is inhibited, nutrients will accumulate in the litter layer in a form which is

Fig. 2. Diagrammatic representation of the cyclic movements of nutrient chemicals in forest ecosystems. Comparison with Fig. 1 reveals some similarities between the movements of energy and nutrients, but points out the cyclic nature of nutrient dynamics as compared with the non-cyclic dynamics of energy. Losses of nutrients from the system are replaced as shown in the diagram, but generally at a rather slow rate.

unavailable to plants, and the nutrient cycle will stagnate. Without an adequate supply of nutrients, energy fixation and storage by the trees will be inhibited and the c.a.i. will drop. Conversely, the loss of the soil organic layers by fire or erosion may radically reduce the ability of the forest to retain the nutrients necessary for future tree growth and is known to result in dramatic losses of forest productivity in many types of forest. Thus, the condition and fate of soil organic layers (including the forest floor) has a far greater significance for site productivity than is realised by many foresters.

Many other apparently inconsequential components of the forest ecosystem are also known to play a vital role in maintaining the circulation of nutrients necessary for forest growth. For example, undergrowth, including mosses, has been implicated as being of great importance in some types of forest (Weetman and Timmer 1967). Thus, since the total quantity and availability of nutrients are both intimately related to site fertility, it is vital that forest managers should acquire as profound a knowledge as is possible of nutrient cycling and the effects of forest management thereupon.

Ecological succession

So far we have considered the two functional aspects of ecosystems, energy flow and nutrient cycling, at one point in time. However, ecosystems are not static entities; they are constantly changing. For example, if an area is logged, scarified, and then left to its own devices, a characteristic series of plant communities will successively occupy and replace each other on the site until a stage is reached which is stable and self-replacing.

The entire sequence of communities (a community being a characteristic, identifiable collection of various plants and animals) replacing each other over time on an area is referred to as a *sere*, while the process of change is called *ecological succession*. The driving force in succession is the change which any community of living organisms effects on its physical environment. Each distinct stage in the sere (identified by having a distinct plant and animal community) alters the area it occupies so that the environment becomes less and less suitable for that community and increasingly favourable for the succeeding community. The change involves a reduction in environmental extremes such as excessive fluctuations of temperature and moisture, an increase in nutrient capital and storage capacity, and a general domination of the physical environment by the living community. This process continues until a community develops which cannot effect any immediate further alterations of its physical environment. This community is therefore self-replacing over a considerable period of time and is referred to as the climax community (Daubenmire 1968).

There are three main types of ecological succession, and *it is vital that their similarities and differences be understood if forest management is to be successful*. Of course, there is a broad spectrum of successional types, the three described below

merely representing the central type and the two extremes. The three types occur in excessively wet (hydrarch succession), moist (mesarch succession), and excessively dry (xerarch succession) environments, respectively (see Kimmins 1972, Fig. 1). The examples given are from coastal British Columbia and different species will be involved elsewhere. However, the principles being discussed are fundamental and therefore are equally applicable in other areas.

- Hydrarch succession (producing a hydrosere) starts in open bodies of water such as lakes which gradually fill up with organic and inorganic sediments. As they become shallow (initially around the margins) bottom-rooted plants appear and speed up the process of organic sedimentation. As the water progressively fills with organic debris, various marsh or swamp plants (e.g., sedges, sphagnum moss) colonise the area, this vegetation sometimes extending out as a floating mat from the edge of the lake. As this vegetation builds up a peat layer (undecomposed plant debris), conditions become dry enough for certain woody shrubs (e.g., swamp laurel, Labrador tea), and in due course soil conditions become dry enough for tree species adapted to the wet, acid, organic conditions (e.g., lodgepole pine, western hemlock). After a long period of accumulation of organic matter in the form of branches, dead foliage, and fallen trees, the depth of soil above the water table may become great enough, or the water table may be reduced sufficiently by transpiration, for a climax community to develop. The time scale of this sere is very long, some stages lasting for thousands of years. As a general rule the early stages last much longer than the later stages in which the process of change is faster. Any factors disturbing the successional process and leading to successional retrogression result in an increased wetness of the ecosystem and a loss of accumulated nutrients. Recovery from successional retrogression is slow, although investment in site treatment can sometimes speed the recovery.
- Mesarch succession (producing a mesosere) occurs on moderately deep to deep inorganic soils which do not become excessively wet or excessively dry. Initially, there may be a brief grass or herb community followed quite rapidly by a shrub stage. This is generally replaced in short order by a pioneer tree stage (which may come in immediately, by-passing the earlier stages just mentioned) although, as foresters know to their cost, early shrub stages can be undesirably prolonged on some sites in terms of production forestry. The pioneer tree stage is in turn replaced by communities dominated by other tree species until the climax community develops. The precise sequence of stages is more variable than hydroseres and xeroseres and one or more of the stages mentioned may be omitted. The length of stages is also variable, but while they may be prolonged from an economic standpoint, in ecological terms and in comparison with the stages of xeroseres and hydroseres they are very short-lived. In particular, the early stages in a mesosere are much shorter than the later stages whereas in the other seres the reverse holds true. This is the result of the relatively favourable conditions of this sere which require much less modification by early seral stages in preparation for later stages than is the case in xeroseres and hydroseres. Disturbance and successional retrogression in a mesosere do not necessarily alter the nutritional and hydrological conditions greatly, and should such changes occur recovery is generally rapid. The very important consequences of this for practical forestry will be discussed later.
- Xerarch succession (producing a xerosere) occurs in environments where the availability of water, at least during the growing season, is limiting. Such a situation might be found on a rocky bluff or on a steep rocky slope which has been subjected to excessive erosion, especially when such areas experience a modest annual or growing season rainfall. The physical micro-environ-

