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EFFECTS OF IONIZING RADIATION ON ECOSYSTEMS*

MASTER

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Man's capacity for altering his environment is prodigious, but his present capacity for increasing levels of ionizing radiation on a world-wide basis looms as one of the most fundamental and potentially destructive changes he could make. We have known for many years that ionizing radiations cause biological effects far beyond the effects normally expected from the same amount of energy in different form, but we have recognized only recently that certain plants are damaged in the same exposure range as man himself. Prior to this recognition the opinion was widely accepted that if man could be protected from ionizing radiation, the other organisms of his environment, especially the plants, would be safe by a wide margin. We know now that levels of radiation which would be a serious threat to man would also cause direct and immediate effects on certain other sensitive organisms which are vital components of the ecosystems which are, in the broadest sense, man's environment. The nature of the changes which might be induced in ecosystems is a topic of vital current interest in biology and the subject which I wish to discuss.

To appraise these effects we must examine the fundamental unit which is the subject matter of ecology: the ecosystem, which has been defined most thoroughly in contemporary context by Eugene Odum and Howard Odum in numerous papers and in a text. For our purposes I shall define an ecosystem as a holistic unit of the biosphere, a unit embracing one or several plant communities, animal communities and all of the physical and biological factors which influence the development of the total system. Clearly, this definition is most broad, since the earth itself fits it as does an island, a garden or a city. I would restrict our considerations further to "naturally occurring"

ecosystems, thereby excluding cities, self-sufficient space capsules, and political boundaries. Naturally occurring ecosystems are recognized and usually named from their most conspicuous component, the plants. Such ecosystems exhibit three distinct types of patterns which we recognize as geographical, temporal and internal patterns. Man exists within a framework largely defined by these patterns and I wish to consider the kinds of changes which ionizing radiation might induce in them.

First, let us examine the patterns. Figure 1 shows the geographical patterns of the principal ecosystems of North America. These ecosystems are named after the plant communities, and the patterns shown approximate the distribution of the stable natural ecosystems which would develop in North America if undisturbed for as long as 100 years or more. The patterns are influenced importantly by climate and the stable ecosystems which develop have counterparts, similar in structure and function although different in species composition, in similar climates throughout the world.

Leading to the development of these ultimate, stable, or "climax" terrestrial ecosystems is a regular succession of systems starting with the simple systems of rock ledges, gravel banks and abandoned fields and including, for example, in large upland areas of eastern North America, an Andropogon stage followed by pine forest and later by the climax deciduous forest. This second type of pattern, the temporal pattern, results in the accumulation of energy within the plant community of the system as suggested by the graph of Figure 2, which was compiled from data published by several authors and approximates the accumulation of energy in abandoned fields in eastern North America. Both the time involved in such successions and the degree of stability achieved

vary with geography and even with locale. An extreme example occurs in the Tundra where frost action churns the soil annually over large areas, maintaining on these unstable soils plant communities which would be early successional stages on stable soils. Even here, however, clear long-term patterns exist and the patterns are stable and therefore predictable.

Within any ecosystem the nature of the long-term patterns is determined not only by climate and soil but also by the internal structure and function of the ecosystem. While we cannot examine here the many and complex physiological mechanisms which cause temporal patterns, it is useful to consider one aspect of the internal structure of ecosystems which seems to have promise as a common denominator for comparison of ecosystems. This is energy flow. Figure 3 shows diagrammatically the distribution and flow of energy through successional, climax or stable, and disturbed terrestrial ecosystems. In the diagram energy flow is indicated by arrows, the relative amounts involved by the width of the arrow, while stored energy is shown by the blocks. When energy fixation exceeds losses through respiration and export, the structure of the ecosystem is changing and we recognize a stage in some succession. When losses exceed energy fixation, as they may immediately after a disturbance, we have a different type of instability, usually resolved within a very few years into some stage of the successional pattern. Losses approximate fixation in stable ecosystems and this third type of energy distribution is one characteristic of climax ecosystems.

This stable condition, the climax, is a most useful reference for consideration of ecological problems, and the concept of the climax is basic to the significance of all three of these patterns. The climax ecosystem is

not only the most nearly stable, but also the most complex, containing the greatest number of different species and the most complex internal structure. Paralleling the development of climax is an increase in the diversity of micro-environments within the ecosystem and an amelioration of the general environment of the system. These changes are particularly well illustrated in eastern North America where the normal old field succession leads from the simple weed-dominated ecosystems of the relatively harsh old field environment to the complex deciduous forest ecosystem with its tempered internal environment.