ment in this type of situation is very severe with great fluctuations in temperature and moisture, and initially the only growth is of lichens and pioneer mosses. As these grow and die they build up a thin organic layer over the soil or rock surface creating a nutrient and moisture reservoir, but this stage is normally very protracted since these particular successional processes are generally very slow. When the mosses and lichens have accumulated sufficient organic matter, drought-resistant shrub species (e.g., salal, bearberry) will grow and their litter accelerates the pace of organic accumulation and site amelioration. After a variable period, tree species tolerant of drought (e.g., lodgepole pine, juniper or Douglas-fir) will take over the site. If, over a protracted period, these species are able to build up a sufficient depth of organic soil they may be replaced by climax species. This may take so long as to effectively never occur, however, in which case the earlier species become self-perpetuating. As in hydrosere, the initial stages of xerosere are very enduring, the successional processes responsible for change operating very slowly. Disturbance leading to successional retrogression renders the ecosystem drier, impoverished in available nutrients and reduces the moisture and nutrient storage capacity. Recovery from successional retrogression is slow and the technical possibilities for speeding the recovery are very limited.

So far, I have used the term **climax** in the sense of the climatic climax: that is, the climax plant community is that which is in self-perpetuating equilibrium with the regional macroclimate (such communities usually being restricted to mesosere). However, seres can terminate before reaching the climatic climax. Permanent site factors such as soil, or variable site factors such as animals and fire can effectively maintain an area in subclimatic climax condition in perpetuity. Thus, a forest growing on a gravel bench in a valley may remain permanently as a mid-successional xerosere community while surrounding mesoseric stands develop into true climatic climax communities; alternatively, a cedar stand in a stream-fed swampy valley bottom may be permanent, never progressing to the cedar/hemlock climatic climax. These sub-climatic climax types are referred to by such terms as edaphic (soils), biotic (grazing), or pyral (fire) climaxes and represent environmental conditions which the plant community is unable to modify further within a reasonable time span.

Many of the characteristics of early seral ecosystems differ from those of late seral ecosystems and this affects both the choice of seral stage for agriculture and forestry and the problems attending the choice. For example, early seral stages tend to be less resistant as compared to late seral stages to physical perturbations such as wind and water erosion, and more susceptible (in terms of degree of successional alteration and rate of recovery therefrom) to biotic perturbations such as insect and disease outbreaks. Thus, maintenance through active forest management of a mid-seral Douglas-fir stage in coastal British Columbia may lead to greater erosion problems than managing climax cedar-hemlock stands in the same area, although the former may have a higher productivity or greater economic value. The grain crops of the farmer may be more productive than later seral shrub and herb communities, but their maintenance leads to greater dangers of wind and water erosion, greater

problems of insects and disease (necessitating use of pesticides), and greater losses of nutrients (resulting in water pollution problems and the need for fertilizer applications).