In general, disturbance of the climax produces simplification of the ecosystem, reduction of species diversity and potential oscillations in populations. Such a pattern is characteristic of any type of disturbance whether caused by ionizing radiation or some other factor. The species inhibited will, of course, vary with the nature and severity of the disturbance. Analysis involves, first, recognition of the nature of the direct effects and, then, consideration of the complex secondary effects attributable to changes in the biological interactions which are an integral part of the ecosystem environment. Since the ecosystems we are considering are dominated by plants, which are the principal elements determining the structure of the systems, the most important direct effects probably involve changes in plant populations. I wish to discuss some recent experiments at Brookhaven National Laboratory which indicate the nature and severity of the direct effects of ionizing radiation on ecosystems and suggests the nature of certain secondary effects as well.

During the past year at Brookhaven we have had an opportunity to

examine the effects of chronic exposure to ionizing radiation on two ecosystems at opposite extremes of the temporal sequence characteristic of the Eastern Deciduous Forest: an old field and a near-climax forest. Two separate facilities are involved, utilizing the same general plan of irradiating experimentally under field conditions. One of these facilities is in a cultivated open field, a section of which was abandoned to provide the first year old-field ecosystem. The second facility has been established recently in a forested area nearby. The old field is representative of abandoned agricultural land on Long Island and contained during the first year a dense stand of pigweed (Chenopodium) and various grasses and other herbs. The forest is an oak-pine stand, containing white oak, scarlet oak and pitch pine. Such forests develop characteristically on glacial outwash sands throughout certain sections of northeastern North America and are part of the Eastern Deciduous Forest Complex.

The plan of both installations includes a centrally located source of gamma radiation arranged as shown in Figure 4 to be shielded from a safe distance by operation of a winch. The source of radiation in each installation is large enough to produce exposure rates ranging from several thousand r/day within a few meters to about 2 r/day at 130 M.

Figures 5 and 6 show that the highest exposures, continued chronically throughout the winter and spring of 1961-62, caused devastation of both ecosystems. The changes in plant community composition with exposure rate are shown diagrammatically in Figure 7, which shows that there were substantial differences between the exposures necessary to cause important effects on the structure of these two ecosystems. The old-field plant community, for example,

was intact at daily exposures below about 300 r/day although there were deleterious effects on growth at 100-300 r/day. The forest suffered loss of the principal species contributing to its structure, the trees, at exposures in excess of 60 r/day. No higher plant of the forest survived exposures in excess of 360 r/day, while in the old-field the radiation-resistant Senecio survived exposures up to several thousand r/day.

It is evident that there is great variation in radiosensitivity among the plant species of these two ecosystems. The Senecio was by far the most resistant and the pine the most sensitive, being killed by exposures between 20 and 30 r/day and showing inhibition of growth between 1-2 r/day. Furthermore, the forest ecosystem, considered as a unit, was much more sensitive than the old-field ecosystem, the difference spanning a factor of 5-10 in exposure necessary to produce equivalent change in structure.

This sharp difference in sensitivity suggests that there may be useful parallels between the structure of ecosystems and resistance to damage from ionizing radiation. More specifically, it would seem to suggest that climax or near-climax ecosystems in general are more sensitive than earlier successional stages, especially the old-field. A logical extension of this reasoning would be that organisms capable of surviving in harsh environments such as the old-field are also more resistant to damage from ionizing radiation than organisms characteristic of more equable regimes such as the forest.

To evaluate this general hypothesis we must consider certain principles which govern radiation damage to plants. First, it is important to recognize that the single most important biological effect of ionizing radiation is to cause changes in the chromosomes, changes which are called "mutations."

I use the term to include both chromosome breaks and the lesser changes sometimes called "point mutations." Much of the work most germane to the present discussion has been done recently at Brookhaven National Laboratory by Dr. A. H. Sparrow and his associates. They have shown that the severity of damage produced in plants by exposure to ionizing radiation is directly related to the amount of energy absorbed by the chromosomes. Since the amount of energy absorbed depends on the size and number of chromosomes as well as on exposure rate, sensitivity to damage is related to these two nuclear characteristics. Plants which have high chromosome numbers and small chromosomes are in general resistant to ionizing radiation while plants with few large chromosomes are sensitive. The relationship between radiosensitivity and chromosome size and number extends to the tissue and cellular levels as well.