Man obtains his food in the form of both plants and animals (primarily herbivores) and he is therefore a member of grazing food chains. Since energy flow in the late seral stages is primarily in decomposer food chains, whereas in early seral stages it is primarily in grazing food chains, it is not surprising that man selected plants and animals for domestication from early seral communities. Thus, most farms represent very early seral ecosystems. Such ecosystems have the advantage that the plants are faster growing and easier to grow in monoculture than the plants of later seral communities, and have a much higher proportion of their stored energy in a form available to herbivores. However, because of the successional process of change, early seral stages are constantly moving towards later, frequently less desirable seral stages. This requires that most farmers periodically arrest the successional process and recreate the conditions of the desired seral stage by such means as ploughing.

The evolution of modern forestry is very much more recent than farming, having occurred essentially within the past millenium. Like the farmer, the forester frequently favours sub-climax crops, although this generally means mid-seral stages (Lutz 1957) as opposed to the farmer's early stages. This confers the advantages of higher productivity and relative monoculture, together with the disadvantage of higher risk of erosion and nutrient loss than in later seral forests. It lacks, however, the ease of maintenance of the farmer's seral stages. Since the arable farmer is aiming for the beginning of the sere, the precise amount of disturbance is not of ultimate importance. A bit too much disturbance can be remedied fairly quickly while too little disturbance can be more serious since it leads to weed problems and possibly to undesirable soil texture. As in farming, too little disturbance in the management of a mid-seral forest ecosystem may result in a possibly "undesirable" succession to later seral stages. Unlike farming, too much disturbance results in retrogression to generally undesirable earlier stages. Thus, while both the forester and the farmer are in the business of successional manipulation, the forester attempting to manage midseral forests faces a much more difficult problem with much greater risks of converting his resource to an undesirable seral stage than does his farming counterpart. Also, the forester is frequently dealing with xerosere or hydrosere manipulation whereas the farmer is manipulating mesoseres in which the consequences of poor management are ecologically much less serious. This would imply the need for great caution on the part of the forester in any forest management practice which can potentially lead to successional retrogression. It also points out that the successful management of mid-seral forest ecosystems is likely to be far more tricky than the successful management of mesoseric

agricultural ecosystems. The term "tree-farm", with its implication that forestry should be as easy as farming, is therefore perhaps a rather unfortunate designation for forest management units.

Conclusions

The forest is an ecosystem. An ecosystem is an ecological system of impressive complexity, containing an extremely large number of interacting components about which we know remarkably little other than generalities. This is a problem for forest managers since it means that they will frequently be rather unsuccessful at predicting precisely either the suitability or the success of any particular facet of their management practices. As a result, forestry is still largely an empirical, "try-it-and-see" endeavour: still as much of an art as a science. This situation is a direct outcome of the maxim that the larger the number of unknown or unpredictable variables in a system, the less predictable that system is. The more we know of the functioning of the forest, of course, and the more we understand the components of forest productivity, the better our ability to predict the ecological suitability and consequences of alternative management practices. However, given the current level of application of that somewhat meagre knowledge in everyday forest practice it is inevitable that "ecological mistakes" will continue to be made in forestry in many parts of the world for some time to come.

I am sure that there will be foresters who have read so far and concluded, "so what"? The point is that whether foresters (as opposed to loggers or timber miners, who are professionally involved in the utilization of an existing resource and not with the creation, renewal, or perpetuation of the resource) like it or not, they are applied ecologists. Their professional life is intimately concerned with the components of productivity (i.e., ecological energetics and nutrient cycling) and the temporal dynamics (i.e., ecological succession) of the forest. They are concerned with optimising energy storage in a specific component(s) of a specific seral stage and their professional competence is (or should be) judged on their success at attaining this objective. To attempt to do this without an adequate knowledge of the basic ecological processes which they are manipulating seems to be totally inappropriate under current social and economic conditions.

The forests around the world show that there

remains considerable room for improvement in forest management. The outcome of forest management frequently falls short of desired objectives and the ecological form and function of forests are frequently changed to a condition that has reduced socio-economic values. Although our knowledge of forest ecology is still woefully inadequate, we do know enough to be able to categorise certain types of forestry practice as unsuitable in certain types of ecosystem: unsuitable in terms of not meeting our management objectives. It therefore seems essential for all professionals engaged in the management of forest resources to acquire and apply in their everyday work the best available understanding of forest ecology. To continue to manage forests in such ignorance of the basic ecological facts of life as appears frequently to be the case is not in the best interests of any nation, economically or socially.

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