An additional factor which influences the radiosensitivity of plants is the rate of cell division in the growing tissues during irradiation. Under chronic radiation exposures such as those used in the field experiments described herein, a cell which is dividing slowly receives a greater total exposure before its next division than a cell which is dividing rapidly. Furthermore, in a tissue which contains rapidly dividing cells, damaged cells may be replaced by undamaged cells nearby, thereby increasing the apparent resistance of the tissue. If we consider two extreme conditions, dormancy and rapid growth, it is clear that individual cells in the dormant bud would accumulate greater total damage per cell in the same period of chronic exposure than rapidly dividing cells in an expanding shoot.

Similar reasoning suggests that seeds would behave much as dormant

buds, accumulating severe damage from long-term exposures, but this does not appear to be the case. While few published data apply directly to this question, seeds are generally recognized to be more resistant than vegetative structures to radiation damage from acute exposures. Recent research at Brookhaven indicates that pine seeds are also comparatively resistant to chronic radiation damage. In the Brookhaven forest experiment 90% of the pine trees exposed to more than 28 r/day were killed in the first year. F. Mergen of Yale University reports that cones collected from pine trees receiving 27 r/day contained seeds 95% of which were viable after total exposures of 12,000 r, an observation which seems to confirm that seeds are substantially more resistant to damage from chronic exposures than buds and other vegetative structures.

From these observations it is apparent that differences in response between ecosystems as diverse as a forest and an old-field must involve a complex of factors which affect the radiosensitivity of organisms. First, the plant communities of the forests are made up of perennials, most of which have aeri ally borne buds. Old-field plants are principally annuals which survive the winter as comparatively radiation-resistant seeds. The grasses and other monocots enjoy still a further advantage under chronic irradiation in that the dividing cells which produce new tissues are at the bases of leaves and may be at or slightly below the surface of the ground, thereby receiving a certain amount of shielding not enjoyed by the woody perennials. In addition, differences in chromosome number and size and in rates of growth contribute important differences in sensitivity. So it is abundantly clear that there are substantial reasons at the cellular level for sharp differences in sensitivity between a forest ecosystem and an old-field.

In general such factors which confer a degree of resistance to ionizing radiation appear to contribute to the ability of an organism to survive other adverse conditions. The seed, for instance, functions not only in dispersal but also in enabling the plant to survive severe environmental conditions which would be lethal to vegetative structures. Desert annuals may survive years of drought as seeds, completing their life cycle in a matter of days after a sudden rain. Other organisms such as grasses and sedges which have their perennating structures at or below the ground surface, are particularly well adapted to certain types of harsh environments, such as the tundra.

Still another adaptation which is of particular interest in a consideration of such parallels as these between radiation resistance and adaptation to other environmental stresses is chromosome number. Sparrow and his co-workers have shown conclusively, for instance, that polyploidy or the occurrence of extra sets of chromosomes in the nucleus confers additional resistance to damage from radiation. Furthermore, by correlating chromosome size and number with radiosensitivity, Sparrow and his group have been able to predict within broad limits the effects on growth of exposure of any plant to any level of ionizing radiation. Although the precision of such a prediction is subject to certain environmental influences as well as to several factors intrinsic to the plant, prediction is possible because the primary site of damage from ionizing radiation is the chromosome and because there is enormous variation in chromosome size and number and hence in radiosensitivity among the species of higher plants.

The geographical distribution of plants with high chromosome

numbers suggests that there is further basis for expecting parallels between radiation resistance and the durability of species. For instance, biologists have recognized for many years that among plants the incidence of polyploidy increases near the periphery of the range of the plant and that in general polyploidy is more frequent among organisms characteristic of harsh environments. Among genera of old-fields, for example, diploid chromosome numbers range from lows of the order of 10 to highs of the order of 200. One species of Chenopodium has been reported with a diploid chromosome number of 18 and a subspecies with 54; Digitaria species range between 18 and 72; Trifolium, between 21 and 180; and Andropogon, between 20 and 180. In general the incidence of polyploidy is known to be high among perennial weeds, grasses and sedges. Chromosome numbers of the principal plant species of the experimental forest ecosystem at Brookhaven on the other hand are 24 for all species including the pine, three species of oak, the blueberries and the huckleberry. Within the genera of trees in general, the incidence of polyploidy is lower than among herbaceous weeds. Polyploidy is most common among plants of the Artic Archipelago where as many as 80% of the species present are reported to be polyploids. Within temperate zone vegetations 30-35% of the species are polyploids.

Such relationships as these provide a reasonable basis for appraising the potential direct effects of various exposures on the three types of ecosystem patterns discussed earlier. First, in the temporal sequence, the early successional stages appear to be substantially more resistant than the more complex stages later in the succession. The mosses and lichens, for instance, which are important components of the early successional plant

communities of bare rock surfaces, have survived six-month exposures of more than 1000 r/day in the irradiated forest at Brookhaven. R. B. Platt and J. F. McCormick of Emory University recently irradiated experimentally an early successional plant community characteristic of rock outcrops in the Southeast. This community suffered important alteration of structure only at total exposures in the range of 20,000-40,000 r administered at rates between about 170 and 340 r/day. Charles Daniel, also working with R. B. Platt at Emory, has shown that the species composition of old-field plant communities in the vicinity of an unshielded reactor in Georgia was altered but that the community persisted after acute exposures of about 28,000 and 44,000 r. Such ecosystems, characterized by plant communities containing annual and perennial herbs, the weeds of gardens, roadsides, and waste places, would survive months of exposure to 100-300 r/day and acute exposures in the range of 20,000-40,000 r without important immediate, direct effects although there would be deleterious effects on the growth rate and form of the plants exposed (Fig. 8). These exposure rates are very high rates indeed and would occur only after war or other equally unacceptable catastrophe.

Near the other end of the temporal sequence of ecosystems, at least in eastern North America, the forest ecosystems have quite a different range of sensitivities. Chronic exposures between 20 and 60 r/day, continued through a period of several weeks or longer, would cause important damage to the trees which are the principal elements determining the structure of forest ecosystems. The Coniferous Forests, for example, would probably suffer severe damage at 20-30 r/day continued during a six-month period. A total exposure of 1000-2000 r in one day would cause equivalent damage. Deciduous forest

ecosystems are somewhat more resistant but would suffer important damage including mortality of the principal trees at exposures in excess of 30-60 r/day and from acute exposures in excess of 5000-10,000 r.

On a geographical basis we would expect the Coniferous Forest ecosystems to be among the most sensitive, the Tundra, Grasslands and probably the Deserts among the most resistant.

In all these ecosystems, however, the exposures necessary to cause direct effects of the magnitude we have been discussing are far beyond exposures from naturally occurring sources and present levels from fallout. Nonetheless, these high levels are well within the ranges possible over very large areas following nuclear explosions as is shown by the fallout pattern in Figure 9 for a 1954 test at Bikini. It is clear from this Figure that exposures in the range of thousands of roentgens might occur as far as 100 miles from a bomb burst. We know now that such exposures would affect not only man, and other mammals, but would also have important deleterious direct effects on the dominant plant populations of natural ecosystems.

The lowest exposure necessary to modify the internal structure and function of ecosystems is a vital but elusive question. Since there is no threshold for the production of mutations, we can assume that any increase in levels of radiation exposure will increase mutation rates, potentially increasing the probability of significant changes in the phenotypes present. These effects would appear only after several generations and are quite unpredictable.

The occurrence of somatic effects can be measured with less precision than mutations. As a result we do not know whether there is a

threshold exposure for the production of somatic effects. Exposures of 1-2 r/day continued during more than six months, cause minor morphological changes in pines, one of the most radiosensitive species known. Such exposures, however, are still well above general levels from fallout. Sparrow and I have estimated recently that the exposure from fallout in New York City during 1958, assuming the maximum rate observed at any time continued through the year, was in the range of $1/4,000$ - $1/8,000$ the minimum exposure necessary to cause measurable morphological effects on pine. If exposure rates in the range of 1-2 r/day or lower prove to have important ecological effects, these effects will probably be through genetic or physiological mechanisms. Such effects become apparent only after months, possibly years, and may be totally obscured in the field by a host of secondary effects.

It is these, sometimes subtle, usually complex, and always possible, secondary effects which generate some of the large, difficult, and frequently open-ended questions of ecology. The effects are attributable to alterations of the "normal" behavior of the various interacting components of the ecosystem and are frequently difficult to verify except by experimentation. They are susceptible of generalization and not yet of prediction in detail. In general we know that disturbance of complex ecosystems produces simplification of internal structure, reduction of the number of species present, and some form of instability. Severe or long continued disturbance favors populations of vigorous organisms which reproduce rapidly and even asexually. Among animals, those whose food chains are short, the herbivores, and especially the herbivorous insects are particularly well adapted to survive any sort of general disturbance. The survival of these populations, even at endemic

levels, can only accentuate the direct effects of radiation damage on the primary producers, the plants. I have shown recently that populations of leaf rollers and tiers in the irradiated forest were more resistant than their hosts, the white oak trees, and, apparently without increasing in absolute numbers, removed a high proportion of the foliage remaining on radiation damaged trees (Fig. 10). A simultaneous increase was observed in populations of bark lice and of pine woodborers. Other insect populations were depressed. Such changes in the relationships between predator or parasite and host generate biological interactions, the general effect of which is to increase the disturbance caused by the direct effects of irradiation.

Research at these ecological levels of organization is complex and slow because the natural units are large and replication is difficult. Large-scale field studies such as those described herein represent an opportunity for "in vivo" study of radiation effects on ecosystems. Supplementary laboratory and greenhouse experiments with isolated components correspond to the "in vitro" studies of the chemist. Such studies, coupled with studies of mineral cycling through these systems with emphasis on points of accumulation of radioactive contaminants, will provide within a few years greater precision in our ability to define the potential which any level of ionizing radiation may have for influencing the structure and function of ecosystems.

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FIGURE LEGENDS

- Figure 1. Major geographically defined natural ecosystems of North America.
- Figure 2. Accumulation of energy within the plant community of the Eastern Deciduous Forest.
- Figure 3. The flow of fixed energy through ecosystems. "Input" is energy fixed through photosynthesis. "Losses" include energy exported from the system through harvest and energy dissipated as heat through respiration.
- Figure 4. The source and handling mechanism used for irradiations in the field. The source is a radioactive isotope of cesium which emits gamma radiation, an electromagnetic ionizing radiation similar to X-rays. The source is suspended from an electromagnet to allow electrical interlocks with safety devices, and can be shielded or exposed at will by operation of the winch in the building a safe distance away.
- Figure 5. (a, b, c) Aerial views of the irradiated forest ecosystem before (a) and after (b, c) 6 months' exposure to gamma radiation ranging in intensity from several thousand r/day to background levels. The exposure rate at the perimeter of the circle of damage was about 60 r/day at the time of these photographs (b, c). (Color transparency)
- Figure 6. An old-field plant community exposed chronically to several hundred r/day, exposure rates which killed all the higher plants of the forest. (Color transparency)

Figure 7. Diagrammatic representation of gross radiation effects on the forest and old-field ecosystems.

Figure 8. Effects of ionizing radiation on the morphology of Chenopodium album, the pigweed. Although the plant survives high chronic exposures, there are obvious gross morphological changes, including effects on seed production, at these exposures.

Figure 9. Fallout pattern following the 1954 Bikini test.

Figure 10. Defoliation of white oak trees by insects in the irradiated forest ecosystem. Insect populations were more resistant than their hosts, the trees, and probably without increasing in total numbers per tree, consumed larger fractions of the foliage present on radiation-damaged trees. The net effect of this type of secondary damage is to reduce tree vigor further, increasing the disturbance to the ecosystem.

Fig. 1

ENERGY STORAGE IN TERRESTRIAL ECOSYSTEMS

Fig. 2

ENERGY FLOW THROUGH TERRESTRIAL ECOSYSTEMS

Fig. 3

21

Fig. 4

COMPOSITIONS OF TWO PLANT COMMUNITIES AS AFFECTED BY CHRONIC GAMMA IRRADIATION

Fig. 7

ESTIMATED TOTAL-DOSE CONTOURS IN ROENTGENS
PER HOURS AT 96 HOURS AFTER THE BRAVO TEST EXPLOSION

24

Fig. 